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EVALUATION OF GAMEBIRD USE AND THERMAL CHARACTERISTICS OF ALFALFA AND PERENNIAL GRASSES IN EASTERN SOUTH DAKOTA

BY

NEAL P. MARTORELLI

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EVALUATION OF GAMEBIRD USE AND THERMAL CHARACTERISTICS OF ALFALFA AND PERENNIAL GRASSES IN EASTERN SOUTH DAKOTA

Neal P. Martorelli

This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science degree and is acceptable for meeting the thesis requirement for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidates are necessarily the conclusions of the major department.

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ABSTRACT

EVALUATION OF GAMEBIRD USE AND THERMAL CHARACTERISTICS OF ALFALFA AND PERENNIAL GRASSES IN EASTERN SOUTH DAKOTA

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The northern Great Plains provide critical breeding habitat for waterfowl and gamebirds in the United States. Peak commodity prices in the late 2000s resulted in increased agricultural production and large-scale conversions of grassland habitat to monoculture row crops. However, recent declines in commodity prices have created a renewed interest for private landowners to diversify crops and enroll in government subsidized conservation programs that convert idle grassland and unproductive cropland to wildlife friendly perennial grassland plantings. Exploring alternative grassland restoration techniques can improve the efficiency of management practices to benefit future wildlife habitat and productivity on both public and private lands. We evaluated gamebird nest production in Roundup Ready© alfalfa (*Medicao sative*, hereafter alfalfa) used to prepare seedbeds for perennial grassland conversion. Nest productivity in alfalfa is often reduced when haying occurs during the peak nesting period. Therefore, we investigated the influence of delaying the first harvest date (July 10) on nest production by systematically nest dragging alfalfa and other typical grassland plantings found on game production areas in eastern South Dakota during the summers of 2015-2016. Additionally, the structural and thermal qualities of grassland nesting habitat that can influence nest site selection and success are poorly understood. Thus, we explored the thermal ecology of upland nesting ducks (*Anatinae*) using black-bulb temperature (T_{bb})

probes. We measured vegetation and thermal characteristics at varying relevant scales to evaluate the relative influence of habitat on nest-site selection and survival. Additionally, we compared rates of nest density and nest initiation dates to further evaluate patterns of use among different cover types. We found levels of vegetation in alfalfa to be consistently lower than in other grassland types, however, rates of nest density and nest survival in alfalfa were comparable or higher than other grassland types. Nests were consistently initiated in alfalfa fields later than other grassland types. Only 9% ($n = 3$) of nests in alfalfa fields were destroyed during haying and suggested that the 10 July delayed harvest date effectively minimized nest losses. Collectively, these results suggested that alfalfa provided important nesting cover for late-nesting and re-nesting grassland nesting ducks and gamebirds. Results of temperature data revealed considerable inter-field heterogeneity, as T_{bb} ranged as much as 35°C, when air temperatures exceeded 30°C. Ducks selected for thermally buffered nest sites with nests being as much as 3°C cooler than non-nest sites. We found that vegetation density ($\beta = -0.05$, $P \leq 0.001$), height ($\beta = -0.04$, $P \leq 0.001$), and litter depth ($\beta = -0.01$, $P \leq 0.001$) influenced T_{bb}. However, only litter depth varied between nest and non-nest sample types ($F_{1,209} = 9.15$, $P = 0.003$) and failed and successful nests ($F_{1,98} = 5.7$, $P = 0.019$), which suggested that this component played an important role in the moderation of temperatures at the nest. Additionally, we found that nest survival was positively associated with increased exposure to cold temperatures ($\beta = 3.25$, SE = 0.21). Overall, these results illustrate the importance of managing for heterogeneous grasslands and will provide land managers with information to maximize quality and available avian nesting habitat in the northern prairie

CHAPTER 1: GAMEBIRD PRODUCTION IN ROUNDUP© READY ALFALFA AND PERENNIAL GRASSES IN EASTERN SOUTH DAKOTA

ABSTRACT

South Dakota Game Fish and Parks manages over 119,000 hectares primarily grassland habitat. To improve the quality and availability of grassland nesting habitat, marginal grassland and cropland cover are cleared and reseeded to perennial grass and forb mixes. Current management techniques for perennial grassland conversion use genetically modified planted row crops and herbicide treatment to remove noxious weeds and enrich the seedbed prior to reseeding. Although this technique is effective, planted row crops provide poor nesting cover. To evaluate other management techniques, we examined the use of Roundup Ready© alfalfa (*Medicao sative*, hereafter alfalfa) for preparing seedbeds for perennial grassland conversion. Nest productivity in alfalfa is often reduced when haying occurs during the peak nesting period. Therefore, we investigated the influence of delaying the first harvest date (July 10) on nest production by systematically nest dragging alfalfa and other typical grassland plantings during the summers of 2015 and 2016 in eastern South Dakota. We measured structural vegetation characteristics at varying relevant scales to evaluate the relative influence of habitat on nest-site selection and survival. Additionally, we compared rates of nest density and nest initiation dates to further evaluate patterns of use among different cover types. We found levels of vegetation in alfalfa to be consistently lower than in other grassland types, however, rates of nest density and nest survival in alfalfa were comparable or higher than other grassland types. Nests were consistently initiated in alfalfa fields later than other grassland types. Only 9% (*n* = 3) of nests in alfalfa fields were destroyed during haying

which suggested that the 10 July delayed harvest date, effectively minimized nest losses. Collectively, these results suggested that alfalfa provided important nesting cover for late-nesting and re-nesting grassland nesting ducks and gamebirds. Further, our results will provide land managers with information to maximize quality and available avian nesting habitat in the northern prairie.

INTRODUCTION

Eastern South Dakota is home to the largest population of ring-necked pheasants (*Phasianus colchicus*; hereafter, pheasant) in North America (Trautman 1982) and leads the country in waterfowl production (Smith et al. 1964, Bellrose and Kortright 1976, Batt et al. 1989). This region was historically dominated by mixed and tall grass prairie (Trautman 1982, Johnson et al. 2008); however, increased agricultural production fueled by rising commodity prices has resulted in large-scale conversion of grassland and pasture to monoculture row crops (Wallander et al. 2011). The fragmentation of grasslands in this region from agriculture has yielded a mosaic of grassland patches within an agriculturally dominated landscape (Smith 1981, Schwegman 1983, Herkert 1994). Fragmentation of nesting habitat has been attributed to declines in waterfowl production (Beauchamp et al. 1996, Klett et al. 1988, Sargeant et al. 1993, Sargeant et al. 1995), caused by increased predation of nests (Cowardin et al. 1985, Garrettson and Rohwer 2001). Additionally, wide spread loss of nesting habitat has led to the decline of several other grassland obligate species (Warner 1994, Herkert et al. 1996, Sauer et al. 2014).

Over 65% of eastern South Dakota’s approximately 9.2 million ha of land have historically or are currently involved in some form of agricultural production (Bauman et al. 2016). Recent studies report that 24% of this region includes undisturbed native grassland cover (Bauman et al. 2016). However, only 4.3% of this remaining undisturbed grassland has permanent conservation status, which protects it from conversion indefinitely (Bauman et al. 2016). The South Dakota Department of Game, Fish and Parks (SDGFP) manages 95,443 ha of land in eastern South Dakota, 42.6% of which is undisturbed native grassland. Furthermore, SDGFP manages land in 43 of the 44 counties in eastern South Dakota. Given that >90% of land in this region is privately owned (NRCM 2000), state managed lands can provide valuable grassland nesting habitat, providing connectivity in a highly fragmented landscape.

The SDGFP manages >730 Game Production Areas (GPA) in the state. These lands are managed broadly for the purpose of enhancing wildlife habitat and providing public hunting access. Hunting in South Dakota is culturally and economically important, with revenues from hunting estimated to yield $303 million annually (SDGFP 2015b). Pheasants and ducks (*Anatidae*) are the most popular game birds in this region and collectively accounted for the sale of >180,000 hunting licenses in South Dakota (Huxoll 2011). Therefore, GPAs in eastern South Dakota are largely managed to enhance nesting habitat for these important game species. Much of the land in this region owned by SDGFP was historically hay or pastureland and was often planted with introduced cool-season grasses (J. Freidel, SDGFP, personal communication).

Cool-season grass plantings in this region typically include species such as smooth brome (*Bromus inermis*), Kentucky bluegrass (*Poa pretensis*), crested wheatgrass (*Agropyron cristatum*) and alfalfa (*Medicao sative*) (J. Freidel, SDGFP, personal communication). Cool season grass stands traditionally requires annual management (e.g.

burning, grazing, and reseeding) to maintain plant species diversity. When left idle, forb components are outcompeted, resulting in largely monotypic stands of smooth brome (Hall and Willig 1994, Greenfield et al. 2002), which was historically planted throughout the northern Great Plains and was favored for its adaptability and forage quality (Sather 1987, Otfinowski et al. 2007). However, monotypic stands of smooth brome offer limited benefits to wildlife (Millenbah et al. 1996, McCoy et al. 2001) and lack the structural complexity favored for grassland nesting birds (Higgins and Barker 1982). Vegetation structure and complexity is an important component for nest productivity in pheasants (Olson and Flake 1975, Dumke and Pils 1979, Purvis et al. 1999) and ducks (Schranck 1972). Thus, decadent smooth brome dominant stands are typically converted to mixed stands of perennial grasses and forbs, which provide the structural complexity preferred by grassland nesting birds.

Idle stands are typically replaced with 1 of 2 popular perennial grass and forb mixes (hereafter conservation plantings), which were developed for use in the Conservation Reserve Program. Cool season (CS) and warm season (WS) conservation plantings are used widely throughout the mid-west and have been found to benefit numerous wildlife species (King and Savidge 1995, Swanson et al. 1999, Reynolds et al. 2001, Haroldson et al. 2006, Nielson et al. 2008). Cool season plantings are comprised of a mix of perennial cool-season grasses and legumes and are predominately of exotic origin. These plantings typically include intermediate wheatgrass (*Agropyron intermedium*), tall wheatgrass (*Thinopyrum ponticum*), green needlegrass (*Nassella viridula*), Canada wild rye (*Elymus canadensis*), alfalfa, and sweet clover (*Melilotus spp.*). Cool season plantings provide early season cover but lack the structural rigidity to withstand ice and snow and therefore offer marginal winter cover (SDGFP 2015*a*). Warm season plantings, are comprised of a mix of warm season native grasses and forbs and typically include big bluestem (*Andropogon gerardii*), sideoats grama (*Bouteloua curtipendula*), indiangrass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), prairie coneflower (*Ratibida columnifera*), purple prairie clover (*Dalea purpurea*), and western yarrow (*Achillea millefolium*) (SDGFP 2015*c*). These plantings exhibit late season growth, offer cover for late and re-nesting hens, and provide shelter during winter (SDGFP 2015*c*).

Successful establishment of conservation plantings require preparatory steps to insure the viability of new stands. Noxious invasive species such as smooth brome, Kentucky bluegrass, field pennycress (*Thlaspi arvense*), and Canada thistle (*Cirsium arvense*) are removed using herbicide treatment (J. Freidel, personal communication). Habitat managers with the South Dakota Department of Game, Fish and Parks have traditionally used Roundup Ready© brand (hereafter, RR) genetically modified row crops and glyphosate herbicide treatment for this purpose. Glyphosate is a commonly used herbicide which inhibits amino acid synthesis in plants (Bryan 2006). Roundup Ready corn (*Zea mays*) is typically planted for 2 to 3 years and sprayed with glyphosate herbicide to remove noxious species, followed by 1 year of RR soybeans (*Glycine max*) to enrich the soil with the nitrogen prior to reseeding (J. Freidel, personal communication). The use of traditional row crops and herbicide treatment are commonly used and effective management techniques for preparing seedbeds. However, row crops offer little or no benefits to wildlife as nesting cover (Higgins and Barker 1982).

Recently, SDGFP managers in region 2 have proposed the use of RR Alfalfa in place of traditional row crops to prepare seed beds for perennial grassland conversion. Alfalfa effectively fixes nitrogen at rates similar to soybeans (Frawley and Best 1991), such that a single planting of alfalfa can be used to achieve the same management goals as 3 years of traditional row crops. Further, alfalfa has been found to provide attractive nesting cover for pheasants (Dustman 1950, Baxter and Wolfe 1973, Olson and Flake 1975, George et al. 1979, Trautman 1982, Higgins et al. 1988, Warner and Etter 1989) and ducks (Burgess et al. 1965, Labisky 1957, Rock 2006). Therefore, RR alfalfa can provide valuable nesting habitat during seedbed preparation that would not exist with the use of traditional row crops.

Alfalfa can serve as a high-protein forage for livestock and is used widely throughout the Midwest (Frawley and Best 1991). Alfalfa is the predominant hay crop in South Dakota and accounts for ~58% of the >1 million ha of hay planted annually (USDA Census 2014). Alfalfa is traditionally harvested at the pre-flower stage, which optimizes yield and nutritional content as well as improves stand persistence (Warner and Etter 1989). Recent first harvest dates in South Dakota typically occur in the first 2 weeks of June (Rock 2006), which falls within the peak nesting period (1 May–1 August) for grassland nesting birds in the mid-west (Olson and Flake 1975). Therefore, the conventional timing of harvest for alfalfa at the pre-flower stage is in conflict with the needs of grassland nesting birds (Frawley and Best 1991). Further, it has been reported that when hay production goals are met, the destruction of nests during harvest render alfalfa to be one of the least productive cover types in terms of nest success and production (Olson and Flake 1975). It has been suggested that the timing of harvest during peak nesting diminishes and possibly eliminates bird production in alfalfa altogether (Labisky 1957, Warner and Etter 1989, Frawley and Best 1991).

Studies evaluating nest productivity in alfalfa and other planted nesting covers in South Dakota are limited. Rock (2006) conducted a paired field study in South Dakota and reported similar rates of duck and pheasant nest rates in alfalfa, CS, and WS plantings, concluding that perennial cover adjacent to alfalfa could provide re-nesting opportunities for hens displaced by haying operations. Keyser (1986) compared pheasant nest production in small grain, alfalfa, pasture, roadside ditches, and CS plantings and reported similar rates of nest success in alfalfa and CS. However, the author also reported that the causes of nest failure in CS were predominately depredation, whereas haying operations were responsible for most failed nests in alfalfa. Olson and Flake (1975) compared pheasant nesting in various cover types including pasture, small grain, flax, alfalfa, idle farmland, shelterbelt, fencerow, roadside, and tame hay. The authors found alfalfa to be one of the poorest (7 of 9) cover types in terms of nest production, reporting 88% of nests destroyed during haying.

Although nest productivity in alfalfa is greatly reduced due to haying, several studies have presented examples of the potential benefits of a delayed harvest date on nest production in alfalfa. However, this relationship has not been explicitly studied. Cowardin et al. (1985) evaluated mallard (*Anas platyrhynchos*) nest production in an agricultural setting in North Dakota. The authors of this study (Cowardin et al. 1985) noted that a delay in harvest due to wet weather in the second year of their study (1978) resulted in the comparatively higher nest survival rate of 50.2%, compared with rates of 0.3% and 0.5% in 1977 and 1979, respectively, when harvest occurred at normal times.

However, the author of this study (Cowardin et al. 1985) also noted an increase in nest success in other cover types during this year; nonetheless, suggested that delaying harvest by as little as 2 weeks could greatly improve nest success. Similarly, Labisky (1957) evaluated blue-winged teal (*Anas discors*) nest production in managed hay fields on a wildlife refuge in Wisconsin and reported an increased hatch rate of 22% in a year when heavy rains delayed harvest by ten days, compared to a rate of 14% in the previous year when harvest was earlier. Olson and Flake (1975), who evaluated pheasant production in South Dakota, opportunistically searched one alfalfa field that was hayed after the first week of July and reported that this field had a comparatively higher rate of 53% nest success as compared to a rate of 11%, for fields hayed 2 weeks earlier. These findings highlight the potential benefits of a delayed harvest date on nest production in alfalfa, and provide impetus for an assessment of nest production in alfalfa when haying operations are delayed intentionally.

Selection of nesting sites has been attributed to vegetation structure because structure at nests is often found to be different from random sites (Clark and Shutler 1999). Numerous studies have found evidence for the importance of vegetation characteristics for nest-site selection (Duebbert and Lokemoen 1976, Lokemoen et al. 1984, Clark and Shutler 1999, Durham and Afton 2003). Previous studies have suggested that vegetation density, height, and litter depth influence nest-site selection by providing concealment from predators (Cowardin et al. 1985), controlling microclimate (Gloutney and Clark 1997), and limiting the foraging efficiency of predators (Cody 1985, Duebbert 1969, Livezey 1981). Understanding the dynamics between vegetation structure and nest-site selection can provide valuable insight for making informed management decisions with respect to vegetation characteristics that may be used to promote viable populations.

Previous studies (Johnson and Igl 1995, Best et al. 1997, Delisle and Savidge 1997, Ryan et al. 1998, McCoy et al. 2001, Reynolds et al. 2001) have used overall avian abundance for assessing benefits to grassland birds. However, Van Horne (1983) cautioned that density may be a misleading indicator of habitat quality, because suitable breeding habitats can be over utilized by territorial birds, leading less fit breeders to disproportionately inhabit lower quality habitats, which can result in biased estimates of habitat quality (Van Horne 1983, Maurer 1986, Hughes et al. 1999). Subsequently, it has been established that better indicators of habitat quality are nest survival, fledgling survival and weights, and overall fecundity (Maurer 1986, Hughes et al. 1999).

South Dakota Game, Fish and Parks manages over 400,000 acres of land as GPAs, which are purchased and managed using hunting license revenues and Pittman-Robertson Wildlife Restoration funds (Bauman et al. 2016). As native grassland habitats have been largely diminished by agricultural development, managing these public lands for wildlife production is critical in maintaining biological diversity and recreational opportunities alike. Exploring alternative grassland restoration techniques can improve the efficiency of management practices to benefit future wildlife habitat and productivity. Therefore, we evaluated nest production in Roundup Ready alfalfa and other cover types typically found on GPAs in eastern South Dakota; specifically, cool season, warm season, and smooth brome dominated stands. Our specific objectives were: 1) evaluate nest survival and density among cover types; 2) evaluate patterns of nest-site selection among cover types; 3) compare vegetation structure and composition among cover types;

4) evaluate the influence of stand age class of RR alfalfa plantings on overall nest production, and; 5) evaluate the use of RR alfalfa as productive nesting cover when harvest date was delayed.

STUDY AREA

Study sites were located in South Dakota east of the Missouri River in Brule, Charles Mix, Hand, Hyde, Potter, and Sully counties (Figure 1). Study sites fell in several ecoregions including the: Missouri Coteau, Southern Missouri Coteau, Southern Missouri Coteau Slope and James River Lowland (Bryce et al. 1998). The Missouri Coteau ecoregions have topography ranging from rolling hills to steep moraines and define the westerly boundary of the Northern Great Plains (Bryce et al. 1998). These ecoregions are commonly tilled for agriculture in flatter areas and used for cattle grazing in steeper areas (Bryce et al. 1998). The James River Lowland ecoregion is comprised of level to slowly rolling plains which are extensively tilled for agriculture (Bryce et al. 1998). These ecoregions feature high concentrations of temporary and seasonal wetlands created by the Pleistocene Glaciation, which contribute to high levels of waterfowl production (Bryce et al. 1998). Elevations range from approximately 450 to 650 m above sea level with mean precipitation and temperature varying little between regions (Bryce et al. 1998).

These regions were historically composed of mixed grass prairie (Samson et al. 1998) with potential native species including: big bluestem, little bluestem, switchgrass, western wheatgrass (*Pascopyrum*), indiangrass, blue grama (*Bouteloua gracilis*) and green needlegrass (Bryce et al. 1998). However, much of the grassland area has been cultivated for agricultural production (49%; Han et al. 2012), with 24% remaining as undisturbed native cover (Bauman et al. 2016). Crops in the region include millet

(*Pennisetum* spp.), barley (*Hordeum vulgare* L.), wheat (*Triticum* spp.), sunflower (*Helianthus* spp.), corn, and soybeans (Bryce et al. 1998).

METHODS

Study Site Selection

All study sites were located on GPAs in SDGFP region 2 (Figure 1). We selected study sites that included both RR alfalfa plantings and an equal representation of other typical perennial grassland plantings found on GPAs in the region. We worked with SDGFP Resource Biologists in region 2 to facilitate sampling across all typical perennial grassland plantings and identified three typical cover types in addition to RR alfalfa. Perennial cool-season grass and forb plantings primarily included intermediate wheatgrass, slender wheatgrass (*Elymus trachycaulus*), and western wheatgrass with alfalfa or red clover (*Trifolium pratense*), which provide structural complexity and early-season growth. Warm-season grass plantings include big bluestem, indiangrass, little bluestem, and switchgrass, which provide vertical structure and mid- to late-season growth. Smooth brome grass dominant stands (SB) include a mix of decadent perennial plantings and idle agricultural fields, which were comprised largely of SB but also included Kentucky bluegrass, intermediate wheatgrass, and slender wheatgrass. Smooth brome dominant stands represented a large proportion of idle land on GPAs that provide early-season growth, yet lack structural complexity.

Roundup Ready alfalfa was planted using conventional methods from 2013 to 2016 in previously tilled agricultural fields and seeded directly in stands of unbroken sod. Stands seeded in tilled fields were planted with an oat (*Avena sative*) nurse crop in the first year to provide rapid soil protection and minimize competition with noxious weeds

(J. Freidel, personal communication). RR alfalfa fields were managed for 3-5 years to fully eradicate noxious weeds prior to reseeding in perennial cover (J. Freidel, personal communication). Thus, RR alfalfa fields were selected from each of the 2013-2016 year classes to account for the variation in habitat structure and quality over time. RR alfalfa fields were hayed on or after 10 July during the 2015 and 2016 field seasons, because mowing public lands in eastern South Dakota is prohibited until this time (South Dakota Legislature 2015).

Study site selection was limited to GPAs in Region 2 that included both RR alfalfa plantings and at least 1 of the additional designated field types. During the 2015 field season, we selected 26 fields located on 10 GPAs (Table 1), representing an approximately equal distribution of all field types. We limited our sampling efforts to one of each field type per GPA if multiple stands were available during 2015. In 2016, we selected 5 GPAs (Table 1) that included multiple stands of each field type, resulting in 21 study fields. We selected 2 fields at random when multiple stands of a field type were available on an individual GPA.

Search Methods, Marking Nests and Determining Nest Fate

We located nests by dragging 50 m of 8 mm chain between two utility terrain vehicles (UTV) through study fields to flush hens without damaging nests (Higgins et al. 1977, Klett et al. 1986). We conducted searches from 0700 to 1400, when hens were most likely to be on nests (Klett et al. 1986). We searched fields 4 times during each field season beginning in early May to mid-July, to account for both early and late-nesting species (Delisle and Savidge 1997, McCoy et al. 2001). We defined nests as ≥1 egg in a scrape or nest and marked them with labeled fiberglass stakes placed 4 m north of the nest bowl. We recorded the following information at each nest: Universal Transverse Mercator coordinates (UTM; using GPS units, Garmin eTrex 20, Garmin Ltd., Olathe, Kansas, USA), date, time, species, number of eggs, and estimated incubation stage based on standard field candling techniques (Weller 1956).. We revisited nests at 2-7 day intervals until ≥1 eggs hatched or the nest was abandoned or depredated. Following each visit, we covered eggs with down and other nest material and marked with 2 pieces of vegetation in the form of an X over the nest bowl to help determine if nests were subsequently abandoned, and considered them so if the X was found undisturbed at the next visit. We considered nests with ≥1 egg broken or removed from the nest bowl to be depredated. We revisited nests to confirm depredation if only 1 egg was broken or removed from the nest and no other evidence of depredation was apparent (i.e., eggs or nest material scattered). We excluded nests destroyed during sampling (i.e., run-over or stepped on) from analyses.

Species Considered

Previous studies found chain-dragging to be inadequate for searching for pheasant nests (Fisk 2010, Bender 2012), because hens will typically run away from their nest before flushing when a predator is perceived. This behavior makes it difficult to locate active nests using chain-dragging. Additionally, pheasants often exhibit high levels of nest abandonment (Olson and Flake 1975, Keyser 1986) due to research activities (Snyder 1984). Conversely, upland-nesting waterfowl are easy to detect and exhibit lower abandonment rates (Klett et al. 1986). Furthermore, previous studies have shown that pheasants and ducks occupying the same habitat have similar rates of nest success

(Bender 2012). Thus, we included pheasant nests but largely considered our analysis of duck nests as a metric for pheasants.

Vegetation

We sampled vegetation at 2 levels in 2016 and 3 levels in 2016 to evaluate differences among field types and between nest and non-nest locations. We sampled for vegetation at nests on the projected hatch date to systematically avoid sampling failed nests earlier than successful nests. We sampled for vegetation at the stand level by assigning 1 sample point per ha to ensure an equal distribution of sampling effort throughout the field. Stand level sample points were designated by overlaying each field with a grid composed of 1 ha blocks with random generated points in each block using Hawths Tools for ArcMap 10.4.1 (Environmental Systems Research Institute [ESRI], Redlands, California, USA). We sampled for vegetation at the stand level once in early May and once in mid-July during both field seasons. We sampled for vegetation at 6 of 10 study sites during 2015 due to time constraints. During the 2016 field season, we additionally sampled for vegetation at paired-random sampling points to further evaluate differences between nests and field level vegetation structure. We established 1 paired-random sampling point for each nest by extending a random compass bearing, 2 m from the center of the nest. These samples were collected on the projected hatch date of the nest which they are paired with.

We characterized vegetation using 4 metrics: vegetation height, vegetation density, species composition, and litter depth. We measured vegetation height in cm at the point at which 80% of vegetation is growing at or below, using a modified Robel Pole (Robel et al. 1970). We measured vegetation density using visual obstruction readings

(VOR), measured in cm using a modified Robel Pole (Robel et al. 1970). We estimated percent composition to the nearest 5% by identifying all plant species, litter and bare ground present within a 1 m^2 quadrant centered on the nest or sampling point. We measured litter depth in cm using a standard ruler at each of the 4 corners of the 1 m^2 quadrant (Haffele 2012).

Statistical Analysis

Vegetation – We evaluated differences in vegetation characteristics among field types, alfalfa stand age classes and between the 2 years in our study with an analysis of variance (ANOVA), and tested for pairwise differences when appropriate ($P < 0.05$), using a Tukey Honest Significant Difference (HSD) test in program R (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria). We developed model sets for both field type and alfalfa stand age class using VOR, height and litter depth as the dependent variables. Field type and alfalfa stand age class were the independent variables. Vegetation density and litter depth values were right skewed, so we square root-transformed these covariates for these analyses.

Nest Survival – We used Program R (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria) to analyze nest survival using a logistic-exposure model (Shaffer 2004), which is a generalized linear model with a binomial response distribution based on the Logistic function (Hosmer Jr et al. 1989) using the Logit-link function $\{\log_e[p/(1-p)]\}$. We were interested in understanding which habitat features might contribute to nest survival among different field types. Thus, we included a field type covariate in all models. Based on previous research, we developed a set of competing models to evaluate the influence of quadratic and linear temporal covariates (Shaffer 2004), habitat type covariates (Klett et al. 1988), and vegetation structure covariates (Livezey 1981) on nest survival. We combined all nests found in 2015 and 2016 to maximize our sample size (Klett et al. 1986). We analyzed pheasant nests separately from ducks. We also analyzed duck and pheasant nest survival among alfalfa stand age classes using all nests found in alfalfa fields from both years of the study.

We used an information-theoretic approach (Anderson and Burnham 2002) to evaluate all higher order combinations of covariates and used the model with the lowest Akaike's Information Criteria (AIC) with a correction for small sample size (AIC_c) to predict daily survival rate (DSR) among all field types. We considered models that were ≤2 AIC_c units of the top model to be strongly supported by the data (Anderson and Burnham 2002). Models that included additional parameters that minimally improved model performance were reported but not considered for analysis (Arnold 2010). The output value for DSR is constrained between 0 and 1 on the log scale and requires transformation to clearly illustrate the probability of survival as a percent. Thus, we transformed estimates of DSR to percent daily survival rate using an inverse log function. Daily survival rates are often transformed to stage specific survival rates (e.g., nest survival rate) to produce a more biologically relevant probability of survival (Klett et al. 1986, Stanley 2000). Therefore, we assumed a 35-day exposure period to convert estimates of DSR to stage specific estimates of nest survival (NS). We used the delta method to calculate variance of transformed NS estimates (Powell 2007).

Nest Selection – We evaluated nest site selection among field types using generalized linear mixed models for each of the vegetation metrics with binomial responses representing nest sites or non-nest sites in Program R (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria). We found no significant influence for random effects in our initial analyses of paired-random data. Thus, so we proceeded with fixed-effect models for the analyses of pair-random data and developed two sets of models for each of the vegetation covariates (vegetation height, vegetation density and litter depth) to compare nest sites with both the stand level and paired-random sample points. We were interested in evaluating the inter-field differences in vegetation characteristics at both the nest and non-nest sites; thus, we modeled each vegetation covariate as a fixed effect and with an interaction with field type. Additionally, we included an interaction term for the vegetation covariates (vegetation height, vegetation density and litter depth) and sample period (e.g., early vs late) in our stand level analysis, to evaluate patterns of selection throughout the growing season. The sample period interaction was not included in our analysis of pair-random data due to limited representation of all field types during each sample period. For our analyses of stand data, we included field ID and GPA as random effects to control for spatial variation. We z-standardized the vegetation covariates (vegetation height, vegetation density and litter depth) to improve model convergence. We initially included covariates for the consolidated vegetation species composition data (e.g., percent grass, forb, sedge, shrub, tree, litter and bare), but removed them after initial modeling showed no significant influence. Additionally, we calculated mean VOR, height and litter depth at nest and non-nest sites to illustrate patterns of selection. We initially analyzed pheasants and ducks independently, but found the limited sample size of pheasant nests caused model-convergence issues, so combined all nests for this analysis.

Nest density and Initiation – Nest abundance is a misleading measure of density because some nests go undetected (Higgins et al. 1977, Gloutney et al. 1993) and nests that were initiated and failed between searches are unaccounted for (Devries et al. 2008). Thus, we calculated the number of hatched nests per ha for each individual field, field type and study year to further illustrate overall field type-specific nest production beyond our estimates of nest survival. For each individual field and field type, for each year, we divided the number of successful nests (≥1 eggs hatched) by the total area search to calculate hatched nests per ha. We evaluated differences in mean nest density among field types and alfalfa stand age classes using ANOVA and Tukey HSD tests for post-hoc multiple comparisons (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria). We developed models for field type and alfalfa stand age class separately, using nest density as the independent variable and field type and alfalfa stand age class as the dependent variable, respectively. We developed a separate model for each year of the study and a model with the additional additive term for year to evaluate differences between years.

Nest initiation date was calculated by subtracting the estimated incubation stage at the last visit and total number of eggs for each nest from the Julian date, assuming a rate of 1 egg per day. Cowardin et al. (1985) suggested the use of non-parametric methods for evaluating differences among nest initiation dates due to their typically skewed distribution. After initial diagnostics, we found our data to fit the assumptions of normality, so we proceeded with traditional parametric methods. We evaluated differences in mean nest initiation date among field types and alfalfa stand age classes using an ANOVA and a Tukey HSD test for post-hoc multiple comparisons when appropriate (*P* < 0.05) (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria). We developed models for field type and alfalfa stand age class separately, using nest initiation date as the independent variable and field type and alfalfa stand age class as the dependent variable, respectively. We developed a separate model for each year of the study and a model with the additional additive term for year to evaluate differences between years.

We analyzed nest density and nest initiation for duck nests and pheasant nests separately. Our analyses for alfalfa stand age classes included all combined duck and pheasant nests from both years, due to lack of representation from either individual species group among age classes and between years. Furthermore, we combined nests from both years for our pheasant analyses due to small sample size.

RESULTS

Vegetation – We analyzed 1,603 stand level sample points among field types from May to August in 2015 and 2016. Vegetation density (VOR; Figure 2) and litter depth (Figure 3) were right-skewed. Mean square root-transformed VOR differed among fields types ($F_{3,1045} = 28.42$, $P \leq 0.001$) and years ($F_{1,1045} = 5.25$, $P = 0.022$). Mean square root-transformed VOR listed in increasing order of mean (± SE) were 4.9 (± 0.19) cm, 5.1 (± 0.1) cm, 5.2 (± 0.1) cm, and 6 (± 0.1) cm in alfalfa, smooth brome, warm season and cool season fields, respectively (Figure 4). The multiple comparisons test revealed cool season had higher mean square root-transformed VOR than all other field types (Figure 4). Mean vegetation height differed among field types ($F_{3,1045} = 20.91$, $P \leq 0.001$) and years ($F_{1,1045} = 13.74$, $P \leq 0.001$). Mean vegetation height listed in increasing order of mean (± SE) were 37.4 (± 1) cm, 38.3 (± 1.2) cm, 45.4 (± 1.2) cm, and 48 (± 1.2) cm in alfalfa, smooth brome, warm season and cool season fields, respectively (Figure 5). The multiple comparisons test revealed cool season and warm season fields had higher mean height than alfalfa and smooth brome (Figure 5). Mean square root-transformed litter depth differed among all fields types ($F_{3,1045} = 465.44$, $P \leq 0.001$), but not between years ($F_{1,1045} = 1.1$, $P = 0.295$). Mean square root-transformed litter depth listed in increasing order of mean (± SE) were 1.2 (± 0.0) cm, 2.3 (± 0.0) cm, 2.6 (± 0.0) cm, and 2.7 (± 0.04) cm in alfalfa, Smooth brome, cool season and warm season fields, respectively (Figure 6). The multiple comparisons test confirmed these results (Figure 6).

