

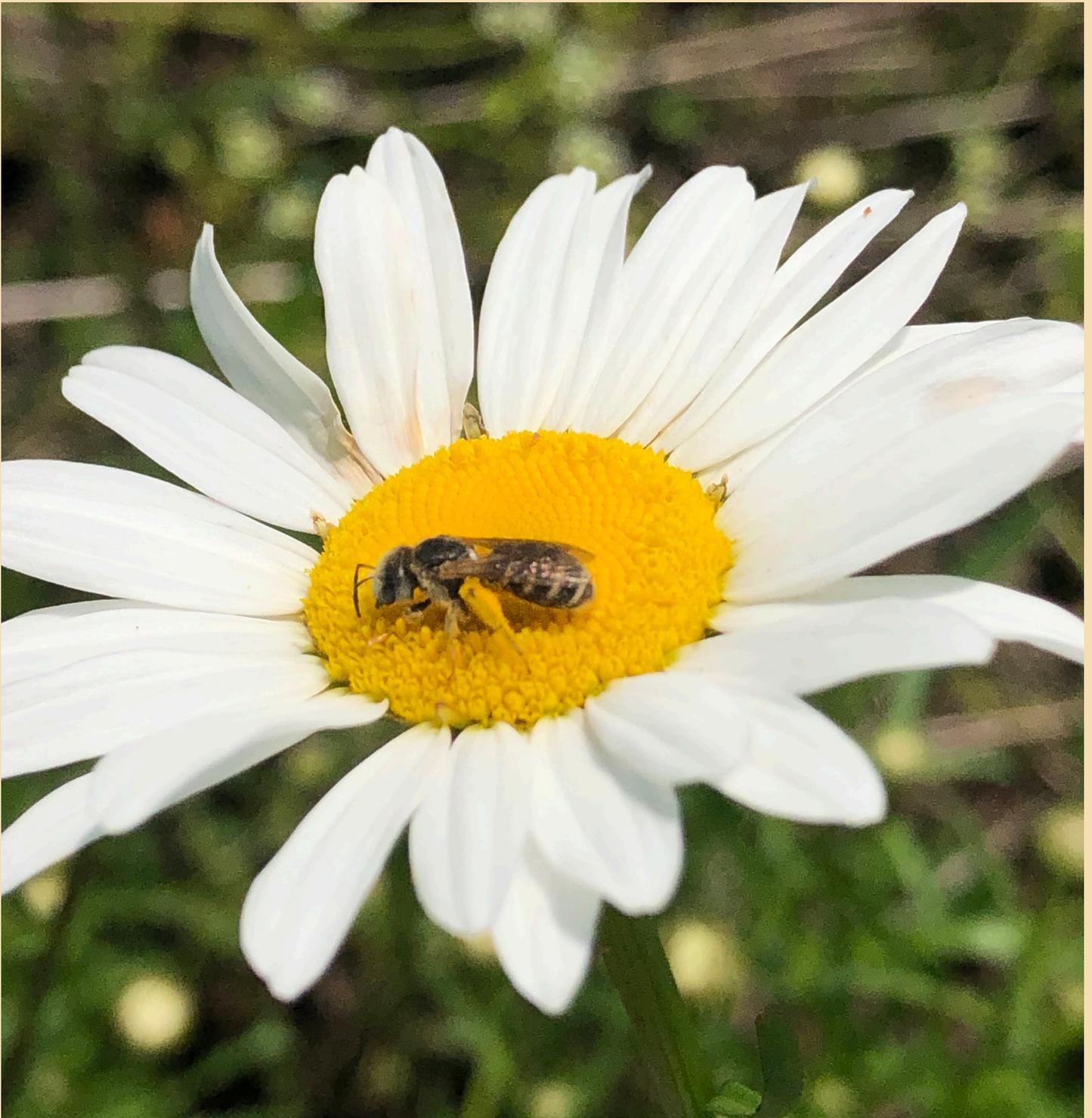


# The Prairie Naturalist

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# The Prairie Naturalist

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# Comparing Native Bee Communities on Reconstructed and Remnant Prairie in Missouri

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**ABSTRACT** The tallgrass prairie of North America is an imperiled ecosystem that has been the subject of considerable restoration effort and research in the past two decades. While native prairie plant species are purposely introduced during restoration, prairie invertebrates, including native bees (Anthophila), are not and must colonize from surrounding remnants. Prairie restorations may not support the same bee communities as remnant prairies because of habitat differences and dispersal limitations. We sampled native bees on reconstructed and remnant prairies in Missouri in the summers of 2016 and 2017 and compared the communities by evaluating species richness, diversity, and community composition. We detected no differences in bee species richness or diversity between reconstructions and remnants; remnants and reconstructions shared all but three of the 57 taxa observed. Community composition of bees on reconstructions was different from that of remnants because of differences in the relative abundance of taxa. Several species were associated with either reconstructed or remnant prairies. At a functional level, stem nesters were more common on reconstructed than remnant prairie. We also examined whether bee communities on reconstructions converged with those observed on remnants over time by comparing bee communities across restorations of different ages and found that reconstruction communities did not appear to be converging with remnants. Reconstructing prairie bee communities may depend on restoring soil conditions and disturbance regimes that influence bee nesting habitat.

**KEY WORDS** Anthophila, community, diversity, grasslands, monitoring, pollinators, restoration.

Substantial losses in the diversity and abundance of native bees in North America (Colla and Packer 2008) have led to increased research and conservation initiatives for bees and other insect pollinators. Habitat loss undoubtedly plays some role in bee decline (Grixti et al. 2009, Cameron et al. 2011), and this is almost certainly true in prairie ecosystems, most of which have been converted to agricultural land (Samson and Knopf 1994). The remaining prairie habitat, though small, is important for conserving bee diversity. Remnant prairies in Iowa contained more bee species, including more rare species, and greater bee abundance than ruderal areas (Kwaiser and Hendrix 2008). In Illinois, while prairie remnants and old fields contained similar bee abundances, bee communities in remnant prairie were more diverse and differed in composition than those in old fields (Tonietto et al. 2017). The growth of restoration science and ecology has opened another potential avenue for bee conservation through the restoration or reconstruction of prairies.

Prairie restoration can range from the rehabilitation of grazing lands to the full-scale reconstruction of prairie from agricultural fields. Scientists and managers reconstructing tallgrass prairie generally attempt to establish a plant community that corresponds to those found in local remnant prairies (Kurtz 2013). Prairie restoration appears to be a promising strategy for native bee conservation; it has been

effective in practice for plants (McLachlan and Knispel 2005), the usual proximate target of reconstruction, and restoration of a variety of habitats has been successful for native bees (Tonietto et al. 2018).

Assessing how well restoration works for native bees can be challenging due to the variability exhibited by insect populations (Fleishman and Murphy 2009) and the substantial regional variation in bee community composition (Williams 2011). Additionally, tallgrass prairie ecosystems are dynamic (Evans 1988, Whiles and Charlton 2006), representing moving targets for restoration (Simberloff 1990). This dynamism makes simultaneously monitoring restored and remnant habitats critical. Studies examining bee communities on restorations have yielded somewhat inconsistent results. There is substantial evidence that bees colonize newly restored habitats quickly, resulting in species richness and abundance similar to remnant habitat within five years (Exeler 2009, Williams 2011, Griffin et al. 2017). The community composition of bees on restorations, however, may converge with that found on remnants over time (Griffin et al. 2017) or remain distinct (Williams 2011, Tonietto et al. 2017). The habitat differences responsible for the difference in bee communities are not entirely known.

Examining functional groups can provide information about the habitat characteristics important to bees on prairie

restorations. Assigning bees to groups based on nesting habitat requirements (Potts et al. 2003, Tonietto et al. 2017) is one useful way of using functional groups. Native bee species may nest in the soil, plant stems or twigs, wood, or cavities (Ascher and Pickering 2017), and the availability of these resources can vary across habitat types and landscapes. Soil and stem nesting habitat may differ between remnant and reconstructed prairies because of differences in plant communities (Kindscher and Tieszen 1998, McLachlan and Knispel 2005, Middleton et al. 2010). The legacy of a site may also affect nesting resources, especially soil nesting habitat. Prairie reconstructions that were previously cultivated fields likely contain more homogenous, shallower soils than remnants (Baer et al. 2005) as well as greater soil compaction and less organic matter (Six et al. 1998). Finally, prairie management can greatly alter the availability of nesting resources. Grazing and frequent fire can increase the abundance of soil nesting bees by exposing bare ground (Potts et al. 2003, Kimoto et al. 2012), whereas less frequent fire benefits some stem and twig nesting bees by providing more stems and twigs (Cane et al. 2007, Cane and Neff 2011).

Research involving simultaneous sampling of different locations and different ages of reconstructions is important to better understand bee communities on prairie reconstructions and whether reconstructions can rescue declining bee species. We had two objectives for our study. First, we compared native bee (*Anthophila*) communities on reconstructions to those on remnants by evaluating species richness, diversity, and community composition at paired reconstructed and remnant prairies in Missouri. We sought to identify species or functional groups associated with remnants or reconstructions that could be used in future monitoring. Our second objective was to compare native bee communities across prairie reconstructions of different ages to determine if bee communities on reconstructions were converging with those on remnants over time. We hypothesized that bee communities of remnant and reconstructed prairies would not differ in species richness or diversity. We also thought community composition would likely differ between reconstructions and remnants, but as the soil and plant community converge over time with those found on remnants, those community differences would diminish on older reconstructions.

## STUDY AREA

We sampled two locations containing prairies managed by the Missouri Department of Conservation. The Wah'Kon-Tah Prairie location, situated in St. Clair County in the Upper Osage Grasslands region of southwestern Missouri, contained remnant (756 ha) and reconstructed (160 ha) prairie (Fig. 1). Prairie reconstruction at Wah'Kon-Tah was initiated in ten parts from 2002 to 2008. The second location was 333 km northeast in the Central Dissected Plains region in Calloway County. This North location consisted of two distinct prairies:

one remnant (Tucker Prairie, 59 ha) and one reconstructed (Prairie Fork Conservation Area, 142 ha), separated by 32 km (Fig. 1). Reconstruction of prairie patches at Prairie Fork Conservation Area in the North location started in 2004 and was ongoing at the start of this study in 2016.

There were various grassland management practices that could confound invertebrate surveys. Therefore, we excluded areas that were scheduled to be hayed, grazed, mowed, or high-clipped in the sampling year because those practices might alter the invertebrate community during the summer months (Humbert et al. 2010). Burning also affects invertebrate communities (Panzer 2002); however, we included burned patches in our sampling because burns were scheduled during the dormant season, outside of the sampling window.

## METHODS

### Sampling Scheme

We sampled bee communities using bee bowls placed at randomly selected locations within each remnant and reconstructed prairie in 2016 and 2017. We used ArcMap 10.3.1 (ESRI 2015) to randomly generate points each year. There were 30 sampling points generated on the Wah'Kon-Tah reconstructions and 30 points on the remnant prairie. At the North location, there were 30 points on the reconstructions and 15 on the remnant in 2016 and 20 points on the reconstruction and 10 on the remnant in 2017. We reduced the samples in the North in 2017 to increase distances between bee bowls and better match sampling intensity with the larger Wah'Kon-Tah. Each sample point was located at least 40 m from the prairie edge to limit edge effects. The two closest sampling points were 120 m apart, and the average nearest neighbor distance was 250 m. Independence in this case means that the bees caught at one sampling point should not have affected bees caught at any other location. However, while we assumed independence among samples, native bee species differ considerably in body size and flight range, with some bees having foraging ranges of 1.5 km or larger (Greenleaf et al. 2007). As some of the samples in this study were located closer than 1.5 km, samples may better reflect bee foraging preference than nest location, especially for larger bees with large flight ranges. Sample independence is a challenge in many bee studies (Davis et al. 2007, Kwaiser and Hendrix 2008, Kimoto et al. 2012). Our experimental design and distance between sampling locations is similar to previous research (Briggs et al. 2013).

### Collecting

We sampled bees using bee bowls made with clear 0.27 L (9-oz) cups (SOLO®) and fluorescent paint (Droege 2012). We placed three bowls, one yellow, one blue (Fluorescent

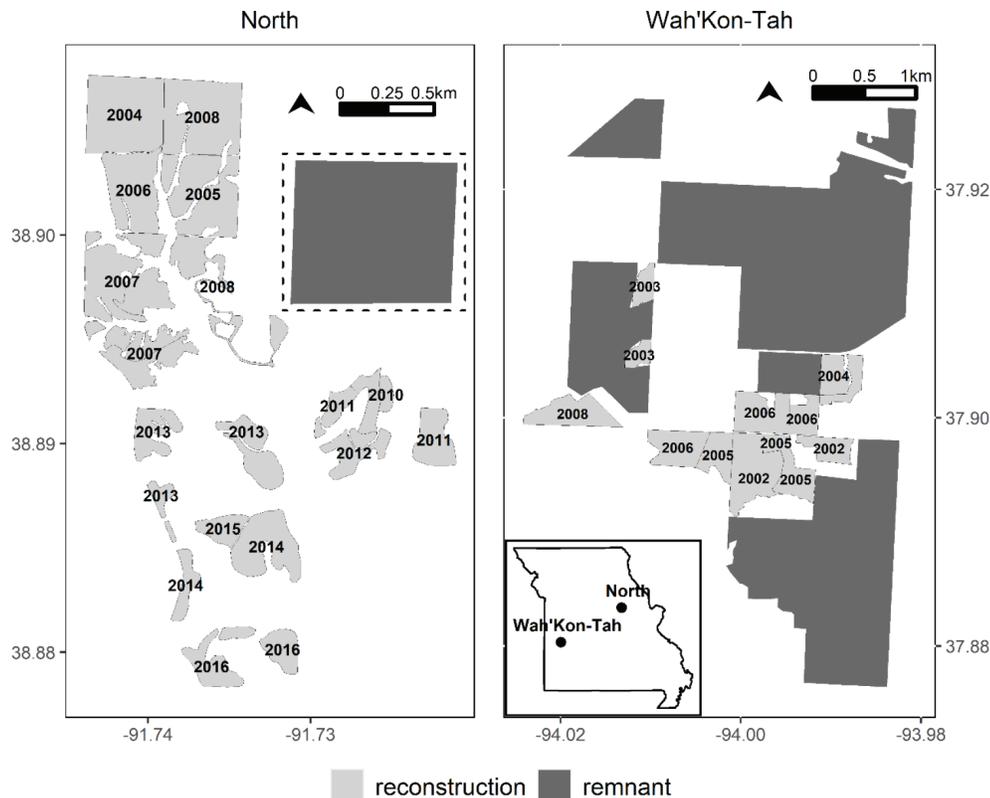


Figure 1. Maps of Wah'Kon-Tah and North prairies in Missouri, USA. The remnant prairie at the North location is 32 km away from the reconstructed prairie, therefore it is displayed to scale as an inset (dashed border). Reconstructed portions of prairie are labeled with the year in which they were seeded.

Yellow, Fluorescent Blue, mixed with Silica Flat; Guerra Paint & Pigment Corporation), and one white (white spray paint; Valspar®), at each randomly generated point. Bowls sat in plastic (PVC) rings that were glued to each other and then mounted on a 12.7 mm dowel rod, which allowed us to modify bee bowl height with growing vegetation. We positioned the bee bowls at half vegetation height to track flower height. Bee bowls are only effective if they are visible (Tuell and Isaacs 2009), thus they must be placed higher later in the growing season to correspond with plant growth. We filled bee bowls with soapy water, and they remained in the field for 48 hr during each sampling period (Droege 2015). The contents of the three bowls were combined into a single sample for each sampling period. In 2016, we sampled monthly from June to August. In 2017, we sampled monthly from April to August. We also caught bees through standardized sweeping as part of a concurrent study on grasshoppers (LaRose et al. 2019). We conducted 40 sweeps along a 60-m transect centered at every bee bowl location concurrent with bee bowl use. Any bees captured were identified and added to bees captured with bee bowls for analyses.

Bees were identified to species, or in cases where species could not be reliably determined, to genus or subgenus, using Arduser (2016) and discoverlife.org (Ascher and Pickering

2017). We grouped bees by family and nesting habitat (Table 1). Representative specimens of every taxon were pinned and stored in the Enns Entomological Museum at the University of Missouri, Columbia.

### Statistical analyses

*Bee diversity and total abundance.* We compared bee taxon richness (species plus genera and subgenera that were not identified further) and diversity in reconstructed and remnant prairies at each location (Wah'Kon-Tah and North) using non-asymptotic techniques. The non-asymptotic approach consisted of rarefaction/extrapolation (Weibull et al. 2003, Gotelli and Colwell 2011, Colwell et al. 2012), which resamples species data to estimate the richness or diversity at other sample sizes. We performed sample-based rarefaction/extrapolation on the locations separately using the package iNEXT (Hsieh et al. 2016), treating each bee bowl location as a sample. We conducted all analyses using R version 3.4.0 (R Core Team 2017).

We generated rarefaction/extrapolation curves for three Hill numbers (Hsieh et al. 2016), which are measures of diversity that combine species richness and abundance. The curves represented the estimated Hill numbers at

Table 1. Bee taxa captured in on Missouri prairies in 2016 and 2017 with family and nesting habitat information. Single asterisk (\*) indicates taxa was unique to remnant prairies; double asterisk (\*\*) indicates taxa was unique to reconstructed prairie.

Taxa	Family	Nest Habitat
<i>Andrena (Andrena)</i>	Andrenidae	Soil
<i>Andrena (Derandrena)</i>	Andrenidae	Soil
<i>Andrena (Melandrena)</i>	Andrenidae	Soil
<i>Andrena (Plastandrena)</i>	Andrenidae	Soil
<i>Andrena (Ptilandrena)</i>	Andrenidae	Soil
<i>Andrena (Rhacandrena)</i>	Andrenidae	Soil
<i>Andrena (Scapteropsis)</i>	Andrenidae	Soil
<i>Andrena (Trachandrena)</i>	Andrenidae	Soil
<i>Andrena arabis</i>	Andrenidae	Soil
<i>Andrena cressoni</i>	Andrenidae	Soil
<i>Andrena rudbeckia</i>	Andrenidae	Soil
<i>Andrena violae</i>	Andrenidae	Soil
<i>Andrena carlini</i>	Andrenidae	Soil
<i>Pseudopanurgus albitarsis</i>	Andrenidae	Soil
<i>Apis mellifera</i>	Apidae	Cavity
<i>Bombus auricomus</i>	Apidae	Soil
<i>Bombus bimaculata</i>	Apidae	Soil
<i>Bombus griseocolis</i>	Apidae	Soil
<i>Bombus impatiens</i>	Apidae	Soil
<i>Bombus pennsylvanicus</i>	Apidae	Soil
<i>Ceratina</i>	Apidae	Stem/twig
<i>Eucera hamata</i>	Apidae	Soil
<i>Eucera rosae</i>	Apidae	Soil
<i>Melissodes agilis</i>	Apidae	Soil
<i>Melissodes bimaculata</i>	Apidae	Soil
<i>Melissodes boltoniae</i>	Apidae	Soil
<i>Melissodes communis</i>	Apidae	Soil
<i>Melissodes comptooides</i>	Apidae	Soil
<i>Melissodes dentriventris**</i>	Apidae	Soil
<i>Melissodes elegans**</i>	Apidae	Soil
<i>Melissodes nivea*</i>	Apidae	Soil
<i>Melissodes trinodis</i>	Apidae	Stem/twig

Taxa	Family	Nest Habitat
<i>Melissodes veronia</i>	Apidae	Soil
<i>Nomada</i>	Apidae	Kleptoparasite
<i>Ptilothrix bombiformis</i>	Apidae	Soil
<i>Xylocopa virginica</i>	Apidae	Wood
<i>Hylaeus fedorica</i>	Colletidae	Stem/twig
<i>Hylaeus illinoisensis</i>	Colletidae	Stem/twig
<i>Hylaeus mesillae</i>	Colletidae	Stem/twig
<i>Agapostemon sericeous</i>	Halictidae	Soil (sand)
<i>Agapostemon texanus</i>	Halictidae	Soil
<i>Agapostemon virescens</i>	Halictidae	Soil
<i>Augochlora pura</i>	Halictidae	Wood
<i>Augochlorella aurata</i>	Halictidae	Soil
<i>Augochlorella persimilis</i>	Halictidae	Soil
<i>Augochloropsis fulgida</i>	Halictidae	Soil
<i>Augochloropsis metallica</i>	Halictidae	Soil
<i>Halictus ligatus</i>	Halictidae	Soil
<i>Halictus parallelus</i>	Halictidae	Soil
<i>Lasioglossum</i>	Halictidae	Soil
<i>Lasioglossum (Dialictus)</i>	Halictidae	Soil
<i>Lasioglossum paralictus</i>	Halictidae	Kleptoparasite
<i>Megachile brevis</i>	Megachilidae	Stem/twig
<i>Megachile montivaga</i>	Megachilidae	Soil
<i>Megachile parallela</i>	Megachilidae	Stem/twig
<i>Megachile petulans</i>	Megachilidae	Stem/twig
<i>Megachile relativa</i>	Megachilidae	Stem/twig

hypothetical sample sizes, ranging from zero to two times the actual sample size. We generated rarefaction/extrapolation of Hill curves for each year separately as well as collectively. We plotted the Hill curves using 95% confidence intervals, calculated with the bootstrap method (Colwell et al. 2012).

