IMPACTS OF WEATHER, HABITAT, AND REPRODUCTION ON THE SURVIVAL AND PRODUCTIVITY OF WILD TURKEYS IN THE NORTHERN BLACK HILLS, SOUTH DAKOTA

by

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ABSTRACT

The study of population ecology is motivated by a desire to understand variation in the factors that drive wildlife population dynamics. Robust vital rate estimates are crucial for effective wildlife conservation and management, particularly for at-risk or harvested species. In avian populations, the survival of females, nests, and young are important drivers of population growth, although the relative importance of each rate can differ among species. Annual and regional variation in vital rates within species is common; further, local climatic and habitat conditions may influence population dynamics. During 2016 – 2018, we used radio telemetry to study the impacts of weather and habitat conditions on the survival and productivity of Merriam's wild turkeys (*Meleagris gallopavo merriami*) in the northern Black Hills of South Dakota. Specifically, we quantified the impacts of 1) precipitation and reproductive effort on hen survival, 2) precipitation and habitat conditions on nest survival, and 3) precipitation and temperature on early poult survival. Precipitation reduced the survival of hens and nests, although the magnitude depended on the hen's incubation status or the vegetation characteristics at the nest site. Based on precipitation data from 2017, the estimated annual survival rate for a hen that did not incubate was 0.535 (SE = 0.038), whereas that and for a hen that incubated for 26 days was 0.436 (SE = 0.054). The probability that a nest would survive from initiation to hatching for a nest initiated by an adult hen on the median date of nest incubation in 2017 was estimated to be 0.432 (SE = 0.084). The estimated probability that a poult would survive from hatching to 4 weeks of age was 0.387 (SE = 0.061). Our results clearly demonstrate a negative cost of reproduction, as predicted by life-history theory, and show that hens and nests in this ecosystem are more vulnerable to predation during or immediately following rainfall, as predicted by the moisture-facilitated nest-predation hypothesis. Survival and productivity of turkeys was lower in our study area than in other portions of the Black Hills; we recommend that managers take steps to limit human-induced hen mortality of this important game species.

CHAPTER ONE

INTRODUCTION TO THESIS

Understanding variation in population vital rates is a principal motivation in the study of population ecology. Additionally, robust estimates of vital rates help wildlife managers best allocate limited resources and is crucial for effective wildlife conservation and management, particularly for populations of at-risk or harvested species. In avian populations, the survival of females, nests, and young are important drivers of variation in population growth, although the relative importance can differ among species (Hoekman et al. 2002, Sandercock et al. 2008, Taylor et al. 2012, Pollentier et al. 2014*a*). Influences of climatic factors and habitat conditions on avian populations dynamics are well documented, but relationships are complex and have been shown to differ by region or year (e.g., Roberts and Porter 1998*a*, Lehman et al. 2008*b*, Webb et al. 2012, Fogarty et al. 2017, Lavoie et al. 2017). Additionally, life history traits that vary among species may act in concert with other biotic and abiotic elements to influence population growth (Stearns 1992, Roberts et al. 1995, Caudill et al. 2014). Further study of these complicated relationships serves to improve both wildlife management strategies and our understanding of life history evolution.

The wild turkey (*Meleagris gallopavo*) is a gallinaceous bird represented by 5 subspecies in North America: the eastern (*M. g. silvestris*), Florida (*M. g. osceola*), Rio Grande (*M. g. intermedia*), Gould's (*M. g. mexicana*), and Merriam's (*M. g. merriami*) (Schorger 1967, Williams 1981, Kennamer et al. 1992). Turkeys experienced a precipitous decline in numbers and range following European settlement due to a combination of overharvest and habitat degradation (Schorger 1967, Kennamer et al. 1992). Early attempts to reestablish turkey populations from birds raised on game farms were largely unsuccessful (Kennamer et al. 1992). However, widespread trap-and-transfer efforts generally were more successful at reintroducing wild turkeys to their native range, and even introduced the species to new areas (Williams 1981, Kennamer et al. 1992).

Merriam's wild turkeys (*M. g. merriami*) originally were found in Colorado, New Mexico, Arizona, Oklahoma, and possibly western Texas (Schorger 1967) and were introduced to the Black Hills of South Dakota beginning in the late 1940s. Wild turkeys are indigenous to the state with the eastern turkey (*M. g. silvestris*) endemic range occurring from southeastern South Dakota west to the mouth of the Cheyenne and Missouri river systems (Grinnell 1910, Mosby 1975). Today, turkeys are a popular game species in South Dakota, with most hunter opportunity in the Black Hills (Flake et al. 2006). Managers use a variety of vital rates data, including hen, nest, and poult survival rates to inform management, yet these rates are based on demographic data collected in the southern and central Black Hills (Rumble and Hordorff 1993, Rumble et al. 2003 Lehman 2005, Lehman et al. 2008*a*, Lehman et al. 2008*b*). Dynamics of turkey populations may differ substantially even between locations in close proximity (Collier et al. 2009, Pollentier et al. 2014*a*, *b*) and the climate and vegetation vary substantially throughout the Black Hills (Flake et al. 2006). Crucially, the northern Black Hills receives substantially more winter snowfall and spring rain than the central or southern

Black Hills; approximately half of annual precipitation in the northern Black Hills falls during late winter and early spring. As a result, turkey population growth and the underlying vital rates in the northern Black Hills might differ greatly from what was measured farther south.

We worked to provide managers with estimates of vital rates that are needed to develop region-specific management strategies for a species of economic and cultural significance. Additionally, we sought add to the body of knowledge regarding the impacts of reproductive tradeoffs, weather conditions, and habitat on gallinaceous bird populations. In Chapter 2, we use radio telemetry data to quantify relationships between hen survival, reproductive effort, and weather conditions. In Chapter 3, we characterize relationships between weather, habitat conditions, and turkey reproduction. Specifically, we explore how precipitation, nesting cover, and predation combine to impact nest survival and how temperature, precipitation and predation affect poult survival. In both chapters, we make comparisons between our study area and other portions of the Black Hills and discuss the implications for turkey population productivity.

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CHAPTER TWO

PRECIPITATION AND REPRODUCTIVE EFFORT COMBINE TO ALTER SURVIVAL OF WILD TURKEY HENS IN THE NORTHERN BLACK HILLS, SD

Contribution of Authors and Co-Authors

Manuscript in Chapter 2

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Contributions: Implemented the study, collected and analyzed the data, wrote the manuscript

Co-Author: Andrea R. Litt

Contributions: Guided study design, helped secure funding, assisted with data analysis, extensive review of manuscript

Co-Author: Chad P. Lehman

Contributions: Conceived initial study idea, secured funding, guided study design, assisted with data collection, reviewed the manuscript

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Precipitation and Reproductive Effort Combine to Alter Survival of Wild Turkey Hens in the Northern Black Hills, SD

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ABSTRACT Tradeoffs between survival and reproduction are predicted by life history theory. Understanding how reproductive tradeoffs act in concert with abiotic elements to impact survival is crucial for effective management and conservation of wildlife populations, particularly for at-risk or harvested species. Wild turkeys (*Meleagris gallopavo*) are a high-interest species for both consumptive and non-consumptive uses, and hen survival is an important driver of turkey population dynamics. During 2016 – 2018, we radio-tracked and collected survival data on 140 Merriam's wild turkey (*M. g. merriami*) hens in the northern Black Hills, South Dakota. We developed and compared a set of candidate models to evaluate the impact of nest incubation, brood rearing, and precipitation during spring and summer on hen survival. Consistent with life-history theory, increased time spent incubating was associated with reduced hen survival.

Additionally, there was some evidence that daily precipitation amount was associated with reduced survival of incubating hens, as predicted by the moisture-facilitated nest-depredation hypothesis. Seasonal survival was lowest during spring and winter. A hen that did not incubate a nest was predicted to have a higher rate of annual survival (0.54, 95% CI = 0.46 – 0.61) than a hen that incubated a single nest (0.44, 95% CI = 0.33–0.55); this prediction is based on precipitation data collected in 2017 and assumes the hen began incubation on the median date. Despite the relative proximity of population segments, we estimated that annual survival for both nesting and non-nesting hens was lower in the northern Black Hills compared to annual hen survival in the southern Black Hills, underscoring the need to inform turkey management with region-specific information whenever possible. Management options to improve hen survival are limited, but we recommend management actions that would reduce hunter-induced hen mortality of this important game species in the northern Black Hills.

KEY WORDS Black Hills, hen survival, *Meleagris gallopavo*, nest survival model, precipitation, wild turkey

Life-history theory predicts trade-offs between survival and reproduction due to competing demands on finite resources (Williams 1966, Stearns 1992). Current reproduction may place costs on current or future survival (Reznick 1985, Stearns 1992, Collier et al. 2009, Blomberg et al. 2013), as well as on the chance of future reproduction (Stearns 1992). Mortality in reproductive individuals can have two effects at the population level: reduced population size and the loss of individuals that could produce offspring. Understanding how reproductive tradeoffs act in concert with abiotic elements is crucial for effective management and conservation of wildlife populations, particularly for at-risk or harvested species.

Hen survival is an important driver of population dynamics for gallinaceous birds (Jarvis and Simpson 1978, Sandercock et al. 2008, Taylor et al. 2012). Reductions in female survival associated with egg production, incubation, or brood rearing have been well documented in many galliform species, including willow ptarmigan (*Lagopus lagopus*) (Hannon et al. 2003), lesser prairie-chickens (*Tympanuchus pallidicinctus*) (Hagen et al. 2007), greater sage grouse (*Centrocercus urophasianus*) (Blomberg et al. 2013), and wild turkeys (*Meleagris gallopavo*) (Collier et al. 2009). However, the impact of mortalities during each reproductive stage on population dynamics may vary by species and location. For wild turkeys in Texas, increased time spent incubating reduced survival during the breeding season (Collier et al. 2009). Similarly, lesser prairie-chickens females that tended nests had lower survival rates than did than non-nesting females (Hagen et al. 2007). Both nest success and brood-rearing success were associated with reduced survival of female sage grouse following the completion of nesting or brood rearing. However, the impact of nest success on future survival during the summer was less than the impact of brood rearing success on future survival during the fall (Blomberg et al. 2013). Other studies have noted reduced survival during nesting or brood rearing, but have been limited in their investigation of the magnitude of reproductive costs (e.g., Vander Haegen et al. 1988, Roberts et al. 1995, Hannon et al. 2003).

Climatic factors also may work in combination with reproductive effort to influence population growth (Caudill et al. 2014). Over shorter time frames, weather conditions, including temperature, snow depth, and rainfall also can influence hen survival (Porter et al. 1980, Rumble et al. 2003, Lavoie et al. 2017). Temperature impacts metabolism (Haroldson et al. 1998), and snow reduces movement ability (Vander Haegen et al. 1989) and limits access to food (Vander Haegen et al. 1989, Lehman 2005). In ground-nesting birds, increased precipitation can exacerbate costs of reproduction by increasing hen and nest predation by mammals, perhaps because predators are able to more effectively locate nesting hens via olfaction during or immediately following rain events (Roberts et al. 1995, Lehman et al. 2008, Webb et al. 2012).

The wild turkey is a gallinaceous bird that experienced a precipitous decline in numbers and range following European settlement due to a combination of overharvest and habitat degradation (Schorger 1967, Kennamer et al. 1992). Early attempts to reestablish turkey populations from birds raised on game farms were largely unsuccessful (Kennamer et al. 1992). However, widespread trap-and-transfer efforts that began in the 1940s and 1950s generally were more successful (Williams 1981, Kennamer et al. 1992). In a relatively short time, turkey populations were reestablished in states where they had been absent for decades. Reintroductions, as well as introductions beyond the native range of wild turkeys, continued into the 21st century (Flake et al. 2006).

Merriam's wild turkeys (*M. g. merriami*) originally were found associated with ponderosa pine (*Pinus ponderosa*) communities in Colorado, New Mexico, Arizona, Oklahoma, and possibly western Texas (Schorger 1967). Valued as a game bird, Merriam's turkeys were introduced to the Black Hills of South Dakota beginning in the late 1940s by the South Dakota Department of Game, Fish, and Parks (SDGFP) where they are prized today for both consumptive and non-consumptive uses (Flake et al. 2006). Managers use data on multiple vital rates, including hen survival, to inform harvest regulations for 3 areas in the Black Hills (northern, central, and southern). Survival data were collected for the central Black Hills from 1990-1993 (Rumble et al. 2003) and for the southern Black Hills from 2001-2003 (Lehman 2005), but currently there is a paucity of data on turkey demography in the northern Black Hills and management decisions are based on demographic data collected in the southern Black Hills. Further, dynamics of turkey populations may differ substantially even between nearby locations (Collier et al. 2009, Pollentier et al. 2014*a*,*b*). The northern portion of the Black Hills differs from the central and southern portions in terms of both climate and vegetation (Flake et al. 2006). Crucially, the northern Black Hills receives substantially more winter snowfall and spring rain than the central or southern Black Hills; approximately half of annual precipitation in the northern Black Hills falls during late winter and early spring (Figure 2.1). We thought these precipitation differences could reduce hen survival during those periods. In the southern Black Hills, seasonal survival of hens was lowest during the spring (Lehman 2005); we expected a similar pattern in our study area. Additionally, we thought winter survival might be lower in our study area due to harsher winter conditions, compared to the southern Black Hills.

We sought to quantify the relationships between hen survival, reproductive effort, and weather conditions for turkeys in the northern Black Hills. Our goal was to develop estimates of hen survival and to evaluate relationships between hen survival and key covariates that could be used to inform region-specific management decisions for wild turkeys. Specifically, we sought to determine how spring and summer precipitation, nest incubation, brood rearing, and hen age were associated with hen survival. Because our expectations about the relationships between hen survival and covariates were tightly coupled with model development, we include specific predictions below.

STUDY AREA

We completed our work in the northern portion of the Black Hills in west-central South Dakota and northeastern Wyoming. The study area (~2675 km^2, Figure 2.2) was in Lawrence, Meade, and Pennington counties in South Dakota and in Weston and Crook counties in Wyoming; most work occurred in Lawrence and southwestern Meade counties. The area was primarily Black Hills National Forest, interspersed with private land and areas managed by the Bureau of Land Management and the state of South Dakota. Elevations ranged from approximately 1000 m to 2175 m above sea level. Mean annual precipitation and temperature (1981-2010) were 77 cm and 6.9° C, respectively (National Climatic Data Center 1981-2010). Ponderosa pine (*Pinus ponderosa*) was the most common tree species, but white spruce (*Picea glauca*) also was a common conifer. Quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) were common deciduous trees, and bur oak (*Quercus macrocarpa*) was locally abundant at low elevations. Common juniper (*Juniperus communis*) was the most common understory shrub; serviceberry (*Amelanchier alnifolia*), kinnikinnik

(*Arctostaphylos uva-ursi*), beaked hazel (*Corylus cornuta*), and snowberry (*Symphoricarpos* spp.) also were common.

METHODS

Capture and Radio Telemetry

We captured wild turkeys from January through March of 2016 and 2017 using rocket nets (Thompson and Delong 1967). Turkeys were lured to netting locations using corn and oat hay. We classified hen age as juvenile (<1 year old) or adult (>1 year old) based on the presence or absence of barring in the ninth and tenth primary feathers (Williams 1961). Each hen was weighed, banded, and instrumented with an 80-g backpack-mounted VHF transmitter that was programmed to provide 3 different signals: an activity signal, a short-term non-moving (loafing) signal, and a mortality signal that activated after 8 hours without movement (Advanced Telemetry Systems, Isanti, MN). Our desired sample size was 80 hens on 1 April, split evenly between adults and juveniles. Once we reached 40 marked hens in an age class, additional hens in that age class were simply weighed, banded, and released without a transmitter.

We monitored hen survival via radio telemetry (White and Garrott 1990). The monitoring schedule varied depending on time of year and logistical constraints. From January through August 2016 and 2017, survival status of most hens was checked via homing or triangulation ≥4 days per week, except during nest incubation when hens were checked daily (see Chapter 3 for full details). During the fall monitoring season (September – December) and during January – March 2018, hen survival was monitored via aerial telemetry 1-2 times per month.

Precipitation Data

To investigate the potential association between precipitation and hen survival during the spring (April-June) and summer (July-August), we established 3 rain gauges across the study area (Figure 2.2) and recorded daily precipitation amounts at these rain gauges from 9 May to 14 August 2016 and from 18 April to 12 August 2017. We also obtained daily precipitation data from 8 National and Oceanic and Atmospheric Administration weather stations (National Climatic Data Center 2016-2017) from 1 April to 31 August in 2016 and 2017. On days when an observation was not available at a rain gauge/weather station, we replaced the missing value with the observation from the next closest gauge/station.