We used 368 stand level sample points to compare vegetation characteristics among alfalfa stand age classes from both years of the study. Stand level mean square root-transformed VOR differed among stand age classes ($F_{3,363} = 6.66$, $P \leq 0.001$) and years ($F_{1,363} = 21.9$, $P \leq 0.001$). Mean square root-transformed VOR listed in increasing order of mean (± SE) were 4.4 (± 0.2) cm, 5 (± 0.2) cm, 5.1 (± 0.1) cm, and 5.6 (± 0.2) cm in age class 3, age class 4, age class 2, and age class 1, respectively (Figure 7). The multiple comparisons test revealed that age classes 1 and 2 had higher mean square root-transformed VOR than age class 3 and age class 4 was in between the 2 groups (Figure 7). Mean vegetation height differed among stand age classes ($F_{3,363} = 14.3$, $P \leq 0.001$), but not between years ($F_{1,363} = 1.86$, $P = 0.173$). Mean vegetation height listed in increasing order of mean (± SE) were 29.3 (± 2.5) cm, 32.8 (± 2.4) cm, 38.2 (± 1.5) cm, and 48.2 (± 2.1) cm in age class 4, age class 3, age class 2, and age class 1, respectively (Figure 14). The multiple comparisons test revealed different vegetation height among all age classes (Figure 14). Further, mean square root-transformed litter depth differed among stand age classes ($F_{3,363} = 11.28$, $P \leq 0.001$) and years ($F_{1,363} = 28.76$, $P \leq 0.001$)

and appeared to loosely increase in a linear fashion with increasing age class, with mean square root-transformed litter depth listed in increasing order of mean (± SE) being 0.8 (± 0.1) cm, 1 (± 0.0) cm, 1.1 (± 0.1) cm, and 1.4 (± 0.1) cm in age class 1, age class 2, age class 4, and age class 3, respectively (Figure 15). The multiple comparisons test revealed that mean square root-transformed litter depth was higher in age class 3 than age classes 2 and 4, which were higher than age class 1 (Figure 15).

Nest Survival – We located 241 nests of 6 species among all 4 field types during the 2015 and 2016 field seasons (Table 3). The number of nests located varied among field type, species, and year (Table 4). We found the most nests in smooth brome (39%, n = 94), followed by cool season (30%, n = 73), warm season (16%, n = 38) and alfalfa (15%, n = 36). We used 128 and 29 nests for our analyses of duck and pheasant nest survival, respectively. Nests not used in analyses were censored due to investigator damage, destroyed during haying, or were not located on a study site that was sampled for vegetation in 2015.

Twenty models were found to support the data for the analysis of duck nest survival (Table 5). Model structures were similar in all competitive models, including the additive covariates field type, number of eggs, nest density and a quadratic term for vegetation density (VOR^2). In addition to covariates supported in all models, the best model (w_i = 0.08) which included the additive covariates percent bare ground, percent litter, percent forb and percent grass was only 0.15 AIC_c units from the second-best model (w_i = 0.08) which included percent litter (Table 5). Thus, we chose to focus on the second-best, more parsimonious model. Additionally, a model with percent litter and year interaction (w_i = 0.06) was included to evaluate nest survival between years. Nest survival was variable among years and field types (Table 6) ranging from 20.5% (SE = 0.8) to 58.9% (SE = 6.5) in 2015 and 32.3% (SE = 1.4) to 68.6% (SE = 6.3) in 2016. Nest survival in alfalfa during 2015 (36.2%, SE = 0.2) was lower than warm season (58.8%, SE = 6.5) but higher than cool season (32.7%, SE = 0.2) and smooth brome (20.5%, SE = 0.8). Nest survival in 2016 followed a similar trend with alfalfa (48.5%, SE = 0.3) being lower than warm season (68.6%, SE = 6.3) but higher than cool season (45.1%, SE = 0.3) and smooth brome (32.3%, SE = 1.4). The number of eggs (β = 0.45, SE = 0.07) and nest density (β = 4.99, SE = 1.87) were positively associated with DSR. VOR^2 (β = -0.0004, SE = 0.0002; Figure 10) and percent litter (β = -0.04, SE = 0.02; Figure 11) were negatively associated with DSR.

We limited the number of covariates included in our pheasant nest survival analysis due to the small sample size (*n* = 29). The distribution of pheasant nests across both years was similar among cool season (35%, *n* = 10), smooth brome (31%, n = 9) and warm season fields (28%, *n* = 8), but considerably lower in alfalfa (7%, *n* = 2). Thus, we were not able to include a term for field type due to minimal representation among field types for both years of the study. Four models were found to strongly support the data for the pheasant nest survival analysis (Table 7). Model structures for all competitive models were similar, with all covariates having a positive association with DSR. All competitive models included either additive or interactive terms for the covariates incubation status plus the number of eggs (hereafter Age2), nest density and year. The best supported model (w_i = 0.07) included the additive covariate for Age2 and an interaction term for nest density and year (Table 7). In addition to the covariates supported in the top model, we also found support from models containing the additive term percent litter (w_i = 0.04), an interaction between Age2 and year (w_i = 0.04) and the additive term vegetation density (w_i = 0.03; Table 7). Pheasant nest survival was variable between years and altogether lower than duck survival estimates, ranging from 0.56% (SE = 0.001) in 2015 to 8.6% (SE = 0.4) in 2016 (Table 8). The covariates Age2 (β = 0.07, SE = 0.03), nest density (β = 14.26, SE = 7.14; Figure 12) and year 2016 (β = 2.78, SE = 1.47) were positively associated with DSR (Table 7). The interaction term for nest density and year (β = -15.55, SE = 8.17) was negatively associated with DSR.

The number of covariates included in our model selection process for nest survival among alfalfa stand age classes was limited due to small sample size (*n* =35; Table 9). We were not able to estimate inter-annual nest survival as we did not have representation of all age classes across both years. Our primary goal was to evaluate differences in nest survival among stand age classes. Therefore, we included a term for stand age class in all candidate models. Only one model was found to strongly support the data (Table 9). In addition to the covariate for stand age class, the best model (w_i = 0.62) included the additive terms for number of eggs and nest initiation date (Table 9). The number of eggs (β = 0.31, SE = 0.05) had a significant and positive association with DSR. Nest initiation date (β = -0.09, SE = 0.03) had a significant and negative association with DSR. Nest survival did not significantly differ among stand age classes (χ^2 = 0.58, *P* = 0.9; Table 10).

Nest Selection – We compared nest and stand level sites using 160 nest and 1050 stand level sample points from 2015-2016. There was a significant and positive influence for the covariate sample period in our analysis of VOR (χ^2 = 51.62, $P \leq 0.001$), vegetation height (χ^2 = 68.65, $P \leq 0.001$), and litter depth (χ^2 = 43.4, $P \leq 0.001$; Table 11). Overall, VOR ($\chi^2 = 34.45$, $P \leq 0.001$; Table 11) significantly and positively influenced the probability of selection, but within field types the influence of VOR was insignificant ($\chi^2 = 1.52$, $P = 0.678$; Table 11). Although, selection was influenced by VOR x sample period ($\chi^2 = 78.35$, $P \leq 0.001$). Means for VOR among all field types appeared higher at nest sites during the earlier sample period, but lower than non-nest sites during the later sample period (Figure 13). Vegetation height positively influenced the nest-site selection, both independently ($\chi^2 = 46.77$, P ≤ 0.001; Table 11) and within field types ($\chi^2 = 10.1$, $P = 0.018$; Table 11). The probability of selection for taller vegetation was similarly evident during the earlier sample period ($\chi^2 = 30.59$, $P \leq 0.001$; Figure 14). Means for vegetation height among all field types appeared higher at nest-sites during the earlier sample period but lower than non-nest sites during the later sample period (Figure 14). Litter depth positively, but insignificantly influenced selection, both independently ($\chi^2 = 0.60$, $P = 0.438$; Table 11) and between sample periods ($\chi^2 = 0.94$, $P = 0.331$; Table 11). Conversely, litter depth within field type ($\chi^2 = 21.27$, $P \leq 0.001$) significantly influenced selection (Figure 15).

We compared nests and paired-random sites using 92 nest and 92 paired-random level sample points from 2016. VOR ($\chi^2 = 1.57$, $P = 0.211$; Figure 16.B), vegetation height ($\chi^2 = 1.62$, $P = 0.203$; Figure 17.B), and litter depth ($\chi^2 = 0.02$, $P = 0.899$; Figure 18.B) all appeared higher at nest than pair-random sites, but was found to have an insignificant influence on selection. Within field types, VOR ($\chi^2 = 0.83$, $P = 0.841$; Figure 16.B), vegetation height ($\chi^2 = 0.14$, $P = 0.987$; Figure 17.B), and litter depth ($\chi^2 = 0.61$, $P = 0.893$; Figure 18.B) similarly had no significant influence on the probability of selection.

Nest Density and Initiation – We included 38 unique fields and 78 and 91 nests from 2015 and 2016, respectively in our analyses of duck nest density. The ANOVA for combined years indicated that there was significant variation in nest density between years ($F_{1,164} = 58.63$, $P \leq 0.001$). Overall, nest density was lower during 2015, averaging 0.10 nests/ha (SE = 0.03) in 2015 and 0.22 nests/ha (SE = 0.04) in 2016. Additionally, there was significant variation among field types ($F_{3,164} = 6.83$, $P \leq 0.001$) and the multiple comparisons test revealed significantly higher rates of nest density in alfalfa than seen in the other field types (Figure 19). Nest density varied among field types during 2015 ($F_{3,74} = 11.72$, $P \leq 0.001$) and during 2016 ($F_{3,87} = 9.64$, $P \leq 0.001$). Nest densities in alfalfa ($\bar{x} = 0.02$ nests/ha, SE = 0.03) were the lowest during 2015, followed by smooth brome ($\bar{x} = 0.10$ nests/ha, SE = 0.01), warm season ($\bar{x} = 0.11$ nests/ha, SE = 0.02), and cool season fields ($\bar{x} = 0.16$ nests/ha, SE = 0.01; Figure 17). The multiple comparisons test revealed variable differences among years (Figure 17). Nest densities were conversely highest in alfalfa ($\bar{x} = 0.33$ nests/ha, SE = 0.02) during 2016, followed by smooth brome ($\bar{x} = 0.26$ nests/ha, SE = 0.02), cool season ($\bar{x} = 0.18$ nests/ha, SE = 0.03), and warm season fields ($\bar{x} = 0.13$ nests/ha, SE = 0.03; Figure 19). The multiple comparisons test results aligned with this apparent trend (Figure 19).

We included 22 unique fields and 43 nests from both years of the study for our analysis of pheasant nest densities. ANOVA indicated that pheasant nest densities varied between years ($F_{1,38} = 23.51$, $P \leq 0.001$) and among field types ($F_{3,38} = 4.27$, $P = 0.011$). Nest densities for both combined years appeared highest in smooth brome ($\bar{x} = 0.18$ nests/ha, SE = 0.02), followed by alfalfa ($\bar{x} = 0.17$ nests/ha, SE = 0.04), cool season ($\bar{x} = 0.16$ nests/ha, SE = 0.02), and warm season ($\bar{x} = 0.09$ nests/ha, SE = 0.03), but the multiple comparisons test revealed no significant difference among field types (Figure 21).

We included 10 unique fields and 35 nests from both years of the study for our analyses of nest density among alfalfa stand age classes. ANOVA indicated that there was no difference in nest density between years ($F_{1,5}$ = 2.65, P = 0.164) and among alfalfa stand age classes ($F_{3,5}$ = 1.00, P = 0.466; Figure 22).

We used the data from our duck nest density analysis for our modeling of duck nest initiation. There was significant variation in median nest initiation dates between years ($F_{1,164}$ = 4.16, P = 0.012) and among field types ($F_{3,164}$ = 4.16, P = 0.007; Figure 20). The multiple comparisons test reported later mean initiation dates in alfalfa, followed by warm season fields, and then cool season and smooth brome fields which were similar (Figure 20). Nest initiation dates did not vary among field types during 2015 ($F_{3,74}$ = 1.2, P = 0.32) but were significantly different during 2016 ($F_{3,87}$ = 8.02, $P \leq 0.001$; Figure 20). The mean nest initiation date in alfalfa appeared to be the latest ($\bar{x}$ = 160 Julian day, SE = 9) during 2015, followed by smooth brome ($\bar{x}$ = 147 Julian day, SE = 3), cool season ($\bar{x}$ = 145 Julian day, SE = 4) and warm season fields ($\bar{x}$ = 139 Julian day, SE = 6; Figure 20). The multiple comparisons test revealed no significant differences among field types (Figure 20). The mean nest initiation date in warm season fields ($\bar{x}$ = 150 Julian day, SE = 4) was the latest during 2016, followed by alfalfa ($\bar{x}$ = 146 Julian day, SE = 3), smooth brome ($\bar{x}$ = 134 Julian day, SE = 3), and cool season fields ($\bar{x}$ = 133 Julian day, SE = 3; Figure 20). The multiple comparisons test reported similarly, later mean initiation dates in warm season and alfalfa than in other field types (Figure 20).

We used the data from our pheasant nest density analysis for our modeling of pheasant nest initiation. Overall, mean pheasant nest initiation dates ($\bar{x}$ = 136 Julian day, SE = 3) were earlier than all combined ducks ($\bar{x}$ = 142 Julian day, SE = 1). There was significant variation in mean nest initiation dates between years ($F_{1,38}$ = 4.77, P = 0.035) and among field types ($F_{3,38}$ = 5.29, P = 0.004). The mean pheasant nest initiation date was the latest in alfalfa ($\bar{x}$ = 158 Julian day, SE = 9) and the earliest and in warm season fields ($\bar{x}$ = 118 Julian day, SE = 6; Figure 21). The multiple comparisons test revealed a significantly later initiation date in alfalfa, followed by cool season and smooth brome fields, which were similar and warm season fields (Figure 21).

We used the data from our alfalfa stand age class nest density analysis for our modeling of nest initiation. There was significant variation in mean nest initiation date between years ($F_{1,5}$ = 9.62, P = 0.004) and among stand age classes ($F_{3,5}$ = 5.33, P = 0.05). Mean nest initiation dates were the earliest in age class 4 stands ($\bar{x}$ = 135 Julian day, SE = 8) and latest in age class 1 stands ($\bar{x}$ = 159 Julian day, SE = 6; Figure 22). The multiple comparisons test revealed a significantly later initiation date in age class 1 stands, followed by age class 2 and 3, which were similar and age class 4 stands (Figure 22).

DISCUSSION

Ducks

Our results suggest that RR alfalfa, if harvest date is delayed, can function as effective nesting cover when used as in perennial grassland conversion. We found that the key measures of nest productivity (nest density and survival) in alfalfa were similar to, and at times higher than, other typical grassland plantings found on GPAs in eastern South Dakota. Our findings suggest that alfalfa can provide vital late season nesting cover for re-nesting hens and that the 1 July harvest date provided adequate time for the majority of nests to hatch successfully.

We found duck nest survival varied among field types and years and that nests in alfalfa fields were consistently more successful than cool season and smooth brome fields. Our overall reported rates of duck nest survival in alfalfa (Table 6) were higher than published in some previous studies (Cowardin et al. 1985, Rock 2006), but comparable to others (Burgess et al. 1965, Duebbert and Lokemoen 1976). The Mayfield estimate of 7% reported by Cowardin (1985) for mallards nesting in alfalfa hayfields in North Dakota, and the apparent nest survival estimate of 15% for Anatids nesting in alfalfa reported by Rock (2006) in eastern South Dakota, were considerably lower than our reported findings. In contrast, the apparent survival estimates of 46% reported by Burgess (1965) for blue-winged teal nesting in mixed hayfields in Iowa and 56% reported by Duebbert and Lokemoen (1976) for Anatids in undisturbed grass-legume cover in north-central South Dakota were similar to our reported rates.

Mechanical destruction of during haying has been found to be the greatest cause of duck nest failures in alfalfa (Labisky 1957, Burgess et al. 1965, Cowardin et al. 1985). Cowardin et al. (1985) and Rock (2006) reported 42% and 90%, respectively, of duck nests destroyed by haying in late June. Further, few studies (Cowardin et al. 1985) identified if nests destroyed during haying were included in their survival analyses. We did not include these nests in our analyses, as we were unable to sample for nest level vegetation measurements after fields were mowed. Cowardin (1985) also reported a nest survival rate of 82% from a separate analysis that excluded nests destroyed by haying, which was higher than our average finding. However, Cowardin (1985) noted that haying which occurred on 20 June destroyed 42% (*n* = 8) of nests, which was higher than our reported proportion of nests (9%, *n* = 3) destroyed by haying on 10 July. Previous studies (Burgess et al. 1965, Cowardin et al. 1985) suggested that a 1 July harvest date was adequate to minimizing nest loss. We projected nest loss to increase by 100% with a 5 July harvest date and 200% with a 30 June harvest date (Figure 23). Thus, our findings indicate that a 10 July delayed harvest date would likely be most effective in minimizing nest loss.

During the course of our study, all study fields were selectively spot treated with herbicide by SDGFP technicians to control noxious forb species several times in each field during both summers. When spraying, technicians would drive UTVs with portable herbicide applicators in a crisscross pattern throughout all of the state managed property. Additionally, alfalfa fields were treated with herbicide 2 times per summer over the course of both years, using a tractor and boom type applicator. SDGFP technicians were made aware of our nests marked with fiberglass stakes and flagging and made attempts to not disturb the area around nests and run over these areas. We did not have any nests destroyed during this process, but it is possible, or even likely, that without our nest markers some nests would have been destroyed. Thus, our estimates of nest survival could be positively biased compared to a more-normal scenario where nests were not clearly marked. Further, past studies on investigator disturbance have shown that such activities can alter and improve nest predator efficiency. As herbicide treatment was typical for all state managed lands in South Dakota, we can assume that any possible increase in depredation caused by this disturbance might be experienced on other state lands. Nonetheless, it is possible that the management practices that occurred on our study sites could have contributed to higher levels of depredation and correspondingly lower nest survival rates.

Most comparable studies that evaluated nest production in alfalfa fields reported either just apparent survival estimates (Burgess et al. 1965, Olson and Flake 1975, Duebbert and Lokemoen 1976, Trautman 1982, Keyser 1986, Rock 2006) or those derived using the Mayfield method (Cowardin et al. 1985). However, more recently developed methods have been shown to better approximate survival and reduce inherent biases (Dinsmore et al. 2002). Our estimates, using the more modern methodology, yielded estimates that would likely be lower than those from apparent and Mayfield estimates. The difference in nest survival analyses could explain some of the differences in our rates as compared to those reported in past studies.

As previously reported (Burgess et al. 1965, Labisky 1957, Rock 2006), our findings indicate that alfalfa is attractive nesting cover for ducks. However, contrary to notion that idle lands have yield higher nest densities than managed lands (Kirsch et al. 1978), we found duck nest densities in alfalfa to vary between years but to be higher overall than for other field types. Burgess et al. (1965) reported the rate of 0.449 nests/ha for Blue-winged teal in mixed alfalfa hayfields to be the second highest among sampled cover types in Iowa. Duebbert and Lokemoen (1976) reported 0.776 nests/ha for ducks nesting in undisturbed grass-legume cover in north-central South Dakota. In a study comparable to ours, Rock (2006) reported 0.3 nests/ha for ducks nesting in alfalfa in eastern South Dakota. Our estimate for duck nest density in alfalfa across years was lower than some previously reported studies (Burgess et al. 1965, Duebbert and Lokemoen 1976), but was higher than reported by Rock during 2016 (2006). However, differences in criteria for reporting nest density could contribute to the apparently lower rates we found. Our reported rates of nest density (successful nests/ha) could appear lower in comparison to nest density defined by nest abundance or all nests per hectare as reported by Burgess et al. (1965), Duebbert and Lokemoen (1976), and Rock (2006). Further, our study fields were composed exclusively of monotypic stands of alfalfa. Of the aforementioned studies, only one (Rock 2006) was similar in this respect. Burgess (1965), Cowardin et al. (1985), and Duebbert and Lokemoen (1976) used alfalfa hayfields that were dominant or co-dominantly planted with introduced grasses. The varying proportion of alfalfa comprised in fields among previous studies could contribute to the range of reported nest survival rates.

Average nest initiation dates were later in alfalfa, than found in all other field types. Growth phenology differs among cover types, and fields with cool season grasses that exhibit early season growth should typically attract more early nesting hens than other field types. Our findings support this hypothesis, as nest initiation dates in cool season fields were earlier than other field types on average. Previous studies suggested that alfalfa does not provide sufficient growth to offer adequate nest concealment until mid-May (Gates 1965), and becomes most attractive to nesting hens after it has reached half of its mature height and density (Cowardin et al. 1985). Cowardin et al. (1985) reported nest initiation dates ranging from 1 June-10 June in alfalfa hayfields and 21 May-31 May in all other cover types and suggested that the later initiated nests in alfalfa hayfields represented second and third attempts for hens that were previously unsuccessful in other field types. Overall, our reported nest initiation dates in alfalfa followed a similar trend and were earlier than for all other field types. Our findings were similar to the nest initiation date range of 25 May-30 May reported by Gates (1965) but later than the range of 1 June-10 June reported by Cowardin et al. (1985). However, our mean nest initiation date in alfalfa during 2015 was similar to the later initiation dates reported by Cowardin et al. (1985). It has been suggested that low spring rainfall can contribute to slower vegetation growth in alfalfa and result in later initiation dates (Cowardin et al. 1985). During 2015, eastern South Dakota received less spring precipitation than during 2016, which could have contributed to the later nest initiation dates during the first year of study.

The alfalfa fields used in our study were composed of monotypic stands of alfalfa. Of the previously mentioned studies (Burgess et al. 1965, Cowardin et al. 1985, Duebbert and Lokemoen 1976, Rock 2006), only Rock (2006) reported a similar composition. Burgess (1965), Cowardin et al. (1985), and Duebbert and Lokemoen (1976) used alfalfa hayfields that were dominant or co-dominantly planted with introduced grasses. Mixed hayfields containing introduced grasses would most likely exhibit earlier growth than monotypic stands of alfalfa. Thus, the varying rates of composition of alfalfa found in fields in previous studies could contribute to the range of reported values for nest survival, nest density, and nest initiation dates.

Pheasants

Pheasant nest survival rates varied between years and were generally higher during 2016 than 2015. Our overall nest survival estimate for pheasants was lower than the apparent survival estimates of 19% reported by Rock (2006) and 35% reported by Keyser (1986), who both evaluated nest production in various cover types in eastern South Dakota. Conversely, our estimates were higher than the apparent survival rates of

8% reported by Olson and Flake (1975) and 7% reported by Trautman (1960), who both conducted similar studies in eastern South Dakota. However, the limited sample size (*n* = 29) of pheasant nests in our study resulted in high variability and reduced our ability to make strong inferences from these nest survival results.

We found pheasant nest densities in alfalfa to be similar to rates found in other cover types. This finding suggests alfalfa was attracting nesting cover for pheasants as reported in past studies (Dustman 1950, Baxter and Wolfe 1973, Olson and Flake 1975, George et al. 1979, Trautman 1982, Higgins et al. 1988, Warner and Etter 1989). Pheasant nest densities among field types during our study were comparable to duck nest densities, with the exception of alfalfa and warm season fields, which were lower than ducks. A possible cause for lower nest density in alfalfa could be the comparatively earlier nest initiation dates in pheasants compared with ducks. Alfalfa becomes most attractive to nesting hens once it has reached half of its mature growth (Cowardin et al. 1985). For this reason, the overall earlier initiation period for pheasants could mean that cover found in alfalfa during the earlier part of the nesting period was simply less attractive.

Mean pheasant initiation dates among field types were similar to our results for ducks, with the exception of warm season fields which were comparatively earlier and the earliest for pheasants among all other field types. Previous investigators (Gates 1965, Trautman 1982) suggested that early nesting pheasants exhibit a preference for stands with significant residual cover until new vegetation growth becomes sufficiently dense. We found that warm season fields consistently had the highest levels of litter depth compared to other field types (Figure 6), supporting this hypothesis. Our reported average initiation dates in cool season and smooth brome fields were similar to the range of 16 May–31 May reported by Olson and Flake (1975). Similar to our findings for ducks, our reported average initiation date in alfalfa was later than all other field types and was similar to the 7 June date reported by Dustman (1950), who evaluated the effects alfalfa mill cutting on pheasants in Ohio. The comparatively later initiation dates seen in alfalfa highlights alfalfa's value for providing late season cover for late and re-nesting pheasants, as reported by Cowardin et al. (1985). Similar to our analysis of pheasant nest survival, the limited sample size (*n* = 43) for our analysis of nest density and initiation yielded high variability and low confidence in our results.

Alfalfa Stand Age Classes

The influence of stand age class on nest production in alfalfa fields has been relatively unexplored. We hypothesized that vegetation growth and, in turn, nest survival and nest density would increase linearly with increasing alfalfa stand age class. Overall, several of our findings were inconsistent with this hypothesis, most likely due to limited sample sizes and the apparent variation in vegetation growth among individual stands (Figure 24). We found VOR (Figure 7) and vegetation height (Figure 8) to generally decrease with increasing age class, whereas litter depth generally increased over time (Figure 9). Litter depth in alfalfa fields was the lowest among all other field types and hens tended to select the deepest litter available. Thus, the linear increase in litter over time suggests that older stands should contain more suitable nesting substrate and subsequently appear more attractive than newer stands to nesting hens.

Nest survival did not vary among stand age classes with the exception of age 4 stands, where survival was significantly greater; we caution, however, that inferences from this result are tenuous at best given our very small sample size for this age class (*n* = 2). Similarly, nest density did not vary among age classes (Figure 22.A). However, our analysis of nest initiation dates revealed a significant negative relationship between initiation date and stand age, such that nests were initiated earlier in older stands (Figure 22.B). This finding suggests that habitat suitability increases with stand age as older alfalfa stands appear to become more attractive earlier in the nesting season. We propose two possible explanations for the pattern of nesting hens appearing to select for taller and denser vegetation. Although we found that VOR and vegetation height appeared to have a negative relationship with increasing stand age, it is possible that inter-stand variation and a small sample size prevented us from capturing the increase in vegetation structure over time, which would have related to cover quality. Conversely, this trend could have been caused by increased levels of litter depth in older stands, further highlighting the importance of residual vegetation for nesting hens in alfalfa.

Vegetation

Our analysis of stand level vegetation indicated that overall levels of VOR, vegetation height and litter depth were significantly lower in alfalfa than all other field types, which could suggest that managed alfalfa fields might not provide the structural complexity and concealment required for nesting hens. However, as previously mentioned, we found rates of nest survival and nest densities in alfalfa to be relative to other cover types. A possible explanation for this apparent discrepancy, would be the disproportionate number of nests produced from a single alfalfa field, seeded in 2015 on Holoubek GPA in Brule County. During the two years of the study, this individual field accounted for 53% (*n* = 19) of all nests found in alfalfa, yielding higher rates of nests per hectare than any other individual alfalfa field (Figure 24). This stand was seeded in a previously tilled agricultural field with a nurse crop of oats in the first year. During the first year, the oats provided additional cover, resulting in higher rates of VOR and height than seen during the second year. During the second year, this field exhibited strong growth which yielded comparatively taller and denser vegetation than seen in most other alfalfa fields sampled during our study (Figure 24). Although, the increased VOR and height during the first year attracted fewer nests (*n* = 3) than during second year (*n* = 16) when vegetation structure more closely resembled that of the other field types (Figure). This field appears to represent the top of the range for vegetation growth and structure possible in alfalfa plantings. While growth can be variable among individual stands, these findings suggests that within this range, alfalfa can provide sufficient cover for nesting hens.

Nest Selection

We found vegetation structure at nest sites to vary from stand level sites across all field types. These results provide evidence of a non-random pattern of nest site selection, as reported in previous studies (Southwood 1977, Clark and Shutler 1999). Vegetation density (Duebbert 1969, Schranck 1972, Livezey 1981, Clark and Shutler 1999) and height (Bue et al. 1952, Livezey 1981, Hines and Mitchell 1983, Clark and Shutler 1999) have long been reported to influence nest site selection. Our results support this hypothesis, because nest sites among all field types generally had higher VOR readings and vegetation heights compared to stand level samples. However, we found strong evidence for this selection during the earlier sample period, but not during the later period, perhaps suggesting that despite the relatively heterogeneous nature of fields prior to peak vegetation growth, hens were able to select nest sites which provided the requisite levels of concealment and cover. We found that when vegetation reached its full, mature growth, adequate nesting cover became abundant and hens selected for intermediate levels of VOR and height. We found nest sites during the later sample period to yield comparatively shorter, less dense vegetation than stand level sites, which provided evidence for a stabilizing selection for vegetation structure, rather than directional (Livezey 1981, Hines and Mitchell 1983, Clark and Shutler 1999, Durham and Afton 2003). Further illustrating this pattern, we found nest survival was negatively related to increasing VOR, similar to the results reported by Haffele (2012) and Skone et al. (2016). This could suggest that a certain threshold of intermediate level of vegetation was the most important factor influencing nest survival. The trend for stabilizing selection was apparent among all field types, despite varying ranges of VOR and height; thus, we can infer that alfalfa can provide the level of structural complexity and concealment required for nesting hens.

Studies evaluating the influence of litter depth on nest site selection are limited (Fisher and Davis 2010). Previous studies have both dismissed (Lokemoen et al. 1984) and promoted (Duebbert 1969) the importance of litter depth as a driver of nest site selection. Our overall findings suggested that litter depth did not significantly influence the probability of selection. However, we found litter depth to differ between nest and stand level sites among all field types, to a varying degree. Litter depth in warm season fields was higher than other field types, which resulted in a negative pattern of selection, as litter depths at nest sites were consistently lower than stand level sites. Conversely, alfalfa fields that were mowed annually had comparatively lower litter depths than all other field types, which resulted in a positive pattern of selection as litter depths at nest sites were consistently higher than stand level sites. Further, it has been hypothesized that litter can contribute to controlling nest microclimate (Gloutney and Clark 1997) and increase concealment for early nesting hens (Duebbert 1969). Supporting this hypothesis, we found that nest locations in smooth brome fields, which were comparatively more structurally sparse than those in cool and warm season fields, to have higher levels of litter during the earlier sample, but lower levels compared to stand level points during the later sample. These findings suggest that hens using smooth brome fields selected for nest sites with deeper litter prior to the stand reaching its full and mature growth, possibly to compensate for the comparatively reduced levels of cover. This apparent stabilizing selection suggested a certain threshold of intermediate litter depth was acceptable for nesting hens. Further, studies (Glover 1956, Burgess et al. 1965) have suggested that managed fields may be less attractive to nesting ducks due to the lack of litter. Our findings evaluating litter depth among alfalfa stand age classes suggested a linear increase in litter for every year of production. Thus, despite the comparatively lower levels of residual litter, hens were able to locate adequate nest sites by selecting for the deepest level of litter available.

Our analyses of nest site selection, comparing nest and paired-random sites, provided no evidence for selection of vegetation structure within 2 m of the nest. This finding suggests that within a relatively homogenous landscape such as northern mixed grasslands, nest site selection appears to occur at a larger spatial extent, likely driven by patches within a stand. Similar to our results comparing nest and stand sites, past studies (Gloutney and Clark 1997, Durham and Afton 2003) have reported differences in vegetation height between duck nests and adjacent sites located 60 m and 0-200 m from nests, respectively. Conversely, another study (Hovick et al. 2014) evaluating habitat selection of greater prairie-chicken (*Tympanuchus cupido*) in tall grass prairie in Oklahoma found nest vegetation to differ from random sites within 2 m of the nest. However, Hovick et al. (2014) described the tall grass prairie in their study as heterogeneous and composed of interspersed patches with variable vegetation height and density. In a study in Saskatchewan, Canada, located in a similar mixed grass habitat as ours, Gloutney and Clark (1997) emphasized the importance of making comparisons to non-nest sites contained within the same patch. Gloutney and Clark (1997) additionally included a covariate for distance from the nest to the patch edge in their analysis of nest site selection. Future research investigating nest site selection in relatively homogenous cover, as often found in the northern prairies, should focus efforts on evaluating the dynamics within grassland patches that appear to drive selection.

SUMMARY AND MANAGEMENT IMPLICATIONS

Recent declines in commodity prices have created a renewed interest for private landowners to diversify crops and seek alternative forms of income. Thus, desire to enroll in subsidized conservation practices (CP), such as the Conservation Reserve Program (CRP), has increased in recent years. This increasing trend of private landowners converting idle grassland and unproductive cropland to subsidized CPs has expanded the potential to use treatments, such as RR Alfalfa, in perennial grassland conversion, thereby providing an opportunity to expand use from public to private lands. However, caveats exist which may restrict its potential for both public and private land managers.

Overall, we found habitat quality to vary among individual stands, but found rates of nest density and nest survival in alfalfa comparable to other field types. These results support the notion that alfalfa can serve as productive nesting cover, when the harvest date is delayed. Our findings suggest that a 10 July delayed harvest date was adequate in minimizing nest loss and recommend this date for public land managers. However, as early haying optimizes yield, nutritional quality, and persistence of stands (Warner and Etter 1989), we acknowledge that production goals of private landowners may restrict them from delaying harvest until 10 July. Although a 10 July delayed harvest date appeared to be effective at minimizing nest loss, our findings suggest that a 1 July harvest date could still yield substantial benefits to nesting birds if a later date is not possible. If private landowners could adjust production goals, roundup ready alfalfa could be incorporated in management plans, maximizing available nesting habitat during the conversion process.