We compared bee abundance on remnants and reconstructions by modeling the total abundance of bees summed across sampling periods using univariate generalized linear models with a negative binomial distribution. Variables included *status* (reconstruction or remnant), *location* (Wah'Kon-Tah or North) and *year* (2016 or 2017). We started with an initial model that included all variables and interactions and then removed interactions and variables

individually. We conducted analyses of variance (ANOVA) on models with and without variables and discarded those variables that did not improve model fit ( $P > 0.05$ ) (Blakey et al. 2016, Clarke-Wood et al. 2016). We used the function *glm.nb* in the package *MASS* (Ripley et al. 2017). We compared the abundance of bees across reconstructions of different ages to determine if bee abundance on reconstructions was changing over time. For these analyses, we used the same ANOVA methods but only included data from reconstructed prairies, replacing *status* with *age* (years since initial reconstruction).

*Community analysis.* To visualize community data, we ordinated the bee communities using non-metric multidimensional scaling (NMS) with a Bray-Curtis

dissimilarity matrix (Paton et al. 2009, Clarke-Wood et al. 2016). Taxa abundances were summed across sampling periods for bee bowl locations for each year separately. Only species that occurred in more than 5% of bee bowl samples were included in the ordination in order to reduce noise that rare species can contribute (Gauch 1982) and to reduce ordination stress, a measure of goodness of fit, to interpretable levels (<0.20) (Clarke 1993). Therefore we used the 24 most common bee taxonomic groups (primarily species and a few genera). Bee bowl samples with zero individuals were removed before analysis for the same reason. We used the function *metaMDS* in package *vegan* (Oksanen et al. 2016) to run NMS. We used the function *dimcheckMDS* to choose the number of dimensions (k) according the stress value and visualized the resulting ordination with the *ordipl* function.

To test whether bee communities in reconstruction and remnant prairies were distinct, we modeled abundances of the same taxa used in the ordinations. Multivariate models were generated in the package *mvabund* (Wang et al. 2012), which incorporates multivariate count data into generalized linear models. The response variables were the abundances of a taxa summed across sample dates for each bee bowl sample; we used a negative binomial distribution for all models. Explanatory variables included *status* (remnant or reconstructed), *location* (Wah’Kon-Tah, and North), *edge proximity* (distance from bee bowl location to closest prairie edge, measured in ArcMAP), *year* (2016 or 2017), and all interactions among them. We tested the significance of variables and interactions with an ANOVA comparing the full model to a model without each variable (Blakey et al. 2016, Clarke-Wood et al. 2016). Because of a significant *status* × *location* interaction, we ran multivariate models for each location as well. To identify which taxa contributed to differences between communities we examined the multivariate model coefficients for each taxon. Coefficients with a *P*-value <0.05 were considered significant.

We used the same methods to compare bee community composition across reconstructions of different ages by removing remnant sampling points (and therefore *status*) and adding *age* as a variable for remaining reconstruction sites. Only the 23 most abundant bees found on reconstructions were used in the models for age effect.

**Functional groups.** We grouped bees by nesting habitat using information from discoverlife.org (Ascher and Pickering 2017) and Arduser (2016). Nesting categories included *wood* (bees that nest in logs or tree cavities), *stem* (twig and stem nesters, hereafter stem nesters), and *soil*. Using the package *mvabund*, we created multivariate models of abundance for each functional group. Explanatory variables in this analysis included *status*, *location*, *edge proximity*, *year*, and all possible interactions. Due to a significant *status* × *location* interaction, we also modeled functional group abundance for each location separately. We used the same methods to compare functional groups across reconstructions of different

ages by removing remnant sampling points (and therefore *status*) and adding *age*.

## RESULTS

### Did bee communities on reconstructions differ from those on remnants?

**Diversity and total abundance.** We collected 3,647 bees from 57 identified species or genera in 2016 and 2017 combined (Table 1). Most of the bees captured were in family Halictidae (71%); Apidae (20%) was the second most common bee family observed. There was little difference in diversity between remnants and reconstructions based on rarefaction/extrapolation curves for species richness, with Shannon diversity and Simpson diversity 95% confidence intervals of reconstruction and remnant diversity overlapping for all three Hill numbers (Fig. 2). At the North location, Simpson diversity was greater on reconstructions than the remnant (Fig. 2).

The best generalized linear model of total bee abundance contained year ( $\chi^2 = 7.87$ ,  $P = 0.005$ ) and an interaction between status and location ( $\chi^2 = 11.27$ ,  $P < 0.001$ ). When locations were modeled separately, bees were more abundant on reconstructions than remnants at the North location ( $\chi^2 = 4.53$ ,  $P < 0.0001$ ), but not at Wah’Kon-Tah ( $\chi^2 = 1.05$ ,  $P = 0.306$ ). Bees were more abundant in 2016 than in 2017.

**Community composition.** Remnant and reconstruction bee communities appeared somewhat distinct in 3-D ordinations (Fig. 3A; stress = 0.19; k = 3), with some overlap in 95% confidence intervals on the centroids. However, communities were clearly different by location (Fig. 3B) and year, indicating that *year* and *location* were more important sources of variation in the bee communities than *status*. The best multivariate model of species abundances contained *year* ( $\chi^2 = 314.9$ ,  $P < 0.001$ ) and an interaction between *location* and *status* ( $\chi^2 = 78.87$ ,  $P < 0.001$ ). However, univariate tests showed that the interaction was only significant for two species, *Melissodes communis* ( $\chi^2 = 11.17$ ,  $P < 0.03$ ) and *Melissodes comptooides* ( $\chi^2 = 17.44$ ,  $P < 0.002$ ). Therefore we focus on results from a model without the interaction term that included *location* ( $\chi^2 = 394.8$ ,  $P < 0.001$ ), *year* ( $\chi^2 = 313.3$ ,  $P < 0.001$ ), and *status* ( $\chi^2 = 145.7$ ,  $P < 0.001$ ). Remnant and reconstruction communities were distinct at Wah’Kon-Tah Prairie ( $\chi^2 = 101.5$ ,  $P < 0.001$ ) and the North prairies ( $\chi^2 = 92.58$ ,  $P < 0.001$ ). Based on model coefficients representing the effects of reconstruction on species abundance, *Eucera hamata*, *Ceratina*, *Apis mellifera*, *Agapostemon texanus*, and *Hylaeus mesillae* were more common on reconstructions than remnants. *Halictus parallelus* and *Augochlorella persimilis* were more abundant on remnants. Beyond the common species used in the ordination and multivariate abundance models, there was one rare species only found on remnants, *Melissodes nivea*, and three species found

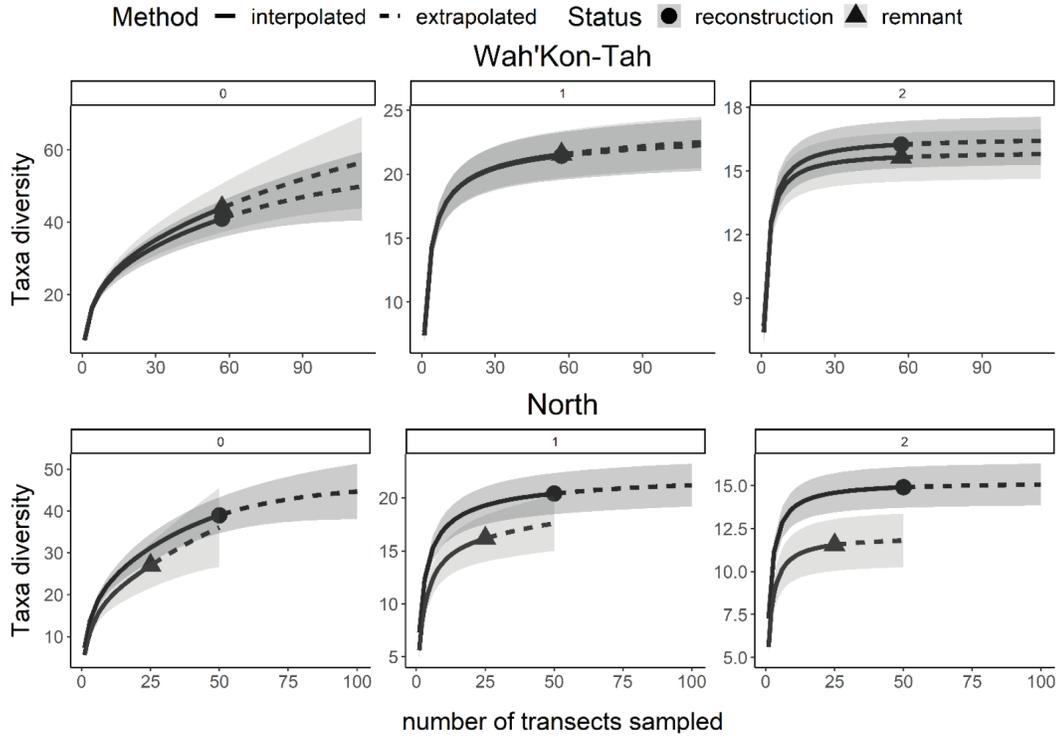


Figure 2. Sample-based rarefaction and extrapolation of Hill number diversity of bees captured on Missouri prairies in 2016 and 2017. 0 = species richness, 1 = Shannon diversity, and 2 = Simpson diversity. Shaded areas represent 95% confidence intervals. Shannon diversity estimates are presented as the exponentials of Shannon indices, and Simpson diversity estimates are presented as inverse of Simpson concentration, such that larger numbers represent greater diversity.

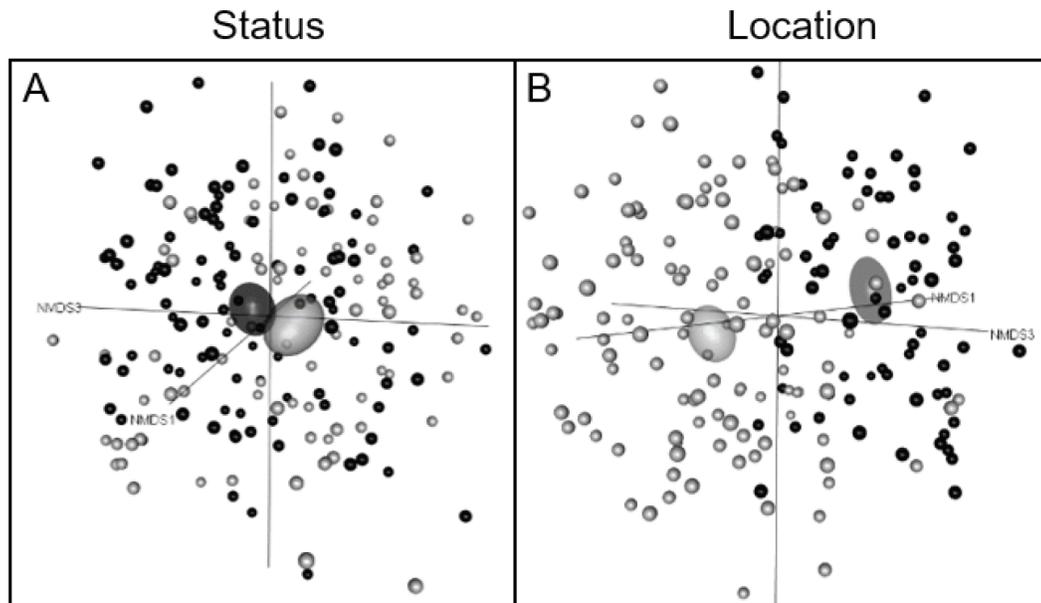


Figure 3. NMS ordination ( $k = 4$ , stress = 0.18) of bee communities from Missouri prairies in 2016 and 2017. Dots represent communities from individual bee bowl samples. Spheres represent 95% confidence intervals around the centroids. A: Remnants (black) and reconstructions (grey). B: Wah'Kon-Tah (black) and North (grey) locations.

only on reconstructions, *Agapostemon sericeus*, *Melissodes dentriventris*, and *Melissodes elegans*.

**Functional groups.** Among nesting functional groups, soil nesters were most abundant (90.5%), followed by stem nesters (7.0%). Overall abundance of stem nesters was greater on reconstructions than remnants (Fig. 4;  $\chi^2 = 12.14$ ,  $P = 0.022$ ); this response was likely driven by the abundance of stem nesters on reconstructions at Wah'Kon-Tah ( $z = -2.02$ ,  $P = 0.043$ ). The genus *Ceratina* and *H. messillae*, identified in the multivariate abundance model as more common on reconstructions, were likely responsible for the greater stem nester abundance on reconstructions. In the North location, soil nesters were more common on reconstructions than on remnants (Fig. 4;  $\chi^2 = 2.059$ ,  $P = 0.039$ ).

#### Did reconstruction age affect community composition?

Ordination ( $k = 4$ , stress = 0.171) revealed no obvious trends based on reconstruction age, but the centroids of newer reconstructions clustered on one side of the NMS space. The best multivariate abundance model contained an interaction between *age* and *location* ( $\chi^2 = 76.04$ ,  $P < 0.001$ ), but univariate tests revealed the interaction was significant

for only two bee species, *Augochloropsis metallica* ( $\chi^2 = 14.6$ ,  $P = 0.006$ ) and *Melissodes bimaculata* ( $\chi^2 = 12.26$ ,  $P = 0.012$ ), as well as marginally significant for *Halictus parallelus* ( $\chi^2 = 9.826$ ,  $P = 0.064$ ). Consequently, and for ease of interpretation, we excluded the *age*  $\times$  *location* interaction term. The model without an *age*  $\times$  *location* interaction included *age* ( $\chi^2 = 61.29$ ,  $P < 0.001$ ) and *year*  $\times$  *location* ( $\chi^2 = 73.7$ ,  $P < 0.001$ ), indicating that bee communities differed across reconstruction age. Excluding *A. metallica* because of a significant interaction, there were three taxa that showed a significant abundance response to reconstruction age: *Lasioglossum* subg. *Dialictus*, *A. aurata*, and the genus *Ceratina*. *Dialictus* abundance decreased with reconstruction age. *A. aurata*, which was the most common native bee captured on reconstructions, and *Ceratina* abundance increased with reconstruction age.

The best bee abundance model for reconstructions included an *age*  $\times$  *location* interaction ( $\chi^2 = 5.81$ ,  $P = 0.016$ ), which was due to a negative relationship between bee abundance and reconstruction age at the North location ( $\chi^2 = 9.99$ ,  $P < 0.002$ ) (Fig. 4).

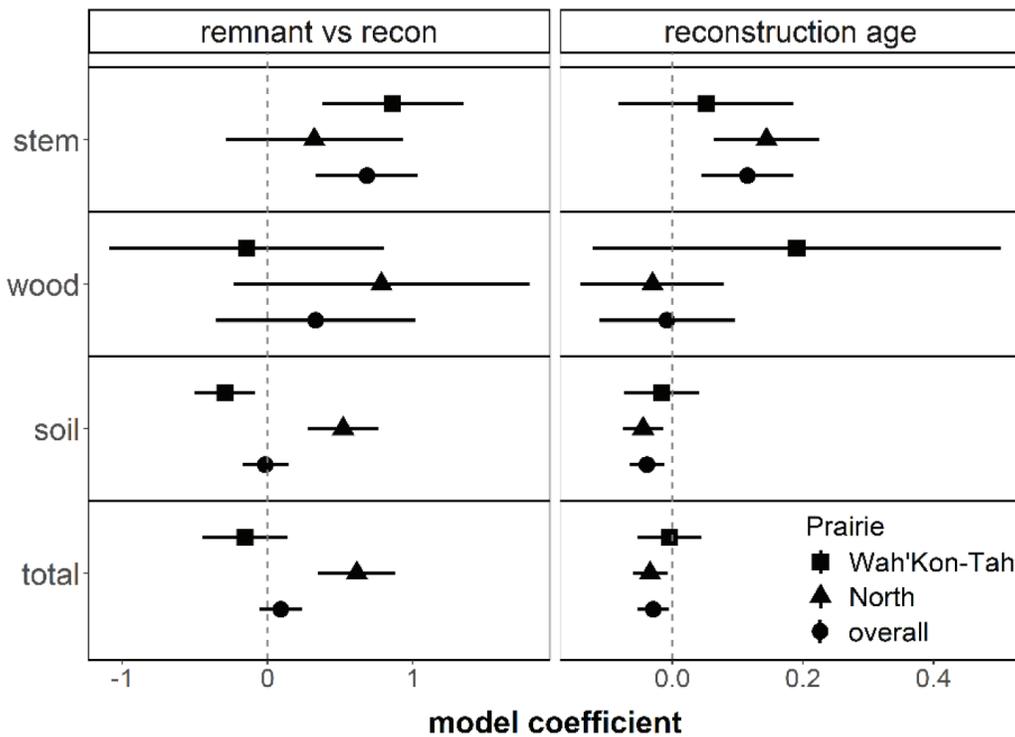


Figure 4. The effect of prairie *status* (left) and *age* (right) on the abundance of three bee nesting groups as well as total bee abundance on Missouri prairies in 2016 and 2017. Symbols represent coefficients, with 95% confidence intervals, from a multivariate abundance model. Positive coefficients signify greater abundance on reconstructions (recon) than remnants (left), or increasing abundance with age (right). There are up to three coefficients for each species, representing the response of taxa for the Wah'Kon-Tah and North areas separately, and for both prairie areas combined with no interaction (overall). Model coefficients with very large standard errors are not shown.

### Functional groups

The best model of nesting group abundances contained age ( $\chi^2 = 17.44$ ,  $P = 0.003$ ) and an interaction between location and year ( $\chi^2 = 19.52$ ,  $P < 0.001$ ). Stem nester abundance was positively associated with reconstruction age, whereas soil nester abundance was negatively associated with reconstruction age (Fig. 4).

## DISCUSSION

Our first objective was to compare bee communities of prairie reconstructions and remnants and identify species or functional groups that can be used to evaluate prairie reconstruction progress and effectiveness. Bee communities on remnant and reconstructed prairies shared nearly all species but were distinct due to differing abundances for some taxa. Although remnants and reconstructions were statistically distinct, communities differed much more between locations and between years. Similar to what studies on restorations have found on Central European grasslands (Exeler 2009), riparian habitats in California (Williams 2011), and Illinois prairies (Tonietto et al. 2017), we found little evidence that remnant and reconstructed prairies in Missouri differed in bee species richness or diversity. It is important to note the possible effect of sample independence and geography in our study when interpreting the observed differences in remnant and reconstructed bee communities. Because the distance between some sampling locations was less than some bees' flight ranges, it is possible that bees nested near one sample location and foraged at another. In this case, we sampled foragers and their foraging preference, not just nesters. As for geography, the reconstruction and the remnant were farther apart at the North location. It is possible that the differences we observed at the North location arise at least partly from differences in background bee communities at the remnant and reconstruction sites, and not necessarily differences between the types of prairie.

Our second objective was to evaluate the effect of reconstruction age on bee communities. Our results suggest that reconstruction bee communities differ along an age gradient, and not necessarily in ways that show convergence with remnant communities. Past studies do not show consistent convergence either. In California, bee communities on restorations remained distinct from remnants after six years (Williams 2011), whereas restoration bee community composition converged with that of remnants after only 2–3 years in Illinois (Griffin et al. 2017). Another study in Illinois reported that bee communities were most different from remnants for several years after reconstruction but became similar to remnants after 20 years (Tonietto et al. 2017).

We identified several bee taxa that were more abundant on either reconstructions or remnants and could hold potential as long-term monitoring subjects. *Ceratina* and *Hylaeus mesillae* are both relatively common twig or stem nesters that were

more abundant on reconstructions. Interestingly, *Ceratina* abundance actually increased with reconstruction age, which is the opposite of what we would expect if reconstructions were converging with remnants, as past studies have shown (Foster et al. 2007, Watts et al. 2008, Carter and Blair 2012, Tonietto et al. 2017). The trends in *Ceratina* and *H. mesillae* abundance could result from amount of stems available for nesting, although without plant community data we are limited to speculation. There are few studies that directly link stem density or abundance with stem-nesting bees; however, prescribed fire, which eliminates stems and twigs, has been shown to negatively impact presence of stem-nesting bees (Eickwort et al. 1981, Cane et al. 2007, Cane and Neff 2011). *Ceratina* and *H. mesillae*, which are generalists, may be more successful nesting in the stems of plants that dominate early reconstructions, some of which are widespread exotics such as wild mustard (*Sinapis arvensis*) and dandelion (*Taraxacum officinale*) (McLachlan and Knispel 2005).