Because patterns of precipitation in the Black Hills can vary spatially, we assigned each hen to a weather station or rain gauge during April – August in each year so daily precipitation amounts could be used as a time-varying individual covariate in the survival analysis. For nesting hens, we selected the weather station nearest the hen's nest. For hens that did not nest, we manually assigned each hen a weather station based on records of each hen's location during each field season using a GIS (ArcMap 10.5.1, Environmental Systems Research Institute, Inc., Redlands, CA, USA). Although assigning each hen a single weather location from April – August is a simplification of hen movements, we viewed this practice as reasonable because hens localized their movements after dispersal from wintering locations.

Logistical constraints prevented us from checking rain gauges at exactly the same time each day, and observation times also varied or were not available for some weather stations. As a result, each daily precipitation record corresponded to ~24 hours. Although we recognized that this could limit our ability to detect patterns between hen survival and precipitation, we considered our data a reasonable approximation of conditions.

Survival Analysis

We estimated survival of all hens that lived for more than 7 days post-capture. We excluded hens that died within the first week following capture to avoid biases due to mortalities that may have been capture related.

Because hen survival was not monitored in equal-length time intervals, we used the nest survival model for ragged telemetry data instead of a known-fate analysis (Dinsmore et al. 2002, Rotella et al. 2004). The minimum data requirements for the nest survival model are: the date the hen was captured and released (FirstFound), the date the hen was checked alive (LastPresent), the date the hen was last checked (LastChecked), and the hen's Fate (0 = alive and 1 = dead). We estimated daily survival rates (DSR) of hens using Program MARK (White and Burnham 1999) via RMark (Laake 2013) in Program R (R Development Core Team 2013).

We used an information-theoretic approach (Burnham and Anderson 2002) to compare 52 candidate models that explored potential impacts of nest incubation, brood-rearing behavior, spring and summer precipitation, and age on hen survival (Table 2.1). In all but 4 simple models, we allowed survival to vary seasonally between the following periods: Winter (1 December – 31 March), Spring (1 April – 30 June), Summer (1 July – 31 August), and Fall (1 September – 30 November). We chose to include these periods *a* *priori* because they align with weather as well as the seasonal behavior and food requirements of wild turkeys in the Black Hills (Flake et al. 2006). We also established annual periods from 1 December – 30 November; we included these annual periods in some models to test for differences in hen survival between years (Table 2.1). When evaluating model-selection results, we considered a parameter uninformative when its addition resulted in an AIC_c score ~2 units larger than a model without it (Burnham and Anderson 2002, Arnold 2010).

Because reproduction in game birds can potentially be costly to hen survival (Collier et al. 2009, Blomberg et al. 2013), we examined the influence of nest incubation and brood-rearing behaviors on hen survival. For models that included incubation, we utilized a time-varying individual covariate to indicate whether a hen was incubating a nest or not (0 = not incubating, 1 = incubating) each day. We used a similar approach to model brood-rearing behavior. However, brood-rearing behavior changes as poults age: notably hens switch from ground roosting to roosting in trees once poults are able to fly (Flake et al. 2006). For this reason, we chose *a priori* to split brood rearing into 2 periods: early (from hatch through 14 days of age) and late (from 15 days of age through 28 days of age). On some occasions, a hen lost her entire brood between poult count visits and we could not determine which day brood-rearing activity ended. When this occurred, we assumed that brood loss occurred on the midpoint day between poult count visits.

Because precipitation has been found to be positively associated with nest predation (Palmer et al. 1993, Roberts et al. 1995, Lehman et al. 2008), we investigated the impact of precipitation on hen survival by using a time-varying individual covariate that indicated the amount of rainfall each day during the Spring and Summer seasons. We expected that precipitation would have a stronger association with hen survival during nesting and early brood rearing (when hens and poults were ground roosted and more vulnerable to predation). Accordingly, we evaluated models that included interactions between precipitation and incubation and between precipitation and early brood rearing. We also thought that the impact of precipitation might be non-linear: that is, low precipitation amounts might have little to no impact on survival, but that higher amounts might have a substantial impact on survival; we included models with a quadratic term for precipitation to test for this potential relationship. Although winter weather conditions (e.g. snow depth, temperature) can impact turkey survival (Porter et al. 1980, Rumble et al. 2003, Kane et al. 2007, Lavoie et al. 2017), we did not explore these relationships because the available weather data did not adequately represent conditions at most turkey wintering locations, and because winter conditions were generally mild during our study (Figure 2.3).

Previous research has indicated that juvenile hens generally have lower survival rates than adult hens (Rumble et al. 2003). Thus, we considered models that included hen age class to allow for such a possibility. Hens captured as juveniles were reclassified as adults at the beginning (1 December) of the winter following capture. To accommodate this change in age, juvenile hens that survived to become adults were represented by 2 lines in the RMark input file (where Age = 0 represented adults and Age = 1 represented juveniles). The first line represented that hen as a juvenile with the following information: FirstFound = Capture Date, LastPresent = 1 Dec, LastChecked = 1 Dec, Fate = 0, Age = 1. The second line represented the hen as an adult with the following information: FirstFound = 1 Dec, LastPresent = last day hen was known alive, LastChecked = last day the hen was checked, Fate = 0 if the hen was alive at the end of the study and 1 if she died prior to the end of the study, and Age = 0.

We estimated DSR from the model best-supported by the data and predicted DSR across relevant ranges of covariate values to evaluate the biological significance of relationships between covariate conditions and estimated rates of hen survival. Because annual and seasonal survival estimates are easier to interpret and provide a better indication of population productivity, we estimated annual and seasonal rates using covariate combinations we considered most useful to managers. We used the delta method to estimate standard errors of these estimates of survival (Powell 2007).

Cause-specific Mortality

Whenever possible, we attempted to determine the cause of hen mortalities by performing necropsies on hen carcasses. We classified mortalities as mammalian predation, avian predation, undetermined predation, starvation, injury or disease, roadkill, transmitter related, or unknown. In addition to performing necropsies, we also searched for tracks, feces, and evidence of carcass caching to help identify predators. Occasionally, we identified predation as mammalian or avian by the presence of hair or feathers from the predator on the turkey carcass or adhered to vegetation at the mortality location. Removal of the head/neck region and accompanying puncture wounds also helped to determine avian predation (Miller and Leopold 1992). When evidence at the mortality site strongly suggested predation but we were unable to completely rule out post-mortality scavenging, we classified the cause of death a probable predation. Carcasses which had not been depredated or scavenged that exhibited emaciated breast muscles indicated a mortality due to starvation. In the absence of evidence of predation, starvation, or external injury, carcasses were examined for disease or injury at the Animal Disease and Diagnostic Laboratory at South Dakota State University by A. Pillatzki, DVM, MS, DACVP. Otherwise we classified the cause of death as unknown.

RESULTS

Turkey Captures

In 2016, we captured 145 female wild turkeys and released 97 (46 juveniles and 51 adults) with VHF transmitters. Twenty-five juvenile hens captured in 2016 survived to enter the adult age class on 1 December 2016. In 2017, we captured 150 female wild turkeys and released an additional 52 individuals (49 juveniles and 3 adults) with transmitters. Twenty-eight juvenile hens captured in 2017 survived to enter the adult age class on 1 December 2017. We excluded 8 hens from the survival analysis because they died within a week of capture; another hen died 9 days following capture but also was excluded because necropsy results suggested that she was injured during capture. Additionally, we right censored data from 4 hens because we lost the transmitter signal or were concerned that the transmitter may have contributed to the female's death.

Hen Survival

We found evidence that incubation status was negatively associated with daily hen survival (Table 2.2). Among the 13 competing models ($\Delta AIC_c \leq 4$), all included incubation. Based on the best supported-model (Season + Incubation), the DSR of incubating turkey hens was lower than the DSR of non-incubating hens and a hen's annual survival rate was associated with the number of days she spent incubating. The estimated annual survival was 0.53 (95% CI = 0.46 – 0.61) for a hen that did not incubate a nest and 0.47 (95% CI = 0.40 – 0.55) for a hen that incubated through the full incubation period (26 days). Although we chose *a priori* to include seasonal periods in all but 4 simple models, we found strong evidence that hen survival differed among seasons: season was included in all competing models and the Season model outperformed the Null model by > 15 AIC_c units (Table 2.2). The data did not support models that included hen age or brood-rearing status (Table 2.2).

We also found some evidence that hen survival was associated with precipitation during the spring and summer; 9 of 13 competing models included daily precipitation. Further, the direction and magnitude of relationships between precipitation and survival were consistent among competing models. In competing models with an additive association with precipitation, $\hat{\beta}_{Precip} \approx -0.0100$ (consistent to the sixth decimal place). In models with an Incubation * Precipitation interaction, $\hat{\beta}_{Incub}$ ranged from -0.6700 to -0.6400, $\hat{\beta}_{Precip}$ ranged from 0.0577 to 0.0585, and $\hat{\beta}_{Incub*Precip}$ ranged from -0.1305 to -0.1299. Precipitation differed notably between spring 2016 and 2017 (Figure 2.4), which likely explains why some well-supported models ($\Delta AIC_c \leq 2$) included a year effect, but not precipitation. The data did not support models that included a non-linear association with precipitation (Table 2.2).

We also found some evidence that the strength of association between precipitation and DSR depended on the hen's incubation status: the second best-supported model (Season + Incubation * Precipitation) had a comparable AIC_c value to the top model, despite the penalty for two additional parameters (Table 2.2). However, 95% confidence intervals associated with precipitation and incubation marginally overlapped zero in some well-supported models ($\Delta AIC_c \leq 2$), preventing unequivocal inferences about the strength of importance.

Because relationships between hen survival and precipitation were consistent among well-supported models, we also present results from the Season + Incubation * Precipitation model. As predicted, incubation activity was associated with reduced daily hen survival on days when precipitation occurred ($\hat{\beta}_{Incub}$ = -0.65, SE = 0.37; $\hat{\beta}_{Precip}$ = 0.06, SE = 0.06; $\hat{\beta}_{Incub*Precip}$ = -0.13, SE = 0.07). To visualize the combined relationships between hen survival, incubation status, and precipitation, we plotted predicted DSRs across a range of precipitation values for incubating and non-incubating hens (Figure 2.5) DSR varied among seasons: DSR was lower during the spring ($\hat{\beta}_{Spring}$ = -0.45, SE = 0.26) and higher during the summer and fall ($\hat{\beta}_{Summer}$ = 0.55, SE = 0.44; $\hat{\beta}_{Fall}$ = 0.90, SE = 0.47) when compared to the winter.

In addition to predictions based on the top model (Season + Incubation, above), we also predicted annual and seasonal survival rates for a hen that did not nest and for a hen that incubated through the full incubation period (26 days) based on the comparable Season + Incubation * Precipitation model. To generate these predicted values, we used the precipitation data from the rain gauge associated with the most hens (~25% of all hen-weather associations) and assumed nest incubation began on the median date (Table 2.3). Survival was lowest during the spring, particularly for incubating hens; estimated spring survival was 0.64 (95% CI = 0.50 – 0.78) for an incubating hen and 0.78 (95% CI = 0.71 – 0.85) for a non-incubating hen, based on precipitation data from 2017. Winter survival was also relatively low at 0.79 (95% CI = 0.73 – 0.85). Most nesting attempts were completed by the end of June and survival was highest during the summer; estimated summer survival for a non-incubating hen was 0.94 (95% CI = 0.89 – 0.98). Survival during the fall was intermediate at 0.87 (95% CI = 0.81 – 0.94). Estimated annual survival from 1 December 2016 through 30 Nov 2017 for a hen that incubated for 26 days was 0.44 (95% CI = 0.33 – 0.55) and for a hen did not incubate was 0.54 (95% CI = 0.46 – 0.61).

Cause-specific Mortality

Predation was the primary cause of hen mortality during our study, with predation and probable predation accounting for 46.8% of all mortalities (44 of 94 mortalities, Table 2.4). Starvation was identified as the cause of 10.6% hen mortalities (10). Three of these hens died of apparent starvation after incubating eggs and then abandoning the nest, another did not attempt to nest and died of apparent starvation in early July. Seven hens (7.4%) died of injury or disease. Three hens (3.2%) were killed in car collisions; these mortalities all occurred at the same location where turkeys frequently crossed and congregated near a road due to landowner feeding practices. A single hen (1.1%) died when her transmitter’s shock cord harness became tangled on a barbed wire fence as she crossed under the bottom wire. We were unable to identify the cause of 30.9% of mortalities (29); 16 of these instances occurred when survival was monitored too infrequently to determine cause of death from turkey remains.

DISCUSSION

Our results provide strong support that variation in DSR of turkey hens during the spring and summer is related to whether the hen was currently incubating eggs, consistent with a negative cost of reproduction predicted by life history theory (Stearns 1992) and with previous studies indicating that nesting hens are especially vulnerable to predation (Thompson 1993, Rumble et al. 2003, Lehman 2005, Lehman et al. 2008). Further, we found evidence that the magnitude of the reproductive cost was related to precipitation amount, as predicted by the moisture-facilitated nest-predation hypothesis (Roberts and Porter 1998, Lehman et al. 2008). We detected this pattern despite the potential for small mismatches between daily survival periods and the associated daily precipitation amount, suggesting that the impact of any such discrepancies was insufficient to mask the influence of precipitation on hen survival.

In sage grouse, raising chicks may place a greater cost on hen survival than egg laying and incubation (Blomberg et al. 2013), and Merriam's turkeys in Arizona experienced higher rates of predation during brood rearing than during incubation (Wakeling 1991). Yet in contrast to these studies and our expectation, we did not find evidence for a reproductive cost of brood-rearing behavior. Three factors may have prevented us from detecting an association between brood rearing and hen survival. First, relatively low rates of nesting and nest survival (Chapter 3) resulted in a modest sample of hatched nests (50 successful nests total in 2016 and 2017). Second, we frequently did not know the exact date of brood loss, forcing us to approximate the days a hen spent brood rearing based on the midpoint between the last day she was observed with poults and the first day she was observed without a brood. Finally, in all our analyses we explored only the potential costs of current reproduction on current survival. Costs of incubation or brood rearing may manifest following cessation of these activities, but the duration of our study prevented us from exploring impacts on future survival. Further, we did not explore potential associations between egg laying and hen survival because our telemetry data was not suited to determining the onset of incubation behavior.

Contrary to our expectation, we did not find evidence that hen age affected survival. We expected smaller-bodied juvenile hens would be more vulnerable to winter weather events (Rumble et al. 2003, Lehman 2005), but winter conditions may have been too mild during our study (Figure 2.3) to impact adult and juvenile survival differently. Juvenile hens nested at lower rates than adult hens (Chapter 3), which may have limited exposure of juveniles to predation during incubation and increased survival.

Demographic data help managers establish management strategies that are rooted in science and make the best use of limited resources. Wild turkey management is best informed by vital rates that are current and region-specific (Pollentier et al. 2014*a*, *b*). Although previous research focused on turkey survival in the Black Hills did not explore quantitative impacts of precipitation or reproduction, our estimates of annual survival for both incubating and non-incubating hens are lower than survival in both the central (Rumble et al. 2003) and southern (Lehman 2005) Black Hills (Table 2.3). We found that lower annual survival in the northern Black Hills is driven mainly by lower rates of survival during winter and spring, as hen survival in summer and fall were comparable between the northern and southern Black Hills (Table 2.3). We believe these seasonal differences are primarily related to the distinctly different climatic conditions hens experience in the northern and southern Black Hills (Figure 2.1). Additionally, survival of an incubating hen through spring (April – June) was lower than survival through winter (December – March), despite the winter period lasting a month longer than spring (Table 2.3), emphasizing the cost nesting imposes on hen survival.