We found that the variation in habitat quality of alfalfa stands was driven largely by the planting method implemented by SDGFP land managers in region 2. Alfalfa stands were either established using 2 different methods: planting in previously tilled agricultural fields or directly into untilled grass fields. Tilled fields were planted using conventional methods and were paired with an oats nurse crop during the first year of establishment. This method appeared to yield significantly higher rates of first year growth and establishment than stands seeded in untilled fields. Untilled grass fields were mowed, treated with herbicide, and directly seeded into the ground using a seed drill. The latter method was less intrusive, because it does not require plowing; however, stands established in this method appeared to exhibit comparatively reduced levels of establishment and overall growth. Conventional planting methods in tilled fields appeared to yield higher quality stands, but the use of this technique is more limited due to increased costs and limited use on rocky or steep slopes. Further, we acknowledge the negative and seemingly counterintuitive consequences of unbroken sod being plowed, solely for the purpose of reestablishing perennial grasses. Thus, we recommend the use of conventional planting methods when possible, but only for establishment in previously tilled fields. Despite our findings that suggested reduced growth with direct seeding in untilled fields, our sample sizes were small and geographic differences could have contributed to the range of habitat quality we found throughout our study sites. Therefore, we suggest that when used appropriately, both planting methods can effectively provide the requisite levels of cover and concealment needed for nesting hens.

Managers with the South Dakota Department of Game, Fish, and Parks in region 2 have used both alfalfa and corn and soybeans to prepare seedbeds during perennial grassland conversion. Managers rely on a crop-share relationship with local producers, wherein tenant farmers plant and harvest both alfalfa and crop fields in exchange for the ability to grow and harvest the crops on state land. Alfalfa seed is typically provided by SDGFP, and tenants plant with their equipment and treat with their own herbicide in exchange for harvesting the hay at a significantly reduced rental rate. Conversely, crop fields are planted with the tenant providing the corn or soybean seeds, as well as herbicide, in exchange for harvesting the crop at a standard, comparatively higher rental rate. Both crop types (alfalfa and row crops) require similar levels of herbicide treatment, but seed costs are less for alfalfa because they only need to be planted one time. Given the disparity in rental rates and seed costs for these two planting types, the overall net cost for SDGFP to use alfalfa for grassland conversion is similar or slightly less expensive than row crops. The reduction in seed costs for alfalfa might also be attractive to private land owners considering the use of RR crops for perennial grassland conversion. However, corn and soybeans will yield higher monetary returns than alfalfa, especially so if alfalfa harvest is delayed to protect nesting birds. Despite the cost differences between the two planting types, private land owners might appreciate the increased ecological benefits associated with using alfalfa.

Given the ongoing threatened state of our grasslands, efforts to maximize available nesting cover have become increasingly important. The use of RR alfalfa during perennial grassland conversion has limitations, but overall can function as a valuable tool for land managers interested in contributing to this effort on both public and private lands. Beyond providing nesting cover that would otherwise be non-existent with the use conventional crops, alfalfa can provide important nesting habitat to late and re-nesting hens.

FUTURE RESEARCH

We acknowledge that the strength of our inferences were limited by both sample size and time. The use of alfalfa for perennial grassland conversion is a somewhat novel management practice, and thus far its use has been limited to SDGFP region 2 in eastern South Dakota which limited the availability of study fields. Future research should incorporate a larger sample of fields, planted using both conventional and no-till methods, to more precisely evaluate and quantify the influence of stand age class on nest production. Further, this management practice was first implemented in 2013 with only 2 stands seeded during the first year. We conducted our study during the summers of 2015 and 2016, which restricted our evaluation to 4 age classes with relatively sample sizes for each age class. Future research should incorporate age classes >4 years old to further investigate this relationship, as well as strive to include more fields of each stand age class. Additionally, by the completion of our field work in 2016, none of the fields which involved this management practice in region 2 had been fully prepped or cleared of noxious weeds. Thus, we were unable to evaluate the effectiveness of Roundup Ready© alfalfa for prepping seedbeds prior to reseeding. One concern noted by SDGFP managers was the level of nitrogen that alfalfa would fix compared to soybeans to aid in the establishment and first year growth of seeded perennial grass. Future research should evaluate the reseeding and establishment of perennial grasses in fields prepped using alfalfa.

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Figure 1: Location of study sites located in Brule, Charles Mix, Hand, Hyde, Potter, and Sully Counties in SDGFP region 2 in eastern South Dakota during 2015 and 2016.

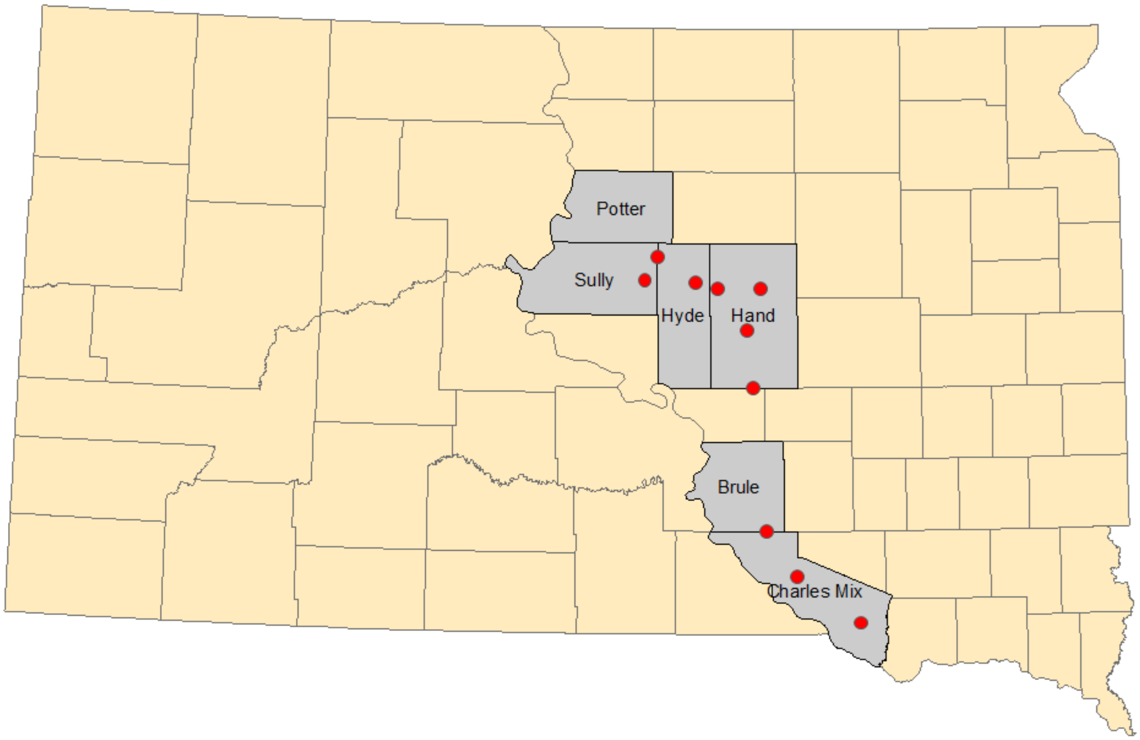


Figure 2. Histogram of vegetation density (VOR) during 2015 and 2016 in eastern South Dakota.

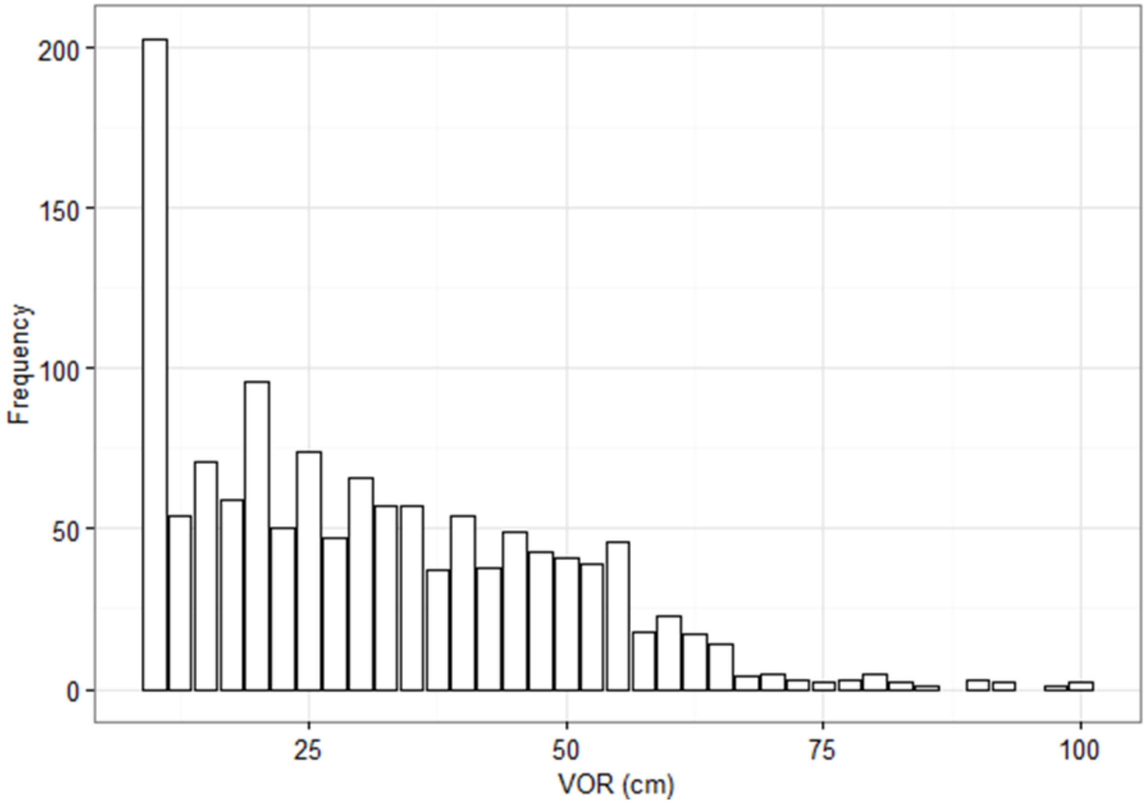


Figure 3. Histogram of vegetation litter depth during 2015 and 2016 in eastern South Dakota.

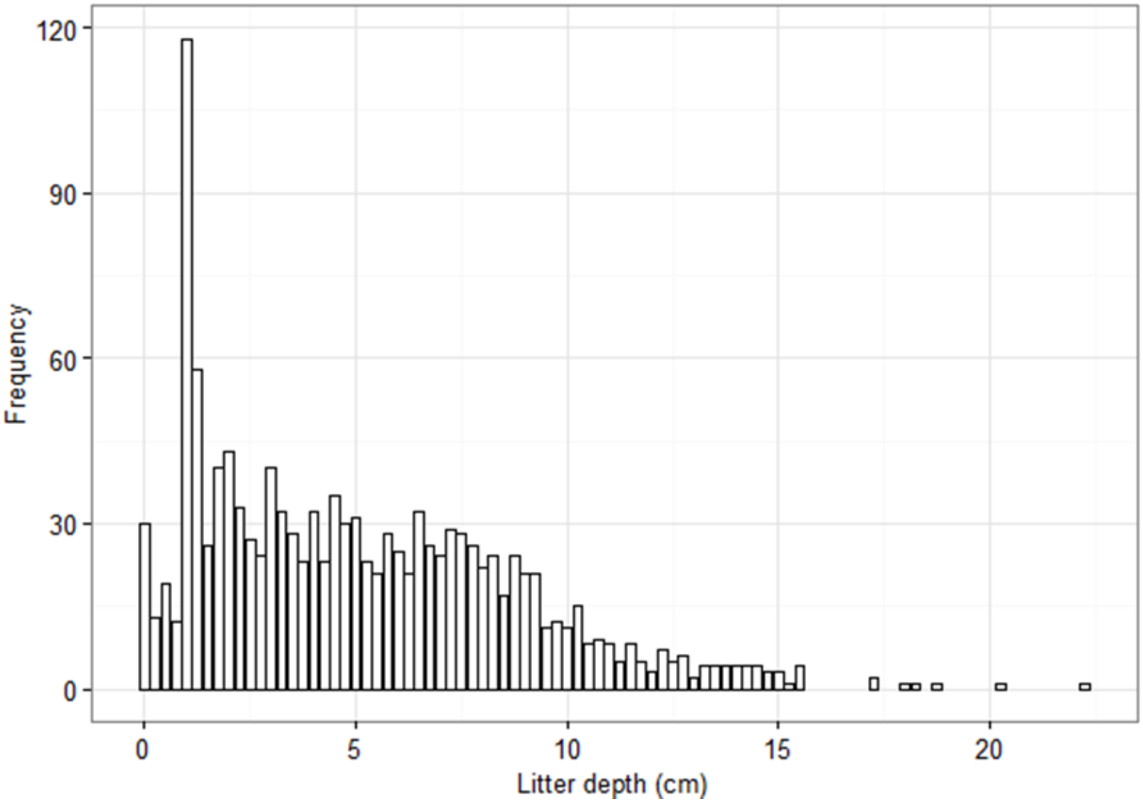


Figure 4: Least-squared means (±95% CI) of square root-transformed vegetation density (VOR) among field types during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test among each individual field type pair.

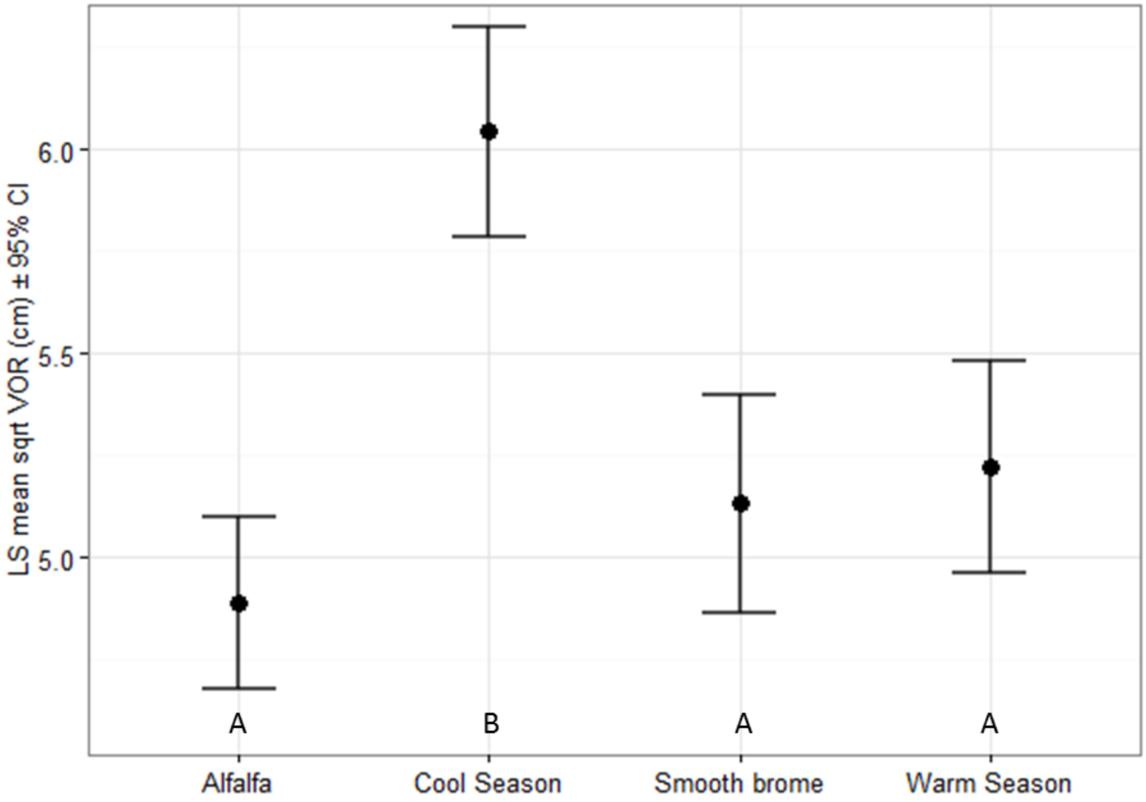


Figure 5: Least-squared means (±95% CI) of vegetation height among field types during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test among each individual field type pair.

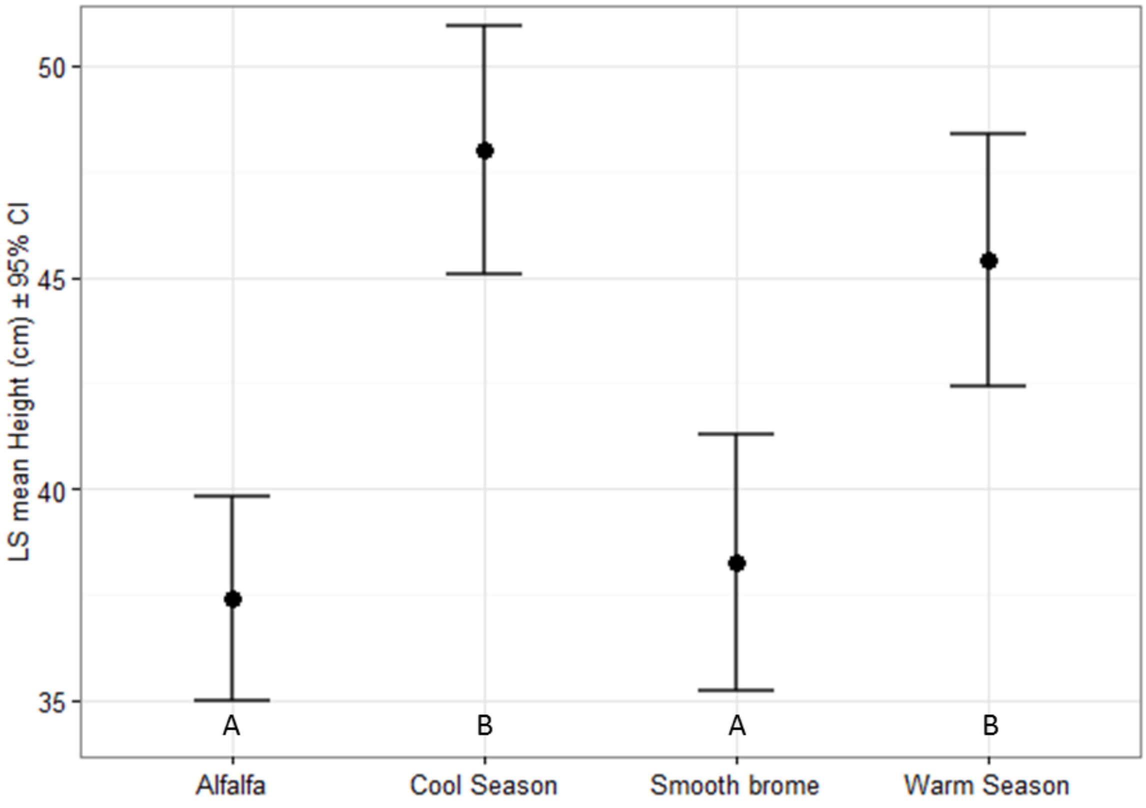


Figure 6: Least-squared means (±95% CI) of square root-transformed litter depth among field types during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences (*P* < 0.05) in a post hoc multiple comparisons test among each individual field type pair.

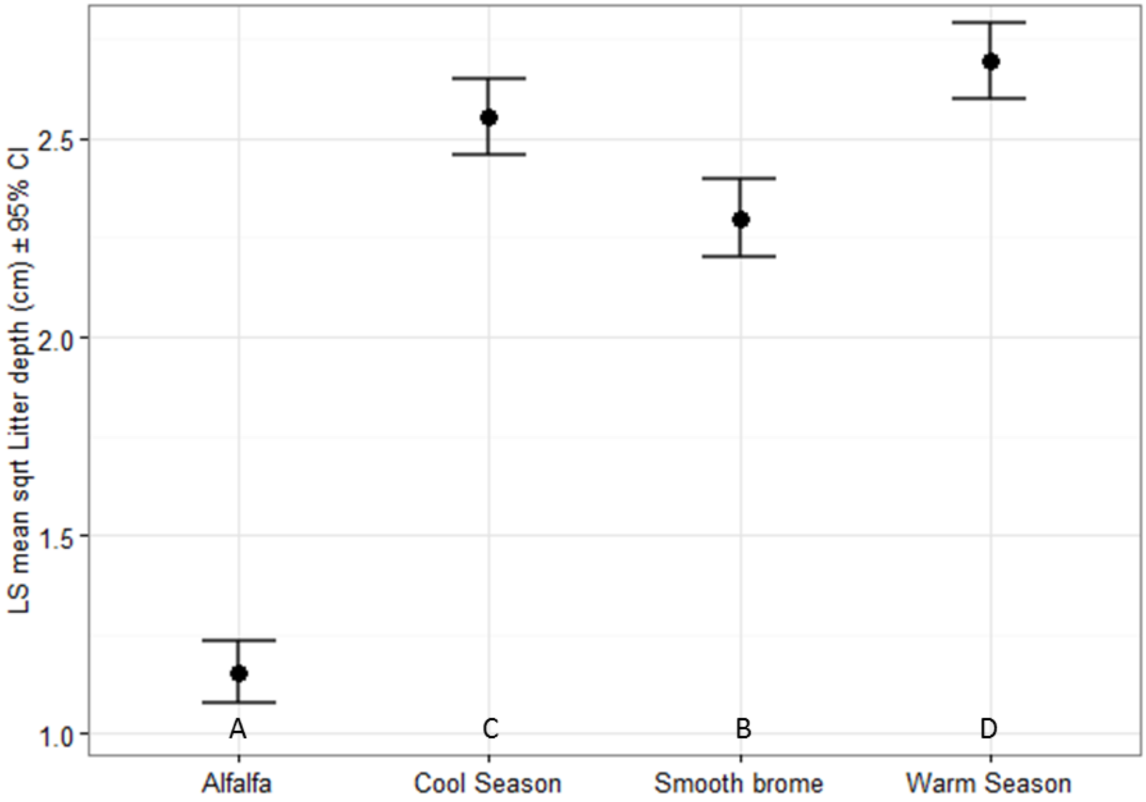


Figure 7: Least-squared means (±95% CI) of square root-transformed vegetation density (VOR) among stand age classes of alfalfa during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test among each individual age class pair.

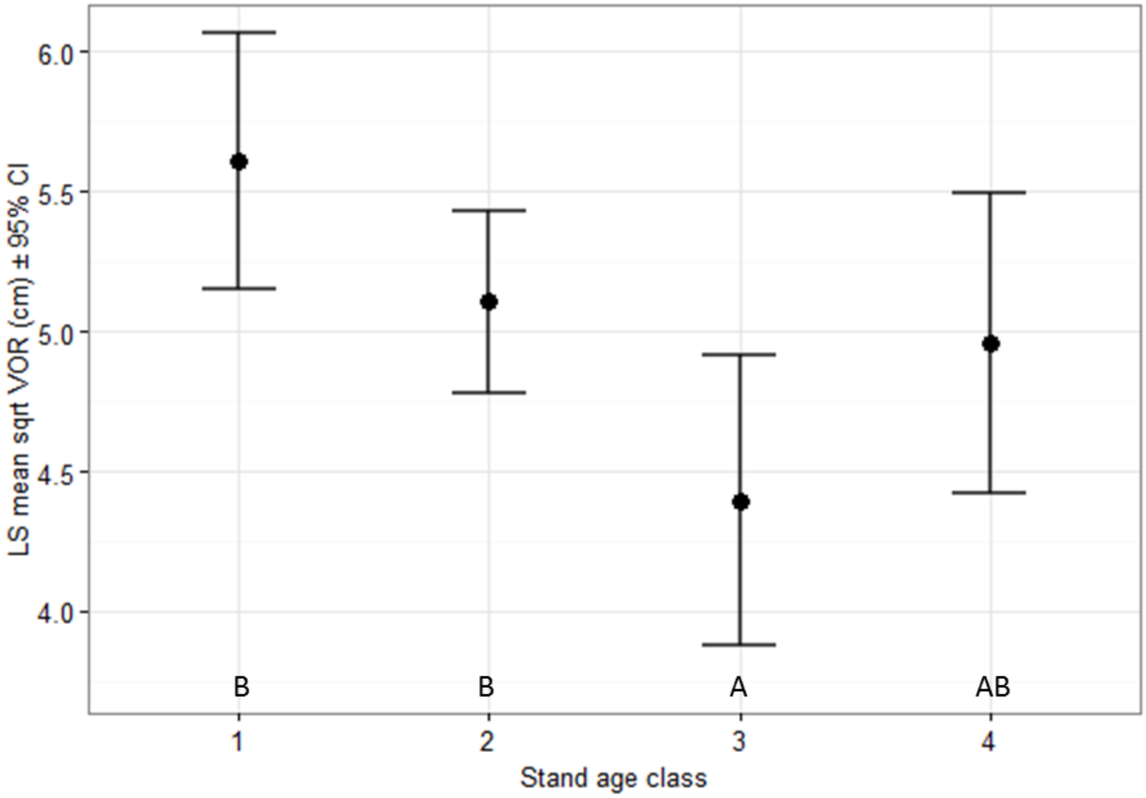


Figure 8: Least-squared means (±95% CI) of vegetation height among stand age classes of alfalfa during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences (*P* < 0.05) in a post hoc multiple comparisons test among each individual age class pair.

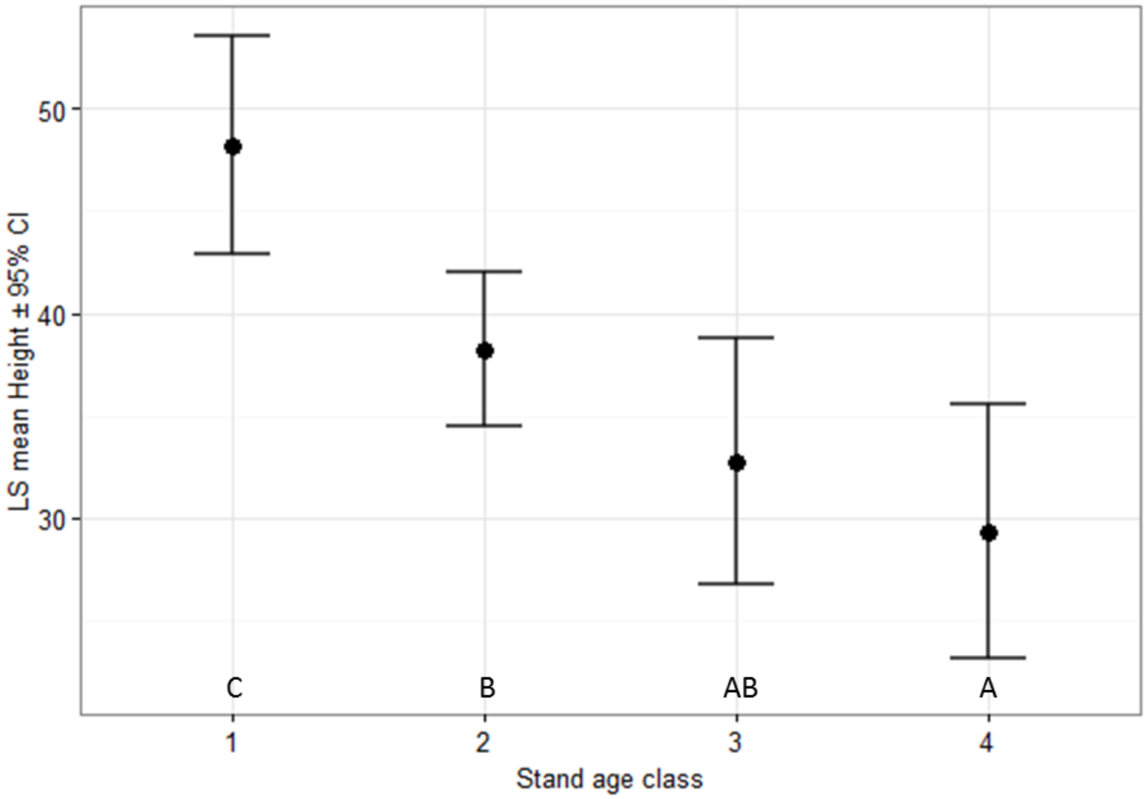


Figure 9: Least-squared means (±95% CI) of square root-transformed litter depth among stand age classes of alfalfa during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences (*P* < 0.05) in a post hoc multiple comparisons test among each individual age class pair.

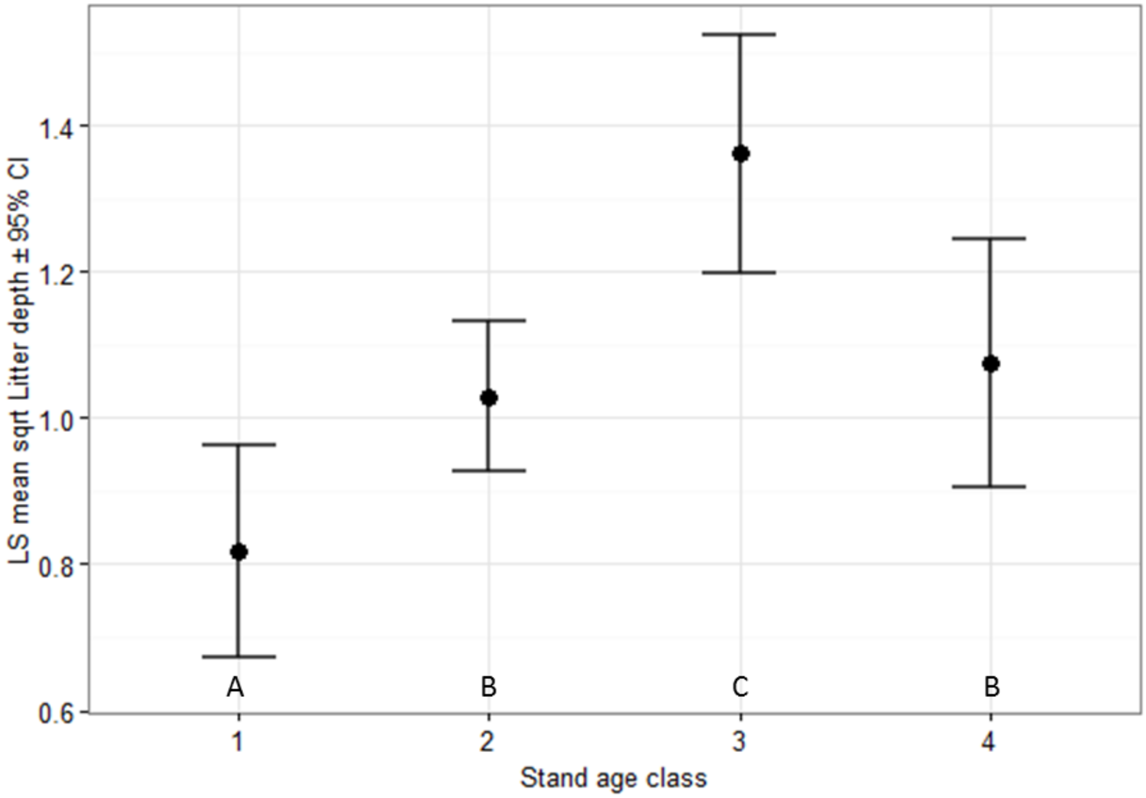


Figure 10: Relationship between daily survival rate (DSR) and vegetation density (VOR) at ducks nests among field types during 2015–2016 in eastern South Dakota.

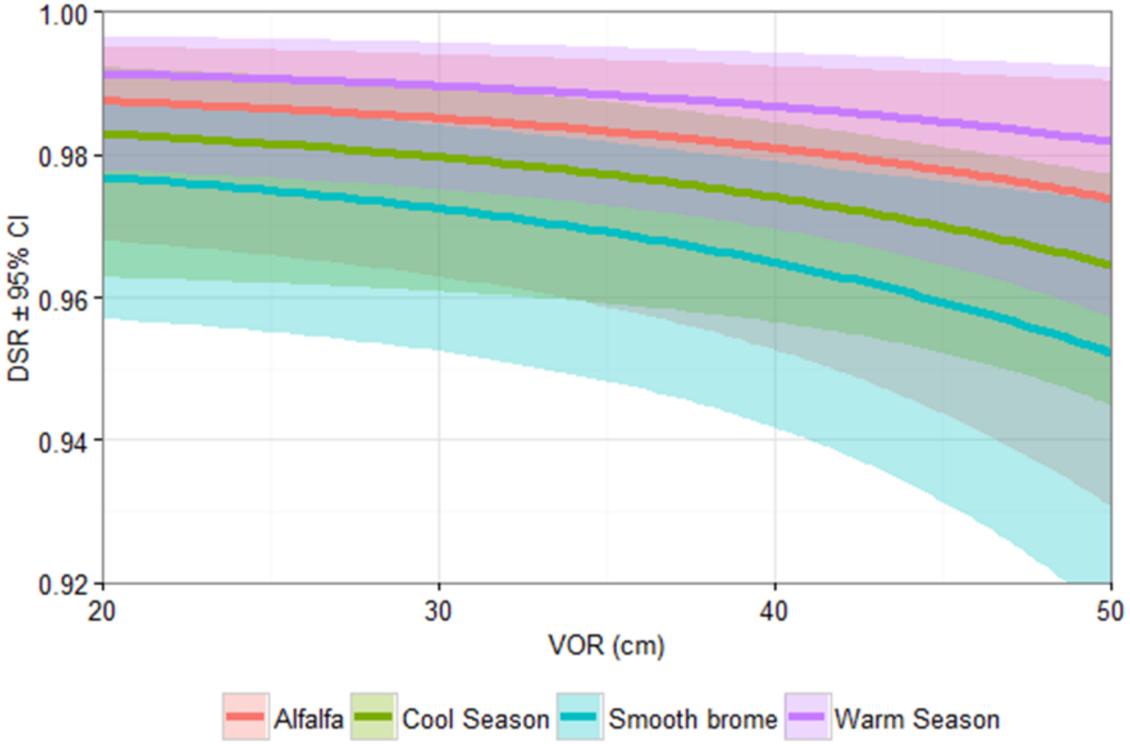


Figure 11: Relationship between daily survival rate (DSR) and percent composition of litter at ducks nests among field types during 2015–2016 in eastern South Dakota.

