





Research Article

Precipitation and Reproduction are Negatively Associated with Female Turkey Survival

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ABSTRACT Understanding how reproductive tradeoffs act in concert with abiotic elements to affect survival is important 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 consumptive and non-consumptive uses, and female survival is a primary factor influencing turkey population dynamics. We radio-tracked and collected survival data on 140 female Merriam's wild turkeys (*M. g. merriami*) in the northern Black Hills, South Dakota, USA, 2016–2018. We developed and compared a set of candidate models to evaluate how nest incubation, brood rearing, and precipitation could be associated with female survival. Increased time spent incubating was associated with reduced female survival. Additionally, daily precipitation was associated with reduced survival of incubating females. Seasonal survival was lowest during spring and winter. A female that did not incubate a nest was predicted to have a higher rate of annual survival (0.53, 85% CI=0.48–0.59) than a female that incubated a single nest (0.47, 85% CI=0.42–0.53). Despite the relative proximity of population segments, we estimated that annual survival for nesting and non-nesting females was lower in the northern Black Hills compared to annual female survival in the southern Black Hills, underscoring the need for region-specific data when possible. © 2020 The Wildlife Society.

KEY WORDS Black Hills, female survival, incubation, *Meleagris gallopavo*, Merriam's wild turkey, nest survival model, precipitation, South Dakota.

Life-history theory predicts trade-offs between survival and reproduction due to competing demands on finite resources (Williams 1966, Stearns 1992). Current reproduction may incur costs on current or future survival (Reznick 1985, Stearns 1992, Collier et al. 2009, Blomberg et al. 2013), and on the chance of future reproduction (Stearns 1992). Mortality of reproductive individuals can have 2 effects at the population level: reduced population size and the loss of individuals that could produce offspring. Abiotic elements (e.g., weather) also can influence population vital rates and may interact with reproductive trade-offs (Caudill et al. 2014). Understanding how reproductive tradeoffs act in concert with abiotic elements is important for effective management and conservation of wildlife populations, particularly for at-risk or harvested species.

Female survival is a primary factor influencing population dynamics for gallinaceous birds (Jarvis and Simpson 1978,

Sandercock et al. 2008, Taylor et al. 2012). Reductions in female survival while egg laying, incubating, or brood rearing have been documented in 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*; Miller et al. 1998, Collier et al. 2009). The effect of mortalities during each reproductive stage on population dynamics may vary by species and location. For wild turkeys in Texas, USA, spending more time incubating reduced survival during the breeding season (Collier et al. 2009). Similarly, lesser prairie-chicken females in Kansas, USA, that tended nests had lower survival rates than did non-nesting females (Hagen et al. 2007). Both nest success and brood-rearing success were associated with reduced survival of female sage grouse after completing nesting or brood rearing; however, the effect of nest success on future survival during summer was less important than the effect of brood rearing success on future survival during fall (Blomberg et al. 2013). Other researchers have noted reduced survival during nesting or brood rearing but have been limited in their investigation of the magnitude of reproductive costs

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(Vander Haegen et al. 1988, Wakeling 1991, Roberts et al. 1995, Hannon et al. 2003).

Climatic factors 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 female survival (Porter et al. 1980, Rumble et al. 2003, Lavoie et al. 2017). Temperature affects 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 female and nest predation by mammals, perhaps because predators are able to locate nesting females via olfaction more effectively during or immediately following rain events (Roberts et al. 1995, Lehman et al. 2008, Webb et al. 2012).

Merriam's wild turkeys (*M. g. merriami*; turkeys) originally were associated with ponderosa pine (*Pinus ponderosa*) communities in Colorado, New Mexico, Arizona, Oklahoma, and possibly western Texas, USA (Schorger 1967). 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 valued for consumptive and non-consumptive uses (Flake et al. 2006). Managers use data on multiple vital rates, including female 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 have been based on demographic data collected in the southern Black Hills. Further, dynamics of turkey populations may differ substantially between nearby locations (Collier et al. 2009; Pollentier et al. 2014a, b). The northern portion of the Black Hills differs from the central and southern portions in climate and vegetation (Flake et al. 2006). The northern Black Hills receives 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 (Fig. 1).