Although we did not explore the impacts of snow depth and temperature on hen survival, persistent deep snow and low temperatures can have substantial effects (Porter et al. 1980, Kane et al. 2007, Lavoie et al. 2017). In the southern Black Hills, turkeys winter in association with livestock operations and farmsteads as well as in ponderosa forest, which represent areas with and without supplemental food, respectively. However, Lehman (2005) did not detect differences in winter survival between these 2 groups of hens. In the northern Black Hills, all turkeys we observed congregated in locations with access to supplemental food during at least a portion of the winter. Despite access to food and milder than average winters (Figure 2.3), we observed lower winter survival in the northern Black Hills compared to farther south (Table 2.3). Additionally, we observed multiple hens that died of starvation during winter and the spring nesting period, as well as one hen that died of starvation during the summer (Table 2.4). Necropsies of hens killed accidentally during capture revealed limited energy reserves. We are unaware of any other turkey studies which have documented hen starvation during nesting or summer. The prevalence of starvation and comparatively low winter survival during the mild conditions encountered during our study suggests that hen survival may be lower when future winter conditions are average or harsh.

MANAGEMENT IMPLICATIONS

Hen survival in the northern Black Hills is lower than in both the central and southern Black Hills. Prior to and during this study, hunter harvest of turkey hens was permitted during the fall turkey season, but not during the spring season. Based on our findings, we recommend that managers should avoid reducing hen survival and subsequent reproduction in the future by allowing a male-only fall harvest or by closing the fall season entirely in the northern Black Hills.

Although weather conditions are outside managers' control, we recommend that survival estimates incorporate the amount of observed precipitation during April – August each year. In the absence of the network of rain gauges we established during our study, we propose that the weather station in Lead, SD could provide a reasonable approximation of daily precipitation in the northern Black Hills. Future investigations of hen survival in the Black Hills should quantify the impact of winter conditions to help managers predict population-level impacts of weather events.

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Table 2.1. List of candidate models for turkey hen survival in the northern Black Hills, SD, 2016-2018. Models constructed with additional time-varying covariates are shown in the first column, models with additional covariates that are not time varying are shown in the second through fourth columns. Covariates are Season (with winter as the reference level and adjustments for spring, summer, or fall), Age (hen age, with adult as the reference level and an adjustment for juvenile hens), Yr (year with 2017 as the reference level, and adjustments for 2016 or 2018), Precip (daily precipitation amount during spring and summer), Incub (hen's daily incubation status), Brood$_1$ (hen's brood rearing status for poults aged 0 – 2 weeks age), and Brood$_2$ (hen's brood rearing status for poults 2 – 4 weeks of age).

Base Model	**+ Age**	**+ Year**	**+ Age + Yr**
Null	Base + Age	Base + Yr	Age + Yr
Season	Base + Age	Base + Yr	Base + Age + Yr
Season + Precip	Base + Age	Base + Yr	Base + Age + Yr
Season + Incub	Base + Age	Base + Yr	Base +Age + Yr
Season + Incub + Precip	Base + Age	Base + Yr	Base +Age + Yr
Season + Incub + Precip + Precip*Incub	Base + Age	Base + Yr	Base +Age + Yr
Season + Incub + Brood$_1$ + Brood$_2$	Base + Age	Base + Yr	Base +Age + Yr
Season + Incub + Precip + Brood$_1$ + Brood$_2$	Base + Age	Base + Yr	Base +Age + Yr
Season + Incub + Precip + Precip*Incub + Brood$_1$ + Brood$_2$	Base + Age	Base + Yr	Base +Age + Yr
Season + Incub + Precip + Precip*Incub + Brood$_1$ + Brood$_2$+ Precip*Brood$_1$	Base + Age	Base + Yr	Base +Age + Yr
Season + Precip + Precip^2	Base + Age	Base + Yr	Base +Age + Yr
Season + Precip + Precip^2 + Incub	Base + Age	Base + Yr	Base +Age + Yr
Season + Precip + Precip^2 + Incub + Brood$_1$ + Brood$_2$	Base + Age	Base + Yr	Base +Age + Yr

Table 2.2. Model selection results for female turkey survival in the northern Black Hills, SD, 2016-2018. Covariates are: incubation status (Incub), precipitation amount (Precip), year (Yr), hen age (Age), and brood rearing status (Brd). All models include a main effect of Season unless otherwise noted and models that include an interaction or quadratic also include main effects of those terms. K is the number of parameters in each model.

Model	**AIC$_c$**	**ΔAIC$_c$**	**AIC$_c$ weights**	**Deviance**	**K**
Incub[a]	1111.18	0.00	0.15	1101.18	5
Incub*Precip[b]	1111.46	0.28	0.13	1097.46	7
Incub+Yr	1112.27	1.09	0.09	1098.27	7
Incub*Precip+Yr	1112.54	1.36	0.08	1094.54	9
Incub+Precip	1113.09	1.91	0.06	1101.09	6
Incub+Age	1113.11	1.93	0.06	1101.11	6
Incub*Precip+Age	1113.41	2.23	0.05	1097.41	8
Incub+Precip+Yr	1114.18	3.00	0.03	1098.18	8
Precip^2+Incub	1114.26	3.08	0.03	1100.26	7
Incub+Age+Yr	1114.27	3.09	0.03	1098.26	8
Incub*Precip+Age+Yr	1114.52	3.35	0.03	1094.52	10
Incub*Precip+Brd	1114.77	3.59	0.03	1096.77	9
Incub+Precip+Age	1115.03	3.85	0.02	1101.02	7
Incub+Precip^2+Yr	1115.34	4.16	0.02	1097.34	9
Incub+Brd+Yr	1115.61	4.43	0.02	1097.60	9
Incub*Precip+Brd+Yr	1115.85	4.67	0.01	1093.85	11
Incub+Precip+Age+Yr	1116.17	4.99	0.01	1098.17	9
Incub+Precip^2+Age	1116.20	5.02	0.01	1100.20	8
Incub+Precip+Brd	1116.43	5.25	0.01	1100.43	8
Incub+Brd+Age	1116.44	5.26	0.01	1100.43	8
Incub*Precip+Brd+Age	1116.72	5.54	0.01	1096.71	10
Incub*Precip+Brd*Precip	1116.76	5.58	0.01	1096.75	10
Season	1116.95	5.77	0.01	1108.95	4
Incub+Precip^2+Age+Yr	1117.33	6.16	0.01	1097.33	10
Incub+Precip+Brd+Yr	1117.52	6.34	0.01	1097.52	10
Incub+Precip^2+Brd	1117.58	6.40	0.01	1099.57	9
Incub+Brd+Age+Yr	1117.60	6.43	0.01	1097.60	10
Incub*Precip+Brd*Precip+Yr	1117.84	6.66	0.01	1093.83	12
Incub*Precip+Brd+Age+Yr	1117.84	6.66	0.01	1093.83	12
Yr	1118.06	6.88	0.00	1106.06	6
Incub+Precip+Brd+Age	1118.36	7.18	0.00	1100.35	9
Incub+Precip^2+Brd+Age+Yr	1118.66	7.48	0.00	1096.65	11
Incub+Precip^2+Brd+Yr	1118.66	7.48	0.00	1096.65	11
Incub*Precip+Brd*Precip+Age	1118.70	7.52	0.00	1096.70	11

Precip	1118.79	7.61	0.00	1108.79	5
Age	1118.88	7.70	0.00	1108.88	5
Incub+Precip^2+Brd+Age	1119.50	8.32	0.00	1099.49	10
Incub+Precip+Brd+Age+Yr	1119.52	8.34	0.00	1097.51	11
Age+Yr	1119.70	8.52	0.00	1105.70	7
Incub*Precip+Brd*Precip+Age+Yr	1119.83	8.65	0.00	1093.82	13
Precip+Yr	1119.90	8.72	0.00	1105.90	7
Precip^2	1119.94	8.76	0.00	1107.93	6
Precip+Age	1120.72	9.54	0.00	1108.72	6
Precip^2+Yr	1121.04	9.86	0.00	1105.04	8
Precip+Age+Yr	1121.55	10.37	0.00	1105.54	8
Precip^2+Age	1121.86	10.69	0.00	1107.86	7
Precip^2+Age+Yr	1122.68	11.50	0.00	1104.68	9
Null[c]	1134.23	23.06	0.00	1132.23	1
Year[c]	1135.40	24.22	0.00	1129.40	3
HenAge[c]	1136.08	24.90	0.00	1132.08	2
Age+Yr[c]	1136.58	25.40	0.00	1128.58	4
Incub+Brd	1201.27	90.09	0.00	1187.26	7

[a] Incub $\hat{\beta}$s (with standard errors) are as follows: $\hat{\beta}_{\text{Intercept}} = 6.24$ (0.18), $\hat{\beta}_{\text{Spring}} = -0.37$ (0.25), $\hat{\beta}_{\text{Summer}} = 0.65$ (0.43), $\hat{\beta}_{\text{Fall}} = 0.91$ (0.47), $\hat{\beta}_{\text{Incub}} = -0.97$ (0.32)

[b] Incub*Precip $\hat{\beta}$s (with standard errors) are as follows: $\hat{\beta}_{\text{Intercept}} = 6.24$ (0.18), $\hat{\beta}_{\text{Spring}} = -0.45$ (0.26), $\hat{\beta}_{\text{Summer}} = 0.55$ (0.44), $\hat{\beta}_{\text{Fall}} = 0.90$ (0.47), $\hat{\beta}_{\text{Incub}} = -0.65$ (0.37), $\hat{\beta}_{\text{Precip}} = 0.06$ (0.06), $\hat{\beta}_{\text{Incub*Precip}} = -0.13$ (0.07).

[c] Models without a main effect of season.

Table 2.3. Estimates of turkey hen survival (annual and seasonal) for the northern, central, and southern Black Hills. Estimates for the northern Black Hills come from the current study (by year, based on the Season + Incub*Precip model), estimates from the south and central regions come from previous research (southern: 2001-2003, Lehman 2005, and central: 1990-1993, Rumble et al. 2003). Standard errors (when available) are shown in parentheses.

	North		South[a]	Central[b]
	2015-2016[c]	2016-2017		
Annual 1 Dec – 30 Nov	0.48 (0.04)[e]	0.44 (0.05)[e]	0.67 (0.09)	0.68
	0.53 (0.04)[f]	0.54 (0.04)[f]		
Winter[d] 1 Dec – 31 Mar	0.79 (0.03)	0.79 (0.03)	0.93 (0.02)	
Spring 1 Apr – 30 Jun	0.70 (0.04)[e]	0.64 (0.07)[e]	0.83 (0.04)	
	0.77 (0.04)[f]	0.78 (0.04)[f]		
Summer 1 Jul – 31 Aug	0.94 (0.02)	0.94 (0.02)	0.96 (0.02)	
Fall[d] 1 Sep – 30 Nov	0.87 (0.03)	0.87 (0.03)	0.86 (0.05)	

[a] Estimate for adult hens.

[b] Estimate for adult and juvenile ages combined.

[c] Based on data collected from January 2016 – November 2016.

[d] Fall and winter estimates are constrained to be the same in each year by model structure.

[e] Estimate for a hen that incubates for 26 days starting on the median date of incubation initiation that year.

[f] Estimate for a hen that does not incubate a nest.

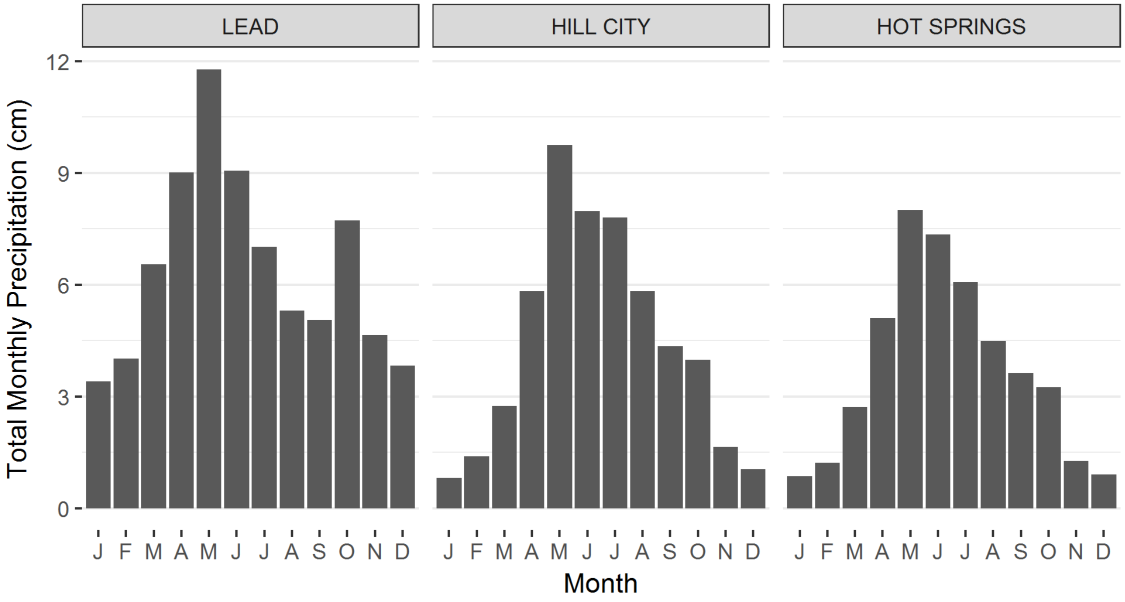
Table 2.4. Cause-specific mortality of turkey hens in the northern Black Hills, SD, 2016 – 2018.

	Winter[a]		Spring[b]		Summer[c]		Fall[d]		Total	
	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
Mammalian	12.1	4	20.5	9					13.8	13
Mammalian (Probable)	6.1	2	11.4	5					7.4	7
Avian	9.1	3	18.2	8					11.7	11
Undetermined Predator	9.1	3	6.8	3					6.4	6
Undetermined Predator (Probable)	9.1	3	9.1	4					7.4	7
Starvation	9.1	3	13.6	6	14.2	1			10.6	10
Unknown	33.3	11	11.4	5	42.9	3	100	10	30.9	29
Injury/Disease			9.1	4	42.9	3			7.4	7
Roadkill	9.1	3							3.2	3
Transmitter[e]	3.0	1							1.1	1
Total	100.0	33	100.0	44	100	7	100.0	10	100.0	94

[a] 1 Dec 2015 – 31
[b] 1 Apr – 30 Jun
[c] 1 Jul – 31 Aug
[d] 1 Sep – 30 Nov
[e] Mortality caused by transmitter snagging on barbed wire fence. Hen was right censored in the survival analysis.

Figure 2.1. Average a) precipitation and b) snowfall by month (cm) for the northern (Lead, SD), central (Hill City, SD), and southern (Hot Springs, SD) Black Hills (National Climatic Data Center 1981-2010).

a)



b)

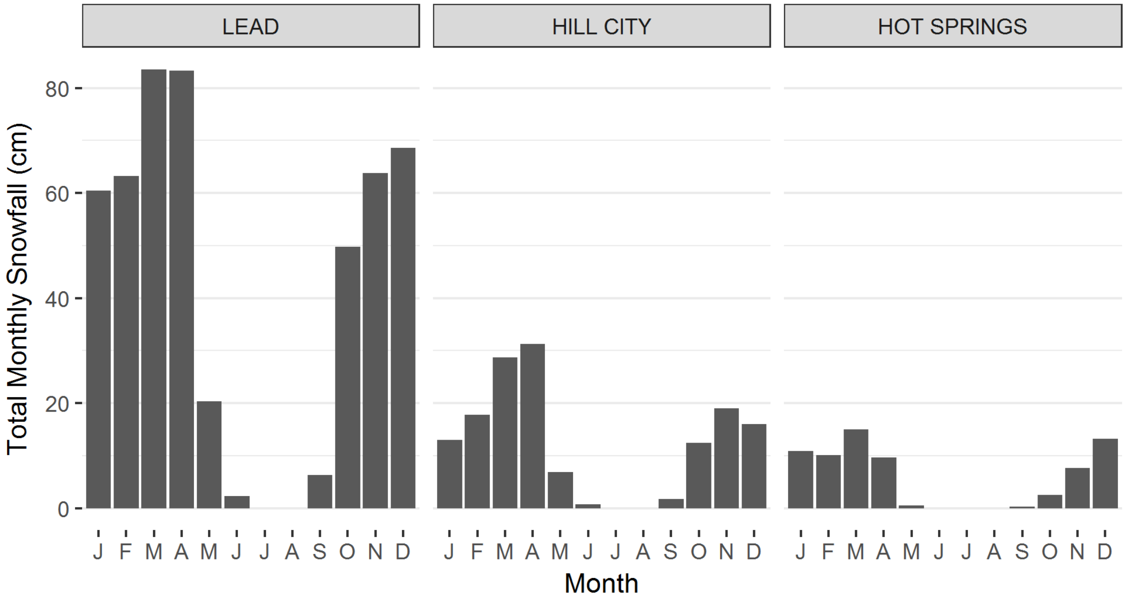


Figure 2.2. Study area with locations of all weather stations/rain gauges, nests, and captures, west-central South Dakota and northeast Wyoming (see inset map), January 2016 – March 2018. Colored weather station symbols correspond to colors in Figure 2.4.