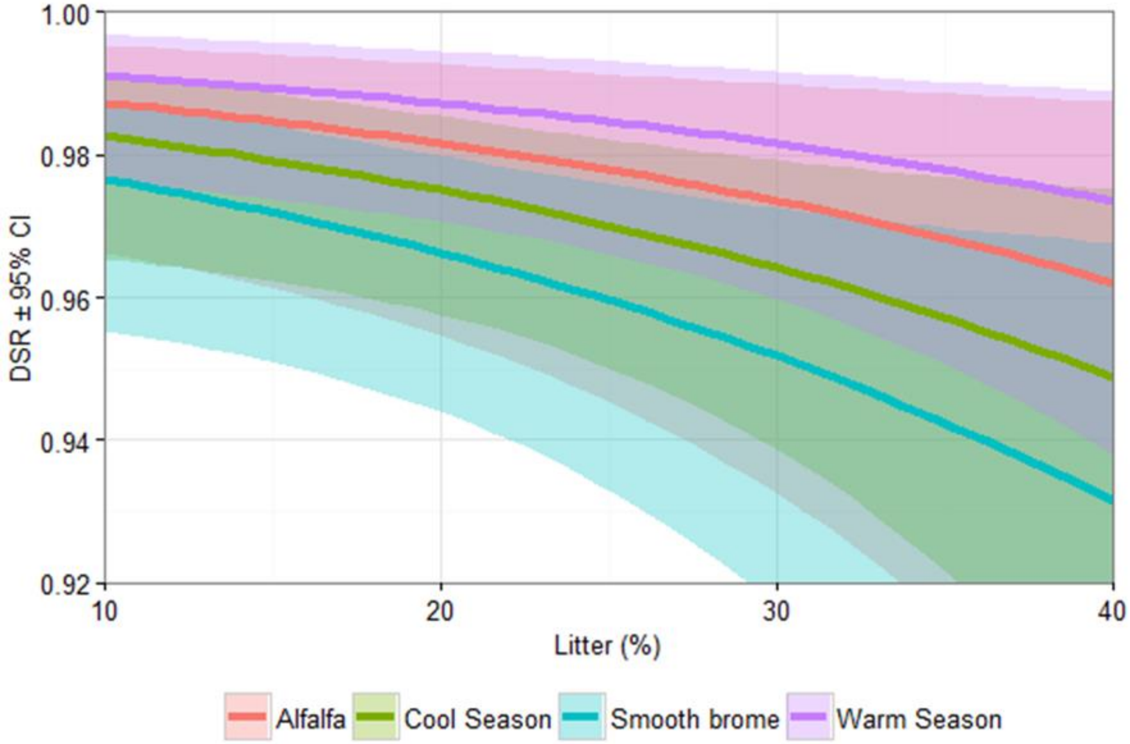


Figure 12: Relationship between daily survival rate (DSR) and nest density (nests/ha) at pheasant nests during 2015–2016 in eastern South Dakota.

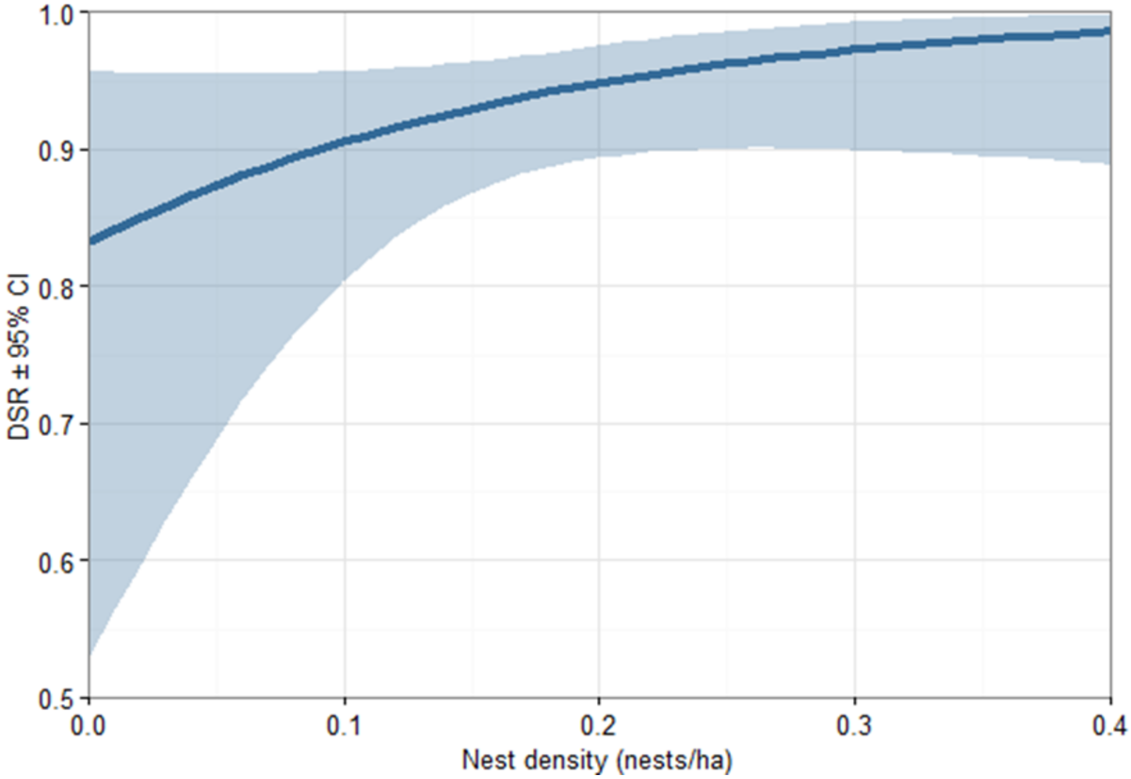
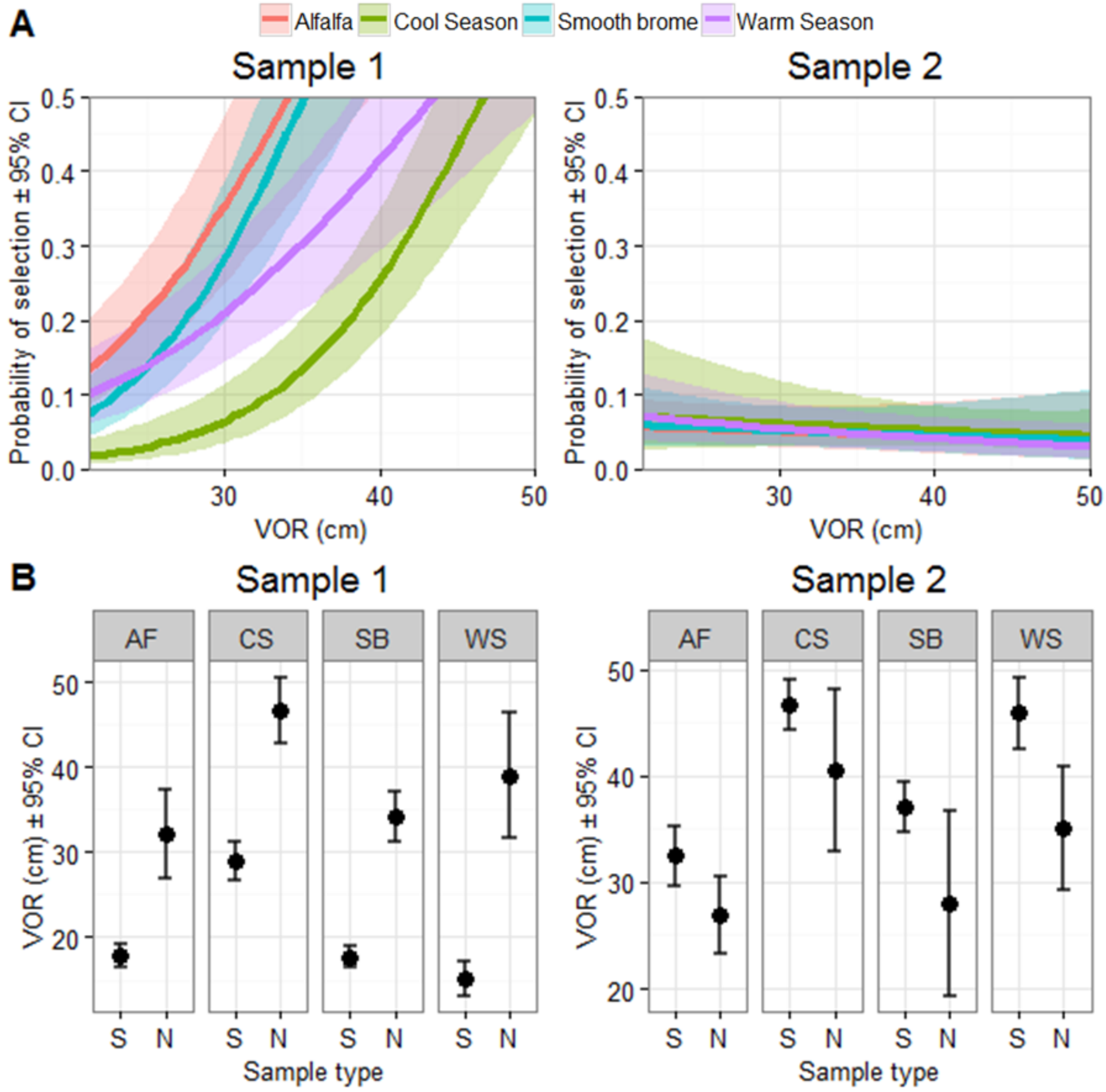
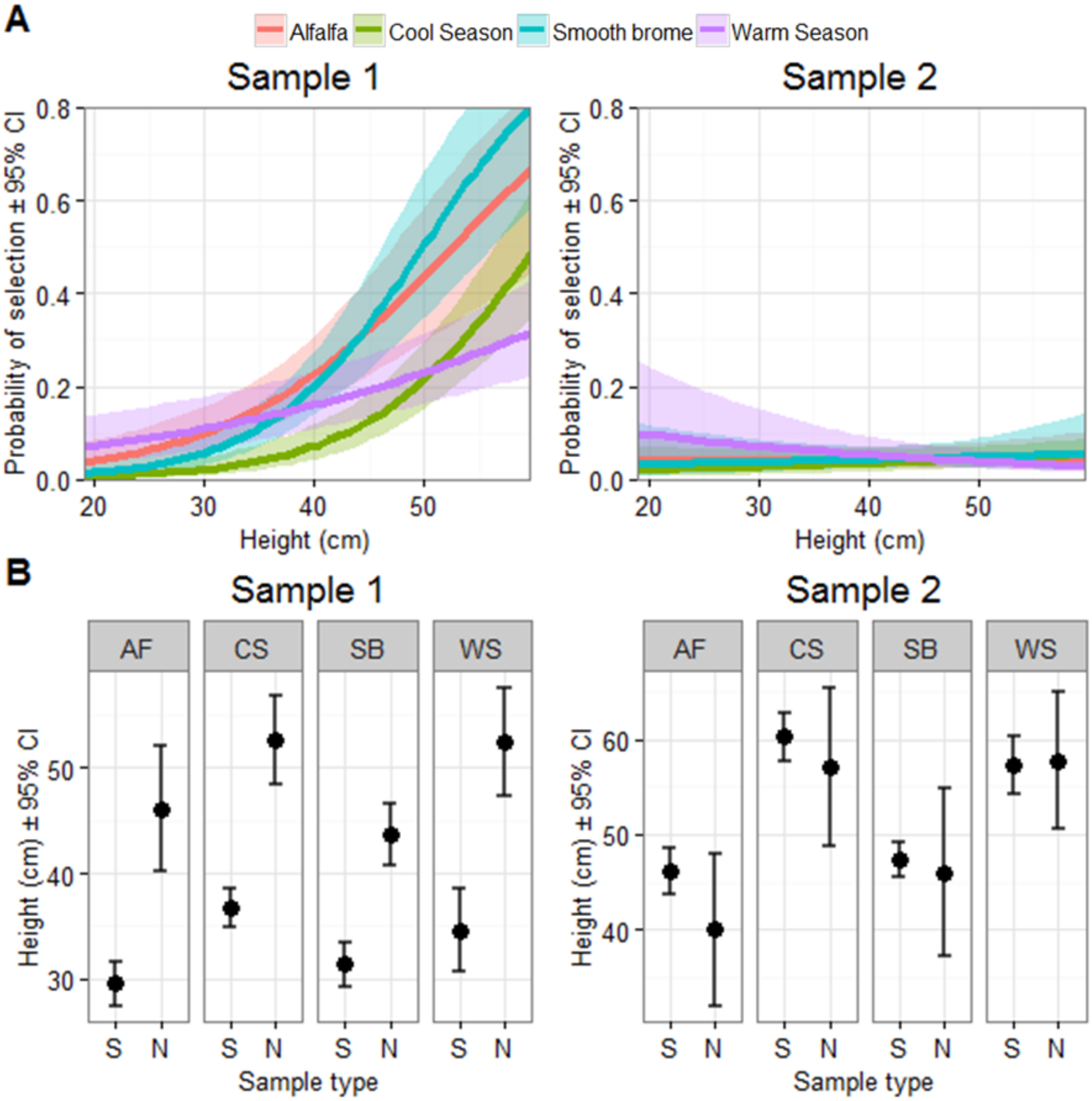


Figure 13: (A) Predicted probability (±95% CI) of nest site selection in relation to stand and nest level VOR from early (Sample 1) and late (Sample 2) samples among field types during 2015–2016 in eastern South Dakota. (B) Means (±95% CI) of VOR from stand (S) and nest (N) level sample points from early (Sample 1) and late (Sample 2) samples among field types during 2015 and 2016 in eastern South Dakota.



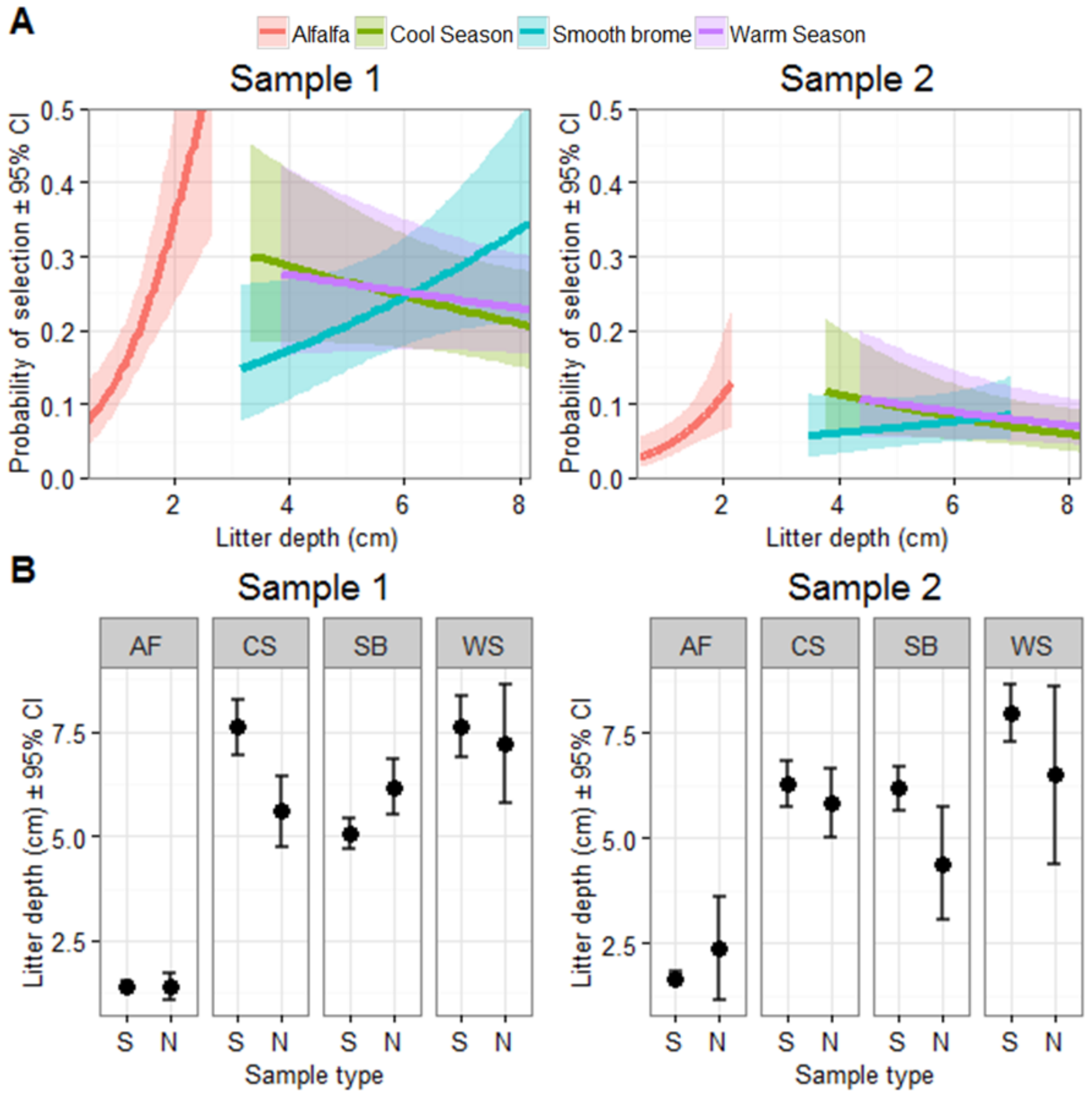
AF = Alfalfa
CS = Cool season
SB = Smooth brome
WS = Warm season
S = Stand
N = Nest

Figure 14: (A) Predicted probability (±95% CI) of nest site selection in relation to stand and nest level vegetation height from early (Sample 1) and late (Sample 2) samples among field types during 2015–2016 in eastern South Dakota. (B) Means (±95% CI) of vegetation height from stand (S) and nest (N) level sample points from early (Sample 1) and late (Sample 2) samples among field types during 2015 and 2016 in eastern South Dakota.



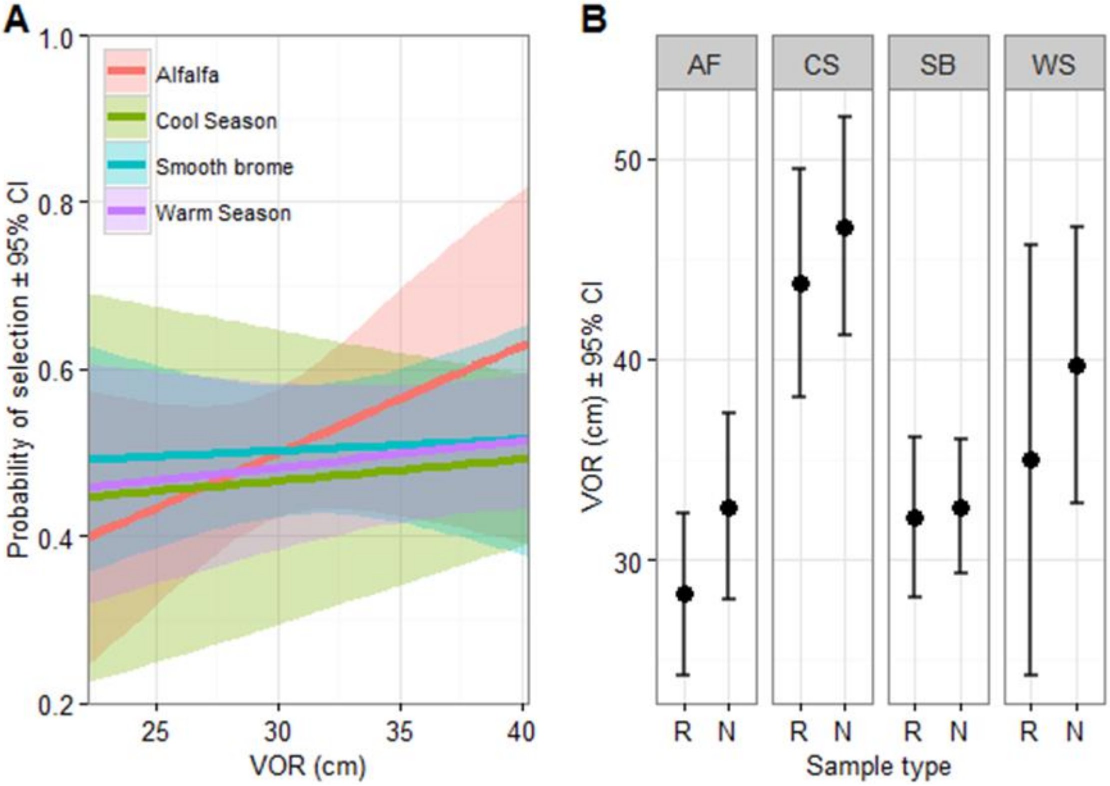
AF = Alfalfa
CS = Cool season
SB = Smooth brome
WS = Warm season
S = Stand
N = Nest

Figure 15: (A) Predicted probability (±95% CI) of nest site selection in relation to stand and nest level litter depth from early (Sample 1) and late (Sample 2) samples among field types during 2015–2016 in eastern South Dakota. (B) Means (±95% CI) of litter depth from stand (S) and nest (N) level sample points from early (Sample 1) and late (Sample 2) samples among field types during 2015 and 2016 in eastern South Dakota.



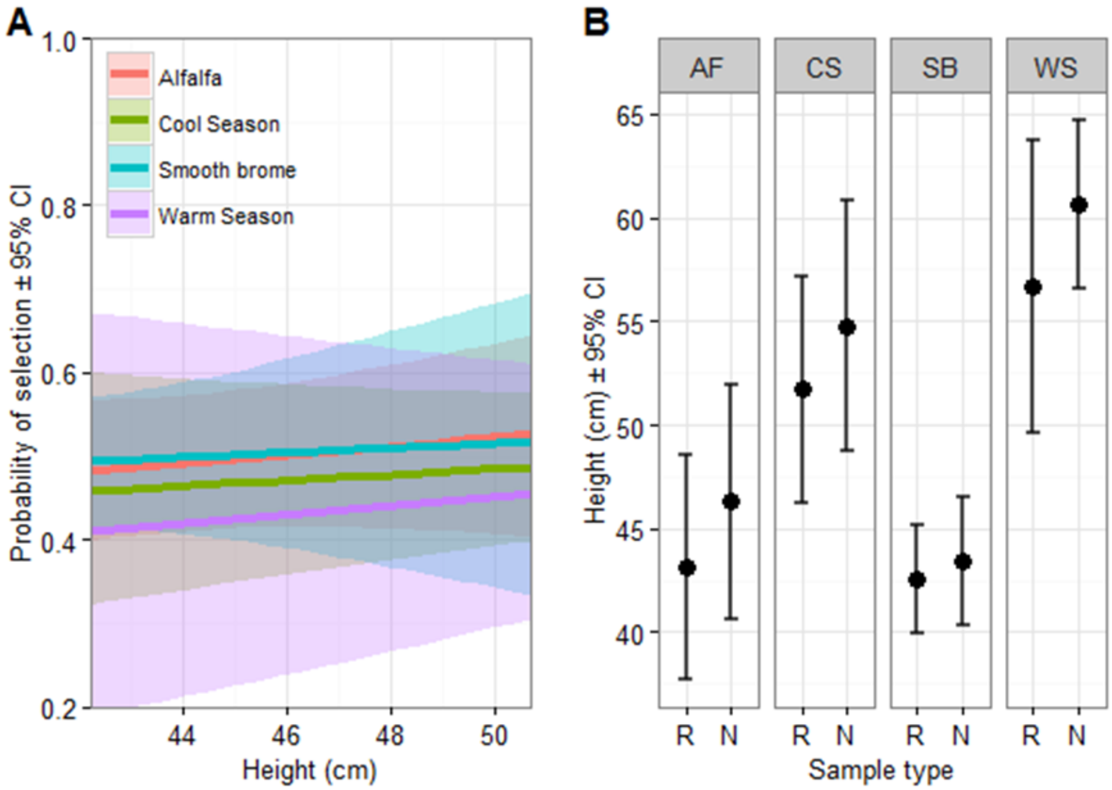
AF = Alfalfa
CS = Cool season
SB = Smooth brome
WS = Warm season
S = Stand
N = Nest

Figure 16: (A) Predicted probability (±95% CI) of nest site selection in relation to paired-random and nest level VOR among field types during 2015–2016 in eastern South Dakota. (B) Means (±95% CI) of VOR from paired-random (R) and nest (N) level sample points samples among field types during 2015 and 2016 in eastern South Dakota.



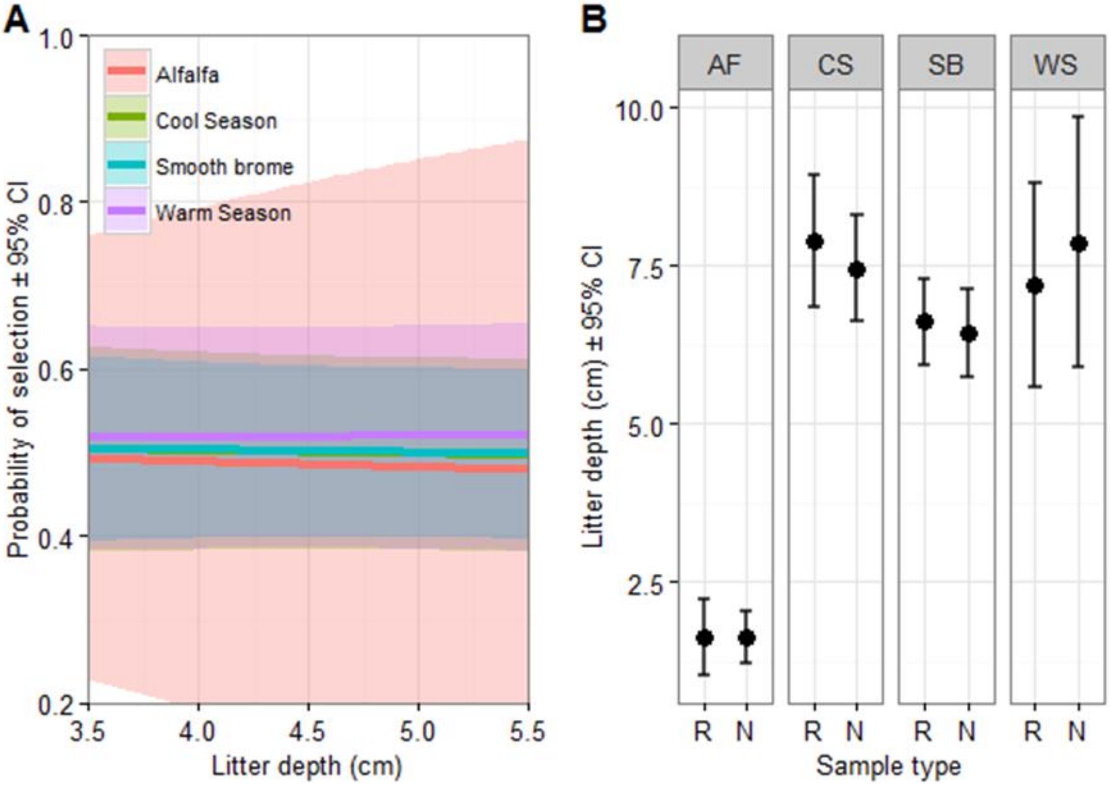
AF = Alfalfa
CS = Cool season
SB = Smooth brome
WS = Warm season
R = Paired-random
N = Nest

Figure 17: (A) Predicted probability (±95% CI) of nest site selection in relation to paired-random and nest level vegetation height among field types during 2015–2016 in eastern South Dakota. (B) Means (±95% CI) of vegetation height from paired-random (R) and nest (N) level sample points samples among field types during 2015 and 2016 in eastern South Dakota.



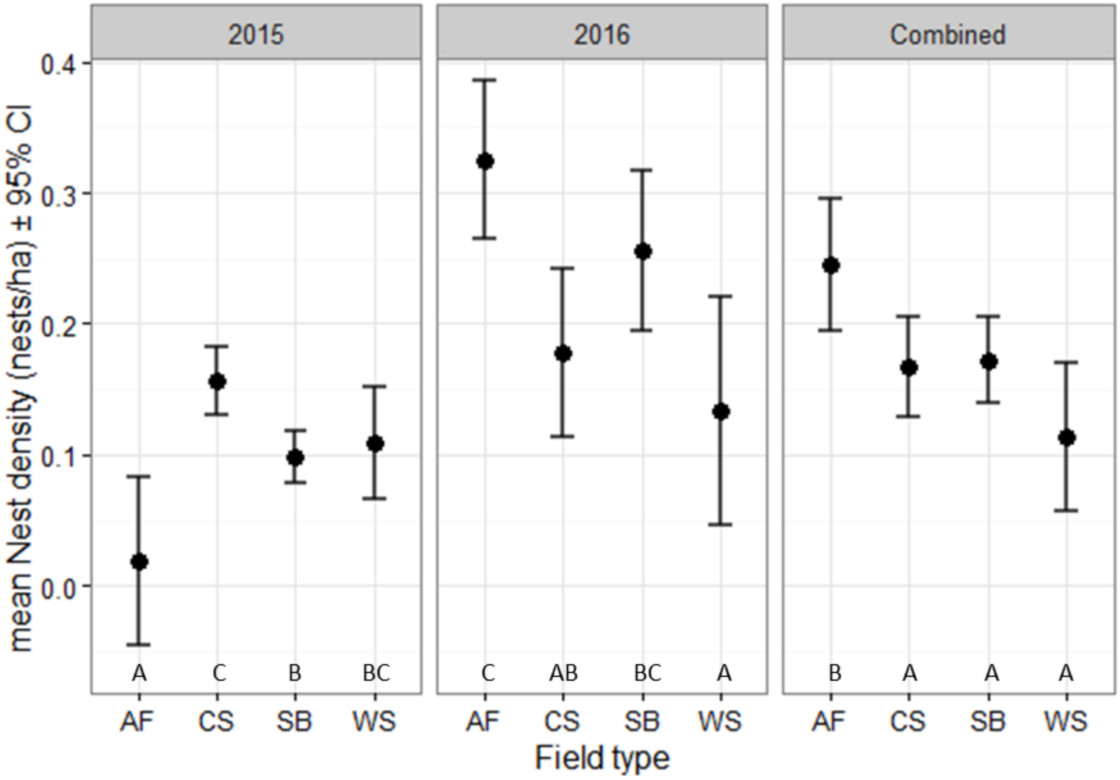
AF = Alfalfa
CS = Cool season
SB = Smooth brome
WS = Warm season
R = Paired-random
N = Nest

Figure 18**:** (A) Predicted probability (±95% CI) of nest site selection in relation to paired-random and nest level litter depth among field types during 2015–2016 in eastern South Dakota. (B) Means (±95% CI) of litter depth from paired-random (R) and nest (N) level sample points samples among field types during 2015 and 2016 in eastern South Dakota.



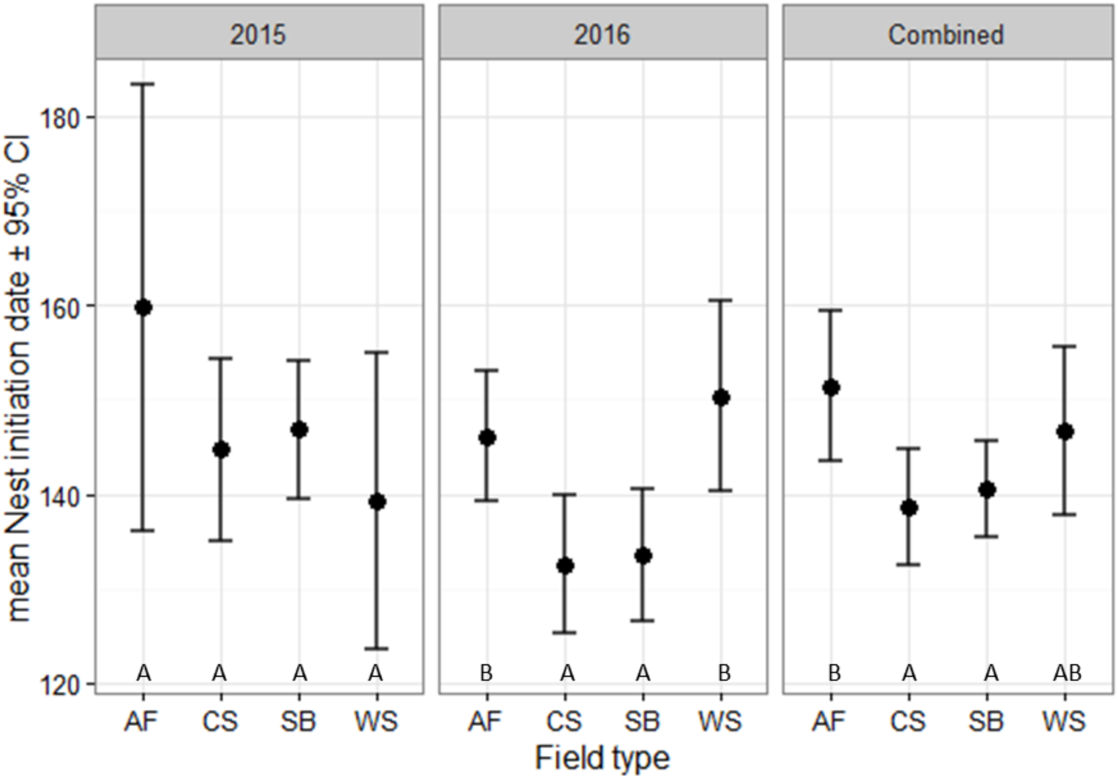
AF = Alfalfa
CS = Cool season
SB = Smooth brome
WS = Warm season
R = Paired-random
N = Nest

Figure 19: Mean (±95% CI) nest density (successful nests/ha) for ducks among field types during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test among each individual field type pair.