Some of the species associated with reconstructions were ground nesters. Like plant community composition, soil characteristics are potential factors in explaining the greater abundance of ground nesters such as *E. hamata* on reconstructions. One of the stronger indicators that soil affects reconstruction community composition in our study comes from the observed trend in *Dialictus* abundance. The genus *Lasioglossum*, and in particular its subgenus *Dialictus*, is associated with disturbed soil (Kim et al. 2006). *Dialictus* abundance decreased with reconstruction age. Recently reconstructed prairies have been recently disturbed and thus likely offer more nesting habitat for soil nesting bees such as *Dialictus*. The trend in *Dialictus* abundance was particularly strong at the North location. There were some soil-nesting taxa whose abundance increased with reconstruction age, such as *A. aurata* that may thrive in soil that has been disturbed less recently than taxa like *Dialictus* or *E. hamata*.

Species or functional groups closely associated with remnants have the potential to be good indicators of reconstruction success and our study identified two candidate species based on results of the multivariate models: *A. persimilis*, and *H. parallelus*. *H. parallelus* is a thought to be a prairie specialist because it has been found mainly on remnants in Missouri (Arduser 2016), and our results provide quantitative support for that hypothesis. Both *H. parallelus* and *A. persimilis* are ground nesting generalists, but *H. parallelus* is a large bee while *A. persimilis* is one of the smallest bees that we captured. Reconstruction soils, which are generally recently disturbed and usually altered by agricultural activity (Kindscher and Tieszen 1998), may lack the ideal soil nesting conditions for those species.

Our results indicated that bee communities on remnant and reconstructed prairies were distinct. The distinction was due to differences in relative abundances of bees, not necessarily the identity, because remnants and reconstructions shared almost all bee taxa. We identified several bee taxa that were

more abundant on reconstructions or remnants and thus hold potential as long-term monitoring subjects. Trends in nesting group abundances emphasize the impacts of management and potential importance of soil characteristics and function on bee communities. More extensive and varied sampling is likely necessary to determine when the entire bee community on reconstructions reaches the target composition found on prairie remnants.

## MANAGEMENT IMPLICATIONS

Prairie restoration and reconstruction efforts that are focused on achieving remnant-like bee communities would likely benefit from considering community measures other than species richness and diversity, as these may not differ between restorations and remnants. Restoration efforts aimed at providing habitat for prairie bees could consider incorporating nesting habitat availability, particularly soil and plant stems, because of its strong association with bee community composition.

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# Patterns and Potential Causes of Changing Winter Bird Distributions in South Dakota

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**ABSTRACT** Average winter temperatures in the north-central United States have been increasing since the 1970s, and this warming might influence winter distributions of birds in the region. Species potentially influenced by such winter warming include short-distance migrants for which the northern boundary of the winter range is influenced by temperature, such as hermit thrush (*Catharus guttatus*), yellow-rumped warbler (*Setophaga coronata*), and fox sparrow (*Passerella iliaca*). We examined winter records during 1974–2017 from a citizen-science bird observation database for South Dakota to determine recent trends in winter records for these three species. We compared their occurrence patterns with those for three benchmark species (i.e., American black duck [*Anas rubripes*], Townsend’s solitaire [*Myadestes townsendi*], and varied thrush [*Ixoreus naevius*]), for which winter records are not expected to respond to warming winters in South Dakota. All three study species showed marked recent increases in the number of winter records in South Dakota. Logistic regression with model selection identified year as an important predictor of occurrence for all three study species, with higher probabilities of occurrence in recent years. This contrasted with winter occurrence patterns for benchmark species, for which year was positively associated with winter occurrence only for Townsend’s solitaire. Early winter temperatures were included in competitive models for hermit thrush and yellow-rumped warbler, with increased probabilities of occurrence in years with higher temperatures. For benchmark species, only winter occurrence of American black duck was positively associated with early winter temperatures. These data suggest that all three study species are expanding their ranges northward in the north-central United States during a period of winter warming, but other factors in addition to winter temperature are also influencing this trend.

**KEY WORDS** birds, climate change, fox sparrow, hermit thrush, temperature, winter distribution, yellow-rumped warbler

Winter climates in North America are showing warming trends, particularly in northern and north-central regions of the continent, with the greatest winter warming in the continental United States occurring in the northern Midwest, including North and South Dakota (Tebaldi et al. 2013, Vose et al. 2017). For example, average daily winter (December–February) temperatures in South Dakota have increased by approximately 1° C per decade since the 1970s (Swanson and Palmer 2009). Numerous studies have examined bird responses to changing climates, focusing primarily on range shifts, changes to migration timing, and changes to breeding and wintering abundance (e.g., Wormworth and Şekercioğlu 2011). Indeed, Princé and Zuckerberg (2015) found that structure of the winter bird community in eastern North America has changed since 1990, with the changes driven largely by warm-adapted species moving their winter ranges northward. Few studies, however, have examined the impacts of warming winters on birds in the north-central United States, despite this being one of the regions with the greatest winter warming (Tebaldi et al. 2013, Vose et al. 2017). Such warming may affect winter bird abundance (Butler et al. 2007) and migration phenology (Swanson and Palmer 2009, Travers et al. 2015) in the region, but these regional studies have not examined whether winter occurrence trends are changing in response to warming winters as a result of shifts

in northern range boundaries.

To detect trends in bird occurrence patterns with warming winter temperatures, we suggest two criteria must be met in the selection of study species. First, the species must be historically rare within a region in winter so that the baseline occurrence pattern for the region is an absence of winter records. An increase in winter detections over time would then imply a change in the winter occurrence pattern for the species. Changes in bird abundances could also meet this criterion, but documenting changes in abundance over time requires a long-term systematic dataset of bird abundance surveys. The National Audubon Society Christmas Bird Count dataset is such a long-term dataset, but it is limited to the early winter period and, therefore, may include straggling late fall migrants rather than true winter residents. No such long-term dataset for mid- or late-winter bird abundance occurs for the north-central United States. Second, for species to respond to warming winter temperatures, their northern range boundary must be associated primarily with temperature rather than with vegetation or other ecological factors. For species with northern range boundaries associated with temperature, increasing winter temperatures should result in a northward movement in the northern range boundary so that individuals will occur in winter in regions where they were formerly absent. The northern

range boundaries for a number of birds wintering in North America are associated with temperature (Root 1988a, Canterbury 2002), including species in the north-central United States (Butler et al. 2007). Short-distance migrant birds meeting these two criteria for South Dakota include hermit thrush (*Catharus guttatus*), yellow-rumped warbler (*Setophaga coronata*), and fox sparrow (*Passerella iliaca*).

Hermit thrush is the most northerly wintering of the *Catharus* thrushes and yellow-rumped warbler is the most northerly wintering Parulid (Hunt and Flaspohler 1998, Dellinger et al. 2012). The northern range boundaries, determined from Christmas Bird Count data, for both of these species are approximately associated with the  $-4^{\circ}\text{C}$  mean minimum January temperature isotherm, extending in the central United States from northern Oklahoma and southern Kansas to southern Missouri and Illinois (Root 1988a, 1988b, Hunt and Flaspohler 1998, Dellinger et al. 2012). The northern and western range limit of winter distribution of the eastern *iliaca* group of fox sparrow extends from eastern Oklahoma and Kansas to southeastern Minnesota, southern Wisconsin, and southern Michigan (Weckstein et al. 2002). The northern range boundary of fox sparrow is loosely associated with the  $-5^{\circ}\text{C}$  minimum January temperature isotherm (Root 1988b). Canterbury (2002) calculated northern range boundaries differently, as the mean minimum January temperature at the coldest Christmas Bird Count site occupied during at least half of the count years, and listed the northern range boundaries for yellow-rumped warbler as  $-9.4^{\circ}\text{C}$  and for fox sparrow as  $-15^{\circ}\text{C}$ . In addition, Princé and Zuckerberg (2015) calculated the average minimum temperatures across the entire winter range of yellow-rumped warbler and fox sparrow as  $-4$  and  $-5^{\circ}\text{C}$ , respectively, also suggesting that northern range boundaries for these species occur at colder temperatures than those suggested by Root (1988a, 1988b). Tallman et al. (2002), reviewing South Dakota bird records prior to 2001, classified hermit thrush as accidental (0–2 records in the preceding decade) and yellow-rumped warbler and fox sparrow as casual (3–10 records in the preceding decade) in winter in South Dakota. Consequently, these three species represent likely candidates to respond to warming winters by increasing their winter occurrence within South Dakota.

Precedent exists for a distributional response of wintering birds, including hermit thrush, yellow-rumped warbler, and fox sparrow, to weather or climate variation (e.g., Valiela and Bowen 2003, La Sorte and Thompson 2007, Zuckerberg et al. 2011, Princé and Zuckerberg 2015). Consequently, northward expansion of these species into formerly unoccupied areas as a function of warming winters might be expected. For example, hermit thrush abundances on Christmas Bird Counts in North America increased from 1965–1966 to 2002–2003 (Niven et al. 2004) while breeding populations remained essentially stable (Sauer et al. 2017), suggesting northward movements of winter populations in response

to recent warming winters. Hermit thrush and fox sparrow also showed significant northward trends in winter range centroids from Christmas Bird Count data from 1965–1966 to 2002–2003, but yellow-rumped warbler did not (Niven et al. 2009). Most studies examining the relationship between winter temperature and bird abundance and distribution for North American birds have used Christmas Bird Count data, which provide a snapshot of early winter distributions (Niven et al. 2009). Fewer studies use data that cover the entire winter period (but see Zuckerberg et al. 2011, Princé and Zuckerberg 2015).

In the present study, we analyzed occurrence data during 1975–2017 for the entire winter period (December–February) for hermit thrush, yellow-rumped warbler, and fox sparrow in South Dakota from a citizen-science bird records database of the South Dakota Ornithologists' Union (South Dakota Ornithologists' Union 2018). We compared occurrence data for the three study species with occurrence data for three benchmark species (see below) not expected to respond to changing conditions over the study period. We hypothesized that the patterns of winter occurrence for hermit thrush, yellow-rumped warbler, and fox sparrow in South Dakota would change in response to recent warming winters. More specifically, we hypothesize that 1) winter records of the three study species in South Dakota will increase in recent years, and 2) these species will be recorded more often in warmer than in colder winters.

## STUDY AREA

Our study encompassed all winter bird observation records for the entire state of South Dakota. Average daily January temperatures for South Dakota range from  $-12.2^{\circ}\text{C}$  in the northeast to  $-3.9^{\circ}\text{C}$  in the southwest, with average annual snowfall ranging from 61–76 cm across much of the state to 152–254 cm in the higher elevations of the Black Hills (Todey et al. 2009). Mean winter temperatures have been increasing in South Dakota since 1970 by as much as  $1^{\circ}\text{C}$  per decade in portions of the state (Swanson and Palmer 2009, Tebaldi et al. 2013).

## METHODS

### Data Sources

We used a citizen-science bird observation database maintained by the South Dakota Ornithologists' Union (SDOU) for winter bird observation records. Quality control for this database is provided by the *Seasons Reports* compiler, who is appointed by the SDOU to this position because of demonstrated expertise with the South Dakota avifauna. The compiler authors a quarterly report of state bird observations from submissions to this database that is published in *South Dakota Bird Notes* (e.g., Palmer 2017).

Any records of rare or out-of-range species are not listed in the database until they have been approved by the Rare Bird Records Committee of the SDOU. Of the three study species and three “benchmark” species (see below), only winter hermit thrush observations required rare bird reports, and winter hermit thrush was removed from the review list after 2005. We supplemented records from the SDOU database by reviewing all winter seasonal reports published in *South Dakota Bird Notes* (the official publication of the SDOU); winter seasonal reports have been published in *South Dakota Bird Notes* continuously since the winter of 1974–1975. We considered December through February records as winter records, although some December records may possibly represent lingering migrants. For yellow-rumped warblers for which more winter records were available than the other two species (Tallman et al. 2002), we also separated out January–February records and conducted logistic regression analyses only for January–February occurrences.

We retrieved all December through February records for 1974–1975 to 2016–2017 from the SDOU database and the Seasonal Reports for hermit thrush, yellow-rumped warbler, and fox sparrow in South Dakota. We similarly chose three “benchmark” species, which we defined as birds that occurred very rarely in South Dakota (or portions of South Dakota) with ranges primarily to the east or west (rather than south) of South Dakota, for which we also extracted winter records. The benchmark species also failed to meet the temperature criterion defined for the study species, so little response to winter warming for these benchmark species was expected. These species included American black duck (*Anas rubripes*), a casual winter visitor in South Dakota, Townsend’s solitaire (*Myadestes townsendi*, eastern South Dakota only because this species is a year-round resident in the western part of the state but a rare winter visitor to the east), and varied thrush (*Ixoreus naevius*), a casual migrant and winter visitor to the state (Tallman et al. 2002). Continuous bird observation records are available in the SDOU database and/or the Seasonal Reports in *South Dakota Bird Notes* for the winter of 1974–1975 through the present, so we extracted all records for winters from 1974–1975 through 2016–2017. We counted records conservatively and treated multiple records for a single species in the same winter from the same or adjacent county (the coarsest location data provided by the SDOU database) as a single record unless different specific locations were mentioned for each record.

For local climate data for South Dakota, we accessed National Oceanic and Atmospheric Association (NOAA) Climate Division data (nClimDiv dataset, NOAA 2018) for November through February, 1974–1975 through 2016–2017. Climate Division data divide South Dakota into nine separate geographic regions. To calculate mean daily minimum temperatures from the Climate Division data, we calculated an average for daily minimum temperature from

the nine regions and used that value for the mean state-wide value. We then calculated average values for state-wide mean minimum temperatures for each month and for all aggregated combinations of months for each year (i.e., one monthly mean or aggregated monthly mean for each year) used in subsequent analyses.

For continental-scale climate data, we used temperature data from the PRISM dataset (PRISM Climate Group 2018) for 1940–1970 and 2000–2018 to map the positions of the  $-4$  and  $-12^{\circ}$  C mean minimum January temperature isotherms for the United States. We focused on these isotherms because northern range boundaries for all three species were associated with the  $-4$  to  $-5^{\circ}$  C mean minimum January temperature isotherms (Root 1988a, 1988b) and the  $-12^{\circ}$  C mean minimum January temperature isotherm extends through South Dakota and is intermediate between predicted northern range boundary temperatures for yellow-rumped warbler and fox sparrow from Canterbury (2002). To calculate isotherms, we averaged continental raster data sets of minimum temperatures for January at a spatial resolution of 4 km for each time period and then calculated the isotherms using the contour function in Arc GIS 10.5 (Environmental Systems Research Institute 2018).

## Statistics

We examined whether winter records for the three study species and three benchmark species have increased temporally by analysis of trends in winter observations. Because the number of bird observations may be related to the amount of observer effort (Butler 2003), we analyzed trends in observer numbers as a function of year with the product moment correlation analysis. To determine observer numbers, we counted the number of observers contributing to the winter Seasonal Reports for the SDOU database (determined from published Seasonal Reports in *South Dakota Bird Notes*). If increased observer numbers are related to increased bird detections, then observer numbers and bird detections should show similar correlations with year (e.g., positive correlations with year).

We conducted logistic regression using PROC LOGISTIC in SAS 9.4 to model winter occurrence patterns for each species from 1974–1975 through 2016–2017 (43 winters) as a function of year, number of observers, and mean daily minimum temperatures for the months of November, December, January, and February, and all aggregated combinations of these months. This strategy produced a single minimum temperature value for each monthly or multi-month period for each year. We included November temperatures in these models because November temperatures, in addition to temperatures in the winter months, could conceivably affect occurrences in the early winter period. We investigated all possible candidate models derived from combinations of the single month and multi-

month winter temperature variables, number of observers, and year. We used Akaike's Information Criterion corrected for small sample sizes ( $AIC_c$ ) to select the best-fitting models and considered all models with a  $\Delta AIC_c$  score within two of the top model to be competitive models. We considered models with higher pseudo- $R^2$  (Cox and Snell 1989) and maximum rescaled  $R^2$  (Nagelkerke 1991) values as providing stronger fits to the data. We considered  $P$ -values  $\leq 0.05$  as statistically significant for correlation analyses. All statistical tests were performed in SAS (SAS 9.4 for Windows). Finally, we calculated the geographic position of the  $-4$  and  $-12^\circ$  C mean minimum January temperature isotherms for North America for 1940–1970 and 2000–2018 from the PRISM dataset and graphically compared the position of these isotherms. We chose these two periods for comparison because 1940–1970 represents the period immediately prior to recent winter warming (Tebaldi et al. 2013) and 2000–2018 represents a period of recent winter warming during which the greatest increases in winter occurrence for the three study species in South Dakota occurred.

## RESULTS

Winter records in South Dakota have increased for all three study species since 1970, with most of the increase since 2000. For winter records of hermit thrush in South Dakota, 89% have occurred since 2000 and 84% since 2003 (Fig. 1). Similarly, winter records for yellow-rumped warbler and fox sparrow have also proliferated recently (Fig. 1). Of the January–February records for yellow-rumped warbler for South Dakota, 36% occurred during 2000–2009 and 52% have occurred since 2010 (Fig. 1). Likewise, 34% of winter records of fox sparrow in South Dakota occurred during 1993–2009, but 52% have occurred since 2010 (Fig. 1). Occurrence records for the three benchmark species were not as skewed toward recent records as for the three study species (Fig. 1). For the benchmark species, 38%, 44%, and 62% of winter occurrence records occurred prior to 2000 for American black duck, Townsend's solitaire, and varied thrush, respectively. Climate data from the PRISM dataset revealed northward movement of the  $-12^\circ$  C, but not the  $-4^\circ$  C, mean minimum January temperature isotherm in central North America (Fig. 2).

Year was positively associated with winter occurrence and was included in top-ranked and competitive models for all three study species (Table 1). In contrast, for the three benchmark species year occurred in competitive models only for Townsend's solitaire, and models were generally weaker for Townsend's solitaire and varied thrush than for study species (Table 1). Winter temperatures occurred in a number of the top-ranked and competitive models for both study species and benchmark species (Table 1). For hermit thrush, the most strongly supported model included a positive influence of year and December temperatures and

a negative effect of January temperatures on occurrence. Monthly or multi-month mean minimum temperatures appear in most hermit thrush models, with positive effects of December temperatures but negative effects of January and February temperatures. Models appear to be stronger for hermit thrush than for other species. Temperature variables occurred in many of the competitive models for yellow-rumped warbler, with positive effects of monthly temperatures in November and December, as well as multi-monthly winter temperatures. Only two candidate models were supported by the data for fox sparrow occurrence. The top model included only the variable year, but the second most strongly supported model included a positive effect of year and a negative effect of January-February mean minimum temperature.

Among benchmark species, temperature variables appeared in some models for varied thrush, with the second most strongly supported model being a single variable model with November mean minimum temperature negatively related to varied thrush presence. Moreover, one two-variable model included a negative relationship of November temperatures and a positive relationship of December temperatures with varied thrush occurrence. A large number of relatively weak models were competitive in predicting Townsend's solitaire occurrence. Monthly or multi-monthly mean minimum temperatures occurred in most models, showing a uniformly negative relationship with solitaire occurrence. Early winter (November, December) monthly mean minimum temperatures were positively related to American black duck winter occurrence, but late winter temperatures (January or February) showed the opposite relationship.

The SDOU database does not quantify observer effort in terms of numbers of days or hours in the field but does include the number of observers contributing to the database for a given season. The numbers of observers reporting to the SDOU database ranged from 17 to 51 per year, with a mean of  $32.0 \pm 1.2$  (SE) observers per year. Number of observers was not correlated with year ( $r_{41} = -0.161$ ,  $P = 0.301$ ). In addition, the number of observers variable was included in some competitive models but not in a consistent manner (Table 1). For example, number of observers was positively related to winter occurrence for varied thrush and American black duck, but number of observers was negatively related to occurrence for yellow-rumped warbler and Townsend's solitaire.