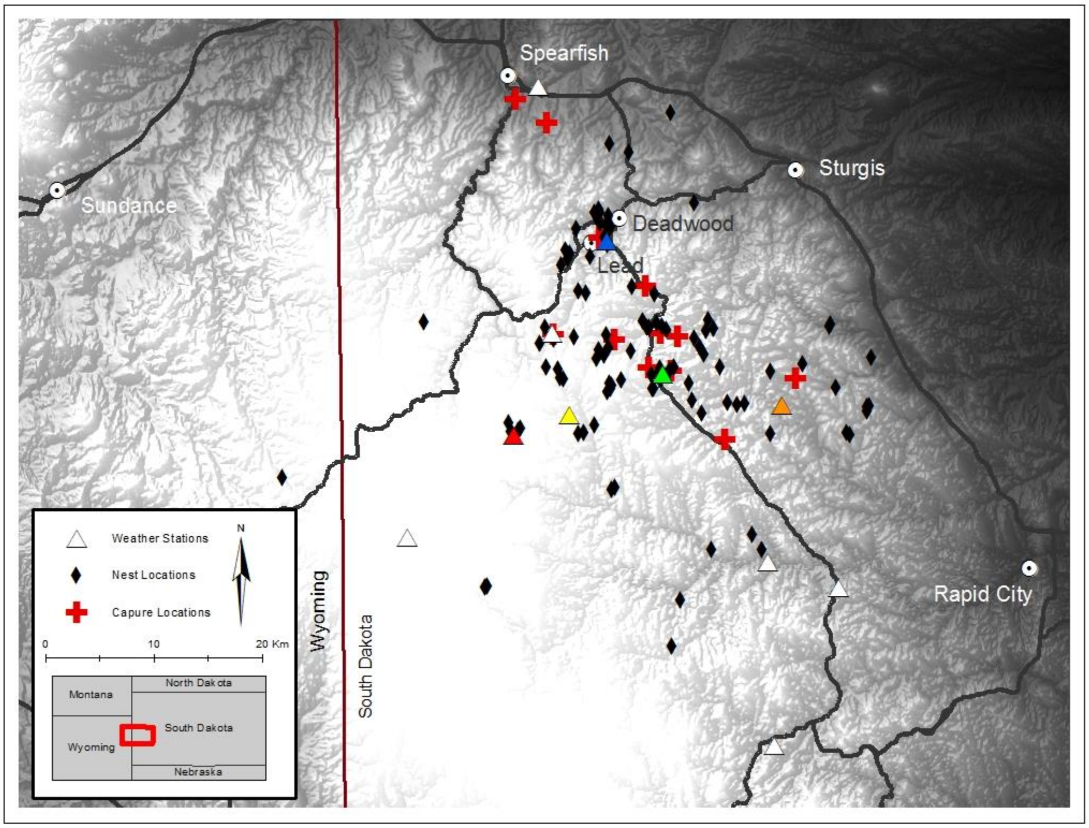


Figure 2.3. Monthly snowfall totals in Lead, SD during December 2015 – May 2016 (left) and December 2016 – May 2017 (middle) compared to long term average snowfall (1981 – 2010, right).

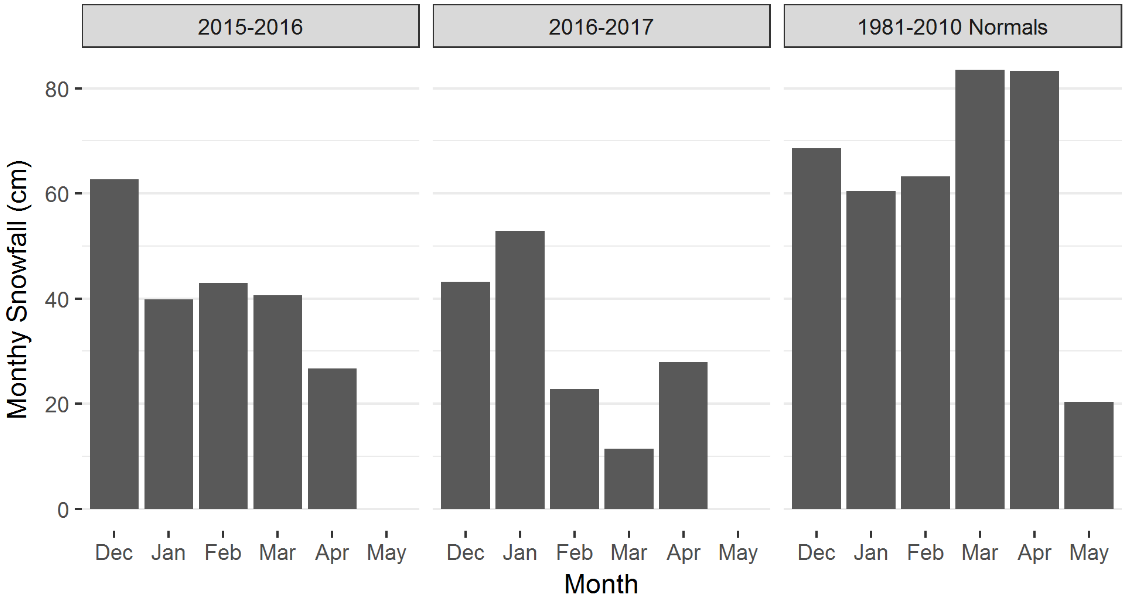


Figure 2.4. Spring precipitation by month at 5 locations in the study area, west-central South Dakota and northeast Wyoming, April – June 2016 and 2017. Colors correspond to weather station symbols in Figure 2.2.

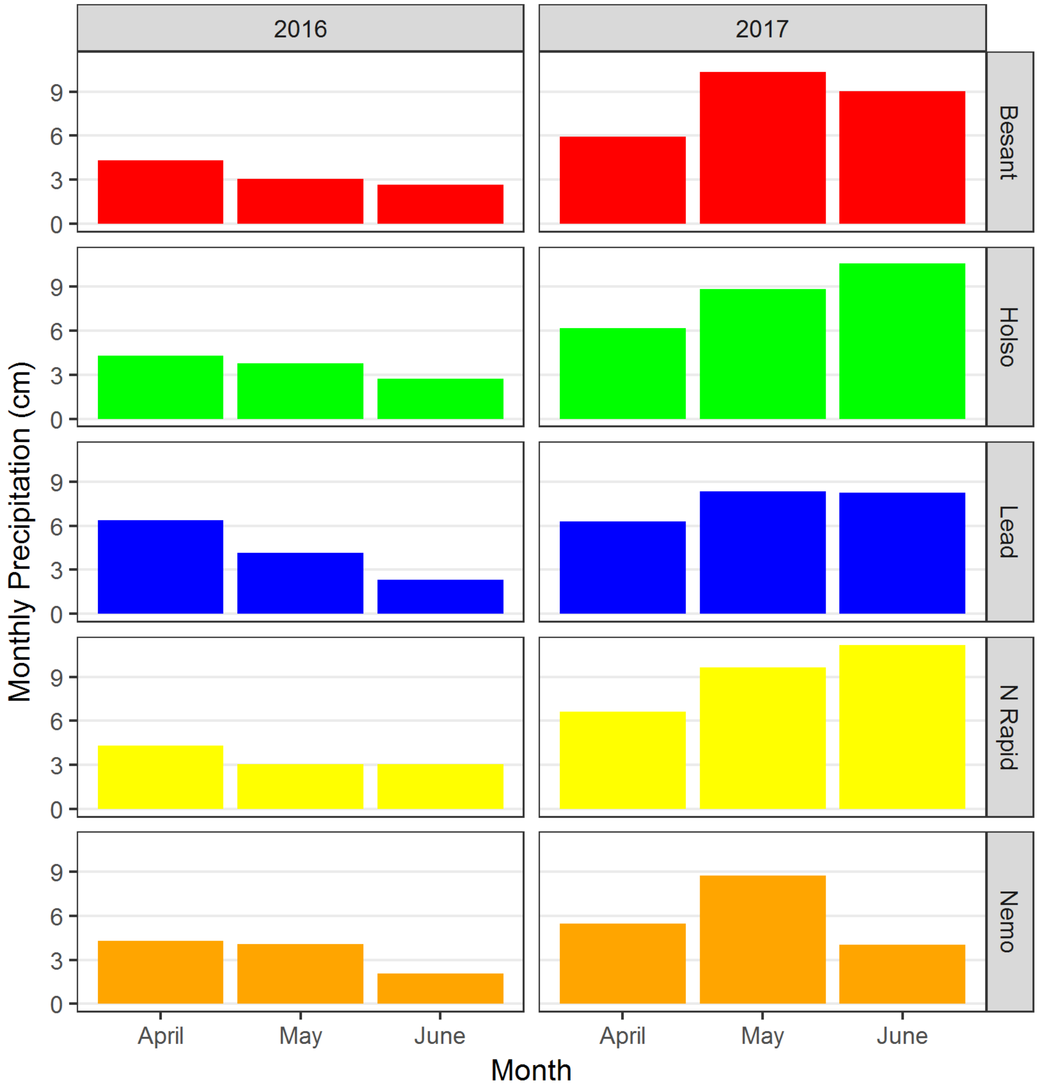
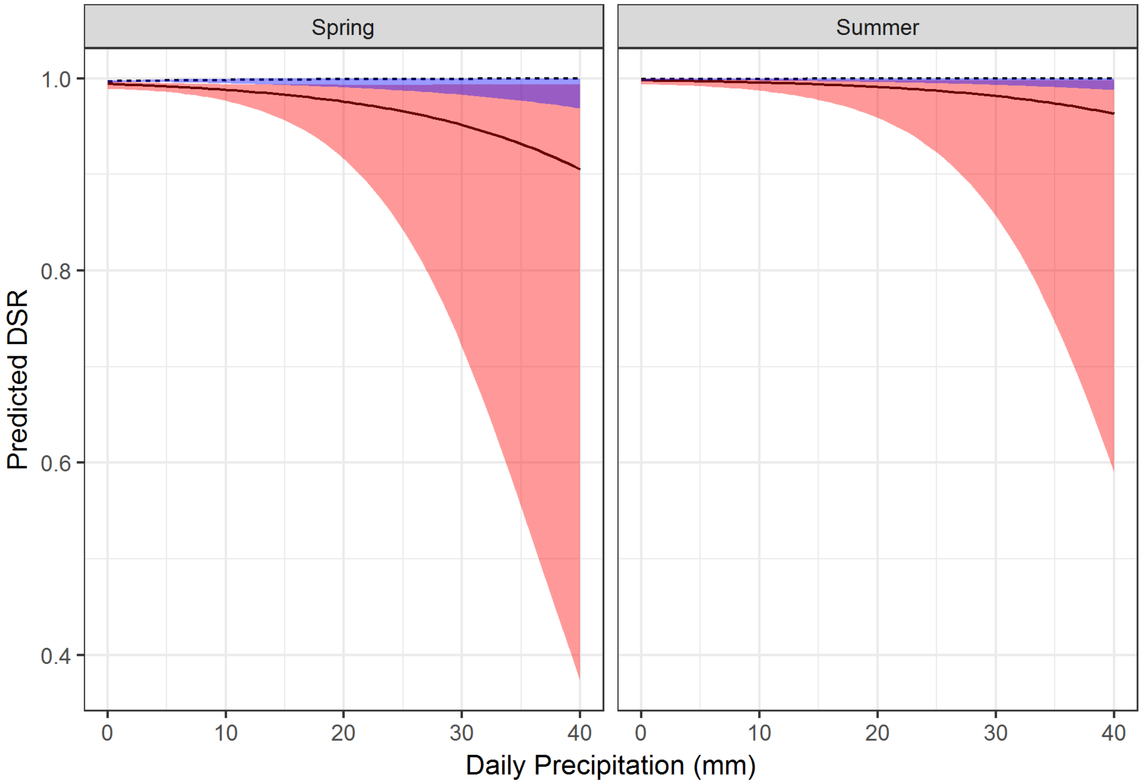


Figure 2.5. DSR predictions and 95% confidence intervals based on the Season + Precip*Incub model for incubating (solid line, red interval) and non-incubating (dashed line, blue interval) hens across a range of precipitation values during spring and summer. Each confidence interval does not overlap the other estimate. Estimates are based on survival data collected in the northern Black Hills, January 2016 – March 2018.



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CHAPTER THREE

IMPACTS OF WEATHER ON REPRODUCTIVE PRODUCTIVITY OF WILD TURKEYS IN THE NORTHERN BLACK HILLS, SD

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Impacts of Weather on Reproductive Productivity of Wild Turkeys in the Northern Black Hills, SD

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ABSTRACT Nesting rate and the survival of nests and young are important factors affecting the productivity of avian populations. Regional and temporal variation in these vital rates is common, and understanding how local weather and habitat conditions affect population dynamics is important for effective wildlife conservation and management. Temperature and precipitation impact the survival of both nests and young galliformes, but the relationships between weather and population productivity are complex and context-dependent. We assessed the associations of weather and habitat conditions with nest and poult survival for Merriam's wild turkeys (*Meleagris gallopavo merriami*) in the northern Black Hills, South Dakota. During 2016 – 2017, we used radio telemetry to collect survival data on 99 nests and 50 broods. We utilized an information-theoretic approach to evaluate the association of precipitation and habitat conditions with nest survival, and the association of precipitation, temperature, and poult age with poult survival. Daily precipitation was associated with reduced nest survival, and larger values of visual obstruction were associated with increased nest survival. We propose that turkey hens and nests are high-reward prey items and that predators using olfactory cues to locate nests more effectively during or immediately following precipitation events. Poult survival increased as poults aged, but we did not detect associations between weather conditions and poult survival. We estimated the rate of nest survival from initiation to hatch was 0.49 (SE = 0.07); this prediction is based on precipitation data collected in 2017 and assumes an adult hen initiated the nest on the median date. The estimated poult survival from hatch to 4 weeks of age was 0.39 (SE = 0.06). Reproductive productivity was lower in our study area than in other portions of the Black Hills. Although managers cannot avoid the impacts of weather, management actions that reduce hen mortality will help prevent further reductions in turkey population productivity.

KEY WORDS Black Hills, *Meleagris gallopavo*, nest survival, nest survival model, poult survival, precipitation, wild turkey

Understanding variation in vital rates is crucial to effectively manage and conserve wildlife populations, particularly for at-risk or harvested species. To affect changes or maintain stable populations, managers should understand the factors that drive temporal changes in vital rates. Survival of nests and young are important drivers of variation in population growth in avian species. However, the relative importance of each rate can differ among species; further, annual and regional variation within species is also common (Hoekman et al. 2002, B. Sandercock et al. 2008, Taylor et al. 2012, Pollentier et al. 2014*a*).

Predation is the most common cause of nest failure in galliformes (Lehman et al. 2008*b*, Webb et al. 2012). Weather conditions, including temperature and precipitation, affect predators' ability to locate hens and their nests, but patterns of influence are likely context-specific (Lehman et al. 2008*b*, Ruzicka and Conover 2012, Webb et al. 2012, Fogarty et al. 2017). Previous studies have quantified decreased nest survival during wet periods and suggested that predators relying on olfactory cues may more effectively locate nests during or immediately following rain events (moisture-facilitated nest-depredation hypothesis, Roberts et al. 1995, Roberts and Porter 1998*a*). Additionally, mesopredators relying on olfaction also may better detect nests during periods of cool temperatures and high humidity (Ruzicka and Conover 2012). Precipitation reduced daily nest survival of wild turkeys in the Black Hills (Lehman et al. 2008*b*) and precipitation (with a 1-day time lag) reduced nest survival in sage grouse (Moynahan et al. 2007, Webb et al. 2012). However, Moynahan et al. (2007) also found that nest survival increased on the day of precipitation, that the net impact of precipitation was positive, and suggested that hen and predator behavior during and following rain events might influence rates of predation. Similarly, precipitation was associated with reduced nest predation in scaled quail (Pleasant et al. 2003), and increased humidity and precipitation increased nest survival of ground nesting birds in Oklahoma (Fogarty et al. 2017).