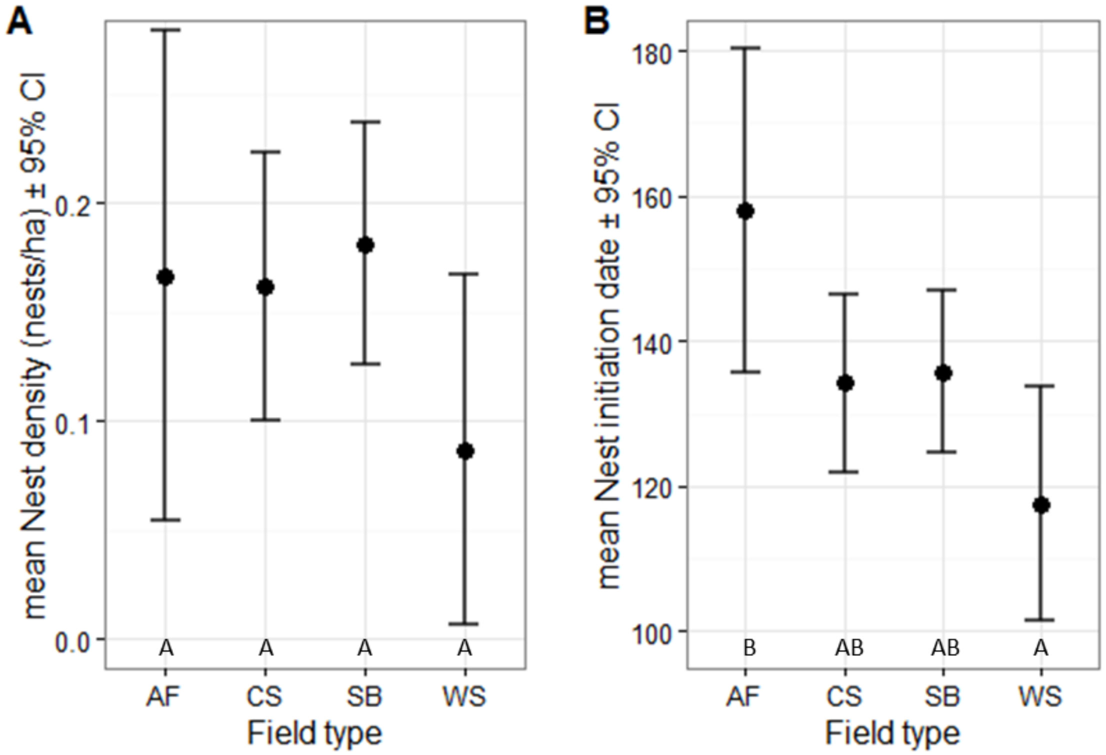
AF = Alfalfa
CS = Cool season
SB = Smooth brome
WS = Warm season

Figure 20: Mean (±95% CI) nest initiation dates for ducks among field types during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test among each individual field type pair.



AF = Alfalfa
CS = Cool season
SB = Smooth brome
WS = Warm season

Figure 21: (A) Mean (±95% CI) nest density (successful nests/ha) for pheasants among field types during 2015 and 2016 in eastern South Dakota. (B) Median (±95% CI) nest initiation dates for pheasants among field types during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences (*P* < 0.05) in a post hoc multiple comparisons test among each individual age class pair.



AF = Alfalfa
CS = Cool season
SB = Smooth brome
WS = Warm season

Figure 22: (A) Mean (±95% CI) nest density (successful nests/ha) for all combined species among alfalfa stand age classes during 2015 and 2016 in eastern South Dakota. (B) Mean (±95% CI) nest initiation dates among alfalfa stand age classes during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test among each individual age class pair.

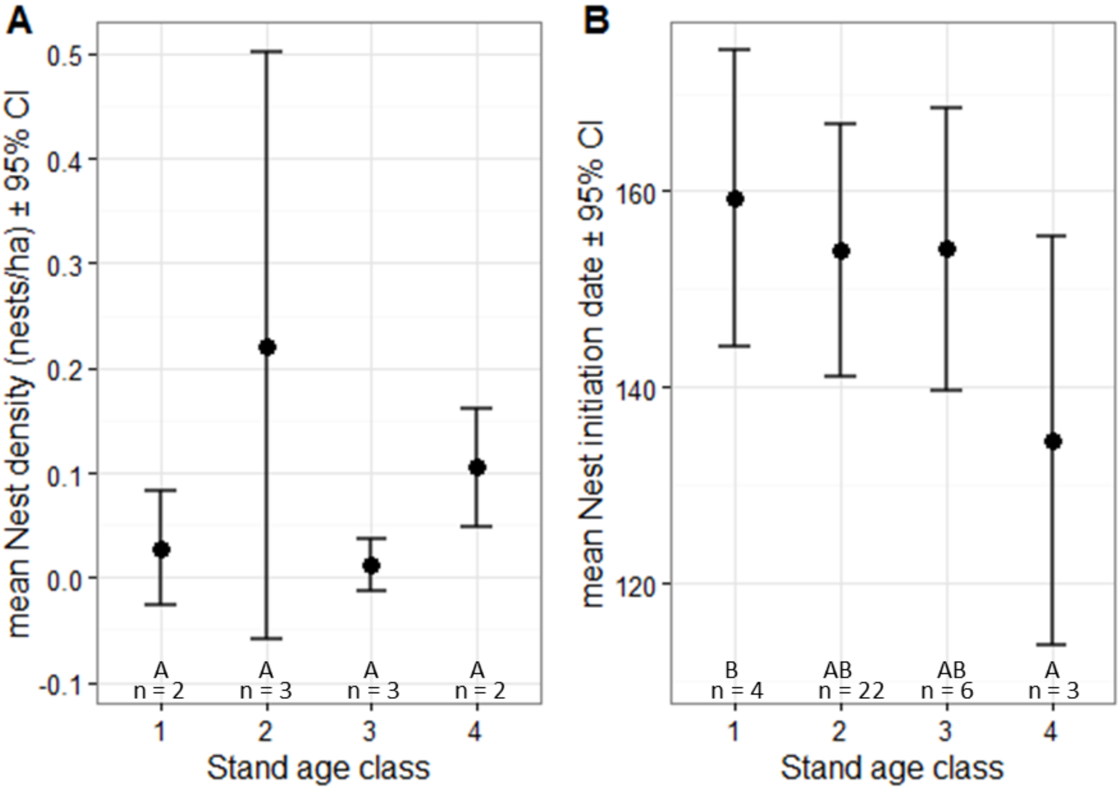


Figure 23: Projected destroyed nests by haying of alfalfa fields given a range of hypothetical harvest dates across 2015 and 2016 in eastern South Dakota.

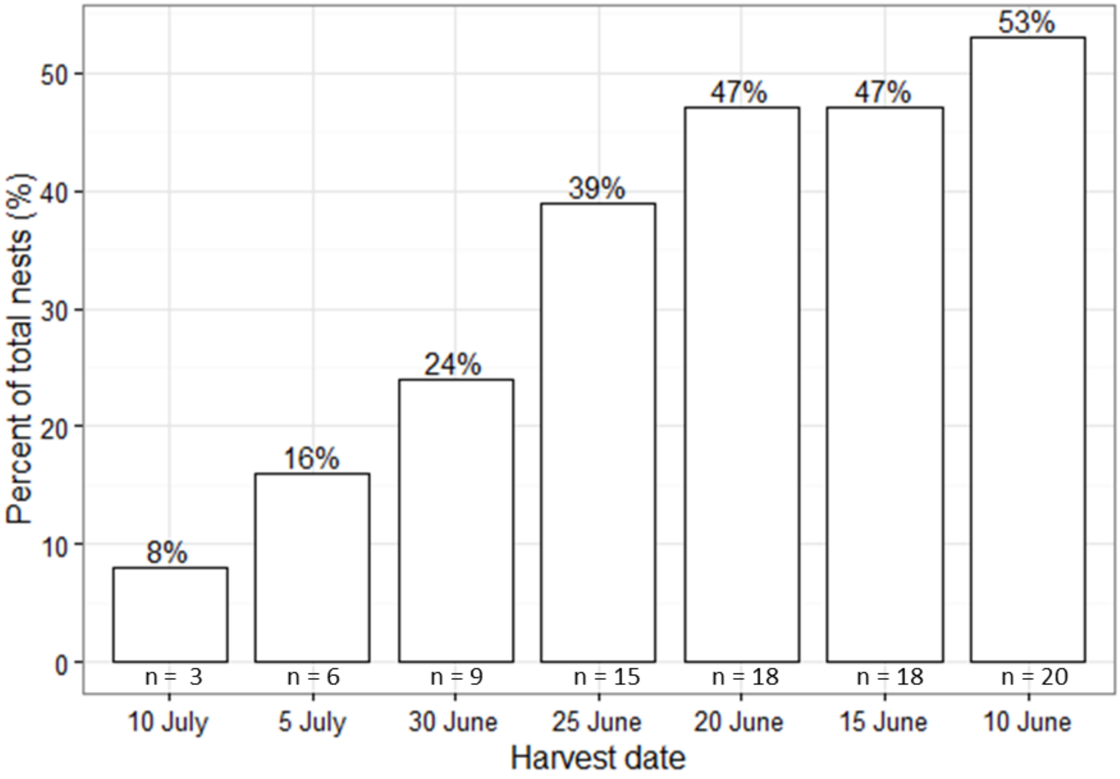


Figure 24: (A) Mean (±95% CI) nest density among alfalfa study fields. **(**B) Mean (±95% CI) VOR in alfalfa study fields during 2015 and 2016. **(**C) Mean (±95% CI) vegetation height in alfalfa study fields during 2015 and 2016. **(**D) Mean (±95% CI) VOR in alfalfa study field HBA51 and other field types during 2015 and 2016. **(**E) Mean (±95% CI) vegetation height in alfalfa study field HBA51 and other field types during 2015 and 2016. Red boxes highlight findings for alfalfa field (HBA51), seeded in 2015 on Holoubek GPA, in Brule County, South Dakota.

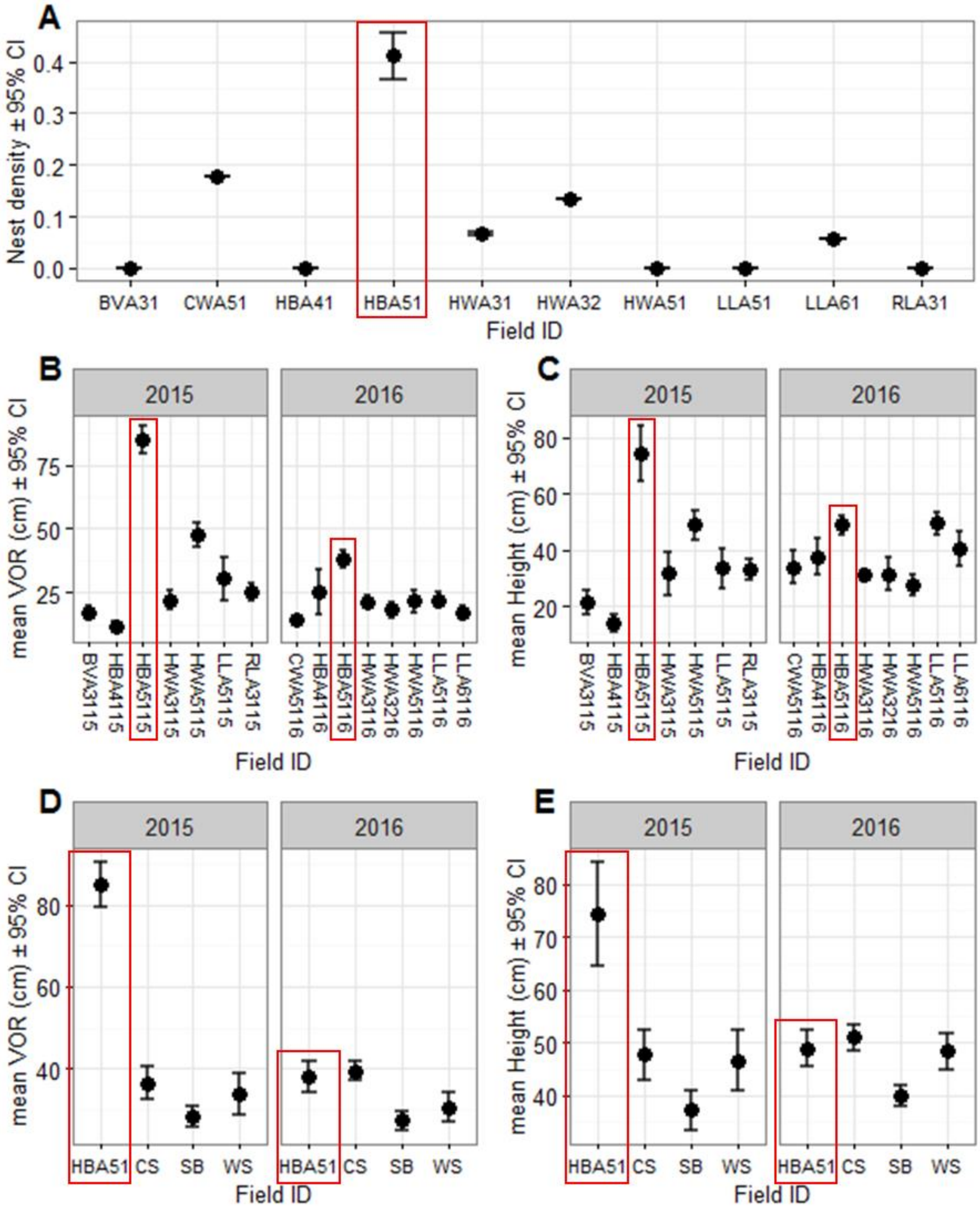


Table 1: List of study sites by year including GPA, field type, field number and area of field.

Year	GPA	Field type	Field number	Area (ha)
2015	Bovee	Alfalfa 2013	1	2.7
		Cool season	1	4.1
		Warm season	1	7.1
	Cottonwood	Smooth brome	1	19.9
		Warm season	1	30
	Holoubek	Alfalfa 2014	1	4
		Alfalfa 2015	1	20.5
		Cool season	1	4
		Smooth brome	1	7.7
		Warm season	1	7.2
	Hawkins	Alfalfa 2013	1	26.1
		Alfalfa 2015	1	14.5
		Cool season	1	17.7
		Warm season	1	20.5
	Lechtenburg	Cool season	1	10.6
		Smooth brome	1	18.1
	Lake Louise	Alfalfa 2015	1	25.1
		Cool season	1	47.6
		Smooth brome	1	53.9
	Pottsdam	Cool season	1	16.5
		Smooth brome	1	10.1
	Rice Lake	Smooth brome	1	47.4
	Red Lake	Alfalfa 2013	1	4.9
		Cool season	1	7.2
		Warm season	1	8.9
	Rezac	Smooth brome	1	28
2016	Cottonwood	Alfalfa 2015	1	17
		Smooth brome	1	19.9
		Warm season	1	30
	Holoubek	Alfalfa 2014	1	4
		Alfalfa 2015	1	20.5
		Cool season	1	4
		Cool season	2	3.4
		Smooth brome	1	7.7
		Smooth brome	2	3.3
		Warm season	1	7.2
		Warm season	2	7.7

Table 1 continued: List of study sites by year including GPA, field type, field number and area of field.

Year	GPA	Field type	Field number	Area (ha)
2016	Hawkins	Alfalfa 2013	1	26.2
		Alfalfa 2013	2	7.5
		Alfalfa 2015	1	14.5
		Cool season	1	17.8
		Warm season	1	20.5
		Warm season	2	9.8
	Lake Louise	Alfalfa 2015	1	25.1
		Alfalfa 2016	1	17.9
		Cool season	1	47.7
		Smooth brome	1	53.9

Table 2: The number of nests found by species in all fields in 2015 and 2016 in eastern South Dakota.

Species	2015	2016
Blue-winged teal (*Anas discors*)	8	35
Gadwall (*Anas strepera*)	32	27
Mallard (*Anas platyrhynchos*)	42	27
Northern pintail (*Anas acuta*)	1	0
Northern shoveler (*Anas clypeata*)	0	4
Ring-necked pheasant (*Phasianus colchicus*)	50	15
TOTALS	133	108

Table 3: The number of nests found by field type in 2015 and 2016 in eastern South Dakota.

Field type	2015	2016
Alfalfa	8	28
Cool season	46	27
Smooth brome	57	37
Warm season	22	16
TOTALS	133	108

Table 4: The number of nests found by species and field type in 2015 and 2016 in eastern South Dakota. Species included blue-winged teal (BWTE), gadwall (GADW), mallard (MALL), northern pintail (NOPI), northern shoveler (NSHO) and ring-necked pheasant (RNEP).

Field type	Species	2015	2016	TOTALS
Alfalfa	BWTE	0	8	8
	GADW	4	12	16
	MALL	0	7	7
	RNEP	4	1	5
	All species	8	28	36
Cool season	BWTE	1	7	8
	GADW	7	7	14
	MALL	18	10	28
	RNEP	20	3	23
	All species	46	27	73
Smooth brome	BWTE	4	13	17
	GADW	19	3	22
	MALL	20	9	29
	NOPI	1	0	1
	NSHO	0	3	3
	RNEP	13	9	22
	All species	57	37	94
Warm season	BWTE	3	7	10
	GADW	2	5	7
	MALL	4	1	5
	NSHO	0	1	1
	RNEP	13	2	15
	All species	22	16	38
TOTALS		133	108	241

Table 5. Model selection results including delta AIC_c (Δ AIC_c), AIC_c weights (w_i) and number of parameters (K), used to evaluate factors affecting nest success of duck nests in 2015 and 2016 in eastern South Dakota. Covariates are field type (Field), incubation status of nest plus the number of eggs at visit (Age2), number of eggs at visit (Eggs), number of successful nests per ha for each field and study year (Density), quadratic term for vegetation density (VOR^2), year, proportion of bare ground around nest (Bare), proportion of litter around nest (Litter), proportion of forbs around nest (Forb), proportion of grass around nest (Grass) and area of field (Ha).

Model	AIC_c	ΔAIC_c	w_i	K
Field+Eggs+Den+VOR^2+Bare+Litter+Forb+Grass	286.36	0.00	0.08	11
Field+Eggs+Den+VOR^2+Litter	286.50	0.15	0.08	8
Field+Eggs+Den+VOR^2+Litter+Age	286.79	0.44	0.07	9
Field+Eggs+Den+VOR^2+Litter×Year	287.06	0.71	0.06	10
Field+Eggs+Den+VOR^2+Litter+Year	287.10	0.74	0.06	9
Field+Eggs+Den+VOR^2+Bare+Litter+Forb+Grass+Age	287.22	0.86	0.05	12
Field+Eggs+Den+VOR^2+Litter+Ha	287.32	0.97	0.05	9
Field+Eggs+Den+VOR^2+Litter+Year	287.37	1.01	0.05	10
Field+Eggs+Den+VOR^2+Bare+Litter+Forb+Grass+Year	287.74	1.39	0.04	12
Field+Eggs+Den+VOR^2+Litter×Year+Age	287.87	1.52	0.04	11
Field+Eggs+Den+VOR^2+Litter+Ha+Year	287.88	1.53	0.04	10
Field+Eggs+Den+VOR^2+Bare+Litter	287.91	1.55	0.04	9
Field+Eggs+Den+VOR^2+Bare+Litter+Age	288.21	1.85	0.03	10
Field+Eggs+Den+VOR^2+Bare+Litter+Forb	288.22	1.87	0.03	10
Field+Eggs+Den+VOR^2+Litter+Ha+Age	288.24	1.88	0.03	10
Null	314.74	28.39	0.00	1

Table 6. Estimated rates of duck nest survival (%) by field type and year during May and July 2015 through 2016 in eastern South Dakota.

Field type	Year	Survival %	SE	95% LCL	95% UCL
Alfalfa	Combined	51.7	1.4	49.0	54.5
	2015	36.2	0.2	35.8	36.7
	2016	48.5	0.3	48.0	49.1
Cool Season	Combined	40.7	0.5	39.6	41.8
	2015	32.7	0.2	32.2	33.1
	2016	45.1	0.3	44.5	45.7
Smooth brome	Combined	29.5	1.3	26.9	32.1
	2015	20.5	0.8	18.9	22.1
	2016	32.3	1.4	29.5	35.1
Warm season	Combined	63.3	5.0	53.6	73.1
	2015	58.8	6.5	46.2	71.5
	2016	68.6	6.3	56.3	80.9

Table 7. Model selection results including delta AIC$_c$ (Δ AIC$_c$), AIC$_c$ weights (w_i) and number of parameters (K), used to evaluate factors affecting nest success of pheasant nests in 2015 and 2016 in eastern South Dakota. Covariates are incubation status of nest plus the number of eggs (Age2), nest density (Den), year, percent litter (Litter) and vegetation density (VOR).

Model	AIC$_c$	Δ AIC$_c$	w_i	K
Age2+Den×Year	55.33	0.00	0.07	5
Age2+Den×Year+Litter	56.48	1.16	0.04	6
Age2^{x}Year+Den×Year	56.55	1.22	0.04	6
Age2+Den×Year+VOR	56.80	1.47	0.03	6
Null	69.26	13.93	0.00	1

Table 8. Estimated rates of pheasant nest survival (%) by year during May and July 2015 through 2016 in eastern South Dakota.

Year	Survival (%)	SE	95% LCL	95% UCL
Combined	10.0	0.0	10.6	10.6
2015	0.6	0.0	0.6	0.6
2016	8.6	0.4	7.9	9.3

Table 9. Model selection results including delta AIC$_c$ (Δ AIC$_c$), AIC$_c$ weights (w_i) and number of parameters (K), used to evaluate factors affecting nest success in alfalfa stand age classes in 2015 and 2016 in eastern South Dakota. Covariates are stand age class (AgeClass), eggs and nest initiation date (Initiation).

Model	AIC$_c$	Δ AIC$_c$	w_i	K
AgeClass+Eggs+Initiation	84.35	0.00	0.62	6
Null	97.21	12.86	0.00	1

Table 10. Estimated rates nest survival (%) among alfalfa stand age classes during May and July 2015 through 2016 in eastern South Dakota.

Age class	Survival (%)	SE	95% LCL	95% UCL
1	45.4	1.5	42.5	48.3
2	46.8	1.4	44.1	49.4
3	44.6	1.6	41.6	47.7
4	100.0	20.4	60.0	140.0

Table 11. Model summaries used to evaluate nest site selection, comparing nest and stand level vegetation characteristics for each field type in 2015 and 2016 in eastern South Dakota. Covariates are vegetation density (VOR), vegetation height (Height), litter depth (Litter) and field type (Field CS, Field SB, Field WS).

Model	Variable	*β*	SE	95% LCL	95% UCL	*P*
VOR+VOR×Field	Intercept	-2.71	0.94	-4.55	-0.87	0.004
	VOR	0.91	0.23	0.46	1.35	≤ 0.001
	VOR×FieldCS	0.35	0.30	-0.24	0.93	0.249
	VOR×FieldSB	0.53	0.32	-0.09	1.15	0.094
	VOR×FieldWS	0.06	0.27	-0.47	0.60	0.811
Height+Height×Field	Intercept	-2.56	0.85	-4.23	-0.89	0.003
	Height	0.97	0.24	0.51	1.43	≤ 0.001
	Height×FieldCS	0.11	0.29	-0.46	0.68	0.705
	Height×FieldSB	0.44	0.34	-0.23	1.10	0.201
	Height×FieldWS	-0.30	0.29	-0.86	0.26	0.297
Litter+Litter×Field	Intercept	-1.85	0.50	-2.84	-0.87	≤ 0.001
	Litter	1.32	0.34	0.66	1.98	≤ 0.001
	Litter×FieldCS	-1.72	0.42	-2.53	-0.90	≤ 0.001
	Litter×FieldSB	-0.90	0.43	-1.74	-0.05	0.037
	Litter×FieldWS	-1.60	0.41	-2.41	-0.79	≤ 0.001

CHAPTER 2: THE THERMAL ECOLOGY OF UPLAND NESTING DUCKS

ABSTRACT

Temperature plays a key role in the life history of many animals and has been found to directly influence behavior, reproduction, survival, and physiology. Despite these findings, the structural and thermal qualities of grassland nesting habitat that can influence nest site selection and success are poorly understood. Thus, we explored the thermal ecology of upland nesting ducks (*Anatinae*) in eastern South Dakota, during 2015-2016, using black-bulb temperature (T_{bb}) probes. We measured vegetation and thermal characteristics at varying relevant scales to evaluate the relative influence of microclimates on nest-site selection and survival. We found that relatively homogeneous grasslands exhibited considerable thermal heterogeneity, as T_{bb} ranged as much as 35°C, when air temperatures exceeded 30°C. We found that this range of thermal environments allowed hens to select for thermally buffered nest sites, as nests were as much as 3°C cooler and experienced more moderate temperatures than non-nest sites. We found that vegetation density (β = -0.05, $P \leq 0.001$), height (β = -0.04, $P \leq 0.001$), and litter depth (β = -0.01, $P \leq 0.001$) influenced T_{bb}. However, only litter depth varied between nest and non-nest sample types ($F_{1,209}$ = 9.15, P = 0.003) and failed and successful nests ($F_{1,98}$ = 5.7, P = 0.019), which suggested that this component played an important role in the moderation of temperatures at the nest. Additionally, we found that nest survival was positively associated with increased exposure to cold temperatures (β = 3.25, SE = 0.21). Collectively, these results provide evidence that variation in vegetation structure is important in moderating thermal environments and highlights the importance of the

management for thermally heterogeneous grasslands that can contribute to duck production in the northern prairies.

INTRODUCTION

Temperature plays a key role in the life history of many animals and has been found to directly influence behavior, reproduction, survival, and physiology (Elmore et al. 2017). Despite these findings, studies evaluating habitat's influence on microclimates and how organisms respond to thermal conditions are limited (Elmore et al. 2017). Research focusing on these aspects of thermal ecology can further elucidate the full and functional extent of an organism's habitat and allow for a better understanding of the specific features that directly influence survival.

The functional benefit of microclimates are experienced on a spatiotemporally and dynamic extent. Thus, thermal ecology studies must focus on an often fine and biologically relevant scale of microclimate to assess habitat suitability and use (Varner and Dearing 2014). In waterfowl, the chronology of migration (Schummer et al. 2010, van Wijk et al. 2012), nesting (Cowardin et al. 1985), molting (Robertson et al. 1997), and reproduction (Jorde et al. 1984) have been related to large-scale seasonal weather patterns. In contrast, in mostly lab settings, waterfowl embryonic development (Snart 1970, Batt and Cornwell 1972), incubation behavior (Caldwell and Cornwell 1975), immunocompetence (DuRant 2011, DuRant et al. 2012), and metabolic responses (Owen 1970, Bakken et al. 1999) have been found to be directly influenced by small-scale variations in temperature. However, inferences made from lab studies should be broadly applied with caution because of: 1) uncertainty in how artificial conditions relate to natural conditions, and; 2) inadequate quantifications of the inherently and spatiotemporally heterogeneous thermal landscape (Elmore et al. 2017). Despite some understanding of how temperature influences waterfowl, evidence of how habitat influences nest temperature, and how hens respond to microclimates, is lacking.

The microclimate selection hypothesis states that hens select nest-sites which minimize physiological stress during incubation (With and Webb 1993). Numerous studies have illustrated that structural vegetation characteristics differ between nest and non-nest sites (Southwood 1977, Hines and Mitchell 1983, Clark and Shutler 1999, Durham and Afton 2003), but few have linked any pattern of selection with temperature (Gloutney and Clark 1997, Solem 2013). Gloutney and Clark (1997) reported interspecific differences among observed nest temperatures but found no difference between nest and non-nest sites. Further, the authors of this study (Gloutney and Clark 1997) did not account for vegetation structure in their analyses, and therefore were unable to quantitatively identify the mechanisms that drove variations in temperature. Conversely, Solem (2013) found that nests consistently experienced cooler and drier conditions than non-nest sites, and suggested that litter depth played an important role in moderating thermal conditions at the nest.

Several recent studies have incorporated the use of operative temperature probes in evaluating the thermal ecology of gallinaceous birds in the Southern Great Plains (Guthery et al. 2005, Hovick et al. 2014, Carroll et al. 2015, Grisham et al. 2016). Operative temperature incorporates the influence of solar radiation, air temperature, wind and humidity (Dzialowski 2005) and offers a better approximation of conditions experienced by organisms (Elmore et al. 2017) than air temperature alone (Helmuth et al. 2005). In a study of greater prairie-chickens (*Tympanuchus cupido*) in Oklahoma, Hovick et al. (2014) reported finding a highly heterogeneous thermal landscape and that temperatures were found to range as much as 23°C at a given time. Further, the authors of this study (Hovick et al. 2014) reported nests to be 4°C cooler than non-nest sites within 2 m of the nest and that successful nests were 6°C cooler than unsuccessful nests. Similarly, Grisham et al. (2016) found nest survival in lesser prairie-chickens (*Tympanuchus pallidicinctus*) to be negatively associated with the proportion of extreme hot and arid conditions and further suggested that vegetation density was responsible for much of the thermal variation experienced at nests.

Nest-site selection plays an important role in duck reproduction as it influences the environmental conditions in which the hen and eggs will be exposed to, for a relatively long period of time (Gloutney and Clark 1997). Moreover, temperatures experienced at the nest can negatively influence egg and nest survival in 2 ways. First, hens are largely away from the nest during the egg laying period, thus potentially exposing eggs to lethal temperature extremes. Second, egg production and incubation are physiologically demanding for nesting hens and increasingly so in extreme hot or cold conditions. Extended bouts of unfavorable weather can lead to more frequent recesses from the nest, which leaves the eggs exposed to the environment and can result in higher rates of depredation, as nest predators are provided with increased opportunity to detect nests. Thus, the selection for adequately buffered nest-sites is critical for moderating nest temperatures during egg laying and incubation. Therefore, our goal was to provide a fine-scale descriptive analysis of the thermal environments in which upland nesting waterfowl reside and explore how nest survival and selection are impacted by temperature.

METHODS

Data Set

The primary focus of this study was to evaluate the thermal ecology of waterfowl, so we excluded pheasant nests from analyses. Additionally, we excluded northern shoveler nests, because the sample size for this species (*n* = 2) prevented us from drawing strong species-specific inferences. Further, we excluded alfalfa fields from these analyses and focused on samples from cool season, smooth brome, and warm season fields, because they are the most common type associated with nesting waterfowl in the northern Great Plains.

Field Sampling

We collected black bulb temperature (i.e., operative temperature; hereafter T_{bb}) among all study fields to characterize thermal conditions at nest and non-nest sites. We measured T_{bb} using a DS1921G ibutton© (Maxim Integrated, San Jose, California, USA), affixed in the center of a 15-cm-diameter, 20-gauge, stainless steel (304 alloy) sphere (Arthur Harris & Company, Chicago, Illinois, USA), painted matte black (hereafter; black bulb) and placed on the ground (Guthery et al. 2005, Allred et al. 2013, Hovick et al. 2014). T_{bb} provides an effective method for extrapolating temperature variation, assuming the primary drivers of variation can be determined and accounted for within a given landscape (Allred et al. 2013). Similar methods have been used in thermal ecology studies for northern bobwhites (*Glinus virginianus*; Guthery et al. 2005, Carroll et al. 2015, Carroll et al. 2016), greater prairie-chickens (Hovick et al. 2014), and lesser-prairie-chickens (Grisham et al. 2016). However, it is likely that T_{bb} does not directly respresent the thermal conditions experienced by real birds, because the thermal conductance and rates of solar absorptivity of black bulbs differ from the plummage of a bird. Given an estimated reflectivity (24%; Stevenson 1979), we assumed the short-wave solar absorptivity was 76% for mallards (Wolf and Walsberg 2000) and 100% for the black bulbs themselves (Guthery et al. 2005). Thus, we expected the black bulbs would experience 24% higher levels of T_{bb} than the ducks in our study. Further, we were unable estimate species-specific rates of short-wave absorptivity for blue-winged teal and gadwall, but assumed that the similarities in plummage would result in a similar response to mallards. Despite these limitations, estimating T_{bb} provided a means of comparing an ecologically relevant measure of thermal conditions experienced at nest sites and within the different cover types included in our study.

We evaluated T_{bb} at the nest, stand, and paired-random sample points described in Chapter 1 (p. 14). We measured T_{bb} at 1092 stand-level sample points at 5-minute intervals for 13–167 hours ($\bar{x}$ = 55.9 hours), during 15–30 April and 1–15 July, for both years of the study to characterize the range of thermal conditions experienced throughout the nesting season. We measured T_{bb} at 156 nest sites (centered in nest bowl) on the projected hatch date, at 5-minute intervals for 9–312 hours ($\bar{x}$ = 80.4 hours) during 5 June–2 August 2015 and 14 May–25 July 2016. We measured T_{bb} at 104 paired-random sites on corresponding projected hatch dates at 5-minute intervals for 9–312 hours ($\bar{x}$ = 83.1 hours) in the second year of the study during 14 May–25 July 2016.

We collected climatological data throughout the duration of the study to provide context to site-specific T_{bb} measurements. We measured air temperature (T_{air}; C°) at each study site using an ibutton enclosed in clear waterproof housing (NexSens Technology, Inc., Fairborn, Ohio, USA) and fixed to a 1 m fiberglass stake, at 5-minute intervals. We measured average Solar radiation (S_{rad}; W/m^2) and wind speed (wind; m/s) at 15-minute intervals using 4 regional weather stations near our study sites (SD Mesonet 2016). We were unable to collect site-specific S_{rad} and wind data, but given the relatively similar slope and aspect of our study sites, within a largely homogenous landscape, we assumed weather station data would be adequate for approximating climatological conditions. We collected all climatological data from 1 May–1 August during 2015 and 2016.

We used data from vegetation sampling described in Chapter 1 (pp. 14-15) to evaluate the relationship between vegetation structure and thermal conditions experienced at nest sites. Vegetation density (Grisham et al. 2016), vegetation height (Hovick et al. 2014), and litter depth (Gloutney and Clark 1997, Solem 2013) have been reported as factors that may moderate temperature extremes at nest sites; thus, we focused our analyses on these structural vegetation metrics.