## DISCUSSION

Winter records for all three study species have increased in recent years, especially since 2000. Single- and multi-variable logistic regression models showed positive effects of year on the probability of occurrence for each of the three study species (Table 1). Consistent with this temporal

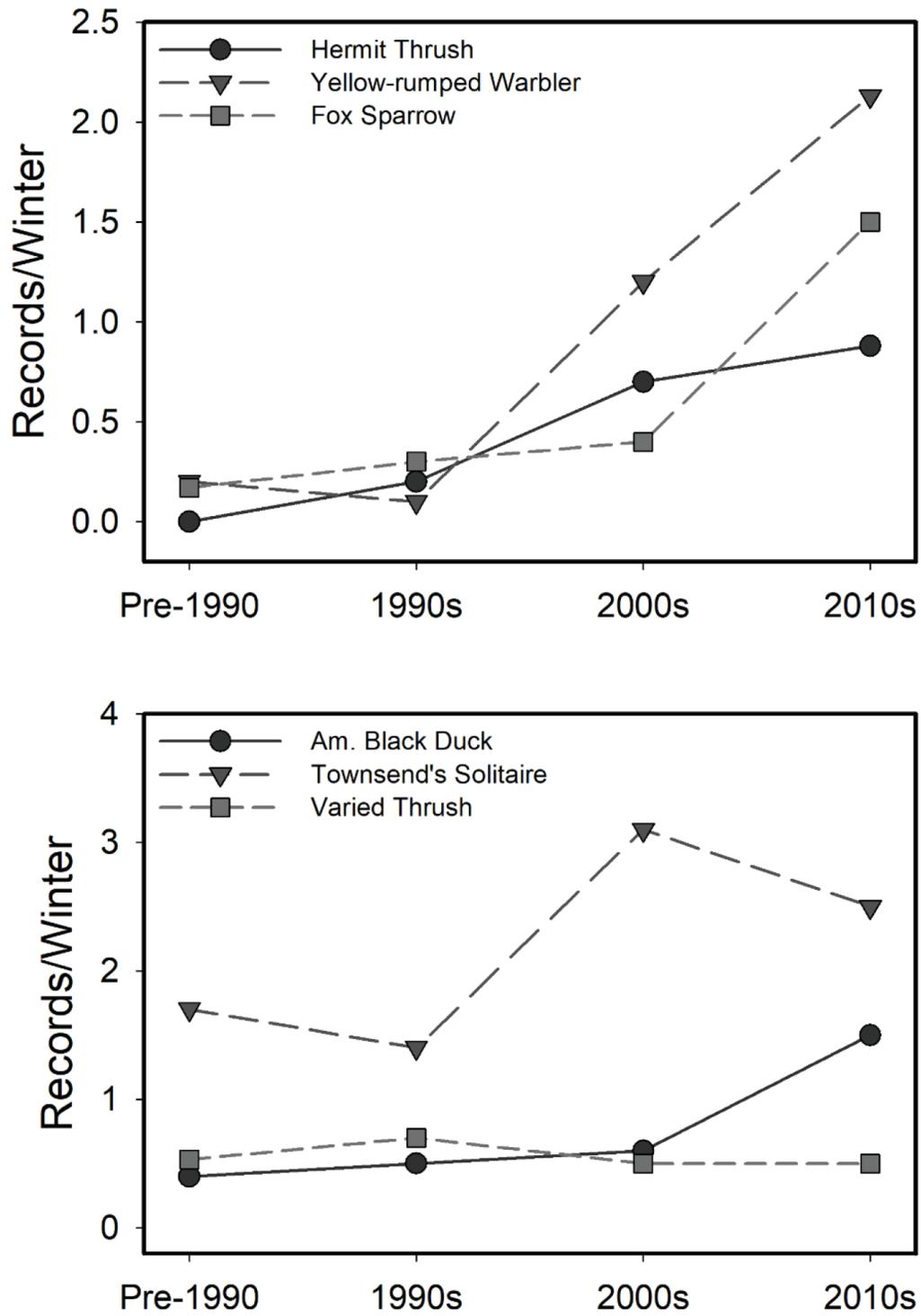


Figure 1. Number of winter records per year for the three study species (top panel) and the three “benchmark” species (bottom panel) for four time periods: 1974–1989, 1990–1999, 2000–2009 and 2010–2017.

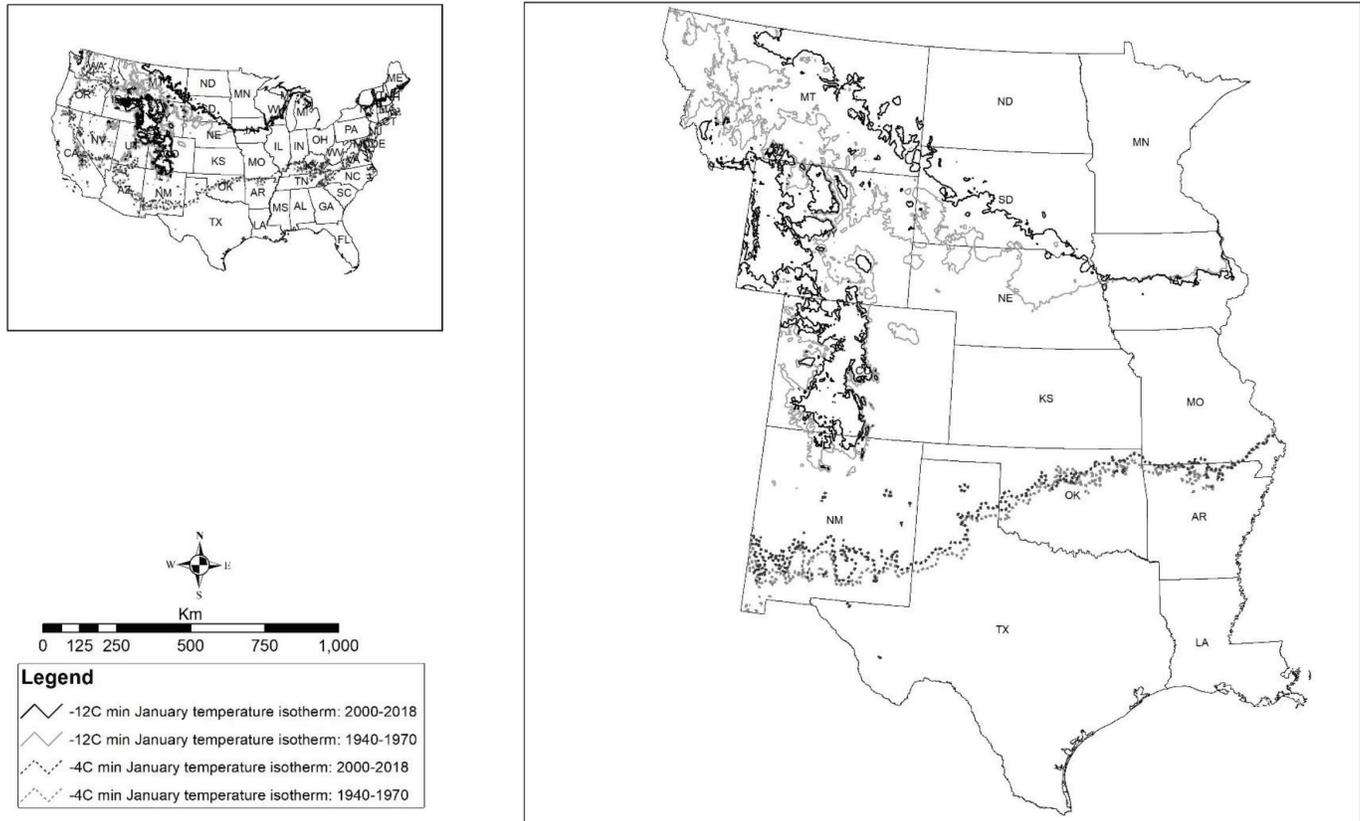


Figure 2. Minimum January temperature isotherms calculated from the PRISM dataset (PRISM Climate Group 2018; <http://prism.oregonstate.edu/>) for North America for the periods 1940–1970 (gray lines) and 2000–2018 (black lines). Both  $-4^{\circ}$  (dotted lines) and  $-12^{\circ}$  C (solid lines) isotherms are mapped, as the  $-4^{\circ}$  C isotherm has been claimed to be associated with northern winter range boundaries for hermit thrush and yellow-rumped warbler (Root 1988a, 1988b), and the  $-12^{\circ}$  C isotherm passes through South Dakota, the study area in this study.

trend in winter occurrence for the three study species is a similar temporal trend in winter warming for South Dakota and the north-central United States during the same period, with rates of winter warming ranging from 0.6 to  $1^{\circ}$  C per decade (Swanson and Palmer 2009, Tebaldi et al. 2013). Early winter temperature variables were generally positively associated with occurrence of study species in our models, but late winter temperatures were either negatively or more weakly associated with winter occurrence, suggesting that early winter temperatures were more likely to affect winter occurrence patterns for the study species. Our analyses, however, identified year as a stronger predictor of winter occurrence than temperature for all three study species, suggesting that other factors, in addition to winter warming, also contributed to this temporal trend.

Benchmark species showed less response to year than the three study species and year occurred in competitive models only for Townsend's solitaire. Winter temperatures occurred in competitive models for all three benchmark species but were often negatively associated with winter occurrence. The

relationship of early winter temperature to occurrence was positive only for American black duck among benchmark species, and this could be related to later ice formation in warm years stimulating later departure for migrant birds. In addition, models for Townsend's solitaire and varied thrush were considerably weaker than those for study species. Thus, patterns of winter occurrence differed between study species and benchmark species, as expected. Collectively, these data suggest weaker influences of year and temperature on winter occurrence for the benchmark species than for the study species. This finding is consistent with winter distributions for the benchmark species, which lie mainly to the east or west of South Dakota, which makes them less likely to respond to temperature variations within the study region. Moreover, northern winter range boundaries for these benchmark species are not limited by winter temperatures to the same degree as for the study species (Root 1988a,b), also making them less likely to respond to winter warming by increasing winter occurrences within the study region.

Several factors might account for year being a stronger

Table 1. Summary of logistic regression results using model selection for the three study species, hermit thrush (HETH), yellow-rumped warbler (YRWA), and fox sparrow (FOSP), and the three benchmark species, varied thrush (VATH), Townsend's solitaire (TOSO), and American black duck (BLDU). The + or - symbols indicate sign of regression coefficient. Bold indicates variables that were statistically significant at  $P \leq 0.05$  and italics indicate variables that were significant at  $P \leq 0.10$ . Only models with  $\Delta AIC_c$  values  $< 2$  are included. Model variables include year, mean minimum temperature for monthly (November [Nov], December [Dec], January [Jan], February [Feb]) or multi-monthly (temp with first letter of corresponding month) periods, and number of observers reporting for a given winter (obs). Pseudo  $R^2$  and Maximum Rescaled  $R^2$  values for models were calculated according to Cox and Snell (1989) and Nagelkerke (1991), respectively. Log Likelihood represents  $-2 \times$  the log-likelihood,  $AIC_c$  is the Akaike Information Criterion with correction for small sample size,  $\Delta AIC_c$  is the model  $AIC_c$  minus the minimum  $AIC_c$  across all compared models for a species, and  $w(AIC_c)$  is the Akaike weight for an individual model.

Species	Variables	Log Likelihood	$AIC_c$	$\Delta AIC_c$	$w(AIC_c)$	Pseudo $R^2$	Maximum Rescaled $R^2$
HETH	<b>year(+)</b> <i>Dec(+)</i> <i>Jan(-)</i>	27.022	36.075	0.000	1.00	0.450	0.637
HETH	<b>year(+)</b> <b>Dec(+)</b> <i>Jan(-)</i> <i>Feb(-)</i>	24.939	36.561	0.486	0.78	0.476	0.673
HETH	<b>year(+)</b> <i>Dec(+)</i> <i>Feb(-)</i>	28.461	37.514	1.439	0.49	0.431	0.610
HETH	<b>year(+)</b> tempJF(-)	30.916	37.531	1.457	0.48	0.398	0.563
HETH	<b>year(+)</b> <i>Jan(-)</i>	31.094	37.709	1.635	0.44	0.395	0.559
HETH	<b>year(+)</b>	33.565	37.865	1.790	0.41	0.359	0.509
YRWA	<b>year(+)</b> tempNDJ(+)	42.48	49.095	0.000	1.00	0.298	0.404
YRWA	<b>year(+)</b> obs(-)	42.61	49.242	0.146	0.93	0.285	0.385
YRWA	<b>year(+)</b>	44.99	49.290	0.195	0.91	0.256	0.347
YRWA	<b>year(+)</b> Dec(+) <i> obs(-)</i>	40.336	49.417	0.322	0.85	0.323	0.436
YRWA	<b>year(+)</b> Nov(+)	42.967	49.582	0.487	0.78	0.290	0.393
YRWA	<b>year(+)</b> tempNDJ(+) <i> obs(-)</i>	40.607	49.688	0.593	0.74	0.318	0.430
YRWA	<b>year(+)</b> Dec(+)	43.337	49.952	0.857	0.65	0.284	0.385
YRWA	<b>year(+)</b> Nov(+) <i> obs(-)</i>	40.882	49.963	0.868	0.65	0.314	0.424
YRWA	<b>year(+)</b> tempNDJF(+)	43.439	50.054	0.959	0.62	0.283	0.382
YRWA	<b>year(+)</b> tempDJ(+)	43.655	50.270	1.175	0.56	0.279	0.378
YRWA	<b>year(+)</b> tempNDJF(+) <i> obs(-)</i>	41.424	50.505	1.410	0.49	0.305	0.412
YRWA	<b>year(+)</b> tempDJ(+) <i> obs(-)</i>	41.685	50.766	1.671	0.43	0.300	0.406
YRWA	<b>year(+)</b> tempDJF(+)	44.159	50.774	1.679	0.43	0.270	0.366
YRWA	<b>year(+)</b> Nov(+) <i> Dec(+)</i> <i> obs(-)</i>	39.16	50.827	1.731	0.42	0.341	0.461
YRWA	<b>year(+)</b> Nov(+) <i> Dec(+)</i> <i> obs(-)</i>	41.878	50.931	1.835	0.40	0.308	0.417
FOSP	<b>year(+)</b>	42.982	47.282	0.000	1.00	0.237	0.327
FOSP	<b>year(+)</b> tempJF(-)	42.631	49.246	1.964	0.37	0.261	0.359
VATH	intercept only	57.843	59.943	0.000	1.00		
VATH	Nov(-)	56.992	61.292	1.349	0.51	0.055	0.073
VATH	obs(+)	57.401	61.709	1.766	0.41	0.011	0.014
VATH	<i>Nov(-)</i> Dec(+)	55.183	61.798	1.855	0.40	0.093	0.125
TOSO	<b>year(+)</b>	45.047	49.347	0.000	1.00	0.128	0.184
TOSO	<i>year(+)</i> obs(-)	43.138	49.770	0.423	0.81	0.116	0.169
TOSO	<b>year(+)</b> tempNDJF(-)	43.256	49.871	0.524	0.77	0.163	0.235
TOSO	<b>year(+)</b> tempNDJ(-)	43.369	49.984	0.637	0.73	0.161	0.232
TOSO	<b>year(+)</b> Nov(-)	43.61	50.225	0.878	0.64	0.156	0.225
TOSO	<i>year(+)</i> tempNDJF(-) <i> obs(-)</i>	41.215	50.296	0.949	0.62	0.155	0.227

TOSO	intercept only	48.303	50.403	1.056	0.59		
TOSO	<b>year(+)</b> tempDJF(-)	43.84	50.455	1.108	0.57	0.152	0.219
TOSO	<b>year(+)</b> tempNDJ(-) obs(-)	41.433	50.514	1.167	0.56	0.151	0.221
TOSO	<b>year(+)</b> Nov(-) obs(-)	41.517	50.598	1.251	0.53	0.149	0.218
TOSO	<b>year(+)</b> tempJF(-)	43.991	50.606	1.259	0.53	0.149	0.214
TOSO	<i>year(+)</i> tempJF(-) obs(-)	41.55	50.631	1.284	0.53	0.149	0.217
TOSO	<b>year(+)</b> tempDJ(-)	44.18	50.795	1.448	0.48	0.145	0.209
TOSO	<b>year(+)</b> Feb(-)	44.181	50.796	1.449	0.48	0.145	0.209
TOSO	obs(-)	46.521	50.829	1.482	0.48	0.042	0.061
TOSO	<i>year(+)</i> tempDJF(-) obs(-)	41.838	50.919	1.572	0.46	0.143	0.209
TOSO	<i>year(+)</i> Jan(-) obs(-)	41.887	50.968	1.621	0.44	0.142	0.207
TOSO	<b>year(+)</b> Jan(-)	44.394	51.009	1.662	0.44	0.141	0.203
TOSO	<i>year(+)</i> Feb(-) obs(-)	42.057	51.138	1.791	0.41	0.138	0.202
TOSO	<b>year(+)</b> Dec(-)	44.66	51.275	1.928	0.38	0.136	0.195
BLDU	<b>Nov(+)</b> <b>Feb(-)</b> <b>obs(+)</b>	42.172	51.253	0.000	1.00	0.316	0.422
BLDU	<i>Nov(+)</i> <i>Dec(+)</i> <b>Feb(-)</b> <b>obs(+)</b>	43.683	52.764	1.511	0.47	0.324	0.432
BLDU	<b>Nov(+)</b> <i>Jan(-)</i> <b>Feb(-)</b> <b>obs(+)</b>	44.144	53.225	1.972	0.37	0.317	0.422

predictor of winter occurrence than annual winter temperatures for the three study species. One possibility is that conditions occurring south of the study area are affecting the winter distributions of the study species more than the winter conditions in South Dakota, such that winter range centroids are shifting northward (La Sorte and Thompson 2007), which might, in turn, increase the likelihood of these species occurring in winter in South Dakota. Alternatively, perhaps longer-term trends in winter warming are shifting species ranges, irrespective of annual conditions during particular winters. Christmas Bird Count data have demonstrated significant northward movement of winter range centroids in North America for fox sparrows (462 km) and hermit thrushes (147 km) but not for yellow-rumped warblers (11 km) (Niven et al. 2009). These results appear generally consistent with the stronger response of yellow-rumped warblers to annual winter temperatures than in the other two species in the present study, but they do not explain why year was still a stronger predictor of occurrence than year-to-year variation in winter temperatures for yellow-rumped warblers.

Factors other than winter temperatures could also account for year being a stronger predictor of winter occurrence than temperature for all three study species. One possible factor influencing this trend is food availability, especially the availability of fruits, as all three study species consume fruits in winter (White and Stiles 1992, Hunt and Flaspohler 1998, Weckstein et al. 2002, Dellinger et al. 2012), and yellow-rumped warbler and hermit thrush may track winter fruit resources (Graber and Graber 1970, Terrill and Ohmart 1984, Borgmann et al. 2004, Kwit et al. 2004). For fruit availability

to serve as a factor influencing the temporal trends in winter occurrence documented in this study, availability of fruits should increase over the study period, particularly since the 2000s. One potential candidate fruiting tree species is eastern red cedar (*Juniperus virginiana*), as all three study species consume the fleshy cones (i.e., “fruits”) of cedars in winter (Hunt and Flaspohler 1998, Weckstein et al. 2002, Dellinger et al. 2012), and cedars can also provide winter cover. Coverage of eastern red cedar has been increasing throughout its range in the Midwestern United States, including South Dakota, since the 1960s (Schmidt and Leatherberry 1995, Briggs et al. 2002, Meneguzzo and Liknes 2015). For example, eastern red cedar forest increased in the central United States by 47.3% from 2005 through 2012, although eastern red cedar forest coverage over this period in South Dakota was relatively small, at less than 16,000 ha (Meneguzzo and Liknes 2015). Nevertheless, eastern red cedar is expanding in South Dakota, both in floodplain forest (Greene and Knox 2014) and upland grasslands (Spencer et al. 2009), as a result of flow regulation by dams and fire suppression, respectively. Thus, the combination of eastern red cedar expansion and warming winter temperatures may synergistically interact to increase recent winter occurrences of the three study species. The positive association of year with winter occurrence in Townsend’s solitaire, the only benchmark species to show such a relationship, is also consistent with a response to eastern red cedar expansion, as solitaires regularly consume their cones and winter records in eastern South Dakota are often associated with this species (Tallman et al. 2002). Future studies documenting eastern red cedar expansion in a spatially explicit manner

in South Dakota, and including cedar forest coverage and fruit production as variables, along with winter temperature, would help to resolve the relative influence of these factors on avian winter occurrence patterns.

A second possibility is that differences in observer effort over time are contributing to increasing numbers of recent winter observations of the study species (e.g., Butler 2003). The number of observers reporting to the SDOU database, however, did not change significantly over the period of the study (1974–2017). In addition, observer numbers were not consistently positively related to winter occurrence patterns for either study species or benchmark species. These results do not support the idea that differences in observer effort are a major contributor to the patterns of winter occurrence documented in this study, but we cannot completely rule out that differences in observer effort (e.g., days or time spent in the field) or other factors, such as increases in bird feeding (Robb et al. 2008, Galbraith et al. 2015), contribute to the temporal trends without better quantification of observer effort.

A final factor that could affect winter occurrence trends for the three study species is population size. If populations are increasing over the study period, then it might be expected that increasing numbers of individuals might be detected outside of the normal wintering range, similar to the probability of detecting individuals earlier on migration with increasing population sizes (Miller-Rushing et al. 2008a). Breeding Bird Survey data from 1966 to 2015, however, suggest that populations of hermit thrush and yellow-rumped warbler are stable over this period, whereas populations of fox sparrow are declining significantly at a rate of -1.4% per year (Sauer et al. 2017). Thus, increasing population sizes for the study species do not seem likely to account for the increasing winter detections in recent years.