Like nests, young galliformes also experience high levels of predation. Predation and exposure during cold and wet weather conditions are the main causes of mortality in neonate galliformes, and mortality rates are highest during the first 2 weeks of life, when young birds are unable to fly or thermoregulate (Riley et al. 1998, Roberts and Porter 1998*a*, Hubbard et al. 1999, Lehman et al. 2008*a*, Goddard and Dawson 2009). In addition to direct mortality, severe weather conditions may limit food intake during early life by reducing feeding time or causing avoidance of areas where food abundance is greatest (Erikstad and Spidso 1982). Further, predation might increase when young are wet (Lehman et al. 2008*a*). However, the relationships between survival, predation, and weather conditions are complex, and the timing of weather events is important. Inclement weather post-hatch may reduce survival, but if the inclement weather occurs before hatching, precipitation may contribute to habitat conditions that increase survival (Erikstad 1985, Goddard and Dawson 2009).

The wild turkey (*Meleagris gallopavo*) is a gallinaceous bird that experienced a precipitous decline in abundance and range following European settlement, due to a combination of overharvest and habitat degradation (Schorger 1967, Kennamer et al. 1992). However, widespread trap-and-transfer efforts that began in the mid-twentieth century allowed turkey populations to reestablish in states where they had been long absent (Williams 1981, Kennamer et al. 1992). Merriam's wild turkeys (*M. g. merriami*) originally were found associated with ponderosa pine (*Pinus ponderosa*) communities in Colorado, New Mexico, Arizona, Oklahoma, and possibly western Texas (Schorger

1967). Reintroductions, as well as introductions beyond the native range of wild turkeys, continued into the 21st century (Flake et al. 2006).

Merriam's turkeys were introduced to the Black Hills of South Dakota beginning in the late 1940s by the South Dakota Department of Game, Fish, and Parks (SDGFP) as a game species; today they are prized for both consumptive and non-consumptive uses (Flake et al. 2006). Turkey management in the Black Hills is informed by a variety of vital rates data, including nest and poult survival, for 3 areas (northern, central, and southern). Nesting and poult data were collected previously for the central and southern Black Hills (Rumble et al. 2003, Lehman 2005, Lehman et al. 2008*a*,*b*), but currently there is a paucity of data on turkey demography in the northern Black Hills. Data from the southern Black Hills are currently used to make management decisions for the northern Black Hills, but dynamics of turkey populations can differ substantially even between locations in close proximity (Collier et al. 2009, Pollentier et al. 2014*a*, *b*). The northern portion of the Black Hills differs from the central and southern portions in terms of both climate and vegetation (Flake et al. 2006), namely in that the northern Black Hills receives substantially more winter snowfall and spring rain. Given that approximately half of annual precipitation in the northern Black Hills falls during late winter and early spring (Figure 3.1), nesting rate, nest survival, and poult survival could be lower than documented farther south.

Our objectives were to quantify reproductive productivity of wild turkeys in the northern Black Hills and to characterize relationships between weather and reproduction. Specifically, we sought to understand how precipitation, habitat conditions, and predation were associated with nest survival and how temperature, precipitation, and predation were associated with poult survival. The resulting estimates would provide an additional test of the moisture-facilitated nest-predation hypothesis and inform region-specific management of wild turkeys in the Black Hills. Because our expectations about the relationships between nest and poult survival and covariates were tightly coupled with model development, we include specific predictions below.

STUDY AREA

We completed our work in the northern portion of the Black Hills in west-central South Dakota and northeastern Wyoming. The study area (~2675 km^2, Figure 3.2) was in Lawrence, Meade, and Pennington counties in South Dakota and in Weston and Crook counties in Wyoming; most work occurred in Lawrence and southwestern Meade counties. The area was primarily Black Hills National Forest, interspersed with private land and areas managed by the Bureau of Land Management and the state of South Dakota. Elevations ranged from approximately 1000 m to 2175 m above sea level. Mean annual precipitation and temperature (1981-2010) were 77 cm and 6.9° C, respectively (National Climatic Data Center 1981-2010). Ponderosa pine (*Pinus ponderosa*) was the most common tree species, but white spruce (*Picea glauca*) also was a common conifer. Quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) were common deciduous trees, and bur oak (*Quercus macrocarpa*) was locally abundant at low elevations. Common juniper (*Juniperus communis*) was the most common understory shrub; serviceberry (*Amelanchier alnifolia*), kinnikinnik

(*Arctostaphylos uva-ursi*), beaked hazel (*Corylus cornuta*), and snowberry (*Symphoricarpos* spp.) also were common.

METHODS

Hen Capture and Radio Telemetry

We captured wild turkeys from January through March of 2016 and 2017 using rocket nets (Thompson and Delong 1967). Turkeys were lured to netting locations using corn and oat hay. Males captured incidentally were fitted with an aluminum leg band and released. We classified hens as adults (>1 year old) or juveniles (<1 year old) based on the presence or absence of barring in the ninth or tenth primary feathers (Williams 1961). After aging, hens were weighed, banded, and instrumented with an 80-gram backpack-mounted VHF transmitter equipped with an activity signal, a short-term non-moving (loafing) signal, and a mortality signal set to activate after 8 hours without movement (Advanced Telemetry Systems, Isanti, MN). Our desired sample size was 80 hens split evenly between adult and juvenile hens on 1 April. Once we reached 40 marked hens in an age class, additional hens in that age class were simply weighed, banded, and released without a transmitter.

During the pre-incubation, nesting, and brood-rearing periods (Apr – Aug), we monitored hens via radio telemetry (White and Garrott 1990) for location and signs of nesting activity. We checked hens at least 5 days per week; nearly all hens were checked daily during pre-incubation, and incubating hens were checked daily.

Nest Marking and Monitoring

We monitored hens for signs of incubation via the activity and loafing signals from transmitters. Hens that localized their daily movements and did not activate the activity sensor for 5-10 minutes were located via triangulation, homing, and visual observation (White and Garrott 1990). When hens were found nesting, we recorded Universal Transverse Mercator (UTM) coordinates for each nest location using a handheld GPS (Garmin GPSMap 64s). We used survey tape to mark least 3 points surrounding the nest at approximately 30 m and used a compass to record a bearing in the direction of the nest bowl. This facilitated location of the nest bowl following nest fate while also minimizing investigator disturbance. Survey tape is used very commonly in the Black Hills to mark timber sales, so we were confident its use would not draw the attention of avian nest predators. After nest marking, we checked each nest 1-2 times daily via radio telemetry to monitor success or failure. To prevent disturbance during subsequent visits, we avoided approaching nests within the flagged circle established during marking; this distance varied depending on terrain and proximity to roads, but nests generally were checked from a distance of at least 200 m.

Annual Reproduction Parameters, Determination of Nest Predators, and Poult Counts

We defined nesting rate as the proportion of females alive on 1 April that attempted to nest at least once during the year, and renesting rate as the proportion of females unsuccessful on a first nesting attempt that attempted to nest again (Cowardin et al. 1985). We defined clutch size as the number of eggs laid in each nest, and hatch rate as the proportion of eggs laid in successful nests that hatched. To determine clutch size, we counted eggs while the hen was away from the nest bowl during the incubation period or eggshell and membrane remains in the nest bowl after nest fate. Hatch rate was determined after hatching by counting eggshell and membrane remains. Although estimates of apparent nest success are biased high if all nests are not found at initiation (Mayfield 1961, 1975), we calculated apparent nest success as the proportion of all nests that hatched ≥1 egg (Cowardin et al. 1985) to enable comparisons with results from previous studies that only provided estimates of apparent nest success.

We attempted to determine the cause of failure for nests that did not hatch. Hair or feathers from predators at the nest site enabled us to classify predators as mammalian or avian. When the hen was killed while incubating, removal of the hen's head/neck region and accompanying puncture wounds helped to determine avian predation (Miller and Leopold 1992). Eggshells which had been pecked open (rather than bitten) were also indicative of avian predation. When we could not find hair or feathers, but eggshells were badly smashed or missing, we classified the nest predator as "likely mammalian", given that avian predators were unable to carry away eggshells.

For nests that hatched young, we monitored poult survival via poult counts (Hubbard et al. 1999). We determined the number of poults at hatch from eggshell remains and counted poults at approximately 2 and 4 weeks of age by locating the hen via radio telemetry and counting the poults associated with her. When possible, we visually observed broods from a distance while they foraged in open areas or flushed the brood to obtain a count (Vangilder et al. 1987, Hubbard et al. 1999). However, these methods were frequently ineffective because broods had formed creches (Vangilder and Kurzejeski 1995) or because dense vegetation inhibited our ability to flush and observe the entire brood. When unable to count poults on the ground, we located the brood in the roost tree in the evening and returned the following morning to complete the count before full daylight. This method allowed us to identify which poults were associated with the radio-marked hen and count them as they left the roost tree (Lehman et al. 2008*a*). For the survival analysis, we excluded any poult counts where field conditions prevented us from obtaining an accurate count of the entire brood.

Nest-Site Characteristics

We characterized nest sites using 4 transects established along each cardinal direction centered on the nest bowl. We measured Visual Obstruction Readings (VOR) by placing a pole marked with 1.27-cm increments in the nest bowl and recording the lowest visible increment when viewed from a height of 1 m and a distance of 4 m in each of the cardinal directions (Robel et al. 1970, Benkobi et al. 2000). Additionally, we collected VOR at a point 1 m from the nest bowl in each cardinal direction. For these points, we only recorded VOR from the 3 cardinal directions not across the nest bowl to avoid duplication (e.g., the 1 m north peripheral measurement was read from the E, N, and W).

We quantified understory canopy coverage of total plant cover using a Daubenmire frame (Daubenmire 1959) placed at the nest bowl and at 1-m intervals along the 4 cardinal transects (4 frames per transect, n = 17). Slope at the nest was recorded using a clinometer to measure the slope in the prevailing downhill direction.

Recent papers have raised concern that collecting habitat data at nest termination regardless of nest fate may introduce bias (Gibson et al. 2016, McConnell et al. 2017, Smith et al. 2018). To avoid potential biases associated with measuring unsuccessful nests immediately following failure and successful nests after hatching, we collected vegetation data within 1-2 days of nest fate for successful nests and within 1-2 days of the expected hatch date for failed nests. Due to logistical constraints, nests that failed within 4 days prior to their expected hatch date were sampled only once.

Weather Data

To investigate potential associations between precipitation and nest or poult survival during the spring (Apr-Jun) and summer (Jul-Aug), we established 3 rain gauges across the study area and recorded daily precipitation amounts at these locations from 9 May to 14 August 2016 and from 18 April to 12 August 2017. We also obtained daily precipitation data from 8 National Oceanic and Atmospheric Administration weather stations (National Climatic Data Center 2016-2017) from 1 April to 31 August during 2016 and 2017. We obtained minimum daily temperature readings from 6 National Oceanic and Atmospheric weather stations from 1 April to 31 August in both 2016 and 2017. On days when a daily observation was not available at a rain gauge/weather station, we replaced the missing value for that station with the observation from the next closest gauge/weather station.

Logistical constraints prevented us from checking rain gauges at exactly the same time each day, and observation times also varied or were not available for some weather stations. As a result, each daily precipitation record corresponded to ~24 hours.

Although we recognized that this could limit our ability to detect patterns between nest or poult survival and precipitation, we considered our data a reasonable approximation of conditions.

Because patterns of precipitation and temperature in the Black Hills can be patchy, we assigned the closest weather station or rain gauge to each nest (for precipitation) and each brood (for both precipitation and temperature). This allowed us to utilize daily weather observations as time-varying individual covariates in the survival analyses. For broods, we first calculated the mean center of all poult count locations for each brood and used the weather station nearest to that point. The mean distance between nests and the nearest weather station was 4.6 km, and the mean distances between brood locations and the nearest weather station were 4.5 and 7.4 km for precipitation and temperature, respectively.

Covariates of Interest: Nest Survival

Based on our questions of interest and previous research on nesting ecology of Merriam's turkeys, we chose to explore potential associations of daily precipitation amount, hen age, visual obstruction, understory canopy cover, and slope with nest survival. We were primarily interested in the association between precipitation and nest survival; we also considered visual obstruction, understory canopy, and slope because we thought the exclusion of habitat covariates might prevent us from adequately quantifying the association with precipitation. Prior to conducting our analysis, we evaluated correlations among habitat variables; all were less than 0.35. We also included year as a covariate to test for differences between nest survival in 2016 and 2017. We considered all possible additive combinations of covariates (Doherty et al. 2012, e.g., Skone et al. 2016) and added interaction terms and quadratics to test for biologically-plausible nonlinearities (described below).

Nesting rates of juvenile turkey hens generally are lower than for adults, but there is less evidence that survival of nests incubated by juvenile hens differs from adults (Vander Haegen et al. 1988, Rumble and Hodorff 1993, Roberts et al. 1995, Lehman et al. 2008*a*, Pollentier et al. 2014*b*). However, previous nesting studies in the Black Hills may have had limited power to detect differential nest survival due to small sample sizes for juvenile hens (Rumble and Hodorff 1993, Lehman et al. 2008*b*). We included models with an additive term for hen age to test for potential differences and expected that nests incubated by juvenile hens would have lower survival.

Turkey hens select nesting locations that provide hiding cover from predators (Lutz and Crawford 1987, Wakeling 1991, Rumble and Hodorff 1993, Lehman et al. 2008*b*). We characterized hiding cover using 2 different metrics. VOR provided a measure of hiding cover when viewed from the side (i.e., vertical structure), whereas understory canopy cover provided a measure of hiding cover when viewed from above (i.e., horizontal structure). Lehman et al. (2008) found evidence that nest survival increased with hiding cover, and we predicted nest survival to be positively associated with both visual obstruction and understory canopy cover. Additionally, steep slopes may improve nest survival (Rumble and Hodorff 1993, Lehman et al. 2008*b*) and we expected to find a similar pattern.

Precipitation may increase risk of nest predation in ground-nesting birds because mammalian predators may more effectively locate nesting hens via olfaction during or immediately following rain events (Roberts et al. 1995, Lehman et al. 2008*b*, Webb et al. 2012). Accordingly, we evaluated evidence for a negative association between precipitation and daily survival rate (DSR) by using a time-varying individual covariate that indicated the amount of rainfall during each day of incubation. We expected that increased hiding cover might help offset the impact of precipitation (Lehman et al. 2008*b*), so we considered models where precipitation was allowed to interact with visual obstruction reading and total understory canopy cover. Additionally, we thought that the relationship between precipitation and nest survival might be nonlinear. Specifically, we were interested in whether small precipitation amounts might have little to no impact on nest survival, but larger amounts would have a substantial impact; we considered models that included a quadratic term for precipitation to test for this association.

Covariates of Interest: Poult Survival

Wet weather is associated with reduced poult survival (Roberts and Porter 1998*a*, Lehman et al. 2008*a*) and cold weather also may reduce survival, particularly for young poults that have more difficulty maintaining homeostasis (Roberts and Porter 1998*a*, Lehman et al. 2008*a*). Previous studies of poult survival used heating degree days (HHD) to quantify the cumulative effect of low temperatures during multi-day survival periods (Roberts and Porter 1998*a*, Lehman et al. 2008*a*), but our analysis allowed for a finer resolution via the estimation of DSR. Consequently, we utilized daily observations for precipitation amount and minimum temperature as time-varying individual covariates to assess associations with poult survival. We expected that poult survival would be reduced by increased precipitation and lower minimum temperatures. Prolonged cold *and* wet periods may reduce poult survival further (Healy and Nenno 1985, Lehman et al. 2008*a*); we included models with an interaction between temperature and precipitation to test for this potential effect.

Most poult mortality occurs before 2 weeks of age because they cannot fly, increasing vulnerability to predation, and because they are more vulnerable to weather events (Healy and Nenno 1985, Speake et al. 1985, Roberts and Porter 1998*a*, Lehman et al. 2008*a*). We investigated the impact of poult age by allowing survival to follow a trend according to age in days (Rotella 2017). We expected that DSR would increase as poults aged. We chose not to consider models that included interactions between poult age and weather covariates *a priori* because we expected the data to be overdispersed and because relatively low rates of nesting and renesting resulted in a modest sample size for poult survival, limiting our ability to detect complex patterns.

Survival of poults reared by juvenile hens was lower than poults reared by adult hens in the southern Black Hills (Lehman et al. 2008*a*). We expected a similar relationship in the northern Black Hills and therefore considered models of poult survival that included hen age.