Statistical Analysis

Microclimate Characteristics – We developed models to compare T_{bb} at nest and paired-random as a function of T_{air}, S_{rad}, wind, and vegetation structure to explain variation in thermal conditions experienced by nesting hens (Guthery et al. 2005, Hovick et al. 2014, Carroll et al. 2015, Carroll et al. 2016). We averaged T_{bb} and weather observations (T_{air}, S_{rad}, wind) by hour, excluding night time hours (2000–0600 h) because there is no solar insolation at night (Gloutney and Clark 1997). We analyzed these data using a linear mixed-model from the nlme package (Pinheiro et al. 2014) in Program R (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria). In this analysis, Tair, Srad, wind, and vegetation structure were fixed effects, whereas sample ID was a random effect intended to account for variation due to multiple observations at the same location.

Our models initially included the explanatory variables: T_{air}, S_{rad}, wind, VOR, the interaction term T_{air} × Srad, and interaction terms for VOR and all other continous predictors. We included the interaction term for T_{air} × Srad because the relationship between these covariates has been previously found to strongly influence T_{bb} (Hovick et al. 2014, Carroll et al. 2015, Carroll et al. 2016). We included interaction terms for VOR and all other continous predictors to account for the relationship between vegetation structure and weather predictors (e.g., shading, insulation). We were limited in our ability to include multiple vegetation metrics (i.e., VOR, height, and litter depth), because correlation tests revealed strong associations between these predictors (Pearson correlation test; $r > 0.6$). Thus, we focused on VOR to characterise vegetation structure because it has been found to strongly influence T_{bb} (Grisham et al. 2016). We scaled and centered (e.g., mean = 0, SD = 1) all continuous predictor variables to improve model convergence (Becker et al. 1998).

We started with the global model and then used a hierarchical procedure in which nonsignificant variables were removed (Alisauskas and Ankney 1994). We additionally limited our model to variables in which parameter estimates only included confidence intervals that did not overlap 0. We determined significance of predictors using a likelihood ratio test ($P < 0.05$; Pinheiro et al. 2014). We used the variance explained by fixed effects (i.e., marginal R^2) and the variance explained by fixed and random effects (i.e., conditional R^2) to assess model fit, using the MuMIn package in Program R (Bartoń 2013).

We used these models to characterise thermal conditions experienced across the entire nest exposure period for nest and pair-random sites, which allowed us to make ecologically relevant comparisons among cover and sample types. We assumed an average egg laying and incubation period of 34-days, to back-predict T_{bb} across each nest's total exposure period (Hovick et al. 2014). We used the predicted nest T_{bb} data for our analyses of nest survival and interspecific differences.

We also developed individual models to evaluate differences in T_{bb} among field types (i.e., cool season, smooth brome, warm season), between sample types (i.e., nest and paired-random), and nest outcomes (i.e., successful and failed). We further developed indepedent models for each each vegetation metric (i.e., height, VOR, and litter depth) to assess their relative influence on T_{bb} (Carroll et al. 2016). For individual models we only included the covariates T_{air}, S_{rad} and all higher order interactions in addition to the specific term of interest, given these variables are known to largely drive variation in T_{bb} (Hovick et al. 2014).

Nest Survival – We assessed nest survival using the methods described in Chapter 1 (pp. 15-17). We were specifically interested in evaluating how interactions between vegetation structure and microclimate influenced daily survival rate (DSR). Ambient temperature progressively increased through the season, so nests initiated earlier experienced more moderate temperatures on average than nests initiated later in the season. Thus, we did not include any temporally specific T_{bb} covariates (i.e., measurements linked to individual exposure days) in our nest survival analyses, which controlled for over-paramterization and allowed for interactions between T_{bb} (multiple observations per sample) and vegetation covariates (1 measurment per sample; Grisham et al. 2016). Instead, we developed 3 independent metrics of T_{bb} by consolidating observations from each nest (Grisham et al. 2016), which were: percent of T_{bb} observations within the thermal neutral zone (PercentNeutral; C°), percent of T_{bb} observations ≤ lower critical temperature (T_{lc}; PercentCold; %), and percent of T_{bb} observations ≥ upper critical temperature (T_{uc}; PercentHot; %).

The T_{lc} and T_{uc} represented the lower and upper bounds of the thermal neutral zone, which is the range of temperatures in which no additional energy is required to maintain homeostasis (Weathers and van Riper 1982). The energetic costs for hens during incubation increases at temperatures below (Ricklefs 1974, Turner 1993) and above (Caldwell and Cornwell 1975) the thermal neutral zone. We used previously published T_{lc} thresholds to assess the influence of thermal stress on DSR. Gloutney and Clark (1997) reported the T_{lc} of 9.5°C for blue-winged teal and 16.5°C for mallards. Because body mass influences an animal's ability to thermoregulate (Gloutney and Clark 1997), the smaller average mass of a blue-winged teal (350 g) compared to a mallard (900 g) meant that blue-winged teal would have higher energetic costs (Gloutney and Clark 1997), illustrated by their respective $T_{lc.}$ We used these reported T_{lc} values to calculate a T_{uc} of 23.5°C and 30.5°C for blue-winged teal and mallard, respectively (Gavrilov 1999). We were unable to find temperature threshold estimates for the gadwall but assumed the relatively similar body mass of mallards (900 g) and gadwall (816 g; Bosco and Grosz. 2014) would result in similar temperature thresholds. Given the comparatively larger body size of mallards, it could be assumed that this species' temperature thresholds would exceed that of a smaller bird, such as the gadwall. Thus, we felt that our approximation of T_{lc} and T_{uc} for gadwalls represented a conservative threshold, given the morphological differences between these species. We recognize that several assumptions must be employed when using these values; however, we believed that they would provide conservative approximations of the thresholds at which these ducks experience thermal stress.

We developed a set of 30 candidate models *a priori* and based on previously published research (Hovick et al. 2014, Grisham et al. 2016). We included 1 model for each consolidated T_{bb} covariate (n = 3), 1 model for each vegetation covariate (VOR and litter depth; n = 2), 1 model for each consolidated T_{bb} covariate and each vegetation covariate as additive effects (n = 6), 1 model for each consolidated T_{bb} covariate and each vegetation covariate as interactive effects (n = 6), 1 model for each consolidated T_{bb} covariate and each vegetation covariate as interactive effects, with only 1 term as an additive effect (n = 12), and 1 model that only contained the term field type (n = 1). We used second-order Akaike's Information Criteria (AIC_c) for small sample sizes, ΔAIC_c, and AIC_c weights (w_i) for our model selection process (Anderson and Burnham 2002). We considered models that were ≤2 ΔAIC_c units and ≤4 ΔAIC_c units of the top model to strongly and moderately support the data, respectively (Anderson and Burnham 2002). We combined all duck nests found in 2015 and 2016 that were sampled for T_{bb} to achieve an adequate sample size (Klett et al. 1986).

Group Comparisons – We used the consolidated T_{bb} terms: PercentCold, PercentHot, and PercentNeutral to evaluate levels of thermal stress experienced by nesting hens among field types, species, and between failed and successful nests with Kruskal-Wallis tests (χ^2 approximation; Siegel and Castellan 1988). We used a Kruskal-Wallis multiple comparisons test when significant differences were reported ($P < 0.05$).

Vegetation – Vegetation characteristics can in part be responsible for the creation of microclimates within a larger landscape (Varner and Dearing 2014). Thus, we tested for differences in vegetation parameters (e.g., VOR, height, and litter depth) among field type and species, between sample type (e.g., nest and paired-random), and between failed and successful nests using ANOVA and used a Tukey Honest Significant Difference (HSD) test when appropriate ($P < 0.05$).

RESULTS

Microclimate Characteristics – We found T_{bb} to increase linearly with T_{air} and to range from 2° to 58°C (Figure 1). When T_{air} exceeded 30°C, we found that T_{bb} was capable of exceeding 53°C (Table 1). The best supported predictive model included the fixed effects T_{air}, S_{rad}, VOR, and wind and the interaction terms T_{air} and S_{rad}, T_{air} and VOR, and wind and VOR. We found T_{air} ($\beta = 0.56$, $F_{1,28357} = 124672.78$, $P \leq 0.001$) and S_{rad} ($\beta = 0.39$, $F_{1,28357} = 13644.45$, $P \leq 0.001$) to largely drive variation in T_{bb}. The effect of all covariates included in the final model were significant ($P < 0.05$; Table 2). The marginal and conditional R^2 for this model and the global model were 0.81 and 0.88, respectively.

We found T_{bb} to vary between sample types ($F_{1,159} = 7.684$, $P \leq 0.001$) as nests were 1° to 2°C cooler than paired-random sites (Figure 2). Moreover, nest sites experienced a slightly wider range of temperatures (2°–58°C) than paired-random sites (3°–58°C; Table 3). Further, we found that T_{bb} did not vary between successful and failed nests ($F_{1,82} = 2.11$, $P = 0.15$; Figure 3) but found that successful nests appeared to experience a wider range of temperatures (2°–58°C) than failed nests (5°–53°C; Table 3).

T_{bb} to varied among field types ($F_{2,666} = 9.00$, $P \leq 0.001$) and the rates of increase in T_{bb} and the range of temperatures experienced among field types varied (Table 3; Figure 4).

In our evaluation of vegetation metrics, we found VOR ($F_{1,28358} = 127.41$, $P \leq 0.001$; Figure 5) and vegetation height ($F_{1,28358} = 65.5$, $P \leq 0.001$; Figure 6) to drive T_{bb}, while litter depth ($F_{1,28358} = 1.84$, $P = 0.175$; Figure 7) did not. However, we found the interaction between VOR (Table 8), vegetation height (Table 9), litter depth (Table 10) and S_{rad} and T_{air} to influence T_{bb}.

Nest Survival – We found 4 and 3 models to strongly ($\Delta AIC_c \leq 2$) and moderately ($\Delta AIC_c \leq 4$) support the data, respectively, for the analysis of nest survival (Table 11). We only found support from models containing the covariates PercentCold ($n = 7$), litter depth ($n = 3$), and VOR (n = 3). The top model ($w_i = 0.28$) included the additive term PercentCold ($\beta = 3.25$, SE = 0.21; Table 12), which was positively associated with DSR (Figure 8). The second best model ($w_i = 0.19$) included the additive term PercentCold ($\beta = 15.03$, SE = 6.84) and Litter depth ($\beta = 0.1$, SE = 0.09), which were both positively associated with DSR (Table 12). The third best model ($w_i = 0.15$) included the additive term PercentCold ($\beta = 14.51$, SE = 6.88) which was positively associated with DSR and VOR ($\beta = -0.1$, SE = 0.02) which was negatively associated with DSR (Table 12). In the model that included the interaction between PercentCold and Litter depth ($w_i = 0.1$) the interaction for these covariates ($\beta = 2.13$, SE = 1.07) was positively associated with DSR, which suggests that higher levels of litter were able to control for colder temperatures at the nest (Figure 9). The model that contained the interaction between PercentCold and VOR and the additive term VOR ($w_i = 0.09$) received moderate support within our candidate set ($\Delta AIC_c = 2.18$). In this model, VOR had a negative influence on survival (β

= -0.02, SE = 0.02), whereas the interaction term for PercentCold and VOR had a positive influence on DSR (β = 0.37, SE = 0.19), which suggests that high levels of VOR were unable to control for warmer temperatures at the nest (Figure 10). Based on our top model, the probability of DSR (± SE) for all nests was 0.98 ± 0.56 (95% CI: 0.97–0.99). Assuming a 34-day exposure period, the probability of nest survival was 47%.

Group Comparisons – We compared T_{bb} among field type, species, sample type and nest outcome using 79 nest and 52 paired-random sample points from 2015–2016. We found that nests experienced lower levels of PercentHot (χ^2 = 6.71, P = 0.01; Figure 11B) and higher levels of PercentNeutral (χ^2 = 4.04, P = 0.045; Figure 11C) than paired-random sites (Table 13). There were no differences in levels of PercentCold (χ^2 = 0.11, P = 0.736; Figure 11A) between sample types (Table 13). The multiple comparisons test confirmed that nests experienced less hot and more neutral temperatures than pair-random sample types (Figure 11).

We found that successful nests experienced higher levels of PercentCold (χ^2 = 9.15, P = 0.002: Figure 12A) than failed nests (Table 13). There were no differences in levels of PercentHot (χ^2 = 0.94, P = 0.333; Figure 12B) and PercentNeutral (χ^2 = 3.23, P = 0.072; Figure 12B) between successful and failed nests (Table 13). The multiple comparisons test confirmed that successful nests experienced higher levels of PercentCold than failed nests (Figure 12A).

We found that PercentHot (χ^2 = 16.6, $P \leq 0.001$; Figure 13B) and PercentNeutral (χ^2 = 18.8, $P \leq 0.001$; Figure 13C) varied among field types, but PercentCold (χ^2 = 0.26, P = 0.879; Figure 13A) did not (Table 13). The multiple comparisons tests revealed that cool season fields experienced lower levels of PercentHot (Figure 13B) and higher levels of PercentNeutral (Figure 13C), than smooth brome and warm season fields.

We found that PercentCold ($\chi^2 = 37.77$, $P \leq 0.001$; Figure 14A), PercentHot ($\chi^2 = 30.31$, $P \leq 0.001$; Figure 14B), and PercentNeutral ($\chi^2 = 48.05$, $P \leq 0.001$; Figure 14C) all varied among species (Table 13). The multiple comparisons tests revealed that blue-winged teal experience a wider and less moderate range of temperatures than gadwall and mallard (Figure 14).

Vegetation – We compared vegetation metrics among sample type, nest outcome field type, species, using 138 nest and 73 paired-random sample points from 2015–2016. We found that litter depth ($F_{1,209} = 9.15$, $P = 0.003$; Figure 15C) differed between nest and pair-random samples, while VOR ($F_{1,209} = 1.2$, $P = 0.274$; Figure 15A) and vegetation height ($F_{1,209} = 0.45$, $P = 0.503$; Figure 15B) did not (Table 14). The multiple comparisons test revealed that nests had lower levels of litter depth than paired-random sample sites (Figure 15C). Similar to our sample type analyses, we found that litter depth ($F_{1,98} = 5.7$, $P = 0.019$; Figure 16C) differed successful and failed nests, while VOR ($F_{1,98} = 1.49$, $P = 0.226$; Figure 16A) and vegetation height ($F_{1,98} = 0.23$, $P = 0.633$; Figure 16B) did not (Table 14). The multiple comparisons test revealed that successful nests had higher levels of litter depth than failed nests (Figure 16C). Conversely, we found that VOR ($F_{2,208} = 15.89$, $P \leq 0.001$; Figure 17A) and vegetation height ($F_{2,208} = 17.27$, $P \leq 0.001$; Figure 17B) varied among field types, but litter depth ($F_{2,208} = 15.89$, $P = 0.154$; Figure 17C) did not (Table 14). The multiple comparisons tests revealed that mean VOR in cool season fields was higher than other field types (Figure 17A) and that mean vegetation height in Smooth brome fields was lower than other field types (Figure 17B).

We found that vegetation height ($F_{2,97} = 4.39$, $P = 0.015$; Figure 18B) differed among species but VOR ($F_{2,97} = 2.74$, $P = 0.07$; Figure 18A) and litter depth ($F_{2,97} = 2.15$, $P = 0.122$; Figure 18C) did not. The multiple comparisons test revealed the highest levels of vegetation height at gadwall nests, followed by mallard and blue-winged teal (Figure 18B).

DISCUSSION

Our results provide support for the microclimate selection hypothesis, as nests experienced more moderate temperatures than non-nest sites within 2 m of nests. Our findings suggest that selection occurs at a finer scale than previously reported by Gloutney and Clark (1997), who suggested that nest-site selection occurs at the patch level. In their study evaluating mallard and blue-winged teal nest-site selection in relation to microclimate in Saskatchewan, Canada, Gloutney and Clark (1997) reported no difference in temperatures at nest and non-nest sites and concluded that selection is driven by both microclimate and predator avoidance which is only partially supported by the microclimate selection hypothesis. Further, the authors of this study reported the proportions of temperatures below the T_{lc} of 25% for mallard and 50% for blue-winged teal, that were considerably higher than our reported proportions of 2% and 50% for mallards and blue-winged teal, respectively. Gloutney and Clarke (1997) reported the maximum temperature found at mallard nests to be 56°C that was similar to the upper range of 54°C found in our study. However, the Gloutney and Clarke’s reported maximum temperature for blue-winged teal was 41°C that was lower than our reported upper range of 58°C. This apparent variation in observed temperatures could be due to the latitude of respective study sites and method for recording nest temperatures. The more northerly latitude of Saskatchewan compared to eastern South Dakota would result in lower mean temperatures, could have resulted in the comparatively higher proportions of temperatures below the T_{lc} and the lower maximum nest temperature for blue-winged teal. Further, the authors of this study reported the use of a stand-alone datalogger that recorded air temperature, humidity, and solar radiation, which was used to calculate operative temperature (e.g., T_{bb}). The method we used, recording temperature inside of black bulbs, would inherently produce higher values of T_{bb}, given the increased rate of absorptivity of the black bulbs compared to a stand-alone probe. However, Gloutney and Clarke (1997) did report that blue-winged teal nests experienced greater T_{bb} than mallard nests, which was similar to our findings.

Much previous research evaluating the influence of temperature on grassland nesting birds has focused on the bobwhite quail (Guthery et al. 2005, Carroll et al. 2015), and lesser (Patten et al. 2005, Hovick et al. 2014) and greater prairie-chickens (Grisham et al. 2016). Further, these efforts have been mostly conducted in the short, mixed-grass and Sand Shinnery Oak southern prairie ecoregions of Kansas (Grisham et al. 2016), New Mexico (Patten et al. 2005, Grisham et al. 2016), Oklahoma, (Patten et al. 2005, Hovick et al. 2014, Carroll et al. 2015) and Texas (Guthery et al. 2005, Grisham et al. 2016). Although the obvious disparity between these studies and ours is apparent, similar inferences can be derived by comparing the mechanisms that drive T_{bb} and subsequently influence nest selection and survival.

Our results illustrate how grassland nesting ducks select for nest-sites that provide refuge from temperature extremes. This pattern was most apparent when T_{air} exceeded 30°C as nests were as much as 3°C cooler than paired-random sites. Hovick et al. (2014)

reported similar behavior in lesser prairie-chickens in Oklahoma, where nests were up to 4°C cooler than non-nest sites, which was thought to be a result of selection for nest-sites in denser vegetation. Similarly, Grisham et al. (2016) and Patten et al. (2005) reported that vegetation density for lesser prairie-chickens was the most important habitat component for moderating microclimates that influence survival. However, it has been suggested that vegetation density is a less important predictor of nest survival in grassland habitat types (Fritts et al. 2016). We found no difference in vegetation density or height between nest and paired-random sites, which supports this notion. However, litter depth in our study was higher at nests than non-nest sites, which suggests that this component plays an important role in moderating temperatures at the nests. Conversely, Hovick et al. (2014) reported no difference in litter depth between nest and non-nest sites, further illustrating the apparent disparity between habitat selection decisions in gallinaceous birds in a shrub dominated heterogeneous landscape and ducks in a largely homogenous grassland habitat.

We found no difference in mean T_{bb} between nest outcomes. However, successful nests experienced higher proportions of colder temperatures than failed nests. Moreover, we found nest survival to be largely and positively driven by the proportion of colder temperatures experienced at the nest. Previous studies have reported that successful bobwhite (Guthery et al. 2005) and lesser prairie-chicken (Hovick et al. 2014) nests were 1°–2°C and 4°C cooler than failed nests, respectively. Further, Grisham et al. (2016) and Patten et al. (2005) reported that nest survival of lesser prairie-chickens in the southern plains was negatively associated with increased exposure to extreme hot and arid conditions and positively associated with cooler and more humid conditions, respectively, and additionally positively associated with increased vegetation density. However, Hovick et al. (2014) reported no difference in vegetation structure between successful and failed nests and suggested this disparity provided support for temperature's influence on survival rather than predator avoidance through concealment. Supporting this notion, we found no difference in vegetation height and density between successful and failed nests. In contrast, Filliater et al. (1994) suggested that when a rich assemblage of nest predators is present, hens are unable to select for reliably safe sites because concealment from one predator may result in vulnerabilities to others. Additionally, it has been suggested that level of concealment around nests alone cannot predict nest fate, except when the primary predators are birds (Clark and Nudds 1991). As nests in our study area were subjected to predation from numerous species (N. P. Martorelli, unpublished data), it is possible that decisions regarding nest placement were driven by considerations for microclimates rather than concealment from predators.

In addition to the proportion of colder temperatures experienced at the nest, we also found evidence that nest survival was negatively associated with increased vegetation density. Although the magnitude of the relationship was modest, our results suggested that vegetation density played a role in moderating temperatures at the nest, which increased survival. Increased vegetation density has been found to be positively associated with nest survival in gallinaceous birds (Guthery et al. 2005, Patten et al. 2005, Grisham et al. 2016) and upland nesting ducks (Schranck 1972, Hines and Mitchell 1983, Lokemoen et al. 1984, Clark and Nudds 1991, Durham and Afton 2003). However, similar to our findings, other studies of waterfowl reported negative associations with increased vegetation density (Stephens et al. 2005, Haffele 2012, Solem 2013, Skone et al. 2016). This differing relationship with vegetation density and nest survival between gallinaceous birds and ducks is most likely a result of the different habitat types associated with these species, as dense cover is thought to be more important for birds nesting in shrub dominant heterogeneous landscapes (Davis 2009, Grisham et al. 2014). For upland nesting ducks, this disparity could be driven by climatic and geographic differences in habitat that may result in selection for varying levels of cover to meet thermoregulatory needs. However, it has been suggested that nest survival is diminished in dense cover because predators key in on dense patches of vegetation (Jiménez et al. 2007). Our findings do not necessarily refute this argument, but may suggest that vegetation density can contribute to moderating microclimate conditions at the nest, thereby influencing survival.

Previous studies have both dismissed (Lokemoen et al. 1984) and promoted (Duebbert 1969, Haffele 2012) the influence of litter depth on nest survival. In addition to finding higher levels of litter at successful than failed nests, our results suggested that higher levels of litter depth provided a buffer from warmer temperatures, positively influencing nest survival. Further, litter depth was the only vegetation metric that differed between both nest and non-nest sites and successful and failed nests; thus, it appears that this metric functions as one of the primary drivers that moderate temperatures at the nest, similar to Gloutney and Clark (1997).

Our findings that nest survival was positively driven by the proportion of cold temperatures experienced at the nest was similar to results reported by Patten et al. (2005). Based on this pattern, perhaps nest survival had an opposing negative relationship with the proportion of hot temperatures experienced at the nest. However, we did not find support or significant effects from models specifying upper temperature thresholds (Table 11). Similarly, we found that the proportion of upper temperature thresholds experienced by successful and failed nests did not differ. Exposure to extreme heat can detrimentally affect nesting hens and their eggs. Caldwell and Cornwell (1975) studied the incubation behavior of mallards and noted that when air temperature was 27°C, hens were observed panting and taking frequent recesses from their nests. Caldwell and Cornwell (1975) further noted that when air temperatures exceeded 32°C, hens were increasingly stressed, but refrained from taking recesses, and that prolonged exposure to air temperatures >40°C can be lethal to embryos (Caldwell and Cornwell 1975). Increased temperatures may also result in higher rates of depredation, because ectothermic predators, such as snakes, are more active (Morrison and Bolger 2002) and hens may leave the nest more frequently, allowing predators increased opportunities to detect and depredate nests.

Nests in our study were exposed to temperatures that exceeded upper thresholds ~54% of the time. However, we did not find any direct evidence that ducks in our study were negatively influenced by these upper temperature thresholds, but contrary to our predictions, they were positively influenced by the proportion of temperatures experienced below the T_{lc}. This pattern was somewhat confounding, as egg production and incubation alone are physiologically demanding (Gloutney and Clark 1991), and increasingly so at temperatures below this lower threshold (Caldwell and Cornwell 1975, Gloutney and Clark 1997). Thus, it appears that the positive association with nest survival and cold temperatures was not a product of microclimates that influence hens during incubation, but possibly its direct influence on the eggs and their development. Developing mallard embryos have been reported to be more tolerant of cold than heat

(Snart 1970, Batt and Cornwell 1972). Further, it has been reported that hatchability of domestic birds increased when eggs were periodically cooled during incubation, and that the optimal range of temperatures for eggs prior to incubation was 8°–13°C (Landauer 1967). Batt and Cornwell (1972) suggested that this trait is advantageous to precocial species, such as ducks, whose eggs undergo a considerable period of dormancy during laying, when the hen is largely away from the nest. In their study of the influence of cold on mallard embryos, Batt and Cornwell (1972) reported the highest rates of hatching success in eggs during early stages of embryonic development that were exposed to temperatures ranges of 0°–8°C. They concluded that unincubated eggs and eggs in the earliest developmental stages were more resistant to cold than more developed eggs. It has been further suggested that periodic chilling of eggs could aid in enhancing the development of thermoregulation (Oppenheim and Levin 1975). Moreover, the reported optimal range of temperatures for eggs prior to incubation falls within the limits of our lower temperature threshold, which was experienced to a greater extent at successful than failed nests. It would appear that nests that experienced a higher proportion of colder temperatures, at least periodically, may have a selective advantage, possibly illustrating a direct mechanism by which temperature influences duck nest survival.

Bird nests exposed to extreme bouts of warm (Lundy 1969, Webb 1987) and cold (Greenwood 1969, Batt and Cornwell 1972) weather have been reported to have reduced rates of hatch. However, Caldwell and Cornwell (1975) reported that in most temperate zone dabbling duck species, when hens are able to stay on the nest, embryonic development is not affected during bouts of warm weather. Thus, it is likely that nests in our study did not experience enough prolonged exposure to the range of upper critical temperatures that would have required hens to seek shelter away from nests. Any upper temperatures that might have negatively affected nest survival were likely mitigated by the incubating hens themselves and by their selecting adequately buffered nest sites. Further, reduced hatching rates have been reported to have been due to abnormally cold spring weather in Manitoba (Batt and Cornwell 1972) and North Dakota (Greenwood 1969). However, it is unlikely that nests in our study were exposed to enough lower critical temperatures to negatively influence hatch rates.

SUMMARY AND MANAGEMENT IMPLICATIONS

It has long been hypothesized that temperature plays an important role in waterfowl nesting ecology, yet research on this topic is lacking relative to the larger body of thermal ecology studies. Our goal was to provide the first major in-depth descriptive analysis of the thermal environments in which upland nesting ducks in the northern Great Plains reside. Our major findings suggested that temperatures at the nest were largely driven by a complex array of interactions between abiotic and biotic factors that resulted in a functionally heterogeneous habitat in an otherwise apparently homogenous grassland landscape. Specifically, we found that VOR, vegetation height, litter depth, and their interaction with T_{air} and S_{rad}, played critical roles in controlling microclimatic conditions for grassland nesting ducks. Further, our findings suggested that litter depth at the nest not only provided concealment from predators (Cowardin et al. 1985), but also contributed to the moderation of temperature extremes and influenced nest survival. In addition to finding support for the microclimate selection hypothesis, we found nest-site selection to occur at a finer-scale than previously reported, because nest sites experienced more moderate temperatures than random sites 2 m of nests. We found that, in temperate prairie grasslands and given the range of temperatures we observed, nest survival was not discernably or negatively influenced by any imposed behaviors by hens, but rather by the nest-site itself. We hypothesize that ideal nest-sites control for potentially detrimental upper temperature thresholds, but also are not overly buffered to allow for adequate cooling and the periodic exposure to colder temperatures, which positively influences rates of nest success (Landauer 1967) and thermoregulatory processes (Oppenheim and Levin 1975).

The dynamic relationship between temperature and habitat likely play vastly different roles among various grassland nesting species. Our findings highlight the importance of managing for heterogeneous grassland habitat that allow for a wide range of thermal environments. Further, past research has primarily identified nest-site selection as a function of predator avoidance. Although this idea is possibly confounded with the role in which temperature plays, it is important to expand beyond this paradigm and consider habitat as a gradient of thermal microclimates that may directly influence species' opportunities for successful reproduction.

FUTURE RESEARCH

Because our study was the first modern attempt with the use of black bulb temperature probes to evaluate the thermal ecology of nesting waterfowl, we acknowledge that the strength of our inferences is constrained by the somewhat limited scale of our efforts. Future research should be continued in the northern Great Plains for its inherent importance to North American waterfowl production, but also expand to different habitat types and species. By gaining a better understanding of the fine-scale habitat features that functionally drive thermal environments in various habitat types, future management and restoration efforts can be developed to more effectively maximize nest production. Additionally, future research should focus on the specific habitat cues that ducks use in nest-site selection, to further explore the inter-relationships between temperature and predator avoidance, and how and when they act alone or together, to influence nest survival.

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Figure 1. Distribution of modeled black bulb temperatures and recorded air temperatures, during 2015 and 2016 in eastern South Dakota.

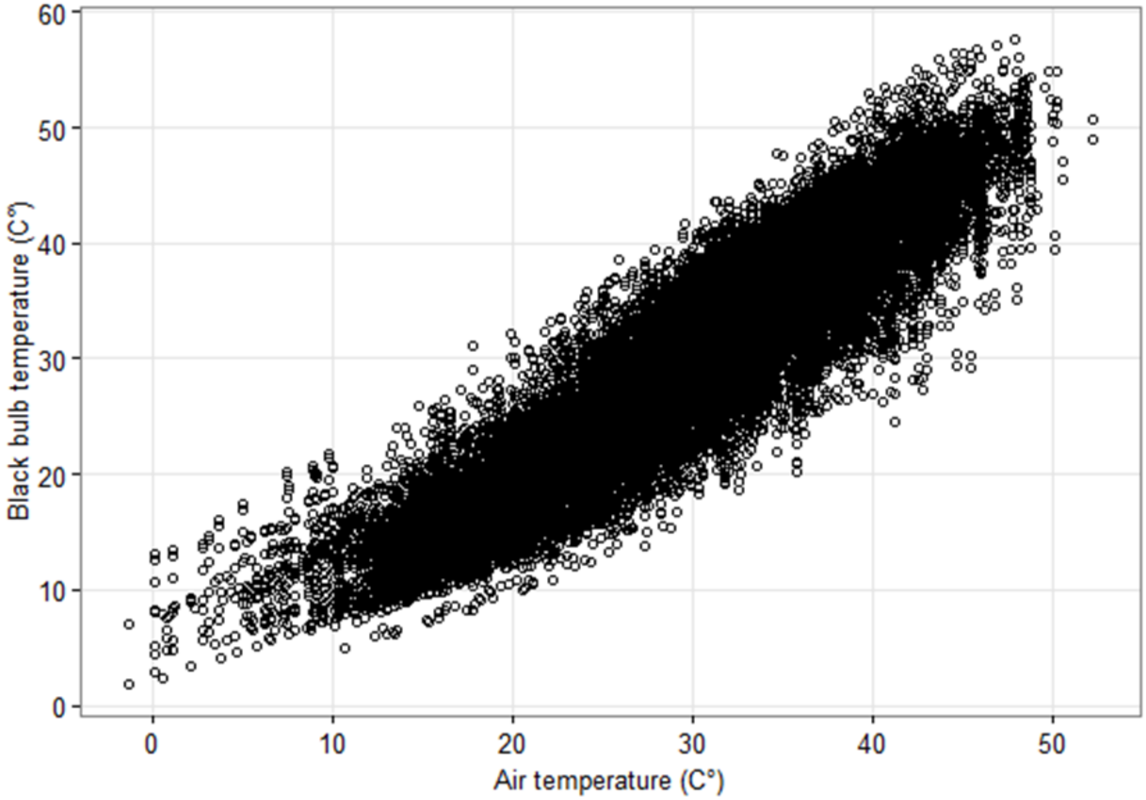

Figure 2. Modeled linear regression of black bulb temperature as a function of air temperature at nest and paired-random sites during 2016 in eastern South Dakota.

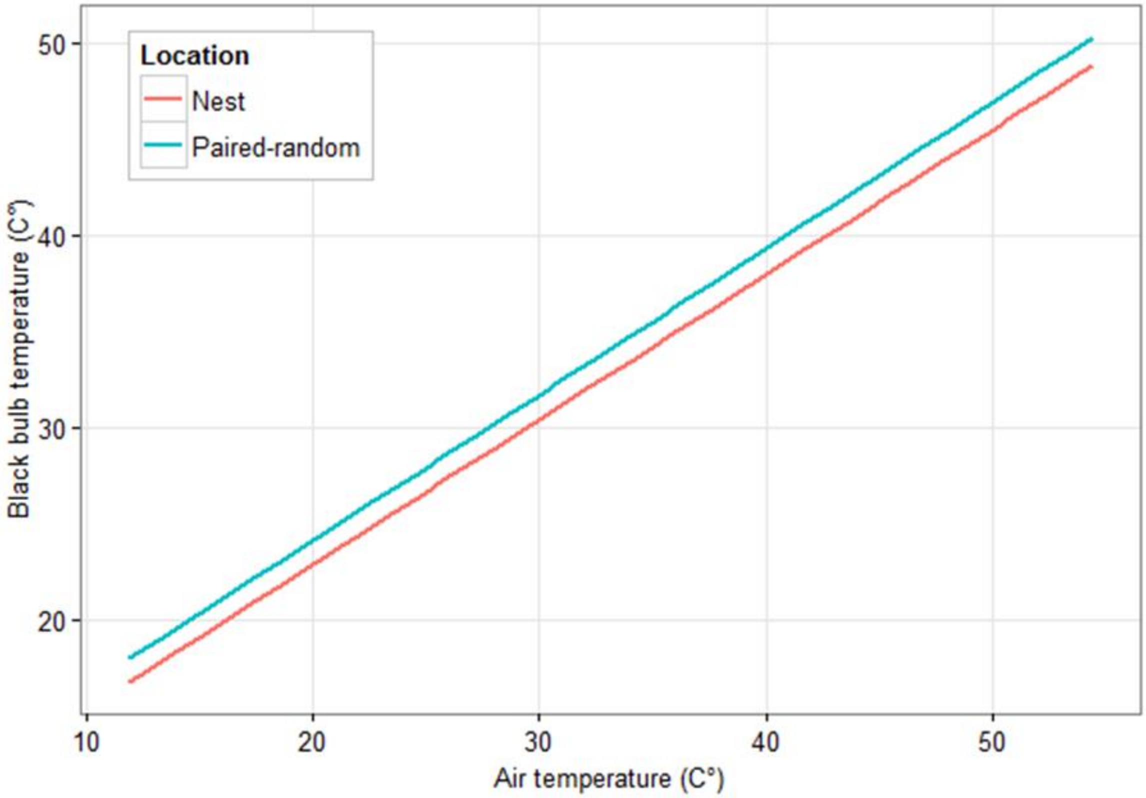

Figure 3. Modeled linear regression of black bulb temperature as a function of air temperature at failed and successful nests during 2016 in eastern South Dakota.