In contrast to our data, which suggest a stronger response to temporal trends (associated with the “year” variable in our study) than to annual winter temperature variables, several studies of non-breeding birds document stronger responses to short-term weather rather than to long-term climate. These include studies of shorebirds in estuaries in the United Kingdom (Austin and Rehfisch 2005), shorebirds in Western Europe (Maclean et al. 2008), the avifauna of Australian tropical savannas (Reside et al. 2010), and feeder birds in the northeastern United States and adjacent Canada (Zuckerberg et al. 2011). In addition, other bird species with ranges limited by temperature in North America seem to respond more strongly to annual variation in winter temperature in the Central Plains states. Christmas Bird Count data for American tree sparrow (*Spizella arborea*), dark-eyed junco (*Junco hyemalis*), and American goldfinch (*Spinus tristis*), all species with northern range boundaries associated with temperature, showed positive responses in relative abundance to warmer winter temperatures (Butler et al. 2007). In contrast, relative abundance of white-breasted

nuthatch (*Sitta carolinensis*), black-capped chickadee (*Poecile atricapillus*), and horned lark (*Eremophila alpestris*), species with ranges limited by vegetation rather than temperature, did not show associations between relative abundance and winter temperatures (Butler et al. 2007).

Our data documenting increasing rates of winter occurrence for the three study species in South Dakota in recent winters are consistent with other studies also documenting northward winter range movements for a number of bird species overwintering in North America. For example, the North American wintering avifauna, except for grassland birds, shows a general northward trend in measures of distribution from Christmas Bird Count data, although individual species showed more variable temporal trends (La Sorte and Thompson 2007, Niven et al. 2009). La Sorte and Thompson (2007) documented northward movements of the northern range boundaries for all three study species, although the centroid measurements for occurrence moved northward only for hermit thrush and fox sparrow and centroids of abundance only for fox sparrow. Interestingly, fox sparrow was the only one of the three study species to show northward movement in all three of La Sorte and Thompson’s (2007) measures of winter distribution (northern range boundary and centroids of occurrence and abundance), and it also showed the largest winter increases in the centroid range measurements, but the lowest northward movement in the northern range boundary. The centroid results of La Sorte and Thompson (2007) are consistent with the analyses of Niven et al. (2009), which also documented that fox sparrow had the greatest northward movement among the three study species.

Winter data from Project FeederWatch in eastern North America from 1989–1990 through 2011–2012 show that winter bird communities are becoming increasingly dominated by species with more southern historical winter distributions, with the strongest signal in more southerly latitudes (Princé and Zuckerberg 2015). This result is similar to La Sorte and Thompson (2007), who provided limited evidence that the northern range boundary for species wintering in southern North America (<36° N latitude) moved northward at a greater rate than for species wintering in northern North America. The centroids of abundance, however, showed the opposite trend, with a greater rate of northward movement in abundance for more northerly wintering species. A similar trend is evident for the winter avifauna of Cape Cod, Massachusetts, USA, which also shows a recent shift toward greater inclusion of species with more southerly affinities over the period of 1930–2000 (Valiela and Bowen 2003).

In addition to winter distribution changes, hermit thrush, yellow-rumped warbler, and fox sparrow may modify migration timing in response to short-term weather variation or long-term climate change, but species-specific responses are often variable. For example, Hagan et al. (1991) documented high among-year variation in timing of

migration arrivals for short-distance migrants, including hermit thrush and yellow-rumped warbler, relative to long-distance Nearctic-Neotropical migrants, suggesting more responsiveness to local temperatures for short-distance migrants. In addition, spring migration timing of hermit thrushes shows significant negative relationships to spring temperatures, with spring migration arrival being earlier in warmer springs, for sites in southern Wisconsin (Temple and Cary 1987), southern Manitoba (Murphy-Klassen et al. 2005), northern Illinois (MacMynowski and Root 2007), Maine (Wilson 2007), and coastal Massachusetts (Miller-Rushing et al. 2008b). In contrast, spring migration timing of hermit thrushes was not significantly associated with spring temperatures in southern Massachusetts (Ledneva et al. 2004) or southern Ontario (Mills 2005). Spring migration timing of hermit thrushes also shows variable responses to temporal trends of warming climates, with significant or nearly significant negative relationships with year (earlier arrival in more recent years) at some locations (Butler 2003, Miller-Rushing et al. 2008b), but not others (Ledneva et al. 2004, Murphy-Klassen et al. 2005). In addition, spring migration phenology of yellow-rumped warblers is negatively related to local spring temperatures in some cases (Van Buskirk et al. 2009, Elwood et al. 2010) but not others (Temple and Cary 1987, Mills 2005, Wilson 2007, Swanson and Palmer 2009). Similarly, spring migration timing of yellow-rumped warblers is moving earlier with climate warming trends in recent years for some locations (Butler 2003, Swanson and Palmer 2009), but not others (Elwood et al. 2010). Fox sparrows also show variable trends in responsiveness of migration timing to year or temperature, with either no relationships (DeLeon et al. 2011) or negative relationships with year (Van Buskirk et al. 2009) or temperature (Wilson et al. 2007).

It might be expected that temporal trends in winter occurrence, such as those documented in this study, would be associated with northward shifts in mean minimum winter temperature isotherms. In an analysis of Christmas Bird Count data, Root (1988a, 1988b) suggested that both hermit thrush and yellow-rumped warbler northern range boundaries were associated with the  $-4^{\circ}$  C mean minimum January temperature isotherm. Maps in Root (1988b) also show that the northern range boundary for fox sparrow is loosely associated with the  $-5^{\circ}$  C mean minimum January temperature isotherm. Our analysis of the position of the  $-4^{\circ}$  C mean minimum January temperature isotherm between 1940–1970 and 2000–2018, however, showed very little movement of this isotherm between the two periods, which suggests that temporal trends in winter occurrences for the three study species are not associated with northward movement of the  $-4^{\circ}$  C mean minimum January temperature isotherm. Canterbury (2002), however, determined range boundaries in a different manner and lists colder mean minimum January temperatures at the northern range

boundary for yellow-rumped warbler and fox sparrow,  $-9.4^{\circ}$  C and  $-15^{\circ}$  C, respectively, than Root (1988a, 1988b). We did find northward movement of the  $12^{\circ}$  C mean minimum January temperature isotherm in the north-central United States (for South Dakota and west), so perhaps this isotherm is more relevant to occurrences of species at the northern end of their winter range in western North America, such as the three species in this study, than the  $-4$  to  $-5^{\circ}$  C mean minimum January temperature isotherms suggested by Root (1988a, 1988b).

In conclusion, hermit thrush, yellow-rumped warbler, and fox sparrow all are short-distance migrant species with winter ranges influenced by temperature (Root 1988a, 1988b, Canterbury 2002, Princé and Zuckerberg 2015). All three species are showing increasing trends in recent winter occurrence in South Dakota, but these trends are associated more strongly with long-term temporal trends than with year-to-year variation in winter temperatures, suggesting that temperature might interact with other factors, such as food availability and vegetation change, to influence long-term patterns of winter occurrence. These results are consistent with other data suggesting that winter ranges of these species are moving northward (La Sorte and Thompson 2007, Niven et al. 2009), and they document that populations wintering in central North America are included in this trend, perhaps associated with northward movement of mean minimum January temperature isotherms and expansion of eastern red cedar (Meneguzzo and Liknes 2015) as a winter source of food and cover in this region. For South Dakota, the winter status of all three species (Tallman et al. 2002) has changed so that all three species are now rare, but regular, winter residents.

Warming winter climates in the north-central United States are likely to continue into the future (Tebaldi et al. 2013, Vose et al. 2017), so this will likely function to increase the winter occurrence of bird species with southern affinities, like the three study species, in the region (Valiela and Bowen 2003, Princé and Zuckerberg 2015). The potential effects of these more southerly species on the wintering avifauna of the north-central United States is not well understood, so additional research is needed to clarify the likely impacts on bird energetics and dynamics of winter bird communities in the region. For example, the interacting factors of climate and land-use/land-cover change (e.g., Sohl 2014) might impose constraints on the wintering avifauna in the north-central United States, but identifying such constraints will require further research. In addition, whether available food resources in the region are sufficient to support the addition of species with more southerly affinities into the wintering avifauna is unknown. The potential ecological responses of the current winter bird community to the influx of new species into the region is also uncertain. Research addressing topics such as these will help inform management decisions that include the winter season in overall habitat management,

conservation and restoration plans for the region.

## MANAGEMENT IMPLICATIONS

Eastern red cedar provides an important winter source of food and cover for the three study species (Hunt and Flaspohler 1998, Weckstein et al. 2002, Dellinger et al. 2012), so removal of invasive cedars may have negative effects on their winter occurrence. Thus, management plans for targeted, rather than wholesale, removal of cedar from invaded areas (Donovan et al. 2018) and consideration of effects of such removal on wintering as well as breeding and migratory birds might be the most appropriate action for bird conservation in South Dakota and other areas experiencing eastern red cedar expansion (Meneguzzo and Liknes 2015).

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## Greater prairie-chickens and sharp-tailed grouse have similarly high nest survival in the Nebraska Sandhills

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**ABSTRACT** The ranges of two native galliform species overlap in the Nebraska Sandhills, the largest contiguous grassland in North America. We monitored nests of greater prairie-chickens (*Tympanuchus cupido*) and sharp-tailed grouse (*Tympanuchus phasianellus*) in Cherry County, Nebraska, in 2015 and 2016. Our objectives were to 1) compare daily probability of nest survival between species, 2) evaluate vegetation structure at nests for potential effects on nest survival, 3) compare nest site topography between species, and 4) use a simple model of breeding season success to evaluate the potential for stable populations at our study sites. We captured and radiomarked 87 birds, and we monitored nests for known fate analyses of survival. The two species did not vary in daily nest survival (pooled DNS = 0.9667, SE = 0.0085), and pooled probability of nest success (24-day) was high (0.4436). Sharp-tailed grouse used nest sites with taller vegetation and nested lower on slopes than greater prairie-chickens, but survival did not vary with vegetation structure. Our modeling suggested that grouse in the Sandhills region have high potential for stable populations with the level of productivity documented in our study.

**KEY WORDS** grouse, Nebraska Sandhills, population model, productivity, *Tympanuchus cupido*, *Tympanuchus phasianellus*

Habitat degradation, habitat loss and fragmentation, and stochastic dynamics of small populations are the largest threats to species of grouse in North America, and in the Great Plains of North America. Conservation of grasslands is especially critical to prairie grouse species in the Great Plains because they are grassland obligate birds (Storch 2007). However, only a small fraction of temperate grasslands of the Great Plains remains intact (Samson and Knopf 1994). The Sandhills region (>50,000 km<sup>2</sup>) of north-central Nebraska is the largest contiguous native grassland in North America because its sandy soils and semi-arid environment prevent widespread tillage for row crop agriculture (Bleed and Flowerday 1998). The region has been used for production of beef cattle since the late 1800s (Vodehnal 1999, Loope and Swinehart 2000).

The Sandhills region offers a unique opportunity to evaluate two sympatric (occurring in the same place) species of grouse, greater prairie-chicken (*Tympanuchus cupido*) and sharp-tailed grouse (*T. phasianellus*). The two species of grouse overlap in a large portion of the central Sandhills region with relatively abundant populations (Fig. 1). The current area of sympatry for the two species is most likely larger than the original, narrow zone of sympatry prior to the effects of agricultural development on the two species' ranges (Johnsgard and Wood 1968). Comparisons of behavior and demographic success of sympatric species may offer unique insights to ecology and wildlife management (Arlettaz 1999, Nudds et al. 1984, Wegge and Kastdalen 2008).

Greater prairie-chickens in the Sandhills are at the

westward portion of their range and are found primarily in the central and eastern Sandhills region. Plains sharp-tailed grouse are at the southern edge of their range, primarily found in the central and western Sandhills region (Fig. 1). Such edge-of-range contexts provide for another unique characteristic of the sympatry (Svedarsky et al. 2000). Greater prairie-chickens were once associated primarily with tallgrass prairies east of the Sandhills (Svedarsky et al. 2000), which have largely been lost to agricultural development, and prairie-chickens are common in the Sandhills region where cover is sparser than tallgrass prairies (Powell et al. 2014, Matthews et al. 2013, Anderson et al. 2015). Throughout its large range, the sharp-tailed grouse uses interspersed cover of grasslands, shrublands, and woodlands with higher shrub components than levels recommended for greater prairie-chickens (Natural Resources Conservation Service 2007).

Although assessments of sympatric grouse species are relatively common in Europe (e.g., Wegge and Kastdalen 2008, Swenson and Angelstam 1993), there are few published studies to inform co-management of greater prairie-chickens and sharp-tailed grouse in the northern Great Plains. Norton et al. (2010) reported that brood-rearing locations differed by topography for the two species, and Flanders-Wanner et al. (2004) used long-term harvest information to describe effects of weather and grazing periods on productivity of both species in the Nebraska Sandhills. Hiller et al. (2019) described macrohabitat differences in habitat use of the two species in the nonbreeding season in the northcentral Sandhills but similar patterns of habitat use during the

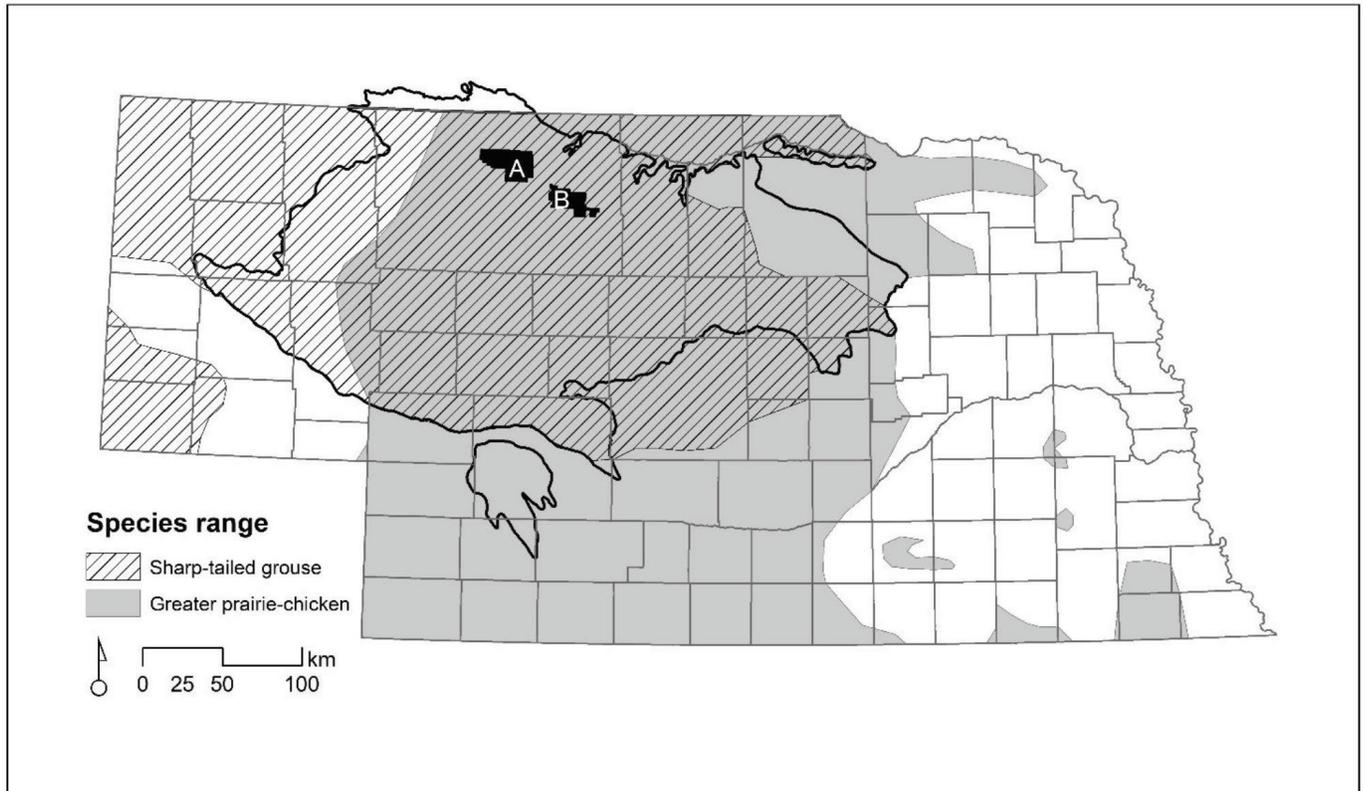


Figure 1. Location of study sites for nest survival of sharp-tailed grouse and greater prairie-chickens at McKelvie National Forest (A) and Valentine National Wildlife Refuge (B) in the Sandhills region (black outline) of Nebraska, USA, with generalized species' ranges (modified from Silcock and Jorgensen 2018).

breeding season. Therefore, our goal was to close a gap in knowledge of breeding season habitat use and demographic success that prevents an informed approach to management of greater prairie-chickens and sharp-tailed grouse in this intact grassland system. Our objectives were to 1) compare daily probability of nest survival between species, 2) evaluate vegetation structure at nests for potential effects on nest survival, 3) compare nest site topography between species, and 4) use a simple model of breeding season success to evaluate the potential for stable populations at our study sites.

## STUDY AREA

The Sandhills are a unique ecosystem of grass-stabilized sand dunes in Nebraska and southern parts of South Dakota (Bleed and Flowerday 1989; Fig. 1). Ninety-two percent of the study area was classified as upland range (grasslands on dune slopes and tops) and the remaining 8% as intermixed, sub-irrigated meadows (flat areas with relatively dense vegetation near creeks, rivers, or lakes with the water table near the soil surface during most of the year) and wetlands

(Hiller et al. 2019). Uplands were characterized by grass-covered sand dunes oriented west by northwest to east by southeast. Upland soils vary from loamy fine sand to fine sand, and meadow (lowland) soils are poorly drained and vary from loam to fine sand (Vodehnal 2000). Average annual precipitation is 41–58 cm (Vodehnal 2000). The dominant plant species in upland areas were sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), prairie sandreed (*Calamovilfa longifolia*), switchgrass (*Panicum virgatum*), sand lovegrass (*Eragrostis trichodes*), blue grama (*Bouteloua gracilis*), and needle-and-thread (*Hesperostipa comata*). Exotic cool-season grasses dominated the meadows and included quackgrass (*Elymus repens*), timothy (*Phleum pratense*), Kentucky bluegrass (*Poa pratensis*), and reed canarygrass (*Phalaris arundinacea*). Warm-season grasses were less prevalent and included big bluestem (*Andropogon gerardii*), indiagrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and prairie cordgrass (*Spartina pectinata*). Red and white clover (*Trifolium pratense* and *Trifolium repens*) were the most prevalent forbs; however, yarrow (*Achillea millefolium*), dandelion (*Taraxicum officinale*), and Aster species were

also common. Sedges (*Carex* spp.) and rushes (*Eleocharis* spp. and *Juncus* spp.) were also commonly found throughout the study site.

Valentine National Wildlife Refuge (NWR) covers 29,045 ha of Sandhills prairie and is dotted with alkaline lakes (Fig. 1). Game bird habitat (i.e., ducks and grouse) is a management priority for Valentine NWR. The NWR uses periodic grazing by cattle to manage rangeland. Generally, light stocking rates and rotational grazing are used to ensure plenty of residual vegetation cover for nesting.

Samuel R. McKelvie National Forest (hereafter, McKelvie NF) covers 46,944 ha, with about 37,000 ha of prairie managed by the U.S. Forest Service for multiple uses (Fig. 1). Most of McKelvie NF is allotted to ranchers who graze cattle at moderate stocking rates each year. The area is mostly comprised of uplands and McKelvie NF has fewer water bodies than Valentine NWR. These sites are representative of the surrounding landscape in terms of topography and land cover.

## METHODS

### Lek surveys and bird capture

We received recent maps of lek surveys from Valentine NWR and McKelvie NF, and we located the mapped leks on the ground in March and April 2015. We selected a subset of leks on which to trap, based on spatial requirements for a concurrent study (Hiller et al. 2019). Leks were selected to provide a gradient of distances from row crop agriculture in the region and to ensure adequate availability of leks of both species of grouse.

We captured female greater prairie-chickens and sharp-tailed grouse during March–April of 2015–2016 using walk-in funnel traps (Schroeder and Braun 1991, Harrison et al. 2015, Anderson et al. 2015). We captured birds in the morning and evening. We fitted females with aluminum leg bands and 18-g necklace style, very high frequency radio transmitters with mortality switches (Model #A4050, Advanced Telemetry Systems [ATS], Inc., Isanti, MN) and released them at the trapping site. We banded these resident game species under the collaborative authority of the Nebraska Game and Parks Commission, and our animal capture and handling protocols were approved by the University of Nebraska-Lincoln's Institutional Animal Care and Use Committee (Permits #901 and #1265).

