2020

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Larkin Powell

Walter Schacht

Julia P. Ewald

Kathryn R. McCollum

The Prairie Naturalist 52:58-75; 2020

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LARKIN A. POWELL, WALTER H. SCHACHT, JULIA P. EWALD, AND KATIE R. MCCOLLUM

School of Natural Resources, University of Nebraska-Lincoln, Lincoln, NE, USA 68583 (LAP, JPE, KRM)
Department of Agronomy and Horticulture, University of Nebraska-Lincoln, Lincoln, NE, USA 68583 (WHS)

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^2) 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

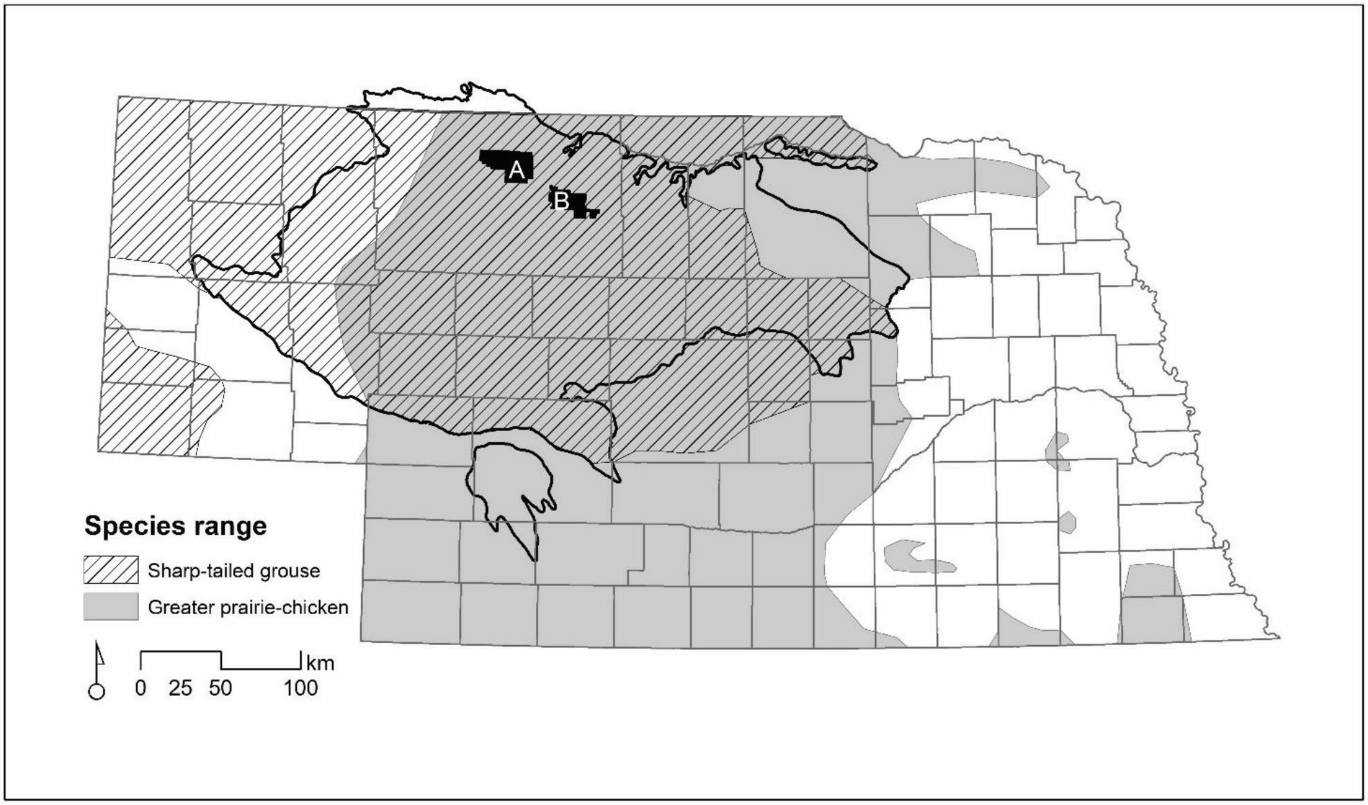

Figure 1. Location of study sites for nest survival of sharp-tailed grouse and greater prairie-chickens at McKelvie National Forest (A) and Valentine National Wildlife Refuge (B) in the Sandhills region (black outline) of Nebraska, USA, with generalized species' ranges (modified from Silcock and Jorgensen 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*), indiangrass (*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 (α= 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 (NS1). We considered a nest successful if ≥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, 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* = 0.75*SA*. 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 ($N_{100} \geq N_1$) 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: 0.9455–0.9799; species model: AIC_c = 96.74, ΔAIC_c = 1.84; DNS, greater prairie-chicken: 0.9729, SE: 0.0154, 95% CI: 0.9193–0.9912; DNS sharp-tailed grouse: 0.9647, SE: 0.0101, 95% CI: 0.9388–0.9799). 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 (β_{SDV} = 0.1156 [SE = 0.0550], $\beta_{SDV*SDV}$ = -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: ΔAIC_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: β_{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 ≥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 ≥0.38