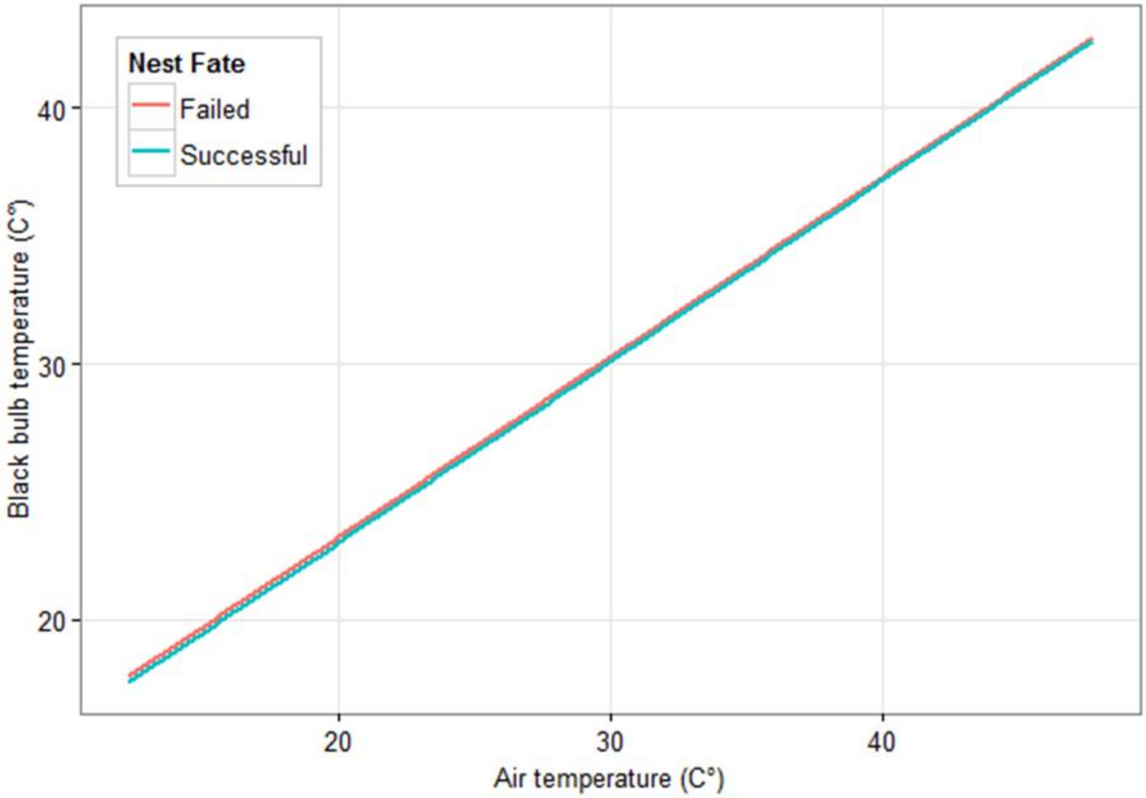

Figure 4. Modeled linear regression of black bulb temperature as a function of air temperature among field types during 2016 in eastern South Dakota.

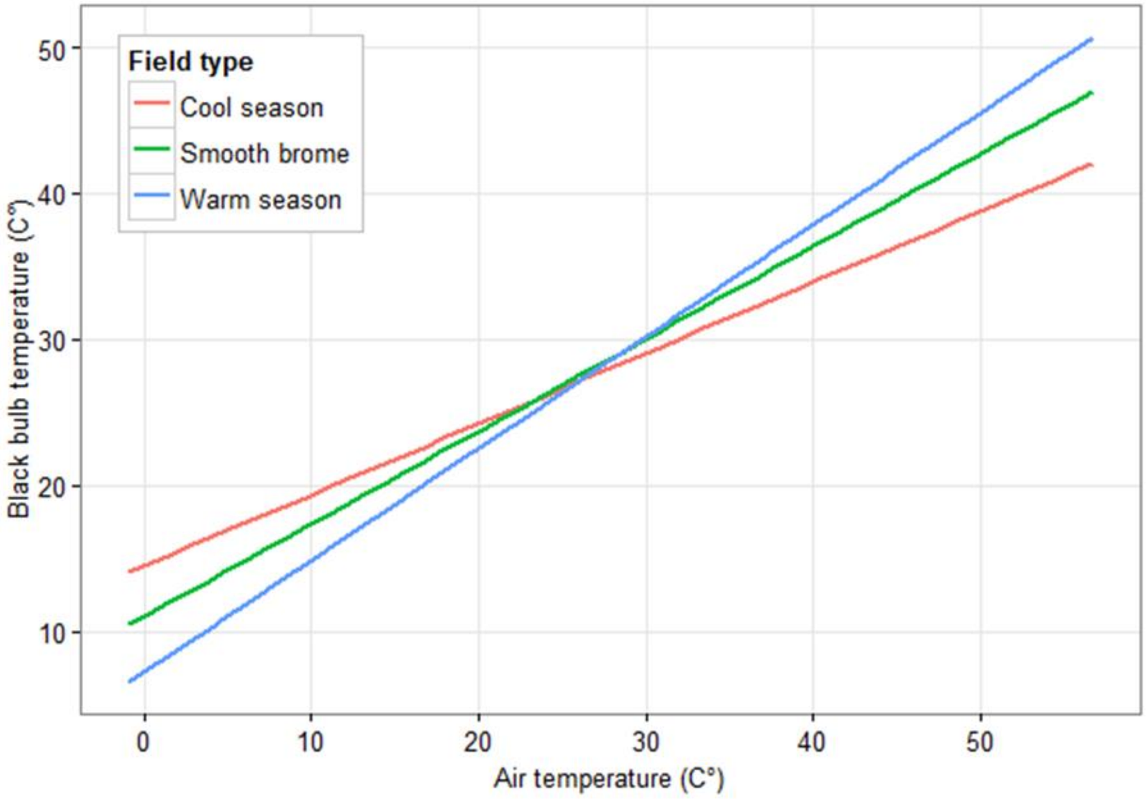

Figure 5. Modeled linear regression of black bulb temperature as a function of air temperature and vegetation density (VOR) during 2016 in eastern South Dakota.

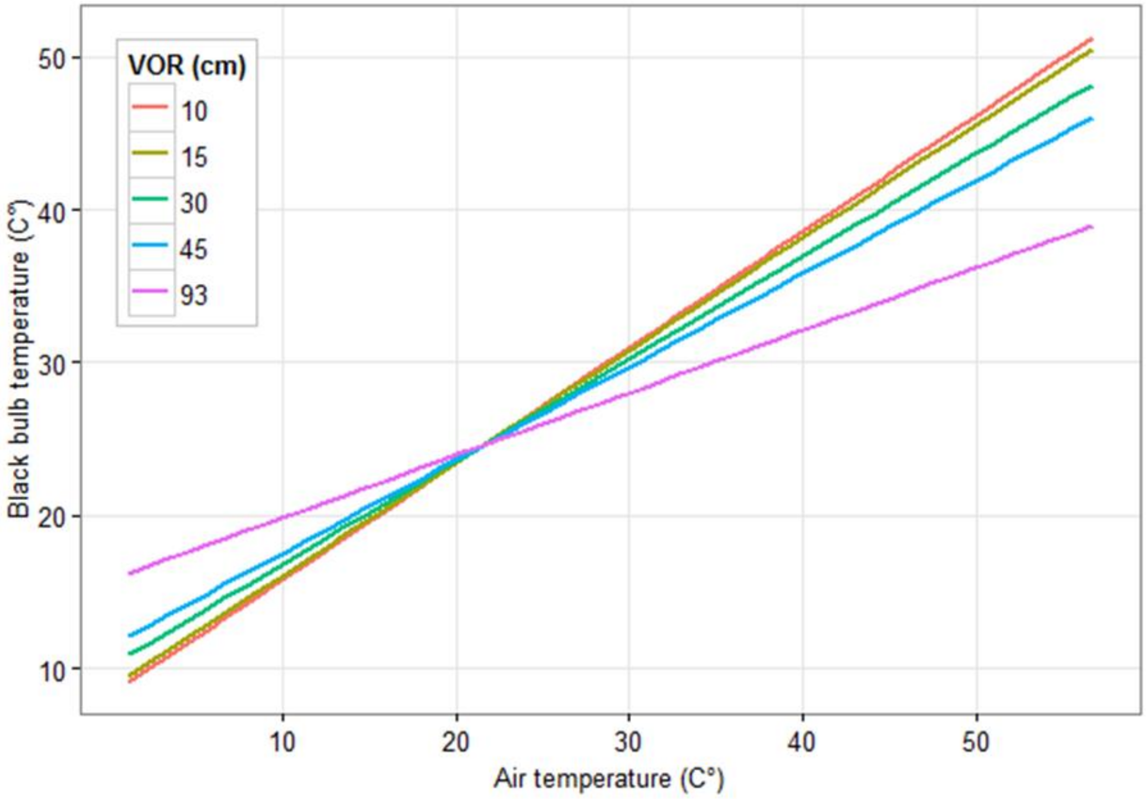

Figure 6. Modeled linear regression of black bulb temperature as a function of air temperature and vegetation height during 2016 in eastern South Dakota.

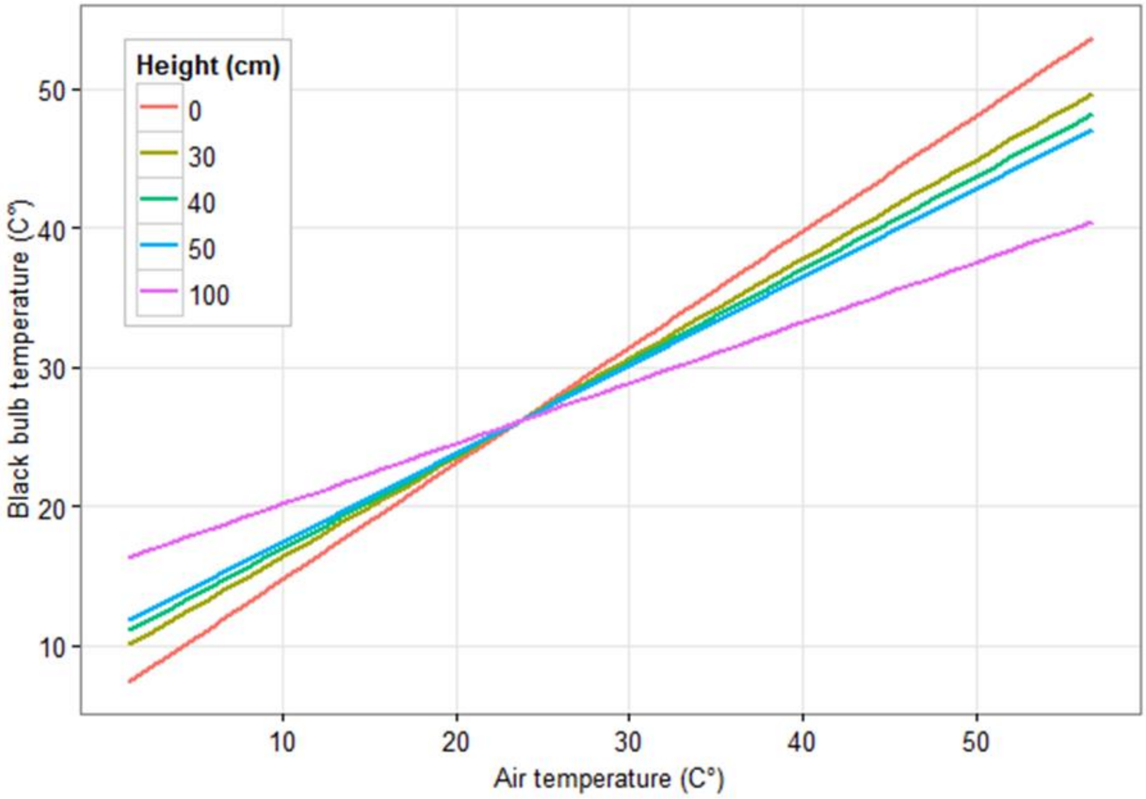

Figure 7. Modeled linear regression of black bulb temperature as a function of air temperature across litter depth during 2016 in eastern South Dakota.

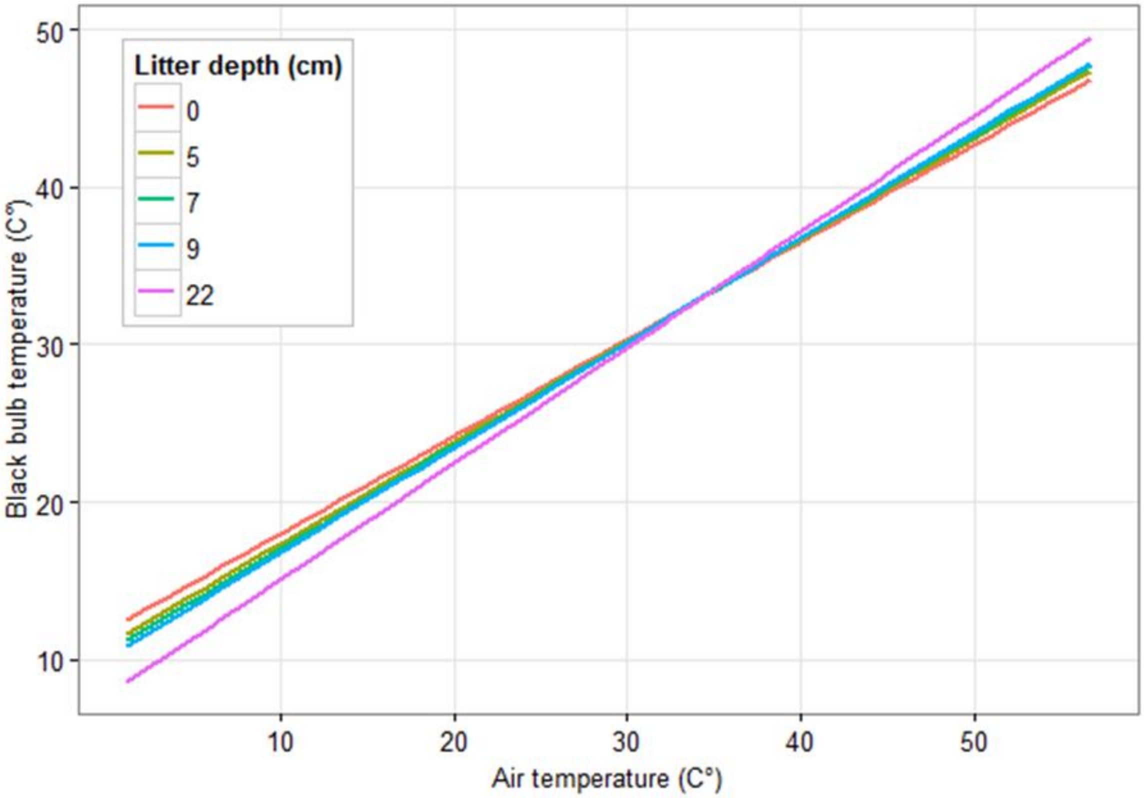

Figure 8. Relationship between daily survival rate (DSR) and the percent of T_{bb} observations below the thermal neutral zone (Percent Cold) for duck nests during 2015 and 2016 in eastern South Dakota.

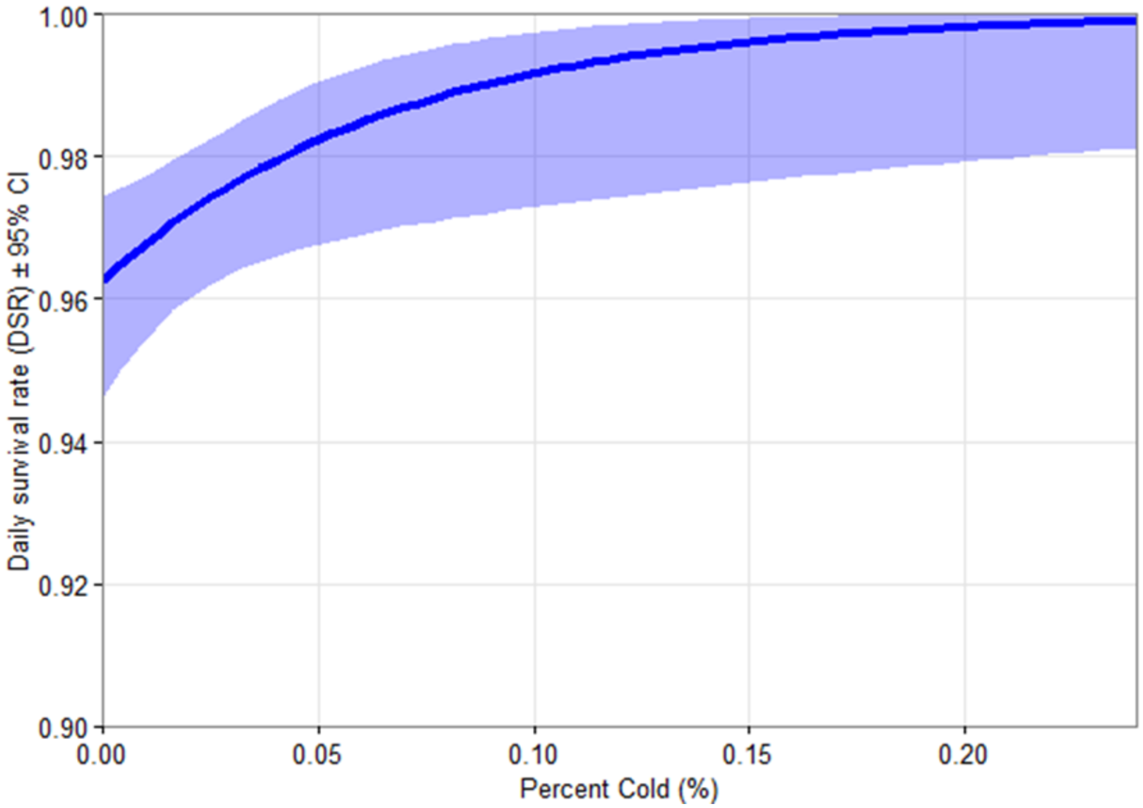

Figure 9. Relationship between daily survival rate (DSR) and the interactive effects of percent of T_{bb} observations below the thermal neutral zone (Percent Cold) and litter depth for duck nests during 2015 and 2016 in eastern South Dakota.

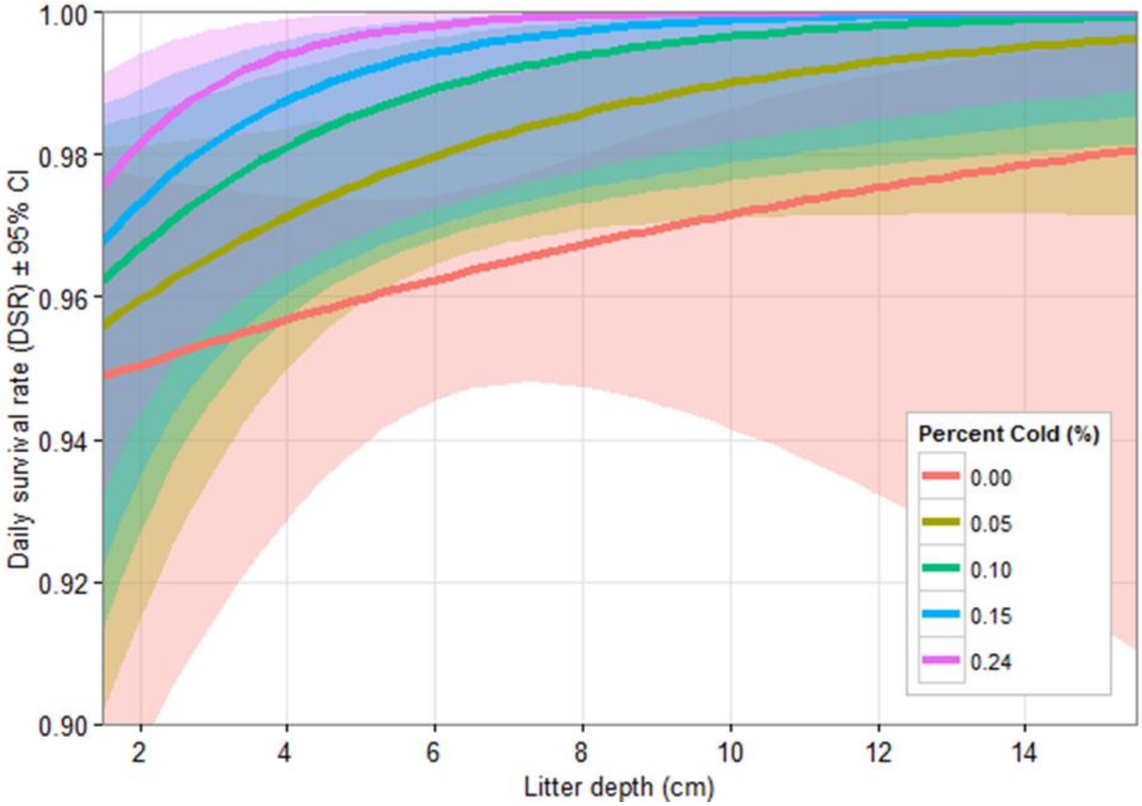

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Figure 10. Relationship between daily survival rate (DSR) and the interactive effects of percent of T_{bb} observations below the thermal neutral zone (Percent Cold) and vegetation density (VOR) for duck nests during 2015 and 2016 in eastern South Dakota.

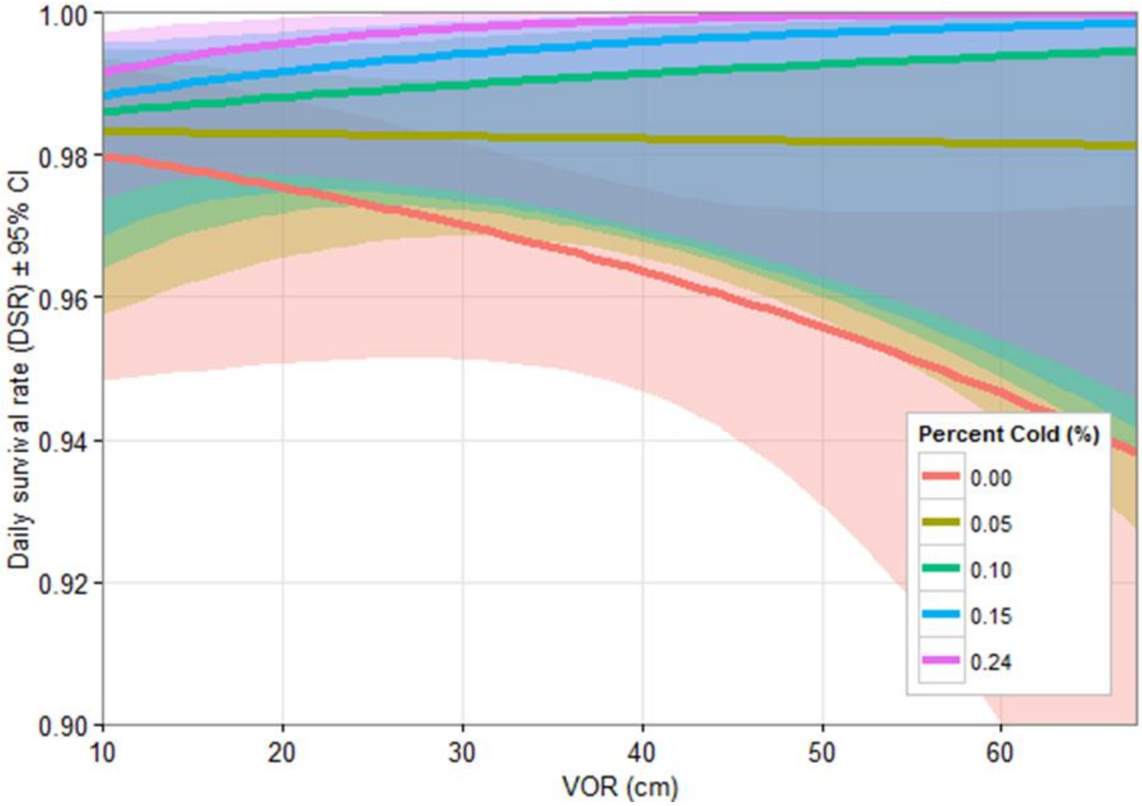


Figure 11. Means (±95% CI) of (A) Percent of T_{bb} observations below the thermal neutral zone (Percent Cold) (B) Percent of T_{bb} observations above the thermal neutral zone (Percent Hot) (C) Percent of T_{bb} observations within the thermal neutral zone (Percent Neutral) for nest and paired-random sample types during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test between sample types.

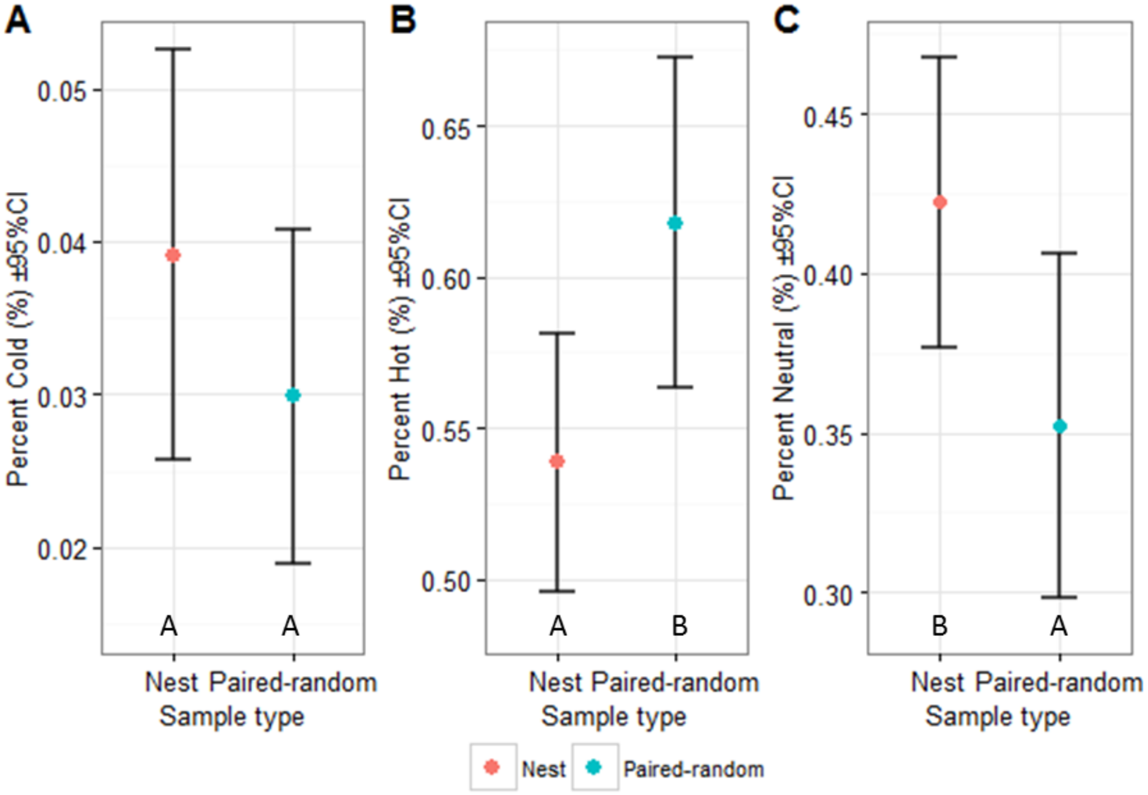


Figure 12. Means (±95% CI) of (A) Percent of T_{bb} observations below the thermal neutral zone (Percent Cold) (B) Percent of T_{bb} observations above the thermal neutral zone (Percent Hot) (C) Percent of T_{bb} observations within the thermal neutral zone (Percent Neutral) for failed and successful nest outcomes during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test between nest outcomes.

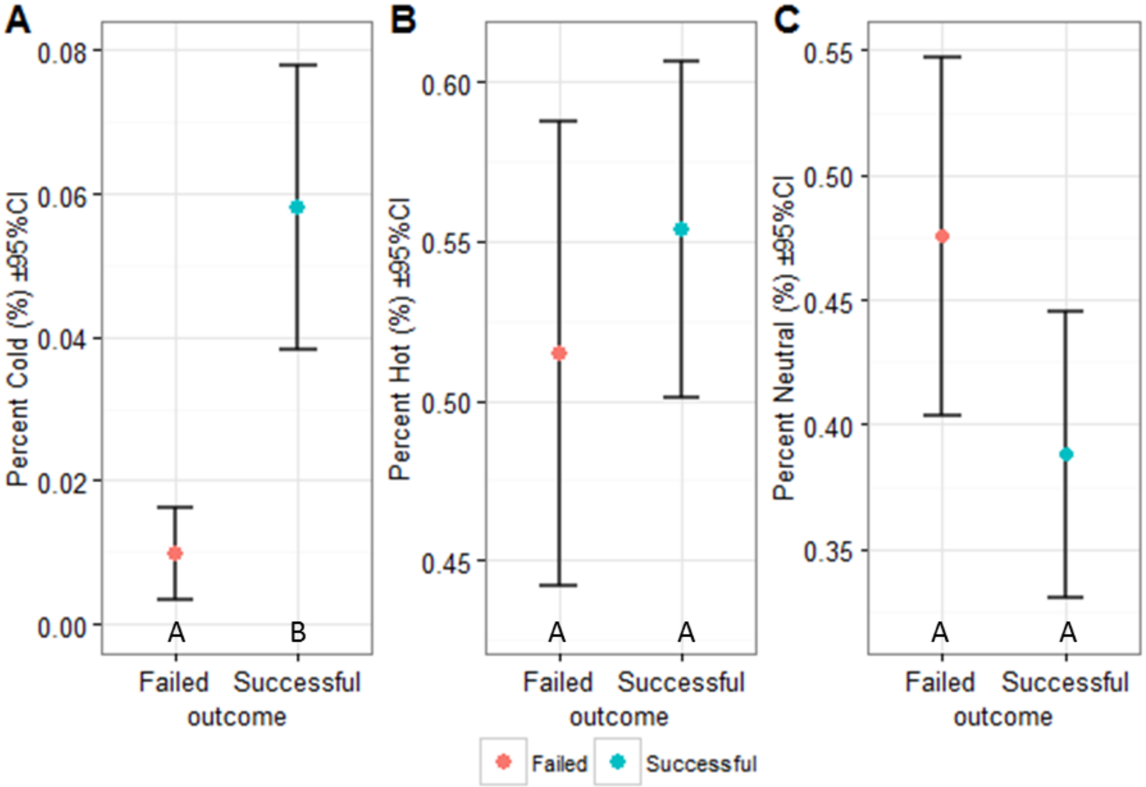
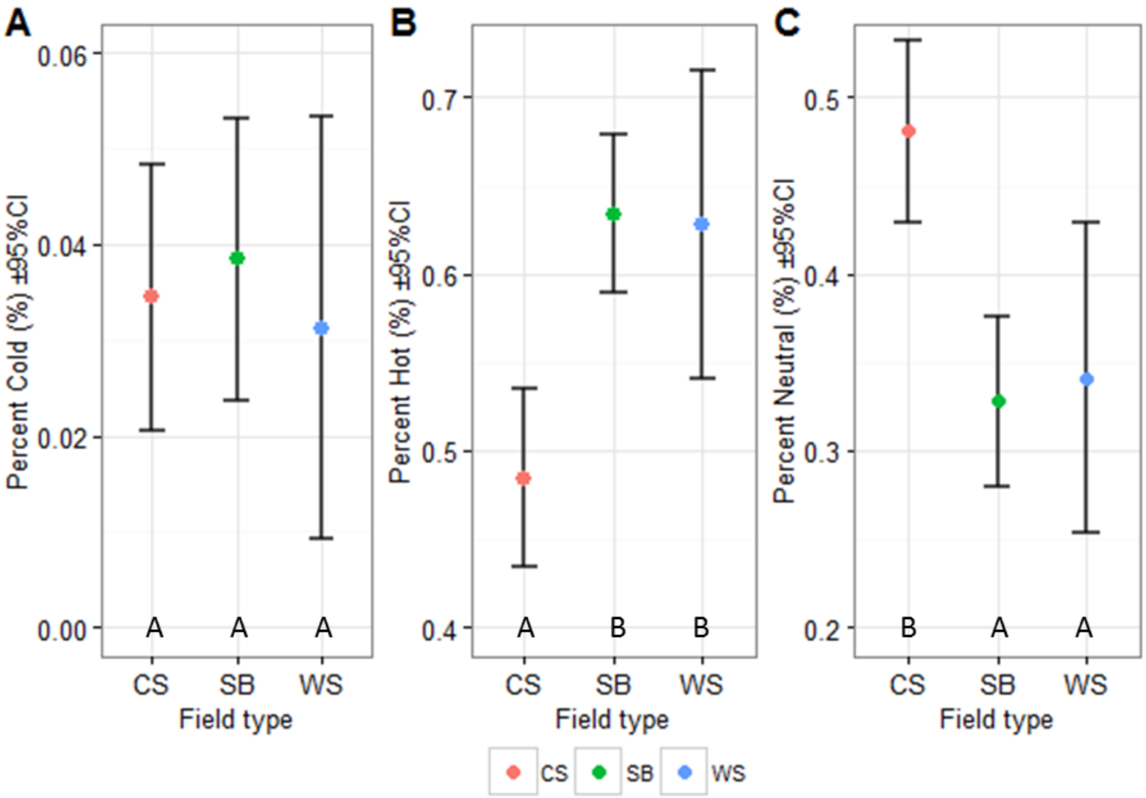
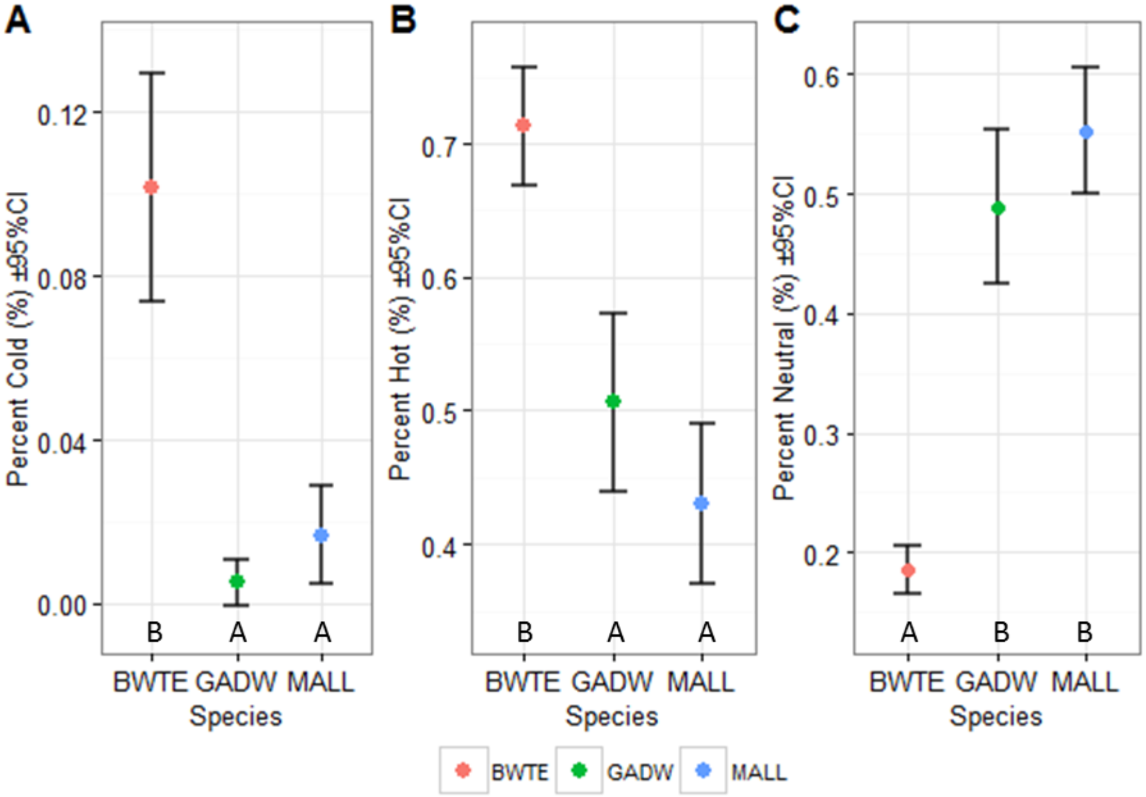


Figure 13. Means (±95% CI) of (A) Percent of T_{bb} observations below the thermal neutral zone (Percent Cold) (B) Percent of T_{bb} observations above the thermal neutral zone (Percent Hot) (C) Percent of T_{bb} observations within the thermal neutral zone (Percent Neutral) among field types during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test among each individual field type pair.