Nest and Poult Survival Estimation

We estimated daily survival rates of nests using the nest-survival model (Dinsmore et al. 2002, Rotella et al. 2004). The minimum data requirements for the nest survival model are the date survival monitoring began (FirstFound, the day the hen began incubating), the last date the nest was known alive (LastPresent), the date the nest was last checked (LastChecked), and the Fate (0 = alive and 1 = dead). We ran our analysis using Program MARK (White and Burnham 1999) via RMark (Laake 2013) in Program R (R Core Development Team 2013). This method uses a maximum likelihood approach to estimate DSR.

Logistical constraints in the field frequently prevented obtaining accurate poult counts at exactly 2 and 4 weeks of age. Because poult survival was not monitored in equal-length time intervals, we used an approach similar to our nest analysis and applied the nest survival model to ragged telemetry data instead of a known-fate analysis (Dinsmore et al. 2002, Rotella et al. 2004, Amundson and Arnold 2011, Garrick et al. 2017) to estimate poult survival. This enabled us to address uncertainty in the exact date of poult mortality. For example, if eggshell remains indicated a brood size of 9 poults at hatch (day 1), 5 poults were counted on day 13, and 4 poults were counted on day 28, then we would use following input data for that brood: 4 poults assigned FirstFound = 1, LastPresent = 1, LastChecked = 13, and Fate = 1; 1 poult assigned FirstFound = 1, LastPresent = 13, LastChecked = 28, and Fate = 1; and 4 poults assigned FirstFound = 1, LastPresent = 28, LastChecked = 28, and Fate = 0.

Because survival of brood mates is not always independent (e.g., a coyote might kill multiple poults during the same predation event), the data could have a lack of independence (Bishop et al. 2008). We used a data-bootstrap to estimate $\hat{c}$, the ratio of the bootstrap variance to the theoretical variance, where overdispersion is indicated by $\hat{c} > 1$ (Bishop et al. 2008, Wilson et al. 2012). We resampled our original data at the brood level to generate 5,000 replicate datasets and estimated DSRs for each replicate using the most complex model from the candidate set (Bishop et al. 2008). For each iteration, we estimated DSR using the mean value of continuous covariates and each combination of discrete covariates. We calculated the variance for each bootstrapped DSR estimate ($\mathrm{Var}(\mathrm{DSR}_{\mathrm{boot}})$) and also estimated the standard error for each DSR based on the original data ($\mathrm{SE}(\mathrm{DSR}_{\mathrm{original}})$). We then estimated c for each DSR: $\hat{c} = \mathrm{Var}(\mathrm{DSR}_{\mathrm{boot}}) / [\mathrm{SE}(\mathrm{DSR}_{\mathrm{original}})]^2$. Finally, we averaged all separate estimates of $\hat{c}$ as the optimal predictor of c (Bishop et al. 2008), and then adjusted AIC_c scores for overdispersion (QAIC_c).

Using an information-theoretic approach (Burnham and Anderson 2002), we compared 120 and 40 models to evaluate relationships between all covariates with nest and poult survival respectively. When evaluating model-selection results, we considered a parameter uninformative when its addition resulted in an AIC_c or QAIC_c score ~2 units larger than a model without it (Burnham and Anderson 2002, Arnold 2010).

We estimated nest and poult DSR from the best fit model and plotted predicted DSR across a range of covariate values to visualize the associations between covariates and nest or poult survival. Because estimates of nest survival to hatch and early poult survival to 4 weeks of age are easier to interpret and provide a better indication of population productivity, we estimated nest survival through a 26-day incubation period and poult survival to 4 weeks of age using covariate combinations we considered most useful to managers. We used the delta method to estimate standard errors of these estimates (Powell 2007).

RESULTS

Turkey Captures, Nests and Broods Monitored

In 2016, we captured 145 female wild turkeys and released 97 (46 juveniles and 51 adults) with VHF transmitters and entered the nesting season with 40 adults and 39 juveniles on 1 April. Twenty-five juvenile hens captured in 2016 survived to enter the adult age class on 1 December 2016. In 2017, we captured 150 female wild turkeys and released an additional 52 individuals (49 juveniles and 3 adults) with transmitters; we entered the nesting season with 40 adults and 41 juveniles. We marked 45 nests in 2016 (42 first nests, 3 renests) and 59 nests (50 first nests, 9 renests) in 2017 (Table 3.1); no hens abandoned their nest as a result of marking activities. Five nests were located during laying; the remainder were marked during early incubation (all but 5 nests were marked on the first day of incubation). We omitted 5 nests from our survival analysis because we were unable to locate the nest bowl or collect the nest site characteristics within 2 days of expected hatch date. In 2016 and 2017, 28 and 22 nests hatched, respectively, and the broods were subsequently monitored to estimate poult survival to 4 weeks of age.

Annual Reproduction Parameters

Within hen age classes, rates of nesting renesting, and hatching and clutch sizes were similar between 2016 and 2017 (Table 3.1); 83% (SE = 4%) of adult hens attempted to nest and 36% (SE = 8%) attempted to renest following an unsuccessful first attempt. Juvenile hens nested and renested at lower rates than adults: 33% (SE = 5%) attempted to nest, but none renested following a failed nesting attempt. Clutches laid by adult and juvenile hens were similarly sized: 9.67 (SE = 0.31) and 9.43 (SE = 0.51) for adults and juveniles, respectively. Hatch rates were also similar: 0.88 (SE = 0.02) and 0.86 (SE = 0.04) for adults and juveniles, respectively. Nests depredated during laying are difficult to locate and count (Lehman et al. 2005); some nests may have failed during the laying period before we could locate them. However, we believe the impact to the estimation of nesting rate was minimal because we checked hen activity frequently and because none of the nests we marked during laying were depredated during the laying period. Apparent nest success averaged 0.51 (SE = 0.06) and 0.39 (SE = 0.10) for adult and juvenile hens, respectively.

Causes of Nest Failure

We determined the cause or probable cause of 53 of 54 failed nests. Mammalian predation was the most common cause of nest failure. Forty-seven percent of nests (25) were confirmed mammalian depredation by the presence of hair or by direct observation. The clutch laid in 1 nest (2%) was infertile; the hen incubated for 43 days until the nest was depredated by a mammalian predator. We were unable to find hair at 13 nests (25%) but classified the cause as probable mammalian predation based on the condition of eggshells. Thirteen percent of nests (7) failed due to avian depredation. Two nests (4%) were depredated, but we were unable to determine if the predator was avian or mammalian. Three nests (6%) were abandoned by hens that died of apparent starvation shortly thereafter. One nest (2%) failed due to a small landslide following an intense rain event.

Nest Survival

We found evidence that larger values of daily precipitation were associated with lower nest DSR, and that hiding cover at the nest was positively associated with nest DSR (Table 3.2). Among well-supported models ($\Delta AIC_c \leq 2$, 13 models), all included precipitation, all but 1 included visual obstruction, and 6 included understory canopy cover. We also found some suggestive evidence that nests incubated by juvenile hens had lower survival than adult hens (5 of 13 well-supported models). Annual variation was included in 9 well-supported models; the 2016 nesting season was associated with higher DSR, suggesting differences in DSR between years that were not explained by daily precipitation observations. Confidence intervals associated with understory canopy cover and hen age, as well as interactions between understory canopy cover and visual obstruction with daily precipitation overlapped zero in some well-supported models, preventing unequivocal inferences about the magnitude of these impacts on DSR (Table 3.2). We did not find evidence for a quadratic effect of daily precipitation amount or that slope at the nest site impacted DSR (Table 3.2).

Although multiple models were well supported, the direction and magnitude of relationships between nest survival, precipitation, and habitat conditions at the nest were consistent. Therefore, we present results from the top model (Precip + VOR + Year). Precipitation was associated with reduced DSR and greater values of VOR were associated with increased DSR. To visualize the influence of precipitation, we plotted predicted DSR in 2017 across a range of precipitation values, while holding visual obstruction at the mean value (Figure 3.3). Similarly, we plotted predicted DSR in 2017 across a range of VOR values while holding daily precipitation at zero and also at the mean of non-zero observations (Figure 3.4). We also predicted nest survival for the entire 26-day incubation period for both years, using the precipitation data from the rain gauge associated with the most nests (~ 26% of all nest-weather associations), the mean values of visual obstruction, and assuming that incubation began on the median date of nest initiation. Estimated survival to hatch was 0.68 (95% CI = 0.53 – 0.83) in 2016 and 0.49 (95% CI = 0.35 – 0.62) in 2017.

Poult Survival

Overdispersion in our poult survival data was substantial ($\hat{c}$ = 6.53). After adjusting AIC_c scores and variances of our survival estimates for overdispersion, we found little evidence that minimum daily temperature, daily precipitation, or hen age were associated with poult survival (Table 3.3). Further, we did not find substantial evidence for a difference in poult survival between 2016 and 2017. There was evidence, however, that survival increased as poults aged (Table 3.3; $\hat{\beta}_{\mathrm{PoultAge}}$ = 0.05, SE = 0.01), and we selected the PoultAge model as the best model to describe turkey poult survival from hatch to 4 weeks of age (Figure 3.5). The estimated survival to 4 weeks of age was 0.39 (95% CI = 0.27 – 0.51).

DISCUSSION

We found evidence that survival of turkey nests in the northern Black Hills is reduced by precipitation, consistent with previous research in the southern Black Hills (Lehman et al. 2008*b*) and as predicted by the moisture-facilitated nest-depredation hypothesis. Predators using olfactory cues likely become more efficient during moist periods.

Increased bacterial growth on wet feathers (Roberts and Porter 1998*b*), and water molecules competing with odorants for binding sites on hens and eggs (Borgo and Conover 2015) have been proposed as potential mechanisms by which scent production could increase during periods of wet weather and increase predator efficiency. But like Lehman et al. (2008*b*), we also found evidence that habitat features, specifically visual obstruction, may improve nest survival, potentially providing additional benefits during periods of wet weather. In addition to providing visual screening, vegetation and other structures may also create turbulence which helps to disperse odorants, making it more difficult for predators to locate the nest (Conover 2007, Fogarty et al. 2018). Although most predation events of nests and incubating hens in our study system were by mammals relying in part on olfactory cues, avian predation was not insignificant. Further, even predators utilizing olfaction to locate nests must also rely on visual information to complete predation attempts, underscoring the importance of both olfactory and visual concealment at nest locations.

In contrast to our findings, precipitation improved survival of sage-grouse nests in Montana (Moynahan et al. 2007) and ground-nesting birds in Oklahoma (Fogarty et al. 2017). Fogarty et al. (2017) suggested that during precipitation, odorants may be released from multiple prey species and predators may focus on the prey items with the greatest reward potential; this could explain why the impact of precipitation varies depending on the study system. Although we were not able to test this hypothesis directly, turkey hens and nests, with their large egg, clutch, and body sizes (Schorger 1967, Flake et al. 2006), likely represent a high-reward item no matter what other species comprise the prey community. Regardless of the underlying mechanism, our results emphasize that understanding the impacts of weather conditions on avian populations likely requires a region-specific accounting for local habitat conditions and the predator-prey community.

Although hen age was not included in the top model, its inclusion in some well-supported models provides suggestive evidence that nests incubated by juvenile hens may have lower survival than nests incubated by adult hens. We are not aware of any studies of Merriam's wild turkey nesting ecology in ponderosa pine ecosystems that have documented differing survival rates between nests laid by adult and juvenile hens. However, previous studies (e.g. Rumble and Hodorff 1993, Thompson 1993, Lehman et al. 2008*b*) may have lacked sufficient sample sizes of nests incubated by juvenile hens to detect differences. We propose that juvenile hens, which typically have smaller body sizes (Flake et al. 2006) might have a greater need to forage during incubation; this potential change in nest attendance behavior might make juvenile hens and their nests more easily detected by predators. Young, less experienced hens might also select nesting locations that are more vulnerable to predation.

We were unable to draw strong inferences regarding the influence of weather on poult survival, possibly due to overdispersion in our poult survival data. However, survival did increase as poults aged, as expected. The ragged nature of our poult count data may have contributed to overdispersion. We typically obtained brood size data at hatch, and again at approximately 2 and 4 weeks of age; this monitoring schedule prevented us from determining if poults lost between counts died due to 1 or more predation or weather events. Further, we had a modest sample size to estimate poult survival (a total of 50 successful nests in both years). Despite our inability to detect impacts of weather on poult survival, we did observe poults that died of exposure during cold and wet events. Further, detrimental impacts of inclement weather on poult survival have been documented previously (Roberts and Porter 1998*a*, Lehman et al. 2008*a*), and managers should be aware that cold and wet events will likely reduce poult survival in the Black Hills. We suggest that future investigations of young galliform survival could be more effective if poults are counted more frequently, but researchers must balance the need for more robust encounter histories with the potential impacts to survival that may result from frequent brood disturbances.

Weather conditions varied markedly over the course of our study. Substantially more spring precipitation fell during the 2017 nesting season than in 2016, but both springs were drier than the long-term average (Figure 3.6a). Additionally, the winters preceding nesting during our study were far milder than average (Figure 3.6b). Despite mild winters, we observed hens that died of starvation during nesting season and necropsies on hens killed accidentally during captures revealed limited energy reserves. Snow cover that persists into late spring may delay or reduce nesting attempts (Lavoie et al. 2017). In years with average or wet springs, nest survival will likely be lower, and during average or harsh winters, hens will enter the nesting season with lower body reserves, which may further reduce nesting rates.

MANAGEMENT IMPLICATIONS

Management of wild turkeys is best informed by current and region-specific vital rates (Pollentier et al. 2014*a*, *b*). Rates of nesting, renesting, and apparent nest success were lower in the northern Black Hills than in the southern Black Hills (Table 3.4), although poult survival to 4 weeks of age was similar (Lehman et al. 2008*a*). Nesting rates also were lower than in the central Black Hills (Rumble and Hodorff 1993, Rumble et al. 2003). Although nest success estimates were lower in the central Black Hills (Rumble and Hodorff 1993, Rumble et al. 2003), small sample sizes limit the strength of comparisons to our study.

Turkey management in the northern Black Hills was previously informed by data from the southern Black Hills. However, the lower rates of nesting, renesting, and nest survival, combined with reduced hen survival (Chapter 2) will limit the productivity of the wild turkey population in the northern Black Hills, when compared to the southern Black Hills. We caution that in wetter than average springs, especially following average to harsh winters, turkey population productivity in the northern Black Hills may be reduced below the levels observed during our study. Prior to this study, hen harvest by hunters was permitted during the fall turkey season. Managers have limited ability to increase turkey productivity in the northern Black Hills, but we recommend that managers avoid human-induced reductions in hen survival and subsequent reproduction by preventing hen harvest, either by allowing male-only harvest during fall or by closing the fall season entirely in this area. We also found that habitat features around the nest provide visual and olfactory concealment important for nest survival, so retaining vegetation cover could also provide another management strategy. However, although we did not explore nest site availability here, our field observations suggest that turkeys are not at all limited by high-quality nesting sites in the northern Black Hills; forest management practices that continue to provide understory structure with ample cover will help maintain turkey populations. Forest management practices in the Black Hills are typically under the purview of the US Forest Service and private landowners. We caution that we considered the impacts of habitat characteristics during nesting alone and a diversity of features are needed to support other stages of the turkey life cycle.

Although turkey productivity is lower in the northern Black Hills than in other portions of the Black Hills, turkeys have persisted and sustained substantial harvest since their introduction (Flake et al. 2006). We documented some juvenile hens that made large spring dispersal movements southward and subsequently wintered in the central Black Hills, and hens from the central and southern Black Hills may make similarly large movements to the north. The population segment in the northern Black Hills may be sustained in part by immigrants from the central or southern Black Hills. However, because we only captured and marked turkeys in the northern Black Hills, we were unable to quantify the potential impact of immigration by turkeys from farther south on population dynamics. Future investigations of turkey ecology in the Black Hills should consider collecting both movement and vital rates data to document the potential for source-sink dynamics.

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Table 3.1. Nesting, renesting, and hatch rates and clutch size for adult and juvenile hens in the Northern Black Hills, 2016-2017. Standard errors shown in parentheses.