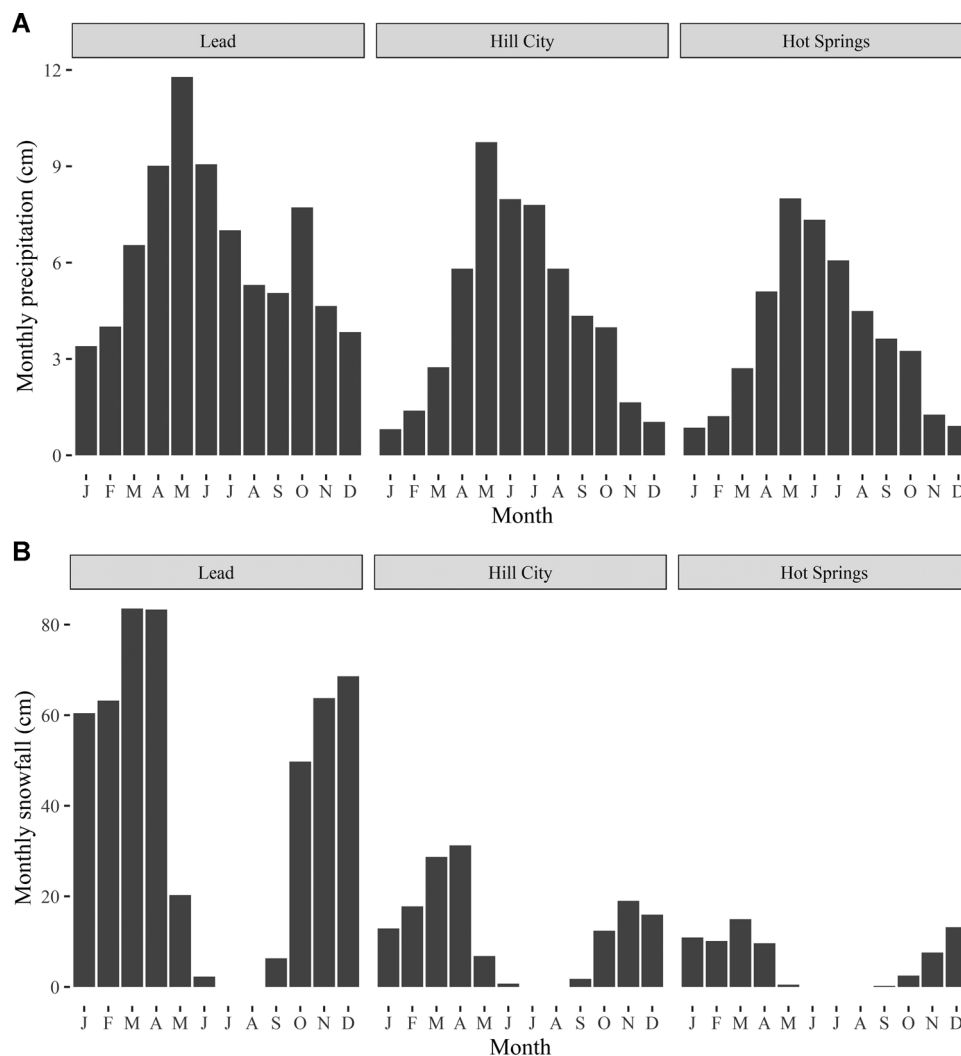


Figure 1. Average precipitation (A) and snowfall (B) by month (cm) for the northern (Lead, SD), central (Hill City, SD), and southern (Hot Springs, SD) Black Hills, South Dakota, USA, 1981–2010 (National Climatic Data Center 2010).