CS = Cool season
SB = Smooth brome
WS = Warm season

Figure 14. Means (±95% CI) of (A) Percent of T_{bb} observations below the thermal neutral zone (Percent Cold) (B) Percent of T_{bb} observations above the thermal neutral zone (Percent Hot) (C) Percent of T_{bb} observations within the thermal neutral zone (Percent Neutral) among species during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test among each individual species pair.



BWTE = blue-winged teal
GADW = gadwall
MALL = mallard

Figure 15. Least-squared means (±95% CI) of (A) vegetation density (VOR) (B) vegetation height (C) litter depth for nest and paired-random sample types during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test between sample types.

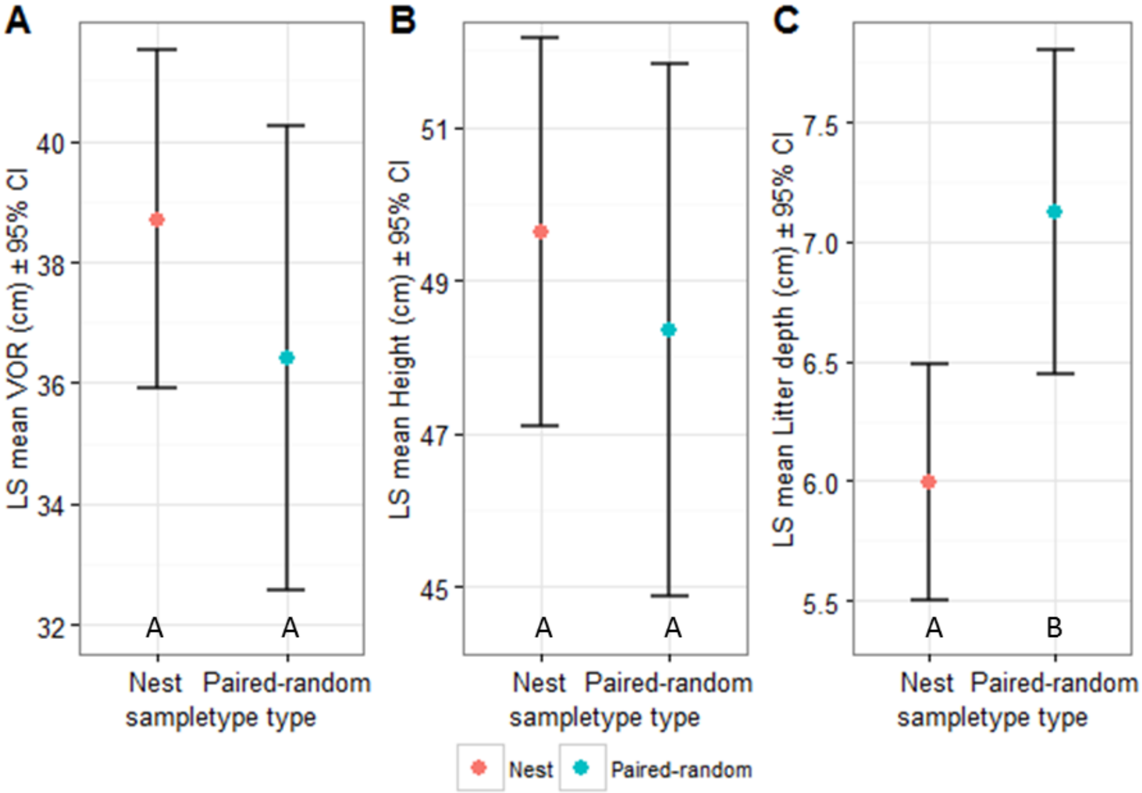


Figure 16. Least-squared means (±95% CI) of (A) vegetation density (VOR) (B) vegetation height (C) litter depth for failed and successful nest outcomes during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test between nest outcomes.

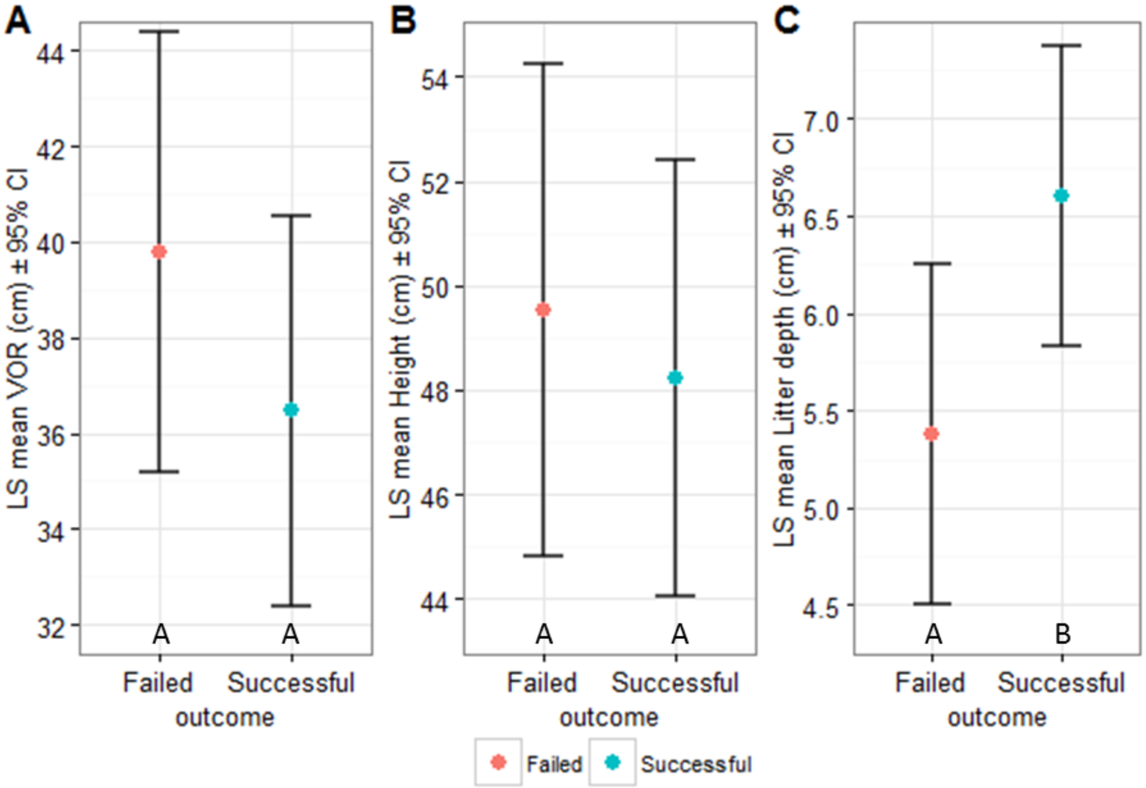
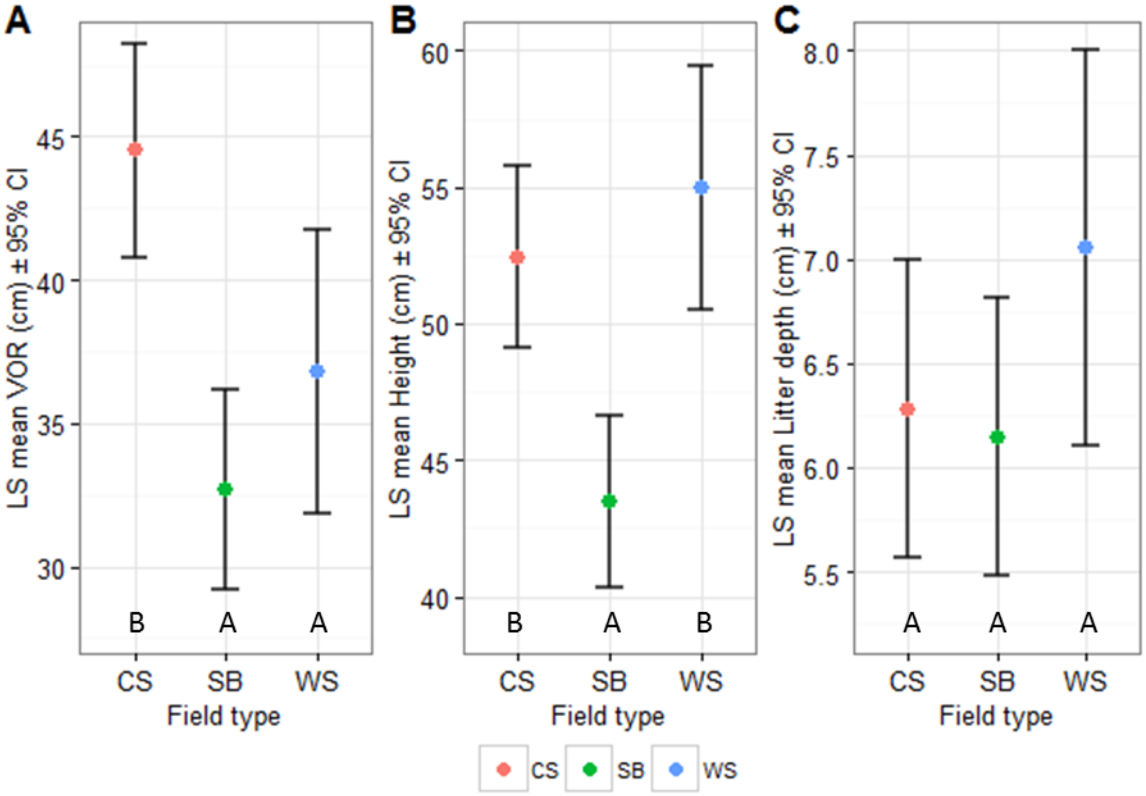
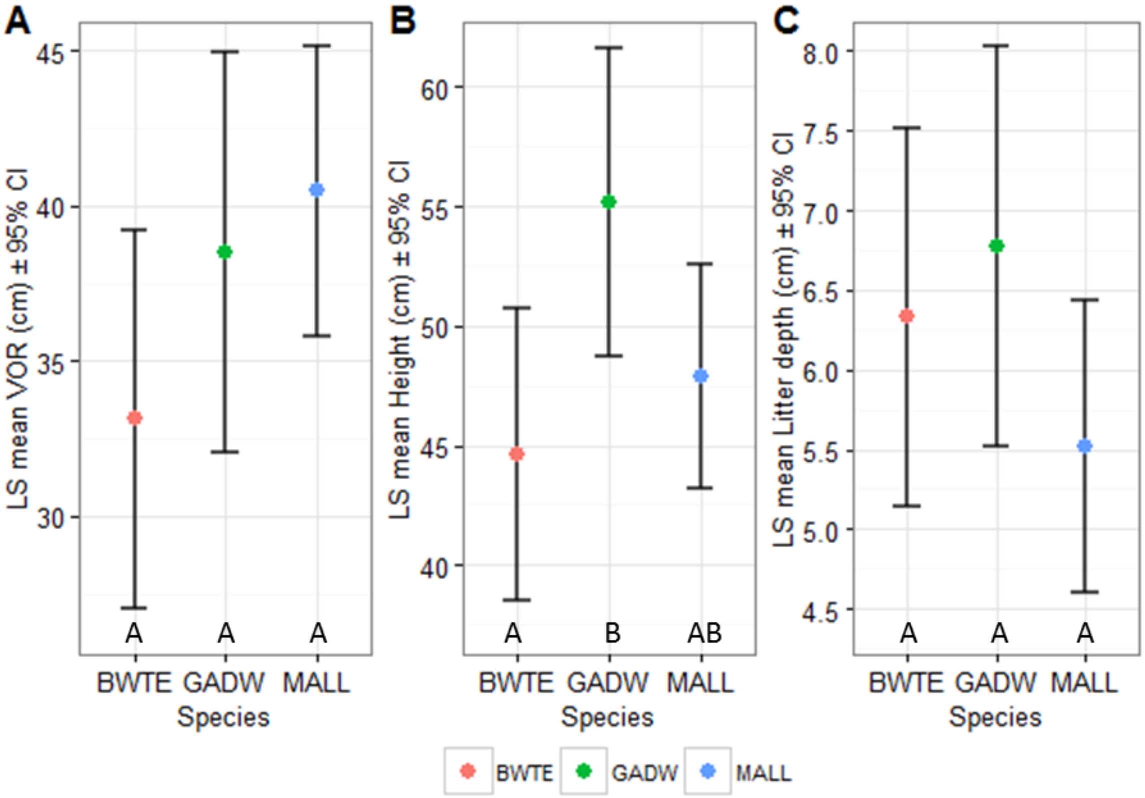


Figure 17. Least-squared means (±95% CI) of (A) vegetation density (VOR) (B) vegetation height (C) litter depth among field types during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences (*P* < 0.05) in a post hoc multiple comparisons test among each individual field type pair.



CS = Cool season
SB = Smooth brome
WS = Warm season

Figure 18. Least-squared means (±95% CI) of (A) vegetation density (VOR) (B) vegetation height (C) litter depth among species during 2015 and 2016 in eastern South Dakota. Letters below each observation represent differences ($P < 0.05$) in a post hoc multiple comparisons test among each individual species pair.



BWTE = blue-winged teal
GADW = gadwall
MALL = mallard

Table 1. Range of air temperature (T_{air}) black bulb temperature (T_{bb}) sampled from 0700 to 1900 during 2015 and 2016 in eastern South Dakota.

T_{air} range (°C)	Mean T_{bb} (°C)	SE	T_{bb} range (°C)
0–9	11.5	±0.2	1.9–21.8
10–19	16.3	±0.1	5.0–32.2
20–29	25.2	±0.0	10.0–42.1
30–39	35.8	±0.0	18.3–53.0
40–49	44.6	±0.1	24.5–57.7
50–58	48.8	±0.9	39.5–54.8

Table 2. Model summary describing black bulb temperature (T_{bb}) during 2015 and 2016 in eastern South Dakota. Covariates are air temperature (T_{air}), solar radiation (S_{rad}), vegetation density (VOR) and wind speed (Wind).

Variable	β	SE	95% LCL	95% UCL	*F*	*P*
Intercept	0.02	0.01	0.00	0.05	667.45	≤ 0.001
T_{air}	0.56	0.00	0.55	0.57	124672.78	≤ 0.001
S_{rad}	0.39	0.00	0.39	0.40	13644.45	≤ 0.001
VOR	-0.05	0.01	-0.06	-0.03	41.74	≤ 0.001
Wind	0.02	0.00	0.02	0.03	32.25	≤ 0.001
$T_{air}\times S_{rad}$	0.08	0.00	0.08	0.08	825.97	≤ 0.001
$T_{air}\times$VOR	-0.07	0.00	-0.07	-0.06	501.59	≤ 0.001
Wind×VOR	0.01	0.00	0.01	0.02	28.40	≤ 0.001

Table 3. Black bulb temperature (T_{bb}) summaries for sample type, nest outcome, and field type models during 2015 and 2016 in eastern South Dakota.

Model	Group	Mean T_{bb} (°C)	SE	Range (°C)
Sample type**	Nest	29.7	±0.1	1.9–57.6
	Paired-random	31.5	±0.1	3.4–57.3
Nest Outcome	Failed	30.0	±0.1	4.8–53.4
	Successful	29.6	±0.1	1.9–57.6
Field type	Cool season	28.9	±0.1	1.9–54.2
	Smooth brome	31.5	±0.1	4.5–57.6
	Warm season	31.5	±0.1	4.9–57.3

*** Indicates significance at $P < 0.001$

** Indicates significance at $P < 0.01$

* Indicates significance at $P < 0.05$

Table 4. Model summary describing black bulb temperature (T_{bb}) at nest and paired-random sample types during 2015 and 2016 in eastern South Dakota. Covariates are sample type (Type), air temperature (T_{air}), and solar radiation (S_{rad}).

Variable	β	SE	95% LCL	95% UCL	*F*	*P*
Intercept	-0.09	0.03	-0.14	-0.03	133.59	$\leq$ 0.001
Type2[a]	0.10	0.04	0.03	0.18	7.68	0.006
T_{air}	0.54	0.01	0.51	0.57	30238.15	$\leq$ 0.001
S_{rad}	0.36	0.01	0.34	0.38	3259.55	$\leq$ 0.001
Type2×T_{air}	0.00	0.02	-0.04	0.05	107.31	$\leq$ 0.001
Type2×S_{rad}	0.10	0.02	0.07	0.13	42.17	$\leq$ 0.001
Tair×S_{rad}	0.08	0.01	0.07	0.09	199.45	$\leq$ 0.001

[a] Type2 denotes paired-random, nest included in intercept

Table 5. Model summary describing black bulb temperature (T_{bb}) at failed and successful nests during 2015 and 2016 in eastern South Dakota. Covariates are nest fate (Outcome), air temperature (T_{air}), and solar radiation (S_{rad}).

Variable	*β*	SE	95% LCL	95% UCL	*F*	*P*
Intercept	-0.06	0.04	-0.15	0.03	42.99	≤ 0.001
Outcome1[a]	-0.02	0.06	-0.13	0.09	2.11	0.150
T_{air}	0.53	0.03	0.48	0.58	14916.14	≤ 0.001
S_{rad}	0.36	0.02	0.32	0.39	1425.28	≤ 0.001
Outcome1×T_{air}	0.00	0.03	-0.06	0.06	5.86	0.016
Outcome1×S_{rad}	0.02	0.02	-0.02	0.07	1.80	0.179
S_{rad}×T_{air}	0.06	0.01	0.05	0.08	64.96	≤ 0.001

[a] Outcome1 denotes successful nests, failed nests included in intercept

Table 6. Model summary describing black bulb temperature (T_{bb}) among field types during 2015 and 2016 in eastern South Dakota. Covariates are field type (Field), air temperature (T_{air}), and solar radiation (S_{rad}).

Variable	*β*	SE	95% LCL	95% UCL	*F*	*P*
Intercept	-0.04	0.02	-0.08	0.00	571.70	≤ 0.001
FieldSB[a]	0.10	0.03	0.05	0.16	9.00	≤ 0.001
FieldWS[b]	0.07	0.03	0.02	0.13		
T_{air}	0.43	0.01	0.41	0.44	127957.90	≤ 0.001
S_{rad}	0.42	0.01	0.41	0.43	13988.22	≤ 0.001
FieldSB×T_{air}	0.13	0.01	0.11	0.16	481.44	≤ 0.001
FieldWS×T_{air}	0.22	0.01	0.20	0.24		
FieldSB×S_{rad}	0.05	0.01	0.04	0.07	257.25	≤ 0.001
FieldWS×S_{rad}	-0.09	0.01	-0.11	-0.08		
Tair×S_{rad}	0.06	0.00	0.05	0.06	632.35	≤ 0.001

[a] FieldSB denotes smooth brome, cool season included in intercept

[b] FieldWS denotes warm season

Table 7. Black bulb temperature (T_{bb}) summaries for vegetation density (VOR), height, and litter depth models during 2015 and 2016 in eastern South Dakota.

Model	Value (cm)	Mean T_{bb} (°C)	SE	Range (°C)
VOR***	10	30.2	±1.8	9.1–51.2
	15	30.0	±1.7	9.5–50.5
	30	29.5	±1.6	10.9–48.2
	45	29.1	±1.4	12.1–46.0
	93	27.6	±1.0	16.2–38.9
Height***	0	30.5	±1.9	7.4–53.6
	30	29.9	±1.7	10.1–49.7
	40	29.6	±1.6	11.1–48.2
	50	29.5	±1.5	11.9–47.0
	110	28.4	±1.0	16.4–40.4
Litter depth	0	29.7	±1.4	12.5–46.8
	3	29.5	±1.5	11.7–47.4
	6	29.5	±1.5	11.2–47.7
	9	29.4	±1.6	10.9–47.9
	22	29.0	±1.7	8.6–49.5

*** Indicates significance at $P < 0.001$
** Indicates significance at $P < 0.01$
* Indicates significance at $P < 0.05$

Table 8. Model summary describing black bulb temperature (T_{bb}) as a function vegetation density during 2015 and 2016 in eastern South Dakota. Covariates are vegetation density (VOR), air temperature (T_{air}), and solar radiation (S_{rad}).

Variable	β	SE	95% LCL	95% UCL	*F*	*P*
Intercept	0.02	0.01	0.00	0.05	670.31	≤ 0.001
T_{air}	0.56	0.00	0.55	0.57	124127.93	≤ 0.001
VOR	-0.05	0.01	-0.06	-0.04	127.41	≤ 0.001
S_{rad}	0.40	0.00	0.39	0.41	13497.96	≤ 0.001
T_{air}×VOR	-0.06	0.00	-0.07	-0.05	161.94	≤ 0.001
S_{rad}×VOR	0.00	0.00	0.00	0.01	105.51	≤ 0.001
T_{air}×S_{rad}	0.08	0.00	0.07	0.08	989.79	≤ 0.001

Table 9. Model summary describing black bulb temperature (T_{bb}) as a function vegetation height during 2015 and 2016 in eastern South Dakota. Covariates are vegetation height (Height), air temperature (T_{air}), and solar radiation (S_{rad}).

Variable	*β*	SE	95% LCL	95% UCL	*F*	*P*
Intercept	0.03	0.01	0.01	0.06	590.68	≤ 0.001
Tair	0.56	0.00	0.55	0.57	123848.08	≤ 0.001
Height	-0.04	0.01	-0.05	-0.02	65.50	≤ 0.001
Srad	0.40	0.00	0.40	0.41	13511.65	≤ 0.001
Tair×Height	-0.06	0.00	-0.07	-0.05	73.66	≤ 0.001
Srad×Height	0.01	0.00	0.00	0.01	207.92	≤ 0.001
Tair×Srad	0.08	0.00	0.07	0.08	898.44	≤ 0.001

Table 10. Model summary describing black bulb temperature (T_{bb}) as a function litter depth during 2015 and 2016 in eastern South Dakota. Covariates are litter depth (Litter), air temperature (T_{air}), and solar radiation (S_{rad}).

Variable	β	SE	95% LCL	95% UCL	*F*	*P*
Intercept	0.02	0.01	0.00	0.04	590.31	≤ 0.001
T_{air}	0.55	0.00	0.54	0.56	123050.50	≤ 0.001
Litter	-0.01	0.00	-0.02	0.00	1.84	0.175
S_{rad}	0.40	0.00	0.40	0.41	13486.89	≤ 0.001
T_{air}×Litter	0.02	0.00	0.01	0.02	112.98	≤ 0.001
S_{rad}×Litter	-0.04	0.00	-0.04	-0.03	223.84	≤ 0.001
T_{air}×S_{rad}	0.06	0.00	0.05	0.06	650.82	≤ 0.001

Table 11. Model selection results, including delta AIC_c, AIC_c weights (w_i) and number of parameters (K), used to evaluate factors affecting DSR of duck nests among field types during 2015 and 2016 in eastern South Dakota. Covariates are percent of T_{bb} observations below the thermal neutral zone (PercentCold), litter depth (Litter), and vegetation density (VOR).

Model	AIC_c	Δ AIC_c	w_i	K
PercentCold	156.70	0.00	0.28	2
PercentCold+Litter	157.44	0.74	0.19	3
PercentCold+VOR	157.95	1.25	0.15	3
PercentCold:Litter+Litter	158.68	1.99	0.10	3
PercentCold:VOR+VOR	158.88	2.18	0.09	3
PercentCold×Litter	159.33	2.63	0.08	4
PercentCold×VOR	159.96	3.26	0.06	4

Table 12. Model summaries used to evaluate DSR among field types in 2015 and 2016 in eastern South Dakota. Covariates are percent of T_{bb} observations below the thermal neutral zone (PercentCold), litter depth (Litter), and vegetation density (VOR).

Model	Parameter	*β*	SE	95% LCL	95% UCL	*P*
PercentCold	Intercept***	3.25	0.21	2.84	3.66	≤ 0.001
	PercentCold*	15.32	6.91	1.78	28.86	0.027
PercentCold+Litter	Intercept***	2.62	0.59	1.46	3.77	≤ 0.001
	PercentCold*	15.03	6.84	1.62	28.44	0.028
	Litter	0.10	0.09	-0.08	0.27	0.267
PercentCold+VOR	Intercept***	3.82	0.67	2.51	5.12	≤ 0.001
	PercentCold*	14.51	6.88	1.03	28.00	0.035
	VOR	-0.01	0.02	-0.04	0.02	0.359
PercentCold:Litter+Litter	Intercept***	2.81	0.59	1.66	3.96	≤ 0.001
	Litter	0.07	0.09	-0.10	0.25	0.420
	PercentCold:Litter*	2.13	1.07	0.03	4.23	0.046
PercentCold:VOR+VOR	Intercept***	4.09	0.66	2.80	5.37	≤ 0.001
	VOR	-0.02	0.02	-0.05	0.01	0.181
	PercentCold:VOR	0.37	0.19	0.00	0.74	0.053
PercentCold×Litter	Intercept***	2.52	0.63	1.29	3.75	≤ 0.001
	PercentCold	23.32	20.61	-17.07	63.72	0.258
	Litter	0.11	0.10	-0.07	0.30	0.233
	PercentCold×Litter	-1.25	2.78	-6.70	4.20	0.652
PercentCold×VOR	Intercept***	3.74	0.73	2.31	5.16	≤ 0.001
	PercentCold	19.61	20.66	-20.88	60.10	0.342
	VOR	-0.01	0.02	-0.05	0.02	0.478
	PercentCold×VOR	-0.14	0.50	-1.13	0.85	0.786

*** Indicates significance at $P < 0.001$
** Indicates significance at $P < 0.01$
* Indicates significance at $P < 0.05$

Table 13. Kruskal-Wallace chi-squared results including mean, SE, χ^2, *P* value and multiple comparisons group for differences ($P < 0.05$) in percent of black bulb temperature (T_{bb}) observations below the thermal neutral zone (PercentCold), above the thermal neutral zone (PercentHot), and within the thermal neutral zone (PercentNeutral) during 2015 and 2016 in eastern South Dakota. Models include sample type (Type), nest fate (Outcome), field type (Field), and species.

Model	Variable	Group	Mean	SE	χ^2	*P*	Group
Type	PercentCold	Nest	0.04	±0.01	0.11	0.736	A
		Paired-random	0.03	±0.01			A
	PercentHot	Nest	0.54	±0.02	6.71	0.010	A
		Paired-random	0.62	±0.03			B
	PercentNeutral	Nest	0.42	±0.02	4.04	0.045	B
		Paired-random	0.35	±0.03			A
Outcome	PercentCold	Failed	0.01	±0.00	9.15	0.002	A
		Successful	0.06	±0.01			B
	PercentHot	Failed	0.51	±0.04	0.94	0.333	A
		Successful	0.55	±0.03			A
	PercentNeutral	Failed	0.48	±0.04	3.23	0.072	A
		Successful	0.39	±0.03			A
Field	PercentCold	Cool season	0.03	±0.01	0.26	0.879	A
		Smooth brome	0.04	±0.01			A
		Warm season	0.03	±0.01			A
	PercentHot	Cool season	0.48	±0.03	16.60	≤ 0.001	A
		Smooth brome	0.63	±0.02			B
		Warm season	0.63	±0.04			B
	PercentNeutral	Cool season	0.48	±0.03	18.80	≤ 0.001	B
		Smooth brome	0.33	±0.02			A
		Warm season	0.34	±0.04			A
Species	PercentCold	BWTE	0.10	±0.01	37.77	≤ 0.001	B
		GADW	0.01	±0.00			A
		MALL	0.02	±0.01			A
	PercentHot	BWTE	0.71	±0.02	30.31	≤ 0.001	B
		GADW	0.51	±0.03			A
		MALL	0.43	±0.03			A
	PercentNeutral	BWTE	0.18	±0.01	48.05	≤ 0.001	A
		GADW	0.49	±0.03			B
		MALL	0.55	±0.03			B

BWTE = blue-winged teal
GADW = gadwall
MALL = mallard

Table 14. ANOVA results including least-squared means, SE, *F* value, *P* value and Tukey multiple comparison group for differences ($P < 0.05$) in vegetation density (cm; VOR), vegetation height (cm; Height) and litter depth (cm) during 2015 and 2016 in eastern South Dakota. Models include sample type (Type), nest fate (Outcome), field type (Field), and species.

Model	Variable	Group	LS Mean	SE	*F*	P	Group
Type	VOR	Nest	38.71	±1.24	1.2	0.274	A
		Paired-random	36.40	±1.70			A
	Height	Nest	49.64	±1.12	0.45	0.503	A
		Paired-random	48.36	±1.55			A
	Litter depth	Nest	6.00	±0.22	9.15	0.003	A
		Paired-random	7.12	±0.30			B
Outcome	VOR	Failed	39.77	±2.03	1.49	0.226	A
		Successful	36.47	±1.80			A
	Height	Failed	49.55	±2.08	0.23	0.633	A
		Successful	48.21	±1.84			A
	Litter depth	Failed	5.38	±0.38	5.70	0.019	A
		Successful	6.60	±0.34			B
Field	VOR	Cool season	44.52	±1.54	15.89	≤ 0.001	B
		Smooth brome	32.67	±1.44			A
		Warm season	36.82	±2.05			A
	Height	Cool season	52.44	±1.39	17.27	≤ 0.001	B
		Smooth brome	43.48	±1.30			A
		Warm season	55.00	±1.85			B
	Litter depth	Cool season	6.28	±0.30	1.89	0.154	A
		Smooth brome	6.15	±0.28			A
		Warm season	7.06	±0.39			A
Species	VOR	BWTE	33.13	±2.50	2.74	0.07	A
		GADW	38.50	±2.65			A
		MALL	40.48	±1.93			A
	Height	BWTE	44.64	±2.51	4.39	0.015	A
		GADW	55.20	±2.66			B
		MALL	47.87	±1.94			AB
	Litter depth	BWTE	6.33	±0.49	2.15	0.122	A
		GADW	6.78	±0.52			A
		MALL	5.52	±0.38			A

BWTE = blue-winged teal
GADW = gadwall
MALL = mallard