### Nest monitoring

We relocated the approximate locations of females during daylight hours every 1–2 days after capture using radio-telemetry via hand-held antennas. When a female was found in the same approximate location for five consecutive days, we flushed the bird to locate the nest. We recorded the

nest location with GPS. To avoid causing nest abandonment, we continued to monitor the female's presence on the nest from >100 m every two days until the nest was successful or failed. When birds could not be relocated with hand-held antennas, searches were conducted using antennas on trucks and fixed-wing aircraft (Hiller et al. 2019).

After each nest had hatched or failed, we recorded habitat data at the nest, including visual obstruction reading (VOR, dm; Robel 1970), grass height (cm), height of standing dead vegetation (cm), mean litter depth (cm, from four samples at corners of a 0.25-cm by 0.50-cm frame centered on the nest), position on slope, aspect, and ecological site defined by U.S. Department of Agriculture's Natural Resources Conservation Service (Natural Resources Conservation Service 2011, Powell et al. 2014). We were not able to collect a full set of topographic information for greater prairie-chicken nests at our study site, so we compared sharp-tailed grouse nest topography to a sample of greater prairie-chicken nests collected from 2009 to 2011 in the Sandhills region approximately 100 km east of our study site (Anderson 2012). We used a general linear model ( $\alpha=0.05$ ) to assess variation in grass height, litter depth, height of dead standing vegetation, and mean VOR between the two species (PROC GLM, SAS; SAS Institute Inc., Cary, NC, USA).

### Nest survival analysis

We used program MARK (White and Burnham 1999) to perform a known fate analysis of daily nest survival (NSI). We considered a nest successful if  $\geq 1$  egg hatched. We used an a priori comparison of our null model (constant survival for both species) and a species-specific survival model to determine if there was evidence for different survival for nests of prairie-chickens and sharp-tailed grouse. We were prepared to conduct separate analysis by species, if warranted. Given that both species have an incubation period of 24 days, we calculated the probability of nest success as 24-day nest survival ( $NS^{24}$ ) as  $NS^{24} = NS_1^{24}$ . We constructed 95% confidence intervals for nest success ( $NS^{24}$ ) using delta methods for approximation of variance described by Powell (2007).

We created linear and non-linear (quadratic) single-factor models to evaluate variation in daily survival of nests. In addition to species comparison, we assessed the following covariates: VOR, grass height, standing dead vegetation height, mean litter depth, and the date of first observation of the nest. The nest observation date was roughly equivalent to the start of incubation because we were able to find nests early in laying using radio-telemetry to track female behavior. We measured VOR, grass height, and standing dead vegetation to quantify the amount of cover at the nest, which we hypothesized should function to protect from nest predators.

We used a model selection framework (Burnham and

Anderson 2002) to evaluate evidence for variation in nest survival with Akaike's Information Criterion corrected for small sample ( $AIC_c$ ). If the top-ranked model was not separated by  $>2.0 AIC_c$ , we were prepared to use conditional model averaging to calculate coefficients.

### Grouse demographic model

We anticipated the need to provide context for our estimates of nest survival with regard to potential impact on population growth for species in our region. We also realized that our parameter space might have some uncertainty, given two years of data and a lack of brood survival information from our study. To explore the influence and sensitivity of nest success, brood survival, and annual survival of females on the rate of population growth, we used a simple model to predict population trends over time (Starfield et al. 1995, Cunningham et al. 2016). We used a deterministic model to calculate future population size of adult females,  $N_{t+1}$ , as a function of the current spring population ( $N_t$ ), production of young, and survival of broods and adult females. We varied the probability of brood survival ( $J_{21}S$ : probability of a brood surviving to day 21 post-hatch) in the model, while keeping all other parameters (nest success,  $NS_{24}$ , and annual adult survival,  $SA$ ) at a given level, to determine at which level of brood survival a constant population would be achieved. Adult females remained in the population as a function of survival ( $SA = 0.30, 0.45, \text{ and } 0.60$ ; after Johnson et al. 2011 and Winder et al. 2013). Juveniles,  $J$ , were produced at time  $t$  as a function of nest success ( $NS_{24} = 0.250, 0.325, 0.400, 0.475$ ; after Anderson 2012 and Harrison et al. 2015), mean number of nests per female ( $n = 1.338$ , Anderson 2012), mean clutch size of females ( $cs = 5.43$ , assuming 50:50 M:F ratio from total  $cs = 10.86$ , Anderson 2012). Our clutch size was a weighted mean, accounting for clutch size of a female's first, second, third, and fourth nests in the Anderson (2012) sample. Thus, the number of juveniles predicted to be produced in a given year was calculated as:

$$J_t = N_t(n)(cs)(NS)(J_{21}S)$$

Estimates for annual juvenile survival (post 21-days following hatch) of prairie-chickens are absent from the literature to our knowledge, so we assumed that annual juvenile survival,  $SJ$ , would be less than adult survival. Following Cunningham et al. (2016), we chose a value of  $SJ = 0.75SA$ . The prediction of the population size for the following year was calculated as:

$$N_{t+1} = N_t(SA) + J_t(SJ)$$

After setting the fixed values for  $n$  and  $cs$ , we adjusted nest success ( $NS_{24}$ ) and adult female survival ( $SA$ ) to create a

unique scenario. We then altered the value for brood survival ( $J_{21}S$ ) until the number of individuals in the population remained stable ( $N_{100} \geq N$ ) over 100 years. Thus, the output of our model was the threshold value for brood survival, at which the population remained stable given our scenarios of  $NS_{24}$  and  $SA$  (Figure 3).

### RESULTS

Nesting season for species in our sample, based on first and last dates of monitoring, lasted from 12 May to 4 July. Structure of vegetation at the nest was similar for the two species (Table 1). However, height of grass and standing dead vegetation tended to be greater at sharp-tailed grouse nests ( $F_{1,36} = 3.65, P = 0.06$  and  $F_{1,36} = 3.54, P = 0.07$ , respectively) than at prairie-chicken nests. Approximately 95% of nests for both species were found on the commonly occurring sands ecological site. Sharp-tailed grouse did not tend to use south-facing slopes (only 3 of 21 [14%] nests were found on south-facing slope), and their nests tended to be located at bottoms of slopes (Table 2).

Our initial comparison of daily nest survival (DNS) between the two species failed to provide evidence of a difference (null model:  $AIC_c = 94.89$ ; pooled species DNS:  $0.9667$ , SE:  $0.0085$ , 95% CI:  $0.9455\text{--}0.9799$ ; species model:  $AIC_c = 96.74$ ,  $\Delta AIC_c = 1.84$ ; DNS, greater prairie-chicken:  $0.9729$ , SE:  $0.0154$ , 95% CI:  $0.9193\text{--}0.9912$ ; DNS sharp-tailed grouse:  $0.9647$ , SE:  $0.0101$ , 95% CI:  $0.9388\text{--}0.9799$ ). Therefore, we continued further modeling with nests of both species pooled together. Nest success was  $0.4436$  (SE =  $0.0936$ ) from the null model with both species pooled.

We found limited evidence for effects of vegetation structure at the nest on daily nest survival, and initial date of incubation did not cause daily nest survival to vary (Table 3). The top model described nonlinear effects of height of standing dead vegetation (SDV) at the nest ( $\beta_{SDV} = 0.1156$  [SE =  $0.0550$ ],  $\beta_{SDV \times SDV} = -0.0011$  [SE =  $0.0005$ ]), and nest survival was predicted to be greater when the height of standing dead vegetation was 30–80 cm (Fig. 2). The 95% confidence interval for each coefficient did not overlap 0, providing support for these effects. However, the second-ranked model was the null model, which was simpler than the top-ranked model, and model weights suggested similar evidence for each as the top model (SDV quadratic model:  $wAIC_c = 0.20$ ; null model:  $\Delta AIC_c = 0.138$ ,  $wAIC_c = 0.18$ ). Other nonlinear effects were ranked lower than linear effects, and none of the effects differed from 0 (e.g., the third-ranked model was effects of VOR:  $\beta_{VOR} = -0.478$ , SE =  $0.542$ ).

Our modeling exercise provided insights into the sensitivity of population growth when varying three critical demographic rates (Fig. 2). For  $SA = 0.4500$  and  $NS_{24} = 0.3250$ , we calculated that 21-day brood survival needed to be  $\geq 0.69$  for a stable population. However, at  $SA = 0.6000$  and  $NS_{24} = 0.3250$ , 21-day brood survival was only required to be  $\geq 0.38$

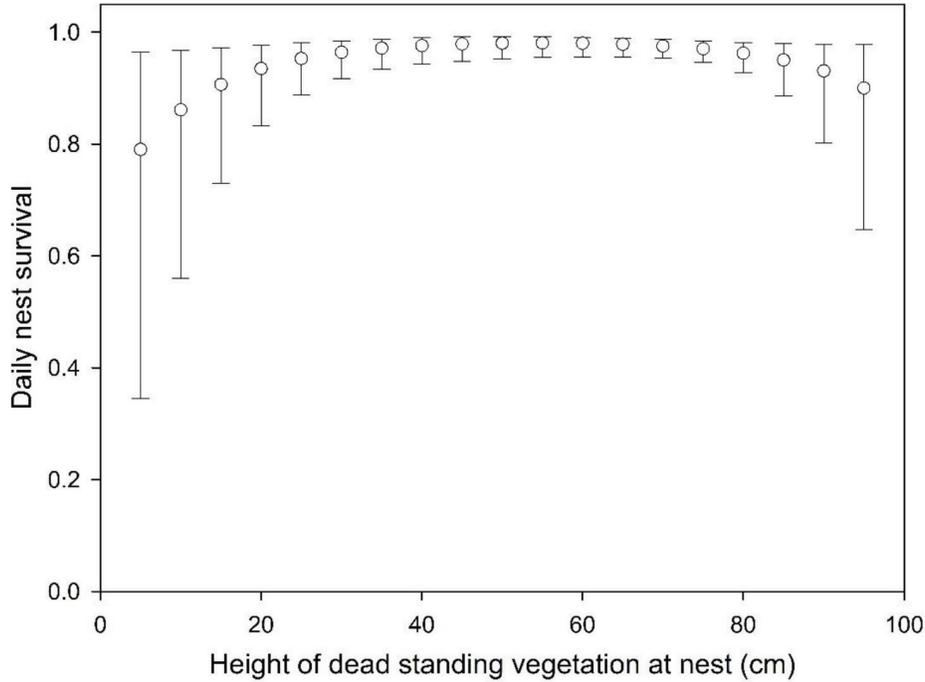


Figure 2. Predicted variation in daily nest survival of sharp-tailed grouse and greater prairie-chickens (species pooled) in the Sandhills, Nebraska, USA, with changes in height of standing dead vegetation (SDV) at the nest from top ranked, known fate survival model.

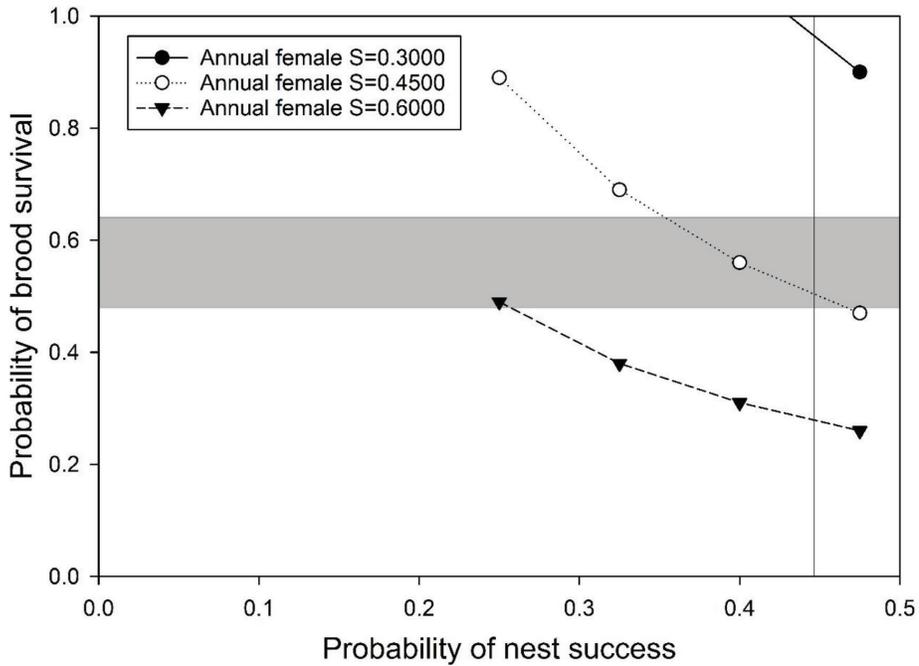


Figure 3. Threshold levels of probability of brood survival (survival to 21 days post-hatch) needed to maintain a stable population of female grouse (greater prairie-chickens or sharp-tailed grouse) in the Sandhills, Nebraska, USA, under four nest success scenarios (0.03, 0.05, 0.10, and 0.15) and three annual female survival (0.7, 0.8, and 0.9) scenarios. See text for other model parameterization and assumptions. Scenarios are not shown when brood survival exceeded 1.0 (100%). For context, empirical nest success estimates (this study) are shown by vertical line, and the range of brood survival rates reported by Anderson et al. (2015) and Harrison (2015) are shown by horizontal box.

Table 1. Comparison of mean, standard deviation (SD), and 95% confidence intervals (CI) for nest-site structural covariates and initiation dates (ordinal date format: May 15 = 135, June 1 = 151), for greater prairie-chickens ( $n = 10$ ) and sharp-tailed grouse ( $n = 29$ ) in Cherry County, Nebraska, USA in 2015 and 2016.

Covariate	Mean	SD	Lower 95% CI	Upper 95% CI
Greater prairie-chicken				
Nest observation start date (Julian date)	144.3 (24 May)	6.0	140.6	148.0
Grass height (cm)	43.8	10.1	37.5	50.1
Standing dead vegetation height (cm)	47.7	21.5	34.4	61.0
Mean litter depth (cm)	7.8	5.5	4.4	11.2
Visual obstruction reading (dm)	1.7	0.5	1.4	2.0
Sharp-tailed grouse				
Nest observation start date (Julian date)	149.6 (29 May)	13.6	144.7	154.6
Grass Height (cm)	56.4	19.9	49.1	63.8
Standing dead vegetation height (cm)	62.3	20.9	54.5	70.0
Mean litter depth (cm)	10.2	8.1	7.2	13.2
Visual obstruction reading (dm)	1.6	0.6	1.4	1.8

Table 2. Comparison of topographic position of sharp-tailed grouse ( $n = 21$ ) nests in Cherry County, Nebraska, USA in 2015 and 2016 in this study with nests of greater prairie-chickens ( $n = 96$ ) in Brown County, Nebraska, USA in 2010 and 2011 (Anderson 2012). Ecological site descriptions from Natural Resources Conservation Service (2011).

Topographic characteristic		Sharp-tailed grouse nests, $n$	Greater prairie-chicken nests, $n$ (Anderson 2012)
Ecological Site	Choppy sands	0	0
	Sands	20	91
	Sandy	1	0
	Subirrigated	0	5
Slope position	Top/middle	7	76
	Bottom	14	30
Aspect	South-facing	3	24
	Not south-facing	18	72

Table 3. Comparison of competing known fate models of survival for greater prairie-chickens and sharp-tailed grouse nests in Cherry County, NE, USA in 2015 and 2016. Models are ranked by Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ):  $\Delta AIC_c$  is the difference in  $AIC_c$  score relative to the highest-ranked model,  $wAIC_c$  is the Akaike weight indicating the relative support of the model, and  $k$  is the number of parameters. Names of non-linear, quadratic models are labeled as  $X^2$ .

Model	$AIC_c$	$\Delta AIC_c$	$wAIC_c$	Model likelihood	$k$
Standing dead vegetation height <sup>2</sup>	94.760	0.000	0.196	1.00	3
Null (constant)	94.898	0.138	0.183	0.933	1
Visual obstruction reading	96.165	1.406	0.097	0.495	2
Dead standing vegetation height	96.575	1.815	0.079	0.404	2
Litter depth	96.580	1.820	0.079	0.403	2
Species	96.736	1.977	0.073	0.372	2
Nest observation start date	96.899	2.139	0.067	0.343	2
Grass height	96.914	2.154	0.067	0.341	2
Visual obstruction reading <sup>2</sup>	97.135	2.375	0.060	0.305	3
Litter depth <sup>2</sup>	97.764	3.004	0.044	0.223	3
Grass height <sup>2</sup>	98.488	3.728	0.030	0.155	3
Nest observation start date <sup>2</sup>	98.822	4.062	0.026	0.131	3

for a stable population. The combination of levels of brood survival previously reported for greater prairie-chickens in the Nebraska Sandhills, nest survival from our study, and typical levels of adult female survival ( $SA \geq 0.45$ ) reported at other sites in the northern Great Plains are sufficient to support populations at stable levels (Figure 3).

## DISCUSSION

### Resource partitioning

Greater prairie-chickens and sharp-tailed grouse are closely related species, similar in size, and are sympatric in much of the Nebraska Sandhills region (Fig. 1). Hiller et al. (2019) reported that the two species use of the Sandhills landscape differs during the breeding season, including use of areas proximate to wet meadows by greater prairie-chickens and more distance from wet meadows by sharp-tailed grouse. Furthermore, prairie-chickens typically use lek sites in flats near wet meadows while sharp-tailed grouse leks tend to be in upper elevations of rolling dune fields (Powell et al. 2014, Hiller et al. 2019). Our study suggests that despite differential proximity to wet meadows, both species select sands ecological sites (rolling hills, sandy soil, slight-to-moderate slopes; Powell et al. 2014, Natural Resources Conservation Service 2011) for nesting. However, the two species appear to use different topographic positions. Sharp-tailed grouse in our study tended to use the bottom of dune slopes for nest locations, while Anderson (2012) reported that greater prairie-chickens tended to use nest sites toward the middle and tops of dune slopes (Table 2). Matthews et al. (2013) also reported that greater prairie-chickens in southeastern Nebraska nested toward the tops of hills. Sharp-tailed grouse in our study nested most commonly away from south-facing slopes, which was similar to prairie-chickens (Anderson 2012, Table 2). Both species may choose locations away from direct southern exposure to provide for cooler nest sites (Raynor et al. 2018).

Height of grass and standing dead vegetation at nest sites were markedly higher for sharp-tailed grouse than for prairie-chickens in our sample. Similar results for both species were reported by Norton et al. (2010) for habitat used for brood rearing in South Dakota. For nest sites, patches with taller residual cover than surrounding sites were critical for sharp-tailed grouse in Nebraska (Prose et al. 2002) and for prairie-chickens in the eastern Sandhills region (Anderson 2012).

### Nest survival

Despite differences between species for structure of vegetation at the nest, our study shows markedly similar probabilities of daily nest survival for both species of grouse in the Sandhills. Further, the height of standing dead vegetation was the only structural measure at the nest to show

effects on daily nest survival, and that effect was not strong (Fig. 2). Hovick et al. (2015) reported lesser probability of nest survival at nests of greater prairie-chickens with lower vegetation heights in Oklahoma, and McNew et al. (2015) reported nonlinear effect of VOR on nest survival of greater prairie-chickens in eastern Kansas. Sharp-tailed grouse select nest sites with high levels of standing dead vegetation in the Sandhills region (Vodehnal et al. 2020, Raynor et al. 2018), and Milligan et al. (2020) reported strong effects of VOR on daily nest survival of sharp-tailed grouse in eastern Montana and western North Dakota. However, Anderson (2012) also reported that variation in vegetation structure at nest sites of greater prairie-chickens in the eastern Sandhills did not affect daily nest survival. Similarly, Harrison et al. (2017) reported stark contrasts between used and available habitat for greater prairie-chicken nests near our study site in the Sandhills, but vegetation structure at nests did not predict the probability of daily nest survival.

Females of both species of grouse in our study placed nests in small patches of thick cover. However, our analysis provided only limited evidence that variation in cover affected survival of nests. One explanation for this dynamic is that that daily nest survival is generally high for grouse in the Sandhills region (Anderson 2012: 0.95; Harrison et al. 2017: 0.96; this study: 0.97), with 24-day nest success rates of approximately 0.30–0.47. Thus, the level of daily nest survival for grouse in the Sandhills appears to be greater than that reported by McNew et al. (2015) in Kansas and Hovick et al. (2015) in Oklahoma but similar to that reported by Milligan et al. (2020) in Montana and North Dakota. Relative to these studies, our nest measurements in the Sandhills show small ranges in height of grass and standing dead vegetation, as well as visual obstruction reading (Table 1), which suggests that the majority of female grouse and prairie-chickens are able to find adequate cover for their nests. Therefore, few females are forced to take nest sites with levels of cover that negatively affects the probability of daily nest survival.