Age	Year	Hens Available to Nest[a]	First Nests	Nesting Rate	Renests	Renest Rate	Mean Clutch Size[b]	Hatch Rate[b]
Adult	2016	40	31	0.78 (0.07)	3	0.33 (0.16)	9.70 (0.52)	0.89 (0.02)
	2017	40	35	0.88 (0.05)	9	0.38 (0.10)	9.64 (0.34)	0.88 (0.03)
	Years pooled	80	66	0.83 (0.04)	12	0.36 (0.08)	9.67 (0.31)	0.88 (0.01)
Juvenile	2016	39	11	0.28 (0.07)	0	0 (0)	10.00 (0.82)	0.87 (0.05)
	2017	41	15	0.37 (0.08)	0	0 (0)	8.86 (0.59)	0.85 (0.06)
	Years pooled	80	26	0.33 (0.05)	0	0 (0)	9.43 (0.51)	0.86 (0.04)

[a] Radiomarked hens known alive on 1 April monitored for nesting activity during the nesting season. Number of adults in 2017 includes hens captured in winter 2016 that survived to the beginning of the 2017 nesting season.

[b] First and renest attempts pooled.

Table 3.2. Strongly-supported models ($\Delta AIC_c < 2$) for nest survival of wild turkeys in the northern Black Hills, SD, 2016-2017. Covariates are: daily precipitation amount (Precip), visual obstruction reading (VOR), total understory plant cover (TOCO), year (Yr), hen age (Age), and slope (Slp). Models that include interactions also include main effects of those terms. K is the number of parameters in each model.

Model	**AIC_c**	**ΔAIC_c**	**AIC_c weight**	**Deviance**	**K**
Precip+VOR+Yr[a]	440.53	0.00	0.05	432.51	4
Precip*VOR+ Precip*TOCO+Yr	440.79	0.26	0.04	426.73	7
Precip *VOR+ Precip*TOCO+Yr+Age	440.85	0.32	0.04	424.77	8
Precip+VOR+Yr+Age	440.91	0.38	0.04	430.88	5
S Precip*TOCO+Yr	441.09	0.56	0.04	431.06	5
Precip*TOCO+Yr+Age	441.43	0.90	0.03	429.38	6
Precip+Yr	441.88	1.35	0.02	435.86	3
Precip*VOR+Precip*TOCO+Age	442.15	1.62	0.02	428.09	7
Precip+VOR	442.18	1.65	0.02	436.17	3
Precip+VOR+Age	442.22	1.69	0.02	434.20	4
Precip*VOR+Yr	442.22	1.69	0.02	432.19	5
Precip*VOR+ Precip *TOCO	442.27	1.74	0.02	430.22	6
Precip+VOR+Slp+Yr	442.29	1.76	0.02	432.26	5

[a] Precip+VOR+Yr $\hat{\beta}$s (with standard errors) are as follows: $\hat{\beta}_{Intercept} = 2.93$ (0.40), $\hat{\beta}_{Precip} = -0.05$ (0.02), $\hat{\beta}_{VOR} = 0.03$ (0.02), $\hat{\beta}_{Yr=2016} = 0.62$ (0.34),

Table 3.3. Results of model selection for turkey poult survival in the northern Black Hills, SD, 2016-2017. Covariates are: poult age in days (PltAge), year (Yr), minimum daily temperature (Temp), hen age (HenAge), and daily precipitation amount (Precip). Models that include interactions also include main effects of those terms. K is the number of parameters in each model.

Model	**QAIC$_c$**	**ΔQAIC$_c$**	**QAIC$_c$ weight**	**QDeviance**	**K**
PltAge[a]	136.92	0.00	0.16	132.91	2
Null	138.51	1.59	0.07	136.51	1
PltAge+Yr	138.53	1.62	0.07	132.53	3
Temp+PltAge	138.64	1.73	0.07	132.64	3
Precip+PltAge	138.67	1.75	0.07	132.66	3
PoultAge+HenAge	138.80	1.88	0.06	132.79	3
Temp+PltAge+Yr	140.09	3.18	0.03	132.09	4
Precip+PltAge+Yr	140.12	3.21	0.03	132.12	4
Year	140.15	3.23	0.03	136.15	2
Precip	140.20	3.29	0.03	136.20	2
Temp	140.29	3.38	0.03	136.29	2
HenAge	140.35	3.43	0.03	136.34	2
Temp+PltAge+HenAge	140.36	3.45	0.03	132.36	4
Temp+Precip+PltAge	140.38	3.47	0.03	132.38	4
PoultAge+HenAge+Yr	140.40	3.48	0.03	132.39	4
Precip+PltAge+HenAge	140.55	3.64	0.03	132.54	4
Temp+Precip+PltAge+Yr	141.63	4.72	0.02	131.62	5
Precip+Year	141.70	4.78	0.01	135.70	3
Temp+PltAge+HenAge+Yr	141.72	4.81	0.01	131.71	5
Temp+Yr	141.84	4.92	0.01	135.83	3
Temp+Precip	141.95	5.04	0.01	135.95	3
HenAge+Yr	141.97	5.06	0.01	135.97	3
Temp+HenAge	141.98	5.07	0.01	135.98	3
Precip+PltAge+HenAge+Yr	141.99	5.07	0.01	131.97	5
Precip+HenAge	142.05	5.13	0.01	136.04	3
Temp+Precip+PltAge+HenAge	142.11	5.19	0.01	132.10	5
Temp*Precip+PltAge	142.29	5.38	0.01	132.28	5
Temp+Precip+PltAge+HenAge+Yr	143.22	6.30	0.01	131.20	6
Temp+Precip+Yr	143.32	6.40	0.01	135.31	4
Temp+HenAge+Yr	143.46	6.55	0.01	135.46	4
Precip+HenAge+Yr	143.53	6.61	0.01	135.52	4
Temp*Precip	143.54	6.63	0.01	135.54	4
Temp*Precip+PltAge+Yr	143.60	6.68	0.01	131.58	6
Temp+Precip+HenAge	143.64	6.73	0.01	135.64	4
Temp*Precip+PltAge+HenAge	144.00	7.08	0.00	131.98	6

Temp+Precip+HenAge+Yr	144.91	7.99	0.00	134.90	5
Temp*Precip+Yr	144.99	8.08	0.00	134.98	5
Temp*Precip+PltAge+HenAge+Yr	145.16	8.25	0.00	131.14	7
Temp*Precip+HenAge	145.21	8.29	0.00	135.19	5
Temp*Precip+HenAge+Yr	146.56	9.64	0.00	134.54	6

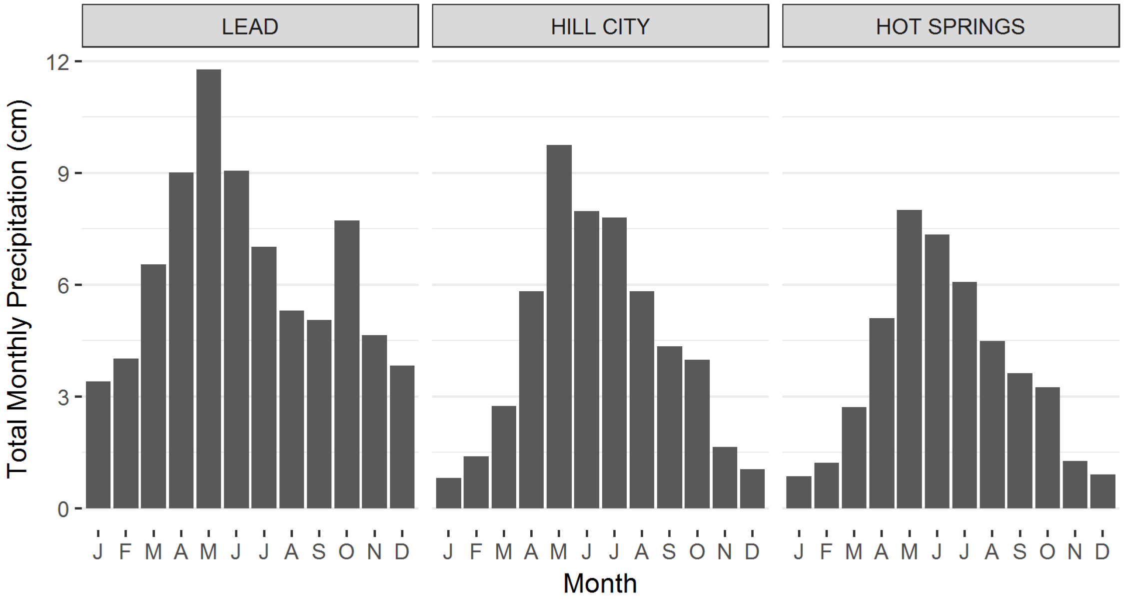
[a] PltAge $\hat{\beta}$s (with standard errors) are as follows: $\hat{\beta}_{\text{Intercept}}$ = 2.741 (0.124), $\hat{\beta}_{\text{PoultAge}}$ = 0.053 (0.012).

Table 3.4. Rates of nesting, renesting, and apparent nest success for wild turkeys in the southern (Lehman et al. 2008*b*) and central (Rumble and Hodorff 1993, Rumble et al. 2003) Black Hills. Standard errors (when available) are shown in parentheses.

Hen Age	**Rate**	**South**	**Central**
Adult	Nesting	0.98 (0.030)	0.97
	Renesting	0.75 (0.063)	–
	Apparent Nest Success	0.59 (0.043)	0.36
Juvenile	Nesting	0.50	0.73
	Renesting	–	–
	Apparent Nest Success	0.83	0.23

Figure 3.1. Average a) precipitation and b) snowfall by month (cm) for the northern (Lead, SD), central (Hill City, SD), and southern (Hot Springs, SD) Black Hills (National Climatic Data Center 1981-2010).

a)



b)

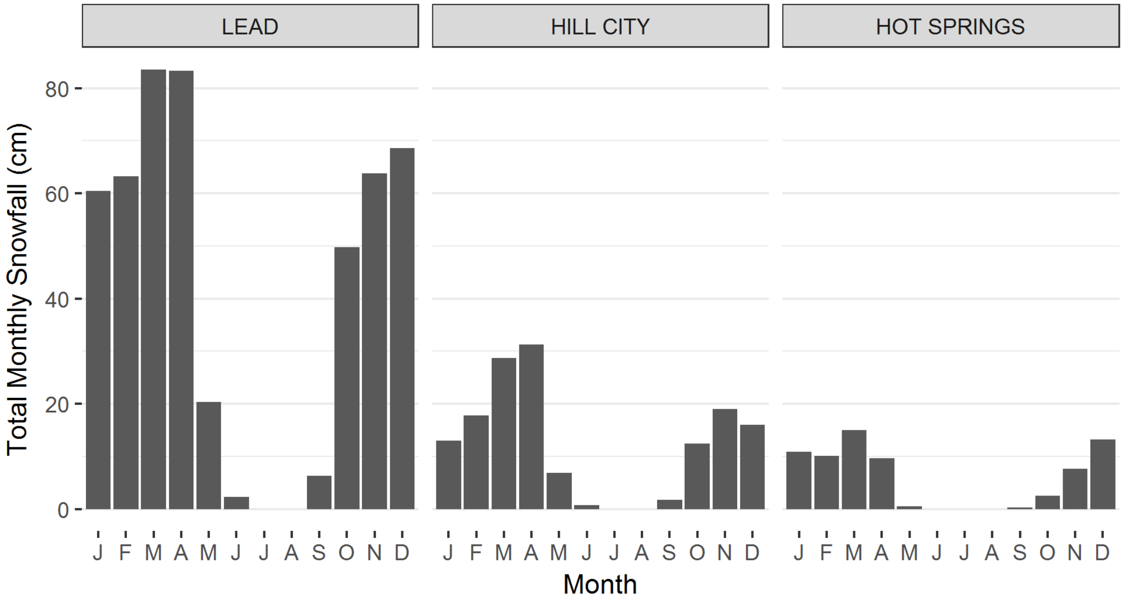


Figure 3.2. Study area with locations of all weather stations/rain gauges, nests, and capture locations, west-central South Dakota and northeast Wyoming (see inset map), January 2016 – March 2018.

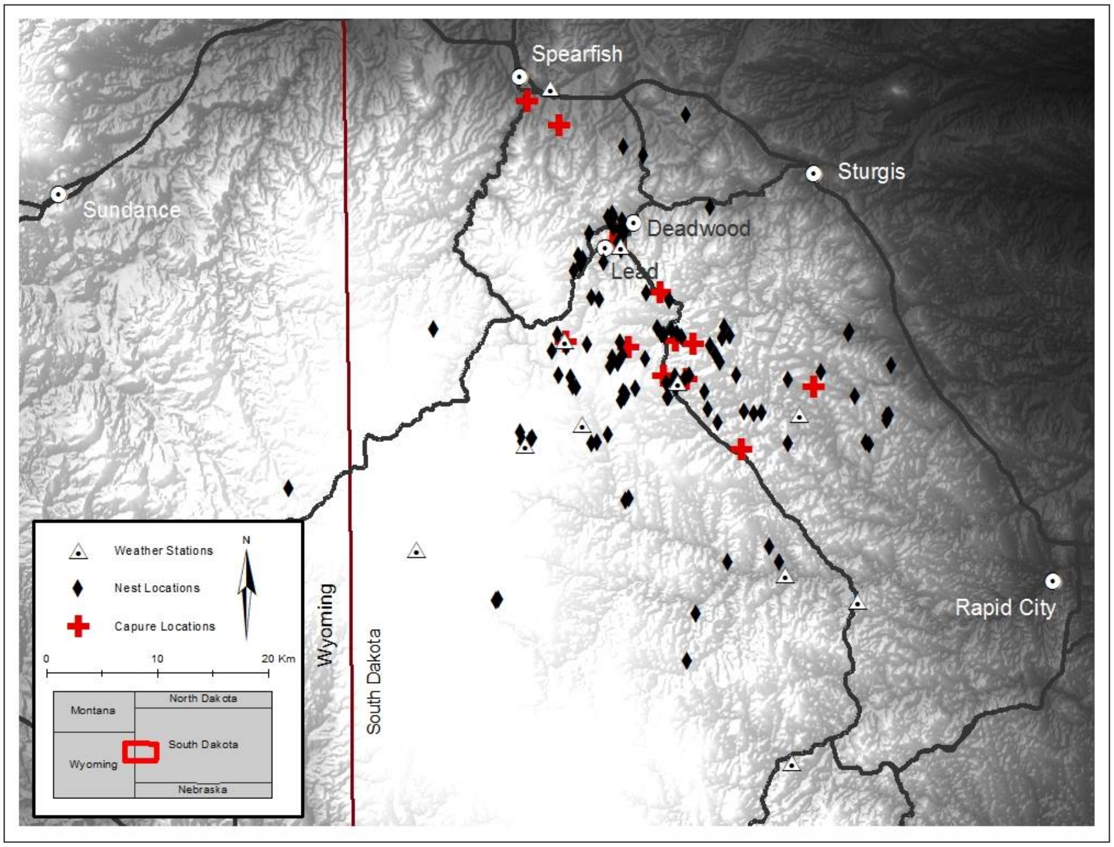


Figure 3.3. Predicted 2017 nest DSR (and 95% confidence intervals) across a range of daily precipitation values when visual obstruction is held at the mean value for wild turkey nests in the northern Black Hills, SD.

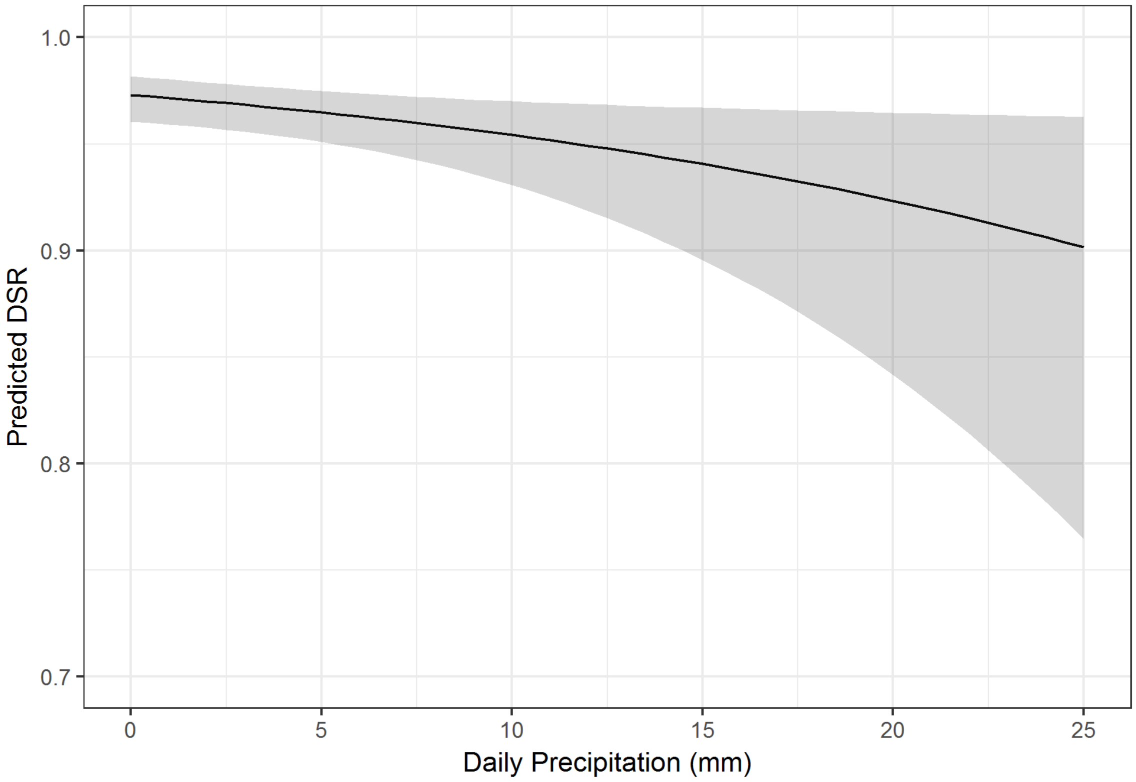


Figure 3.4. Predicted 2017 nest DSR (and 95% confidence intervals) across a range of visual obstruction (VOR) values when daily precipitation is held at zero and the mean of non-zero precipitation values for wild turkey nests in the northern Black Hills, SD. VOR is measured in 1.27 cm increments.