Our objectives were to estimate female survival, quantify relationships between survival, reproductive effort, and weather conditions, and provide information that could be used for region-specific management decisions for turkeys in the northern Black Hills. Specifically, we sought to determine how nest incubation, brood rearing, spring and summer precipitation, and female age were associated with female survival. We thought reproductive efforts would reduce female survival (Collier et al. 2009) and that spring and summer precipitation might be associated with lower survival. Additionally, we predicted that the largest declines in female survival associated with precipitation would be during nesting and early brood rearing, when females and poults were ground roosting and more vulnerable to predation. We expected that seasonal survival of females would be lowest during spring (Lehman 2005) and that juvenile females would have lower survival than adults (Rumble et al. 2003). Finally, we thought winter survival might be lower in our study area because of the harsher winter conditions, compared to the southern Black Hills.

STUDY AREA

We completed our work during 2016–2018 in the northern Black Hills in west-central South Dakota and northeastern Wyoming, USA. The study area (~2,675 km², Fig. 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 1,000 m to 2,175 m above sea level. Mean annual precipitation and temperature (1981–2010) were 77 cm and 6.9°C, respectively (National Climatic Data Center 2010). Potential predators of turkeys included coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), raccoon (*Procyon lotor*), great horned owl (*Bubo virginianus*), and northern goshawk (*Accipiter gentilis*). Ponderosa pine was the most common tree species, but white spruce (*Picea glauca*) was also common. 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 (Larson and Johnson 1999).

METHODS

Capture and Radio-Telemetry

We captured turkeys from January through March of 2016 and 2017 using rocket nets (Thompson and DeLong 1967). We lured turkeys to netting locations using corn and oat hay. We classified female age as juvenile (<1 yr old) or adult (>1 yr old) based on presence or absence of barring in the ninth and tenth primary feathers (Williams 1961). We weighed each female (kg), banded, and instrumented each with an 80-g backpack-mounted very high frequency (VHF) transmitter that was programmed to provide 3 different signals: an activity signal, a short-term non-moving (loafing)

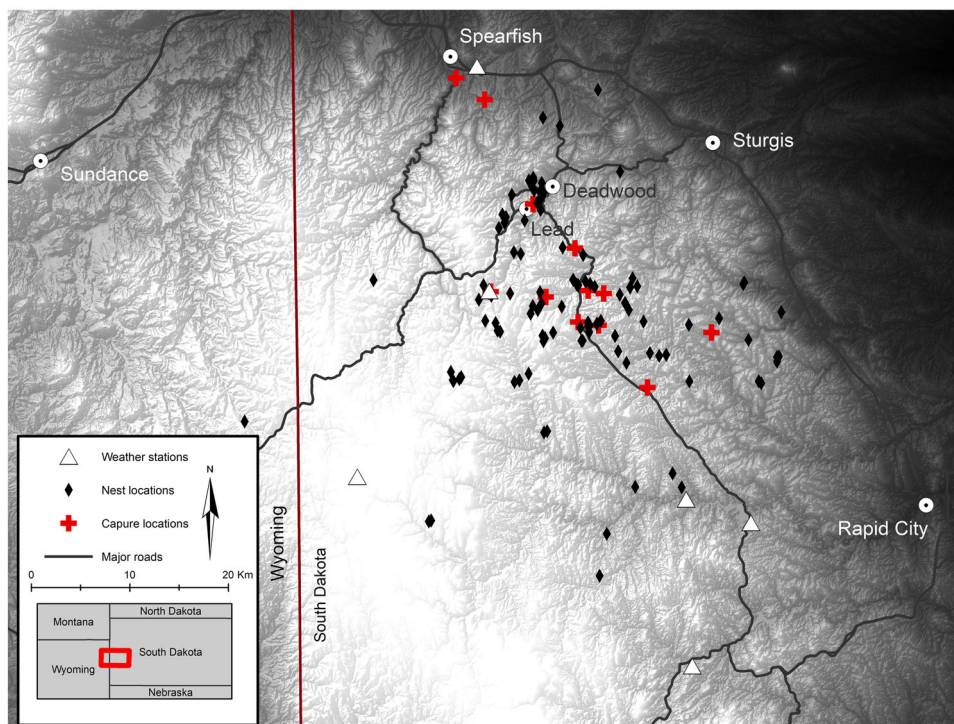


Figure 2. Study area with locations of weather stations and rain gauges, and locations of turkey nests and captures in west-central South Dakota and northeast Wyoming, USA, January 2016–March 2018.

signal, and a mortality signal that activated after 8 hours without movement (Advanced Telemetry Systems, Isanti, MN, USA). Our desired sample size was 80 females on 1 April, split evenly between adults and juveniles. Once we reached 40 marked females in an age class, we simply weighed, banded, and released additional females in that age class without attaching a transmitter.