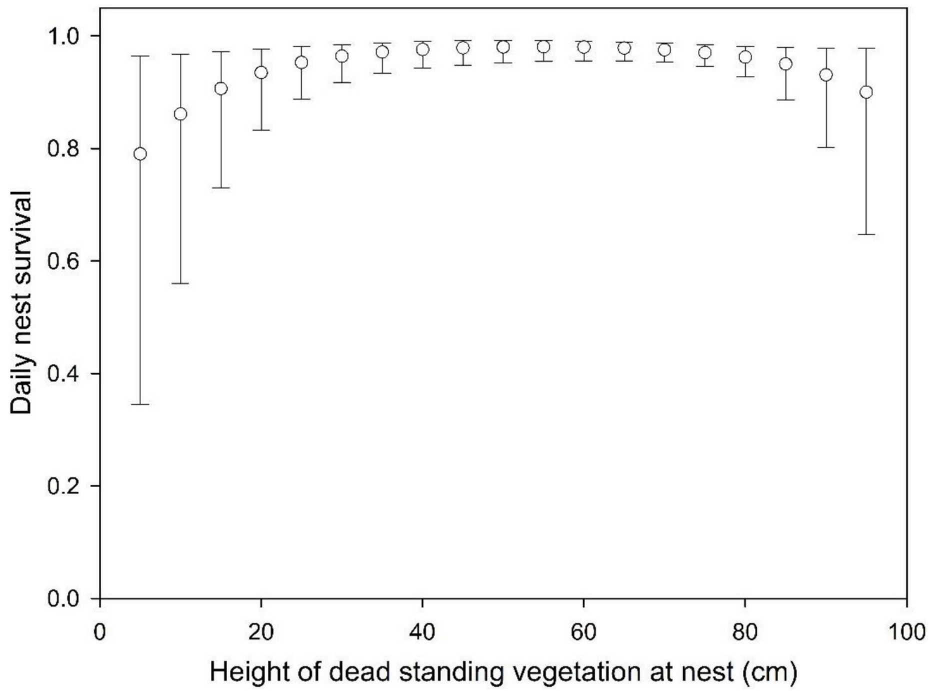

Figure 2. Predicted variation in daily nest survival of sharp-tailed grouse and greater prairie-chickens (species pooled) in the Sandhills, Nebraska, USA, with changes in height of standing dead vegetation (SDV) at the nest from top ranked, known fate survival model.

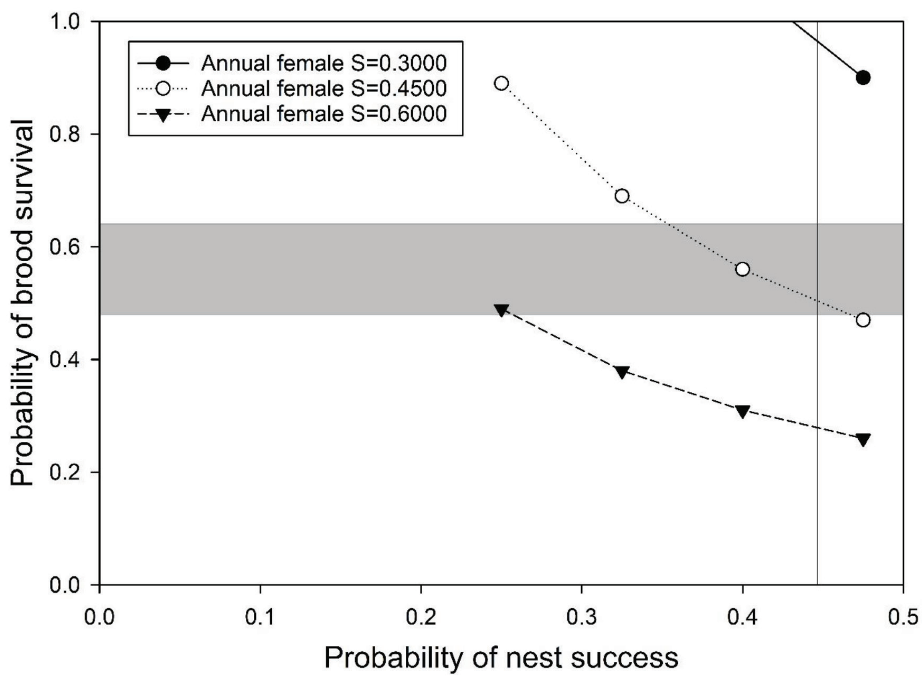

Figure 3. Threshold levels of probability of brood survival (survival to 21 days post-hatch) needed to maintain a stable population of female grouse (greater prairie-chickens or sharp-tailed grouse) in the Sandhills, Nebraska, USA, under four nest success scenarios (0.03, 0.05, 0.10, and 0.15) and three 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	144.3	6.0	140.6	148.0
(Julian date)	(24 May)			
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	149.6	13.6	144.7	154.6
(Julian date)	(29 May)			
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): ΔAIC_c is the difference in AIC_c score relative to the highest-ranked model, ωAIC_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	ΔAIC_c	$wAIC_c$	Model likelihood	*k*
Standing dead vegetation height^2	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^2	97.135	2.375	0.060	0.305	3
Litter depth^2	97.764	3.004	0.044	0.223	3
Grass height^2	98.488	3.728	0.030	0.155	3
Nest observation start date^2	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° 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.

ACKNOWLEDGMENTS

We thank our research technicians for assistance with data collection. We are grateful to J. Geise, M. Nenneman, G. Wright, and other personnel for permission and assistance with our work on Valentine National Wildlife Refuge and the Samuel R. McKelvie National Forest. Two anonymous reviewers provided valuable feedback on an earlier version of the manuscript, and we are grateful to the editorial team for their guidance to improve the manuscript. This project was funded with U.S. Fish and Wildlife Service Wildlife Restoration dollars administered by the Nebraska Game and Parks Commission. LAP and WHS were supported by Hatch Act funds through the University of Nebraska Agricultural Research Division, Lincoln, Nebraska. The model used in this work is available upon request from LAP.

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Submitted: 8 July 2019. Accepted: 8 July 2020.
Associate Editor: Heath Hagy