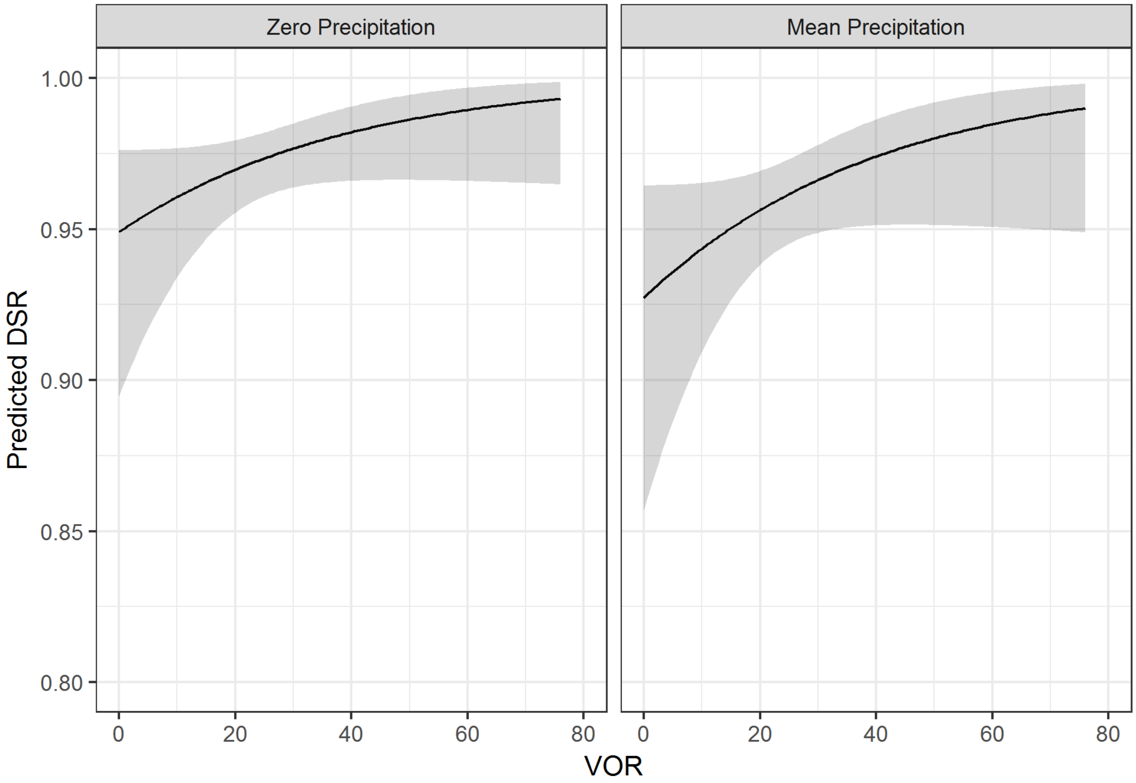


Figure 3.5. DSR estimates (and 95% confidence intervals) for turkey poults from hatch to 4 weeks of age as predicted by the PltAge model, northern Black Hills, SD (2016-2017).

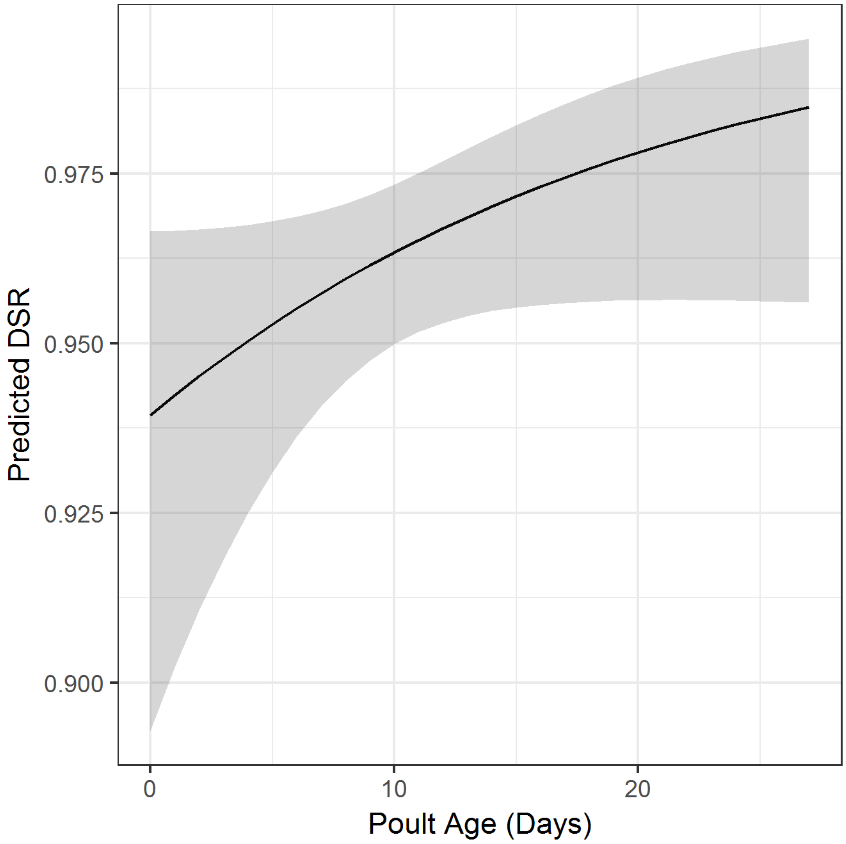
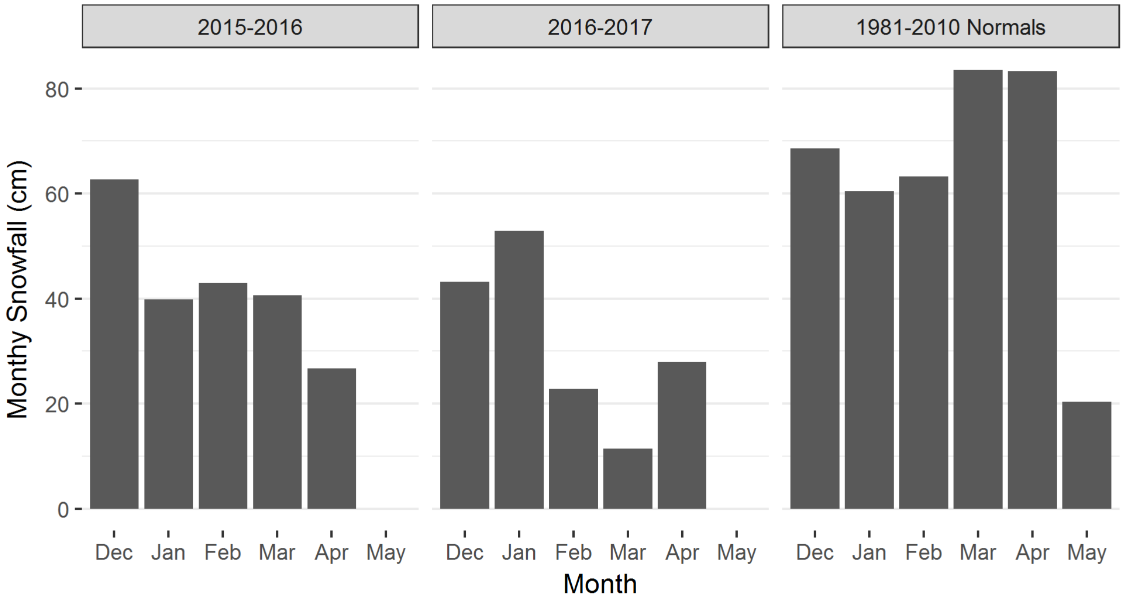
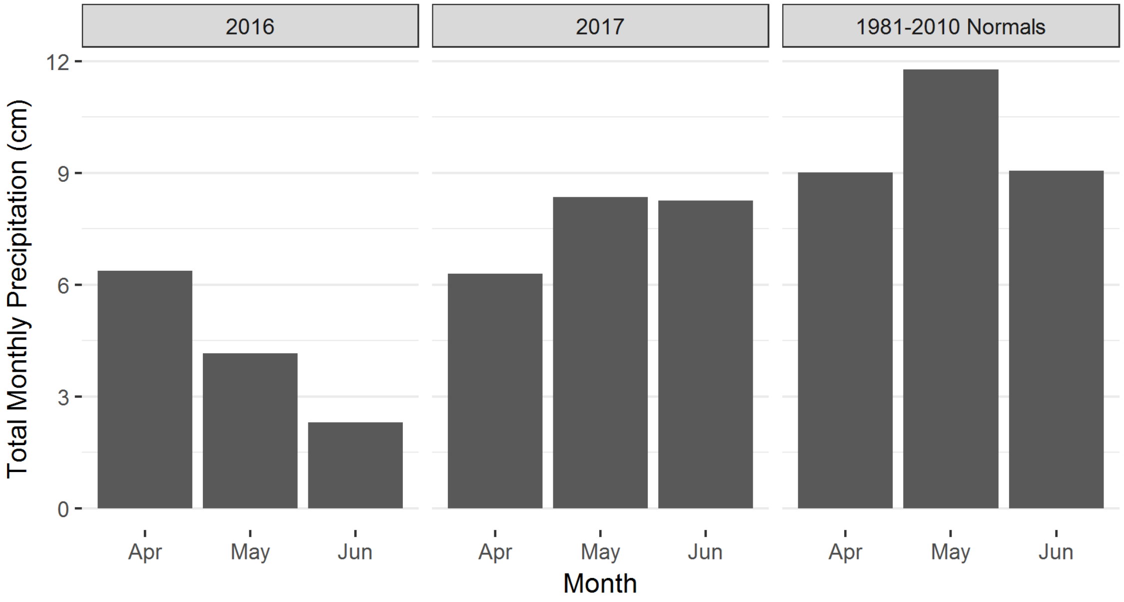


Figure 3.6. Total monthly snowfall (a) and spring precipitation (b) in Lead, SD during 2016 and 2017 compared to long term averages (1981-2010).

a)



b)



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CHAPTER FOUR

CONCLUSIONS

General Conclusions

We found clear evidence that time spent incubating reduced survival of turkey hens, consistent with tradeoffs associated with reproduction predicted by life history theory (Stearns 1992). Additionally, survival of incubating hens was reduced further by precipitation (Chapter 2), as suggested by the moisture-facilitated nest-predation hypothesis (Roberts et al. 1995, Lehman et al. 2008*b*). Precipitation also reduced the survival of nests (Chapter 3), although vegetation cover at the nest may ameliorate the impact of precipitation. We were unable to draw strong conclusions regarding the impact of weather conditions on poult survival but provided managers with an estimate of survival to 4 weeks of age (Chapter 3).

Current reproduction had clear costs for current hen survival (Chapter 2), but tradeoffs between reproduction and survival also may manifest following the cessation of reproductive activity (Blomberg et al. 2013). The duration of our study did not allow us to explore the impacts of current reproduction on future survival or reproduction. Long-term studies longer durations are needed to quantify how reproductive tradeoffs influence the life histories of avian species.

In aggregate, our results show that turkey population growth is less productive than in other portions of the Black Hills (Rumble and Hodorff 1993, Rumble et al. 2003, Lehman 2005, Lehman et al. 2008*b*). We believe that climatic conditions, specifically more winter snowfall and spring rain, in the northern Black Hills underlie these demographic differences. This supports the assertion by us and others (Collier et al. 2009, Pollentier et al. 2014*a*, *b*) that turkey populations in relatively close proximity can exhibit biologically-meaningful differences in demography, requiring alternate management strategies.

Our results add to a growing body of literature that show weather conditions impact nest survival of ground-nesting birds, and that impacts are context-specific (e.g. Lehman et al. 2008*b*, Ruzicka and Conover 2012, Webb et al. 2012, Borgo and Conover 2015, Fogarty et al. 2017). Fogarty et al. (2017) suggested that the relative food value of nests to predators, compared to other prey items, may influence the impact of precipitation on nest survival. Characterizing other portions of the local predator-prey community (e.g., identifying nest predators or quantifying the availability of other prey items) will enhance understanding of nest survival for ground-nesting birds. Additionally, both our nest and hen survival analyses were subject to the potential for small mismatches between the timing of data collection for survival and precipitation. All ecological studies face challenges related to field conditions and logistics, but future studies focused on nest or hen survival may benefit from study designs which promote consistent timing for the collection of precipitation data (e.g., through dedicated personnel or automated gauges).

Management Implications and Future Directions

Regardless of whether the goal is to increase or reduce abundance, wildlife managers often have few options to affect population-level changes. Our results indicate that productivity of turkeys in the northern Black Hills is reduced by lower hen survival during winter and spring, reduced rates of nesting and renesting, and lower nest survival, yet managers have limited ability to increase these values. Managers can, however, reduce human-induced hen mortality by preventing hunter harvest of hens. Given that we also found that habitat features around the nest provide visual and olfactory concealment important for nest survival (Chapter 3), retaining vegetation cover could also provide another management strategy. Although we did not explore nest site availability in this analysis, our field observations suggest that turkeys are not at all limited by high-quality nesting sites in the northern Black Hills. Forest management practices that continue to provide understory structure with ample cover will help maintain turkey populations. We recognize that we focused on habitat characteristics during nesting and that a diversity of features are needed to support turkeys throughout their life cycle.

When compared to other portions of the Black Hills, turkey productivity in our study area is limited by low rates of hen and nest survival, as well as by lower rates of nesting and renesting. Although we did not explore it during our study, we noted that the turkey population in the northern Black Hills may be supported by immigrants from the south. Future studies in the Black Hills or other locations where game bird populations face a variety of climatic conditions in a small area should consider collecting movement data and/or simultaneously quantifying vital rates in multiple locations (e.g. Lavoie et al.

2017). A combination of data on movement and current vital rates would improve our understanding of how source-sink dynamics may operate across a range of environmental conditions.

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APPENDIX A

SUPPORTING INFORMATION FOR CHAPTER 3

Table A.1: List of candidate models for poult survival. Models constructed with additional time varying covariates are shown in rows, additional covariates that are not time varying are shown in columns.

Base Model	**+ HenAge**	**+ Year**	**+ HenAge + Year**
Null	Base + HenAge	Base + Year	Base + HenAge + Year
PoultAge	Base + HenAge	Base + Year	Base + HenAge + Year
Precip	Base + HenAge	Base + Year	Base + HenAge + Year
Precip + PoultAge	Base + HenAge	Base + Year	Base + HenAge + Year
Temp	Base + HenAge	Base + Year	Base + HenAge + Year
Temp + PoultAge	Base + HenAge	Base + Year	Base + HenAge + Year
Temp + Precip	Base + HenAge	Base + Year	Base + HenAge + Year
Temp +Precip + PoultAge	Base + HenAge	Base + Year	Base + HenAge + Year
Temp + Precip + Temp*Precip	Base + HenAge	Base + Year	Base + HenAge + Year
Temp + Precip + Temp*Precip + PoultAge	Base + HenAge	Base + Year	Base + HenAge + Year