We monitored female survival and reproductive activity via radio-telemetry (White and Garrott 1990). Our monitoring schedule varied depending on time of year and logistical constraints. From January through August 2016 and 2017, we checked the survival status of most females ≥ 4 days/week, except during nest incubation when we checked females daily. We monitored females for signs of incubation based on activity and loafing signals from transmitters. When females initiated nesting behavior, we marked and then monitored the female's transmitter daily for success or failure. For nests that hatched young, we monitored brood rearing activity with poult counts (Hubbard et al. 1999). Yarnall (2019) provided details of nest and brood monitoring. During fall monitoring (Sep–Dec) and during January–March 2018, we monitored female survival via aerial telemetry 1–2 times/month. All procedures were reviewed and approved by the Institutional Animal Care and Use Committee at Montana State University (protocol 2015-25).

Precipitation Data

To investigate the potential association between precipitation and female survival during spring (Apr–Jun) and summer (Jul–Aug), we established 3 rain gauges across the study area (Fig. 2) and recorded daily precipitation amounts 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 2017) from 1 April to 31 August in 2016 and 2017. On days when an observation was not available at a rain gauge or weather station, we replaced the missing value with the observation from the next closest gauge or station.

Because patterns of precipitation in the Black Hills can vary spatially, we assigned each female 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 our survival analyses. For nesting females, we selected the weather station nearest the female's nest (distance to weather stations: $\bar{x} = 4.6$ km, range = 0.3–14.7 km). For females that did not nest, we manually assigned each female a weather station based on records of each female's location during each field season using a geographic information system (GIS; ArcMap 10.5.1, Esri, Redlands, CA, USA). Although assigning each female a single weather location from April–August is a simplification of female movements, we viewed this assignment as reasonable because females 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 approximately 24 hours. Although we recognized that this could limit our ability to detect patterns between female survival and precipitation, we considered our data a reasonable approximation of conditions.

Survival Analysis

We estimated survival of all females that lived for >7 days post-capture (Kurzejeski et al. 1987). We excluded females that died within the first week following capture to avoid biases due to mortalities that may have been related to capture. Because we did not monitor female survival in equal-length time intervals, we used the nest survival model for known-fate data (Dinsmore et al. 2002, Rotella et al. 2004). We estimated daily survival rates (DSR) of females using Program MARK (White and Burnham 1999) via RMark (Laake 2013) in Program R (R Core Development Team 2018).

We used an information-theoretic approach (Burnham and Anderson 2002) to compare 52 candidate models that explored potential effects of nest incubation, brood-rearing behavior, spring and summer precipitation, and age on female survival (Table S1, available online in Supporting Information); we selected these covariates based on the relevant literature. We ran all possible linear additive combinations of the covariates because all represented biologically plausible hypotheses (Doherty et al. 2012). We included additional models with interactions between precipitation and reproductive activities to test specific hypotheses regarding non-linearities among these covariates. In all but 4 simple models, we allowed survival to vary seasonally among the following periods: winter (1 Dec–31 Mar), spring (1 Apr–30 Jun), summer (1 Jul–31 Aug), and fall (1 Sep–30 Nov). We chose to include these periods *a priori* because they align with weather and with seasonal behavior and food requirements of 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 female survival between years. When evaluating model-selection results, we considered a parameter uninformative when its addition resulted in an Akaike's Information Criterion score corrected for small sample sizes (AIC_c) approximately 2 units larger than a model without it (Burnham and Anderson 2002, Arnold 2010).