Another explanation for the use of thick cover for nest sites, without a corresponding benefit for nest survival, is that managers may have misinterpreted the role of cover with regard to the success of sharp-tailed grouse and prairie-chicken nests. Generally, cover has been assumed to provide for protection from predators. For example, Powell et al. (2014) stated that female prairie-chickens use small patches of cover because “they want to find protection for their nest in these denser clumps while still being able to see any coming predators.” However, recent explorations of the thermal environment at nest sites have suggested that ground-nesting birds in grasslands, such as quail and grouse, may select nest sites to avoid unfavorable environmental conditions. Nest sites of sharp-tailed grouse in the Sandhills region were  $>1.5^\circ\text{C}$  cooler than random locations in the landscape during the day, and shading by shrubs and standing dead vegetation

provided the thermal cover (Raynor et al. 2018). Therefore, it is possible that females of both species of grouse are selecting nest sites with a suitable level of cover to provide shade, rather than selecting patches of cover to increase avoidance of nest predation. Harrison (2015) and Anderson (2012) reported that greater prairie-chickens used nest sites with mean live vegetation height just over 20 cm on private rangeland, while nest sites in our study on public lands had live vegetation heights of 48 cm for greater prairie-chickens and 56 cm for sharp-tailed grouse. Public lands used in our study were grazed with more conservative stocking rates than those used on private rangelands (Sliwinski et al. 2019). Nest survival estimates on private rangeland (Harrison et al. 2017, Anderson 2012) were not markedly less than the levels of nest survival in our study. Although Hovick et al. (2015) demonstrated effects of vegetation height on nest survival in Oklahoma, our results suggest that vegetation heights of <20 cm (Fig. 2) may be the threshold at which nest survival is affected in the Sandhills. Most nests in our study and previous Sandhills studies have had vegetation heights greater than this threshold.

Nest survival estimates are not useful for management without other key demographic rates to assess population growth (Knutson et al. 2006). Our simple population growth simulation model demonstrated that the levels of nest success in our study and other recent studies on greater prairie-chickens in the Sandhills region should be sufficient for stable or growing populations, given reported levels of brood survival and conservative assumptions for annual survival of adults. Wisdom and Mills (1997) reported that variation in nest and brood survival were the most critical parameters when assessing population growth. For stable populations of prairie grouse, our model suggested that low levels of annual adult survival ( $S = 0.3000$ ) required extremely high levels of brood survival at the highest rates of nest success. In contrast, nest success could be as low as 0.25 at typical levels of brood survival in years when adult survival was 0.6000, which is the highest annual survival reported in Kansas for a single year of a study (Winder et al. 2014).

As sympatric species, sharp-tailed grouse and greater prairie-chickens demonstrated a moderate degree of resource partitioning during breeding season, which is useful information for managers of public and private lands. Nests of sharp-tailed grouse tended to be further from subirrigated meadows, nearer the bottom of slopes, and in taller patches of vegetation. Our study suggests that sharp-tailed grouse and greater prairie-chickens in the Sandhills region are able to find suitable nesting sites on private and public lands to support relatively high levels of nest survival, regardless of differential use of micro- and macroscale features. The lack of influence of vegetation structure on nest survival may suggest habitat resources at nest sites provide critical cover to enhance survival of incubating females, as suggested for greater prairie-chickens in tallgrass prairie (Matthews et

al. 2013) and greater sage-grouse (Moynahan et al. 2006). Management for both species of grouse during the breeding season in the Sandhills requires knowledge of use of habitat resources within the landscape. Our study suggests that provision of patches of vegetation of 20–45 cm in height will provide suitable nest sites and allow for levels of nest success sufficient for stable or growing populations, given reported levels of brood survival and conservative assumptions for annual survival of adults.

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# Captive Ring-necked Pheasant Response to Very High Experimental Doses of Lead

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**ABSTRACT** Ingestion of spent lead pellets is a well-documented source of lead exposure in free-ranging birds, although the consequence of lead ingestion varies widely among avian guilds. Ring-necked pheasants (*Phasianus colchicus*) appear to be less susceptible to lead poisoning than other game birds. Our objectives were to determine survival, liver lead accumulation, and body mass change of 129 captive-raised pheasants in response to being gavage-fed 5, 10, 20, or 40 lead pellets. All pheasants survived the 21-day experiment. Liver-lead levels were positively correlated with the number of lead pellets retained and negatively correlated with beginning body mass. Change in percent body mass varied by sex and liver-lead concentration. Higher liver-lead levels were associated with higher percent mass loss for males but not females. Our experiment coincided with the breeding season, which may have contributed to the sex-specific responses. Our pheasants survived lead doses and liver-lead accumulation levels associated with acute lead toxicosis and death for a variety of avian guilds.

**KEY WORDS** acute toxicosis, lead, lead poisoning, *Phasianus colchicus*, ring-necked pheasant, South Dakota

Exposure to lead adversely affects wildlife, and ingestion of spent pellets or bullet fragments is the primary source of lead exposure in free-ranging birds (Pokras and Kneeland 2009, Tranel and Kimmel 2009). Lead ingestion causes reduced body function resulting in anemia, loss in body mass, reduced reproductive parameters, suppressed brain function, lowered blood oxygen capacity, and changes in behavior which can decrease survival (Sanderson and Bellrose 1986, Kendall et al. 1996, Tranel and Kimmel 2009). Although ingested lead has been documented in >130 avian species (Tranel and Kimmel 2009), the risk profile for a particular species depends on a combination of the individual response to lead exposure and overall population exposure rate. Lead poisoning can be acute and cause death within days of exposure (Schulz et al. 2006) or chronic, in which toxicosis symptoms persist during a prolonged period of elevated body lead level (Sanderson and Bellrose 1986, Gasparik et al. 2012). The severities of lead exposure effects can be influenced by diet (Damron and Wilson 1975, Sanderson and Bellrose 1986), made more severe by stressors such as changes in temperature (Kendall and Scalon 1984), and be less severe in captive-raised versus wild individuals (Jordan and Bellrose 1950).

Among game birds, the issue of lead poisoning has been particularly problematic for waterfowl because hunting deposited concentrated amounts of lead in high-use areas and the individual effects of lead poisoning were severe. Prior to the 1987–1991 phased-in ban on lead ammunition for waterfowl hunting, an estimated 1.6–2.4 million waterfowl died annually from lead poisoning (Friend and Franson 1999). Additionally, an estimated 1.66 million mourning doves (*Zenaidura macroura*) may die annually from ingesting

lead pellets (Plautz et al. 2011). Both waterfowl and mourning doves are highly susceptible to acute lead toxicosis, which causes reduced survival after ingestion of as few as 1–3 pellets (Jordan and Bellrose 1950, Schulz et al. 2006).

Reported mortality from lead exposure is more common in waterfowl than resident upland game birds (Friend and Franson 1999), and gallinaceous birds in particular seem less susceptible to lead poisoning than most other birds (Franson 1996, Friend and Pain 2011). Nonetheless, isolated cases of acute fatal lead poisoning from ingesting shot have been documented in ring-necked pheasants (*Phasianus colchicus*, hereafter pheasant) (Calvert 1876, Hunter and Rosen 1965). Ingested lead pellets were found in 34% of a small sample of captive-raised pheasants from a shooting preserve in Canada (Kreager et al. 2008). In a large sample of hunter-harvested wild pheasants from throughout South Dakota excluding shooting preserves, only 0.8% had ingested lead shot (Runia and Solem 2016). In the same study, the prevalence rate of ingested lead was 3.9% for pheasants harvested on shooting preserves where heavy lead deposition occurred. In pheasants that ingested lead ( $\geq 1$  pellet), the mean number of ingested lead pellets was 2.40 (range: 1–11) for non-preserve areas and 2.65 (range: 1–13) for preserve sites. In a mixture of wild and released pheasants harvested on shooting preserves in Great Britain, 3% contained ingested lead shot (Butler et al. 2005).

Pheasants ingest lead shot in the wild, but the individual effects of lead exposure have not been adequately investigated in this species. No mortality or significant mass loss was observed when captive female pheasants were gavage-fed 2, 4, or 6 lead pellets weekly for 10 weeks (Gasparik et al. 2012). However, egg mass, fertilization, and hatchability were lower

for treatment groups than the control groups (Gasparik et al. 2012). In a 21-day experiment, Runia and Solem (2017) did not detect mass loss or reduced survival when captive female pheasants were gavage-fed a one-time dose of 1 or 3 lead pellets even though liver-lead levels reached a concentration consistent with lead poisoning in other birds.

Lethal dose measures are often used as a way of comparing relative susceptibility of lead poisoning among bird species or guilds. Because the lethal dose of lead for pheasants remains unknown, we expanded upon past pheasant dose-response studies by increasing the experimental dose of lead to much higher levels. Our objectives were to estimate survival, liver-lead concentration, and change in body mass of captive-raised adult pheasants after being gavage-fed 0, 5, 10, 20, or 40 lead pellets.

## STUDY AREA

We studied captive pheasants within the poultry building of the South Dakota State Fairgrounds in Huron, South Dakota, USA (44.3633° N, 98.2143° W). The enclosed brick building was 48 m by 23 m with a 10-m high ceiling and was not temperature controlled. The mean daily temperature was 7.1° C during the 47-day acclimation period and 11.4° C during the 21-day post-treatment period (NOAA 2016).

## METHODS

We conducted a dose-response feeding trial experiment using captive-raised adult pheasants hatched from captive stock. We randomly assigned 129 pheasants (57 females and 72 males) to each of four treatment groups ( $n = 119$ ) and a control group ( $n = 10$ ) (Table 1). After a 47-day acclimation period, we administered the treatments on 26 April 2016

and monitored survival during a 21-day post-treatment period. We used #5 lead shot size as it is one of the more popular shot sizes used for pheasant hunting. The shot was obtained from a commercial shotshell source; therefore, it was assumed there was very little variability in weight/size from pellet to pellet and we did not use any pellets that were obviously damaged or malformed. We gavage-fed 5, 10, 20, or 40, #5 lead pellets one time by inserting a flexible tube (6-mm outside diameter) down each pheasant's esophagus and inserting the pellets into the crop. We replicated this process for birds in the control group without inserting lead pellets. We placed the birds in individual cages (38 cm × 44 cm × 46 cm) within the enclosed building and provided them with unlimited commercial poultry food, water, and gravel grit. Nutritional content of the food was 16.00% crude protein, 0.70% lysine, 0.30% methionine, 2.50% crude fat, 8.00% crude fiber, 3.40–3.90% calcium, 0.45% phosphorus, 0.25–0.65% salt, and 0.15–0.23% sodium.

We weighed birds at the beginning and end of the acclimation period and at the end of the 21-day post-treatment period to the nearest 5 g using a WeiHeng® digital hanging scale (model 40KG, Guangzhou Weiheng Electronics Company, Guangzhou, Guangdong, China). We euthanized all birds by cervical dislocation and removed livers and gizzards from each bird at the end of the 21-day post-treatment period. We stored individual livers in plastic freezer bags and kept them frozen prior to testing. We radiographed and necropsied each gizzard to confirm the presence and number of lead pellets. Each liver was tested for lead concentration (parts per million wet weight [ppm]) by atomic absorption spectroscopy by the University of Missouri-Columbia Veterinary Medical Diagnostic Laboratory, Columbia, USA. Animal care guidelines as outlined in Fair et al. (2010) were followed.

Table 1. Number of #5 lead pellets gavage-fed to captive-raised pheasants by treatment group and sex in South Dakota, 2016.

Treatment Group	No. lead pellets	No. females	No. males
Control	0	5	5
Low	5	11	17
Medium	10	13	16
High	20	14	17
Very High	40	14	17

## Statistical Analysis

Although we administered lead pellets at specific doses (treatment groups), we expected a retention rate of <100% and anticipated a range of lead exposure among all birds. We tested for a difference in pellet retention rate among treatment groups using analysis of variance (ANOVA). Because the pellet retention rate was similar among groups and there was a range of lead exposure among all birds, we assumed overall lead exposure was best described by the number of lead pellets retained by each bird, not the treatment group. We used linear regression to model post-treatment liver-lead concentration as a function of pre-treatment mass, sex, and lead pellets retained. Data from the control group was not used in the regression models predicting liver-lead concentration. For the acclimation period, we tested for a difference in body mass change among treatment groups using ANOVA and between sexes using a *t*-test. We used linear regression to model post-treatment percent change in body mass as a function of pre-treatment mass, sex, lead pellets retained to end of experiment, and liver-lead concentration.

We followed information-theoretic methods to evaluate our candidate model sets for the most parsimonious model(s) (Burnham and Anderson 2002, Arnold 2010). We inspected our model set for uninformative variables by identifying nested models where the addition of one parameter only improved model fit by trivial amounts of deviance (e.g., 1–2). We also evaluated parameter estimate 85% confidence limits (CLs) relative to zero (Arnold 2010). We report estimates and 85% CLs for the most parsimonious model while holding all other continuous variables at their mean. We used the program R (R Version 3.1.3, [www.r-project.org](http://www.r-project.org), accessed 9 March 2015) for all statistical analyses.

## RESULTS

All pheasants survived the acclimation and post-treatment periods. Of the 2,290 gavage-fed pellets, 873 (38%, range: 0–35/bird) were retained to the end of the experiment. Pellet retention rate did not vary by treatment group ( $F_{3,118} = 0.651$ ,  $P = 0.584$ ). Of the 119 pheasants that were administered lead pellets, 112 (94%) retained  $\geq 1$  lead pellet. Mass increased 3.57% (SE = 0.99,  $n = 129$ ) during the acclimation period and did not differ between sexes ( $F_{1,127} = 1.575$ ,  $P = 0.212$ ) or among groups ( $F_{4,124} = 0.398$ ,  $P = 0.810$ ).

Our top-ranked model for predicting liver-lead concentration included mass at beginning of treatment period and number of pellets retained through the post-treatment period (Table 2). The second-ranked model was identical to the top-ranked model except for the addition of the variable for sex, which had 85% CLs that overlapped zero. Because the second ranked model contained an uninformative variable, we considered it to be uncompetitive with the top model. Additionally, no other models were within 4  $\Delta$ AIC<sub>c</sub>

of the top model, so we only used the top-ranked model for parameter estimation. Liver-lead concentration was positively correlated with the number of pellets retained through the treatment period and negatively correlated with beginning pheasant mass (Fig. 1).

Our top-ranked model for body mass change during the post-treatment period included liver-lead concentration, sex, and an interaction between liver-lead concentration and sex (Table 2). The second-ranked model was identical to the top-ranked model except beginning mass was included. Because beginning mass was not informative (85% CL overlapped zero), the second-ranked model was not considered competitive. The third-ranked model differed from the top model by the variables mass and an interaction between mass and sex, both of which were uninformative variables (85% CLs overlapped zero). Therefore, we selected the top-ranked model as most parsimonious. Body mass loss was highly correlated with increasing amounts of liver-lead concentration for males but had very little influence for females (Fig. 2). Females lost more body mass than males during the post-treatment period when liver-lead concentration was  $\leq 15$  ppm.

## DISCUSSION

Gallinaceous birds are known to be resistant to the effects of lead toxicosis, and pheasants appear the least affected within the Galliformes. Our pheasants survived the largest single experimental dose of lead administered to the species to date and one of the largest doses administered to any species. We are only aware of one study that administered a larger one-time dose to any species. Cook and Trainer (1966) experimentally fed 25–100 lead pellets to Canada geese (*Branta canadensis*); all died in  $\leq 10$  days. Pheasants also survived the more chronic but still large dose by Gasparik et al. (2012) (2–6 pellets weekly for 10 weeks) and the lower dose of 1–3 pellets by Runia and Solem (2017). Northern bobwhites (*Colinus virginianus*) exhibited 95% survival to 56 days after being gavage-fed up to 3 spent lead pellets (Tannenbaum 2014). Most (90%) northern bobwhites survived a 5-lead pellet/week dose for six weeks, but mortality was 92% when the dose was increased to 10 lead pellets three times per week for four weeks (Damron and Wilson 1975). In the same study, mortality was over 67% when the dose was 10 lead pellets per week for four weeks. In willow ptarmigan (*Lagopus lagopus*), an experimental dose of three or six lead pellets caused increased mortality (Fimreite 1984).

Comparatively, a single lead pellet causes reduced survival in captive chukars (*Alectoris chukar*; Bingham 2011), mallards (*Anas platyrhynchos*; Jordan and Bellrose 1950), and mourning doves (Burger et al. 1986). Wetmore (1919) found six pellets were always lethal to captive mallards while Jordan and Bellrose (1950) observed 60–70%

Table 2. Linear regression model selection results for predicting liver-lead concentration (parts per million wet weight [ppm]) and body-mass change (%) of lead-dosed captive-raised pheasants after a 21-day post-treatment period, South Dakota, 2016. Only models with differences in Akaike's Information Criterion corrected for small sample sizes ( $\Delta AIC_c \leq 4.0$ ) of the first-ranked model are presented.

Model <sup>a</sup>	AIC <sub>c</sub>	$\Delta AIC_c$	K <sup>b</sup>	$\omega_i^c$
Liver lead concentration (ppm) models				
Pellets + mass	674.9	0.0	2	0.41
Pellets + mass + sex	675.8	0.9	3	0.26
Pellets $\times$ sex + mass	676.3	1.4	4	0.21
Body mass change (%) models				
Lead ppm $\times$ sex	860.1	0.0	3	0.46
Lead ppm $\times$ sex + mass	861.2	1.1	4	0.26
Lead ppm $\times$ sex + mass $\times$ sex	863.4	3.3	5	0.09

<sup>a</sup> Predictor variables included in each candidate model. Lead ppm—liver-lead concentration in parts per million at end of post-treatment period, sex—male or female, mass—pheasant mass (g) on day of treatment, pellets—number of lead pellets in gizzard after 21-day experiment.

<sup>b</sup> Number of parameters used in each candidate model.

<sup>c</sup> Akaike model weight.

mortality for wild mallards after ingestion of a single lead pellet. Nearly all captive mallards died after a dose of eight lead pellets (Irby et al. 1967). Ingestion of as few as two lead pellets caused 50% mortality (20 days) in mourning doves (Schulz et al. 2006).

As expected, at the conclusion of the experiment, liver-lead concentration levels were positively correlated with the number of lead pellets remaining in the gizzard. Varying liver-lead concentration interpretations have been suggested for poisoning thresholds. Our liver-lead level model predictions for birds with 0 pellets retained were still about 6 ppm, which is the lower suggested threshold for clinical poisoning in Galliformes (Franson 1996). For birds that retained  $\geq 21$  pellets, the predicted liver-lead level (15 ppm) was consistent with severe clinical poisoning and death in Galliformes (Franson 1996). We are unaware of suggested liver-lead toxicity thresholds specific to pheasants, but Friend and Franson (1999) suggested 5 ppm was toxic and 16 ppm was fatal for grouse. Our highest observed liver-lead level was 30 ppm for a female pheasant that retained 35 lead pellets, and in previous work we observed a hunter-harvested male pheasant with nine ingested lead pellets and a liver-lead

level of 25 ppm (Runia and Solem 2017).

Based on this study, Gasparik et al. (2012), and Runia and Solem (2017), accumulation of lead in the liver of pheasants exhibits an approximate linear relationship ( $\sim 1\text{--}2$  ppm liver-lead level per pellet administered/retained). However, lead accumulation has been shown to be highly variable in other species, which might explain why lower survival has been observed in other species given similar lead doses as pheasants. With mourning doves administered one, two, or four lead pellets, liver-lead levels were 1.0, 6.8, and 1.5 ppm respectively for birds surviving to 35 days, but 26.8, 29.8, and 31.1 ppm respectively for birds that died during the 35-day experiment (Buerger et al. 1986). Liver-lead levels ranged from 32 to 83 ppm for captive mallards that died after ingesting six lead pellets (Longcore et al. 1974), whereas the predicted liver-lead ppm for our pheasants that retained six pellets to day 21 of the experiment was only 7.7 ppm (85% CI = 7.2–8.3).