Because reproduction in gallinaceous birds can potentially be costly to female survival (Wakeling 1991, Collier et al. 2009, Blomberg et al. 2013), we examined the influence of nest incubation and brood-rearing behaviors on female survival. For models that included incubation, we used a time-varying individual covariate to indicate whether a female was incubating a nest or not (0 = not incubating, 1 = incubating) each day (a single intercept adjustment for incubation on any day an individual female was nesting). We used a similar approach to model brood-rearing behavior during the first 4 weeks after the nest hatched. But brood-rearing behavior changes as poults age; notably,

females 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 female 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 of the potential relationship between seasonal periods and reproductive activities, we created an indicator variable to account for incubation and brood rearing occurring only during spring and summer. We created a factor variable to indicate whether the season was spring or summer ($spr.sum = 1$ if season was spring or summer, $spr.sum = 0$ otherwise), and we interacted that variable with incubation and brood rearing status but without including the main effects for the interaction. In this manner, we made it explicit that incubation can only occur during the spring and summer. Additionally, we used caution when interpreting beta coefficients and survival estimates. That is, we avoided interpreting season and incubation status as though they were completely independent. Instead, we specify the season and reproductive status in our interpretations.

Because precipitation is positively associated with nest predation in some systems (Palmer et al. 1993, Roberts et al. 1995, Lehman et al. 2008), we investigated the effect of precipitation on female survival by using a time-varying individual covariate that indicated the amount of rainfall each day during spring and summer. We evaluated models that included interactions between precipitation and incubation and between precipitation and early brood rearing, to test for a stronger association between precipitation and female survival during periods of reproductive activity. We also thought that the effect of precipitation might be

non-linear. That is, low precipitation amounts might have little to no effect on survival, but higher amounts might have a substantial effect 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, temp) can affect 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 our primary questions of interest were related to costs of reproduction and precipitation during spring and summer. Additionally, winter conditions during our study were mild and varied little (Fig. 3; M. J. Yarnall, Montana State University, unpublished data) and available weather data was too coarse to adequately represent conditions at most turkey wintering locations.

Juvenile females generally have lower survival rates than adult females (Rumble et al. 2003). Thus, we considered models that included age class to allow for such a possibility. We reclassified females captured as juveniles as adults at the beginning (1 Dec) of winter following capture. To accommodate this change in age, data for juvenile females that survived to become adults were presented on 2 lines in the RMark input file: one line with data for the juvenile year and the second with data for the female's time as an adult.

We estimated DSR from the model best-supported by the data and predicted DSR across relevant ranges of covariate values to evaluate the biological relationships between covariate conditions and estimated rates of female survival. We estimated annual and seasonal rates using covariate combinations that we considered most useful to managers. When predicted survival estimates required incubation or precipitation values, we assumed that incubation began on the median date of nest initiation and used observed precipitation amounts from the rain gauge associated with the most females (~25% of all female-weather associations). We used the delta method to estimate standard errors of these estimates of survival (Seber 1982, Powell 2007).