Although liver-lead accumulation did not vary by sex, trends in body-mass loss were influenced by sex and liver-lead levels. Our experiment occurred during the breeding season and we routinely observed our roosters cackling and

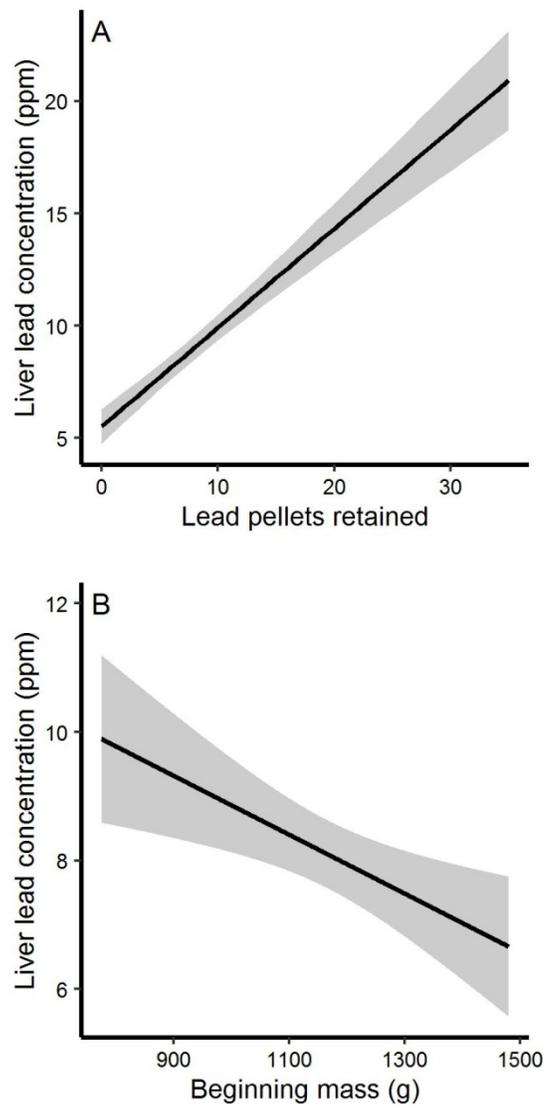


Figure 1. Predicted liver-lead concentration (parts per million wet weight [ppm]) of lead-dosed captive-raised pheasants in response to (A) lead pellets retained and (B) beginning body mass (g) after a 21-day experiment in South Dakota, 2016. Shaded areas represent 85% confidence intervals. All other continuous variables were set to their observed mean.

carrying out territorial wing-flapping behavior. Our females were actively laying eggs, but the facility was not designed to contain eggs within individual cages, so we were not able to estimate egg production for individual birds. Similar mass loss in both male and female wild pheasants has been observed during the breeding season (Edwards et al. 1964). When liver-lead concentration was low, females lost more body mass than males, which suggests the benchmark reproductive energy demand was higher for females than males. Our captive males may have lost less body mass when compared to females because some of the reproductive

energy demand in wild males is behavioral in nature (gather harem, protect territories) and thus there is less energy expended in a captive setting.

Body mass loss of approximately 20–40% has been associated with chronic effects of lead exposure in Canada geese (Sileo et al. 1973), ducks (Irwin 1977, Beyer et al. 1988), northern bobwhite (Damron and Wilson 1975, Beyer et al. 1988), and chukars (Bingham 2011). However, lead exposure has not been linked to significant body mass loss in captive female pheasants (Gasparik et al. 2012, Runia and Solem 2017). We have no obvious explanation to why our female

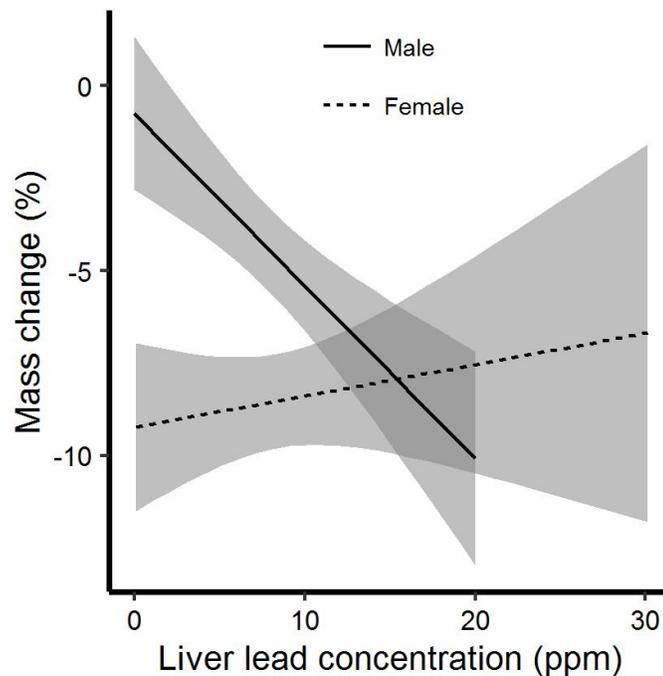


Figure 2. Predicted mass change (% of body mass) of lead-dosed, captive-raised pheasants in response to observed liver-lead concentration (parts per million wet weight [ppm]) after a 21-day experiment in South Dakota, 2016. Shaded areas represent 85% confidence intervals.

pheasants did not lose body mass as liver-lead concentration increased while males did. However, sex-specific responses to lead accumulation have been noted with inconsistent responses. In northern bobwhite, Kerr et al. (2011) found feed consumption, body mass gain, packed cell volume, and plasma protein concentration were adversely affected in lead-dosed males but not females. In domestic chickens (*Gallus gallus domesticus*), Mazliah et al. (1989) found no body mass loss in lead-dosed females, which laid more eggs than controls. However, lead-dosed female Japanese quail (*Coturnix japonica*) lost 21% of their body mass whereas that of males was stable (Edens et al. 1976). Our study is yet another example of the high variability in response to lead exposure between sexes as males lost body mass with increasing liver-lead ppm whereas females did not.

A higher resistance to lead poisoning during the breeding season by females has been demonstrated in mallards and is thought to be related to a high metabolic rate and mobilization of energy sources for egg laying (Finley and Dieter 1978). Spring is also the only season in which food intake is higher for female ducks than male ducks (Jordan and Bellrose 1950).

Diet is probably the single most important factor that influences lead absorption into the body and toxicity once absorbed. This makes it difficult to predict the consequences

of lead ingestion in wild birds based on captive studies or directly compare results of captive studies when the food provided was not similar. Diets high in protein and calcium have been found to consistently reduce the negative impacts of lead exposure (Sanderson and Bellrose 1986). Diets high in carbohydrates such as grain and a variety of weed seeds have been associated with increased symptoms of lead toxicosis (Sanderson and Bellrose 1986). Among captive bird experiments evaluating lead poisoning, feed and available grit has been highly variable. Of the lead-poisoning pheasant studies, Gasparik et al. (2012) did not report the specific feed or grit, Runia and Solem (2017) fed high-protein poultry food and oyster shell grit, and this study fed high-protein commercial poultry food and gravel as grit. It is possible that the high-protein feed in our study mitigated lead absorption and the deleterious impacts of lead poisoning.

Northern bobwhite have shown resilience to the effects of lead poisoning when on a primarily corn/soybean meal diet (Damron and Wilson 1975) and seed-based diet (Tannenbaum 2014), but both diets included limestone or calcium supplements. In captive chukars, a dose of one or five lead pellets never caused mortality in birds on commercial feed, but five out of 16 died when on a mixed seed diet (Bingham 2011). Waste grain, especially corn and wheat, constitutes  $\geq 70\%$  of wild pheasants' diet (Trautman

1982). Corn is only 9% protein (USDA 2018) compared to 16% in the commercial feed fed to our birds. Calcium intake further confounds the potential differences in the effects of lead poisoning between wild and captive pheasants. In wild pheasants, calcium is consumed through calcareous grit or crustaceans (Trautman 1982). About 20% of a pheasant's spring diet is mineral matter and animal matter, both of which contain calcium, but the exact percentage of calcium in the diet is difficult to quantify and compare to commercial poultry feed (Trautman 1982). Calcium intake peaks in spring particularly in females that need increased calcium for egg production (Trautman 1982). Future research should investigate pheasant response to lead exposure when provided food that would resemble the season- and sex-specific diets of wild birds.

### MANAGEMENT IMPLICATIONS

Translating results of captive studies to wild situations is challenging, but pheasants appear to be less susceptible to lead poisoning than other birds. Our pheasants survived and exhibited minimal body-mass loss in response to lead doses far higher than observed in wild pheasants. Dosing wild birds with lead and estimating survival and reproduction may ultimately be the most reliable way of estimating the effects of lead exposure on wild pheasants. However, pheasants are a widespread, popular game bird and shooting occurs in a variety of habitats, including wetlands. Lead deposition from pheasant hunting and its possible impacts to other susceptible birds such as waterfowl may be a more relevant management consideration than the direct impacts to pheasants.

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## NOTES

### TRENDS IN A GREATER PRAIRIE CHICKEN POPULATION ESTABLISHED BY TRANSLOCATION IN NORTH DAKOTA

—In 1992, an effort was undertaken by the North Dakota Game and Fish Department (NDGFD), U.S. Fish and Wildlife Service, and North Dakota Chapter of the Wildlife Society to reestablish a viable population of greater prairie chickens (*Tympanuchus cupido pinnatus*; hereafter prairie chickens) in northeast North Dakota. The release area was centered on the Prairie Chicken Wildlife Management Area located 22.5 km northwest of Grand Forks, North Dakota, in the northern part of Grand Forks County. Topography consists of poorly drained, saline flats and swells separated by poorly drained swales and sloughs in the Red River Valley (Beringer 1995). Permanent grasslands in the release area at the time of the first translocations in 1992 were wildlife areas managed by the state of North Dakota (1,908 ha) and federally owned waterfowl production areas and Kellys Slough National Wildlife Refuge (3,106 ha). Within 9.6 km of the release sites, there were approximately 14,000 ha of grasslands on private lands enrolled in the Conservation Reserve Program (CRP) (Beringer 1995, Kobriger 1999).

The release area had populations of both prairie chickens and sharp-tailed grouse (*Tympanuchus phasianellus*; hereafter sharp-tails) in the past. NDGFD census data that began in 1954 showed that prairie chickens disappeared in 1980. Sharp-tails peaked in 1981 at 118 males but were down to four by 1989, and none were observed in 1992 (Beringer 1995, Kobriger 1999). Since the 1980's, grassland cover in the area increased through state and federal acquisition and the CRP. Management activity (tree removal, prescribed burning, and brush control) on the state and federal lands also increased. A viable prairie chicken population exists 50 to 70 km away in northwest Minnesota. These factors, and a past history of prairie chickens inhabiting the area made this a viable site to reestablish a breeding population of prairie chickens (Kobriger 1999).

Three hundred sixty prairie chickens were translocated to the release area between 1992 and 1998 (Beringer 1995, Svedarsky et al. 1997, Kobriger 1999, Toepfer 2003) (Fig. 1). Between 1992 and 1995, birds were trapped on booming grounds (prairie chicken leks) in northwest Minnesota during spring (April and May) with walk-in traps (Toepfer et al. 1988), radio-marked, and released at the capture site. Birds were recaptured in summer (late July and August) by night lighting, radios replaced, and transported by vehicle to the release area in North Dakota. Sex ratio of released birds was about equal and most of the females were documented by telemetry to have lost nests or broods. Two hens with broods of three were translocated with the brood. These summer-

released birds stayed in the desired area and established booming grounds the following spring near the release sites. In 1996, birds came from both Minnesota and South Dakota (Crow Creek Indian Reservation and Ft. Pierre National Grassland). These birds were also captured in spring, radio-marked, and later recaptured and translocated in summer except four males that were translocated in spring. In 1997 and 1998, birds were obtained from the Sandhills area near Burwell, Nebraska. These birds were captured in spring on booming grounds and translocated immediately to the North Dakota release area to bolster populations on the newly established booming grounds.

An annual census of prairie grouse in the release area was conducted by making booming and dancing ground (sharp-tail lek) surveys following procedures established by Hamerstrom and Hamerstrom (1973) and NDGFD protocols. Spotting scopes and binoculars were used to count and sex birds on leks. Due to the flat terrain and tall grass, many of the leks were not reliably counted unless birds were flushed. Prior to making a flush count, male activity was assessed for the presence of females. Flush counts were conducted later in the morning when males were not active or whooping to avoid the presence of females. Birds that flushed from a greater distance well ahead of the main flush of birds were considered females. Booming grounds were located by listening at stops 1.6 to 3.2 km apart on section line roads and trails. Dancing grounds were located incidental to searching for booming grounds or by listening in areas where sharp-tails had been observed. A systematic search for dancing grounds with listening stops 0.8 to 1.6 km apart was not conducted and dancing grounds may have been missed.

The population peak for prairie chickens was 330 males in 2004 (Fig. 1). During this peak time period, prairie chickens occupied at least 3.5 to 4 townships (32,635 to 37,297 ha) and covered an area 32 km north to south and approximately 13 km east to west. After the peak in 2004, a precipitous decline began; by 2018 only one booming ground with nine prairie chicken males was observed on Kellys Slough National Wildlife Refuge and four single prairie chicken males were observed with sharp-tails on dancing grounds. Numbers of sharp-tails naturally increased in the area and the population peak was 309 males in 2008 (Fig. 1). Sharp-tails declined after 2010 but not as dramatically as prairie chickens; in 2018 173 males were observed.

The reason for the steep decline in prairie chickens is not readily apparent. Private lands enrolled in CRP in Grand Forks County reached a peak in 2007 (U.S. Department of Agriculture-Farm Services Agency, Grand Forks County Office) and have gradually declined since (Fig. 1). The prairie

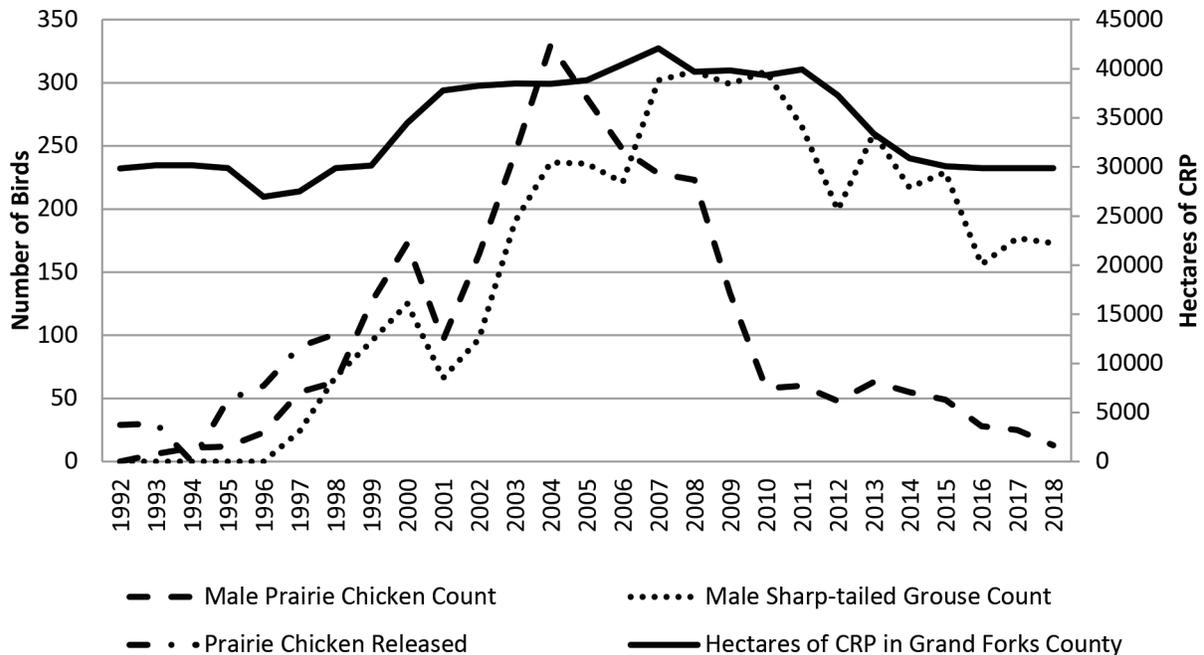


Figure 1. Trends in numbers of male greater prairie chickens and male sharp-tailed grouse counted on the Prairie Chicken Wildlife Management Area and surrounding area of Grand Forks County, North Dakota, USA; number of greater prairie chickens translocated to the Prairie Chicken Wildlife Management Area; and hectares of grassland on private lands enrolled in the Conservation Reserve Program (CRP) in Grand Forks County, North Dakota, 1992–2018.

chicken population decline began before the decrease in CRP grasslands and continued to decline at a much faster rate than the hectares of private lands enrolled in CRP (Fig. 1). In contrast, trends in the sharp-tail population closely followed the amount of grass in CRP.

Weather variables generally affect prairie chicken and sharp-tail production similarly (Flanders-Wanner et al. 2004) and probably do not account for the difference in population trends observed. Winter weather may affect adult survival differently between the species. Snow cover can limit access to the corn, soybeans, and grains that make up most of the winter prairie chicken diet in the northern states and has less effect on the availability of shrub and tree buds that comprise the winter diet of sharp-tails (Johnson et al. 2020). Differences in how the two species deal with winter could be a factor in the observed population trends.

The number of crowing and observed male ring-necked pheasants (*Phasianus colchicus*) was recorded while conducting the prairie grouse census. There were never more than five males heard and or observed in any year. At this low density, we do not believe competition from ring-necked pheasants was an issue in this area as reported in other places with high densities of ring-necked pheasants (Vance and Westemeier 1979, Kimmel 1988, Westemeier et al. 1998, Toepfer 2003).

There were several instances where a dancing ground

became established within 100 to 500 m of a booming ground. After the prairie chicken population peaked in 2005, the number of prairie chicken males on the booming ground would diminish to zero over a 3–4 year period. The sharp-tail dancing ground was maintained or sometimes the dancing ground moved to the location of the original booming ground. An example of each is presented in Table 1. Direct confrontation between males of the two species was occasionally observed on leks, but it is unknown if interspecific competition occurred between females for nesting territories. Hybrid males between prairie chickens and sharp-tails were observed on leks in eight of the years beginning in 2005. The most hybrids observed in one year was three. More hybrids may have been present, but most of the leks in this area do not lend themselves to the close observation required to differentiate hybrids. Hybrids have been documented since the late 1800s where sharp-tails and prairie chickens overlap (Johnsgard and Wood 1968) but are thought to have been rare prior to the expansion of prairie chickens following European settlement. Johnsgard and Wood (1968) stated that sharp-tails are the intruder species onto prairie chicken booming grounds more frequently than the reverse. While the possibility of sharp-tails dominating and causing prairie chicken populations to decline in marginal range for prairie chickens has been informally discussed, there is a lack of documentation of the mechanism or “quantification of the

Table 1. Number of male greater prairie chicken (PC) and male sharp-tailed grouse (ST) observed on leks of different species in close proximity to each other. Mekinock booming ground and dancing ground are approximately 100 m apart. Tire booming ground and Stewart dancing ground are approximately 450 m apart.

Year	Mekinock booming ground		Mekinock dancing ground		Tire booming ground		Stewart dancing ground	
	PC	ST	PC	ST	PC	ST	PC	ST
2004	11	0	0	22	26	0	0	20
2005	5	0	0	16	21	0	0	15
2006	2	0	0	16	2	0	0	8
2007	0	0	0	8	4	0	0	12
2008	0	0	0	22	10	0	0	14
2009	0	0	1	24	5	0	0	17
2010	0	0	1	35	0	4	0	9
2011	0	0	0	25	0	12	0	0

degree of hybridization and the potential loss of fitness with the breakdown of reproductive isolation between the species” (Johnson et al. 2020). Augustine and Trauba (2015) looked at hybridization in a prairie chicken population in west-central Minnesota that was established by translocation. They found that the only mechanism acting to keep the species reproductively isolated was behavioral differences; however, there was 8% incidence of hybrids in the population they examined and they did observe one backcross. Toepfer (pers. obs.) documented radio-marked hybrid and backcross hens successfully fledging broods. We offer our hybridization and observations of the take-over by dancing grounds as a plausible factor in this prairie chicken decline that should be examined in future studies where the two species overlap.

Although disputed by Ross et al. (2006) based on DNA analysis, prairie chickens were not considered indigenous to

North Dakota prior to European settlement based on accounts of early explorers and settlers (Johnsgard and Wood 1968, Johnson and Knue 1989, Kobriger 1999, Houston 2002). Houston (2002) does present one account of several chickens killed by David Douglas in 1827 between Pembina and the Red River, which is northeast of our study area. Johnson et al. (2020) acknowledge Ross et al.’s (2006) assertion that prairie chicken range extended across pre-settlement North Dakota but also state that it is unknown if the prairie chickens were restricted by sharp-tails in this northern range. If prairie chickens were found in North Dakota prior to European settlement, it likely was at very low densities. Prairie chickens have been maintaining booming grounds 70 km east of the study area in Minnesota (personal observations, 2005, 2013). However, these booming grounds represent the northern limit of the larger extant prairie chicken population in Minnesota

(Svedarsky et al. 1997) and, other than a few individuals (personal observations and personal communications with Minnesota Department of Natural Resource personnel), have not extended further north into what is considered primary sharp-tail range (Berg 1997). The factors that limited prairie chickens in North Dakota prior to European settlement might still be at work, and additional translocation efforts should be carefully considered. Funding for the census was provided by the NDGFD and Society of Tympanuchus Cupido Pinnatus, Ltd. We thank J. Kobriger, S. Kohn, and A. Robinson with the NDGFD for their support and coordination. We thank P. Beringer for helping with the census and field work during the first years of the translocation project.—*Gary Huschle, retired Fish and Wildlife Service, Leonard, Minnesota, USA 56652; John E. Toepfer (Deceased, 7 September 1948–11 October 2018). Corresponding author's email address: honkerharmony@gvtel.com.*

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