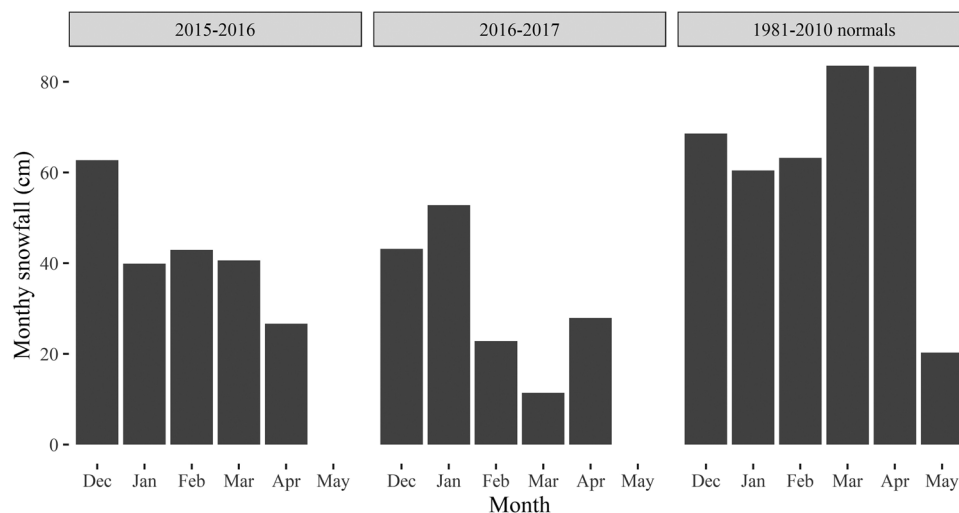


Figure 3. Monthly snowfall totals in Lead, South Dakota, USA, December 2015–May 2016 (left) and December 2016–May 2017 (middle) compared to long term average snowfall (1981–2010, right).

Cause-Specific Mortality

Whenever possible, we attempted to determine cause of female mortalities by performing necropsies on female carcasses. We classified mortalities as mammalian predation, avian predation, undetermined predation, probable predation, starvation, injury or disease, roadkill, transmitter related, or unknown. In addition to 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 presence of hair or feathers from the predator on the turkey carcass or adhered to vegetation at the mortality location. Removal of the head and neck region and accompanying puncture wounds also helped to determine avian predation (Miller and Leopold 1992). If trauma was consistent with predation, but we could not identify the predator as avian or mammalian, we labeled the cause of death as undetermined predation. When evidence at the mortality site suggested predation, but we were unable to completely rule out post-mortality scavenging, we classified the cause of death as probable predation. When carcasses were located near roadways and exhibited significant hematomas but showed no evidence of depredation, we classified the cause of death as roadkill. Carcasses that had not been depredated or scavenged that exhibited emaciated breast muscles indicated a mortality due to starvation (Lehman et al. 2007). 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. Otherwise we classified the cause of death as unknown.

RESULTS

In 2016, we captured 145 female turkeys and released 97 (46 juveniles and 51 adults) with VHF transmitters.

Twenty-five juvenile females captured in 2016 survived to enter the adult age class on 1 December 2016. In 2017, we captured 150 female turkeys and released an additional 52 individuals (49 juveniles and 3 adults) with transmitters. Twenty-eight juvenile females captured in 2017 survived to enter the adult age class on 1 December 2017. We excluded 8 females from the survival analysis because they died within a week of capture; another female 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 females because we lost the transmitter signal or were concerned that the transmitter may have contributed to the female's death.

Female Survival

Incubation status was negatively associated with daily female survival (Table 1). 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 females was lower than that of non-incubating females (Fig. 4; $\hat{\beta}_{\text{incubation} \times \text{spr.sum}} = -0.97$, 85% CI = $-1.43 - -0.50$). The estimated annual survival rate was 0.53 (85% CI = 0.48–0.59) for a female that did not incubate a nest and 0.47 (85% CI = 0.42–0.53) for a female that incubated through the full incubation period (26 days). Although we chose *a priori* to include seasonal periods in all but 4 simple models, female survival differed among seasons; season was included in all competing models and the best of these outperformed the null model by $>20 AIC_c$ units (Table 1; Fig. 4A). The data did not support models that included female age or brood-rearing status (Table 1).

Precipitation alone did not improve model fit; as a solely additive relationship (incubation + precip model), precipitation was an uninformative parameter (Table 1). But the influence of precipitation on female survival during the

Table 1. Competing models (i.e., within 4 Akaike's Information Criterion corrected for sample size [AIC_c] units of the top-ranked model) for female turkey survival in the northern Black Hills, South Dakota, USA, 2016–2018.

Model ^a	AIC_c	ΔAIC_c	AIC_c weights	Deviance	K
Incub ^b	1,111.18	0.00	0.15	1,101.18	5
Incub \times precip ^c	1,111.46	0.28	0.13	1,097.46	7
Incub + yr	1,112.27	1.09	0.09	1,098.27	7
Incub \times precip + yr	1,112.54	1.36	0.08	1,094.54	9
Incub + precip	1,113.09	1.91	0.06	1,101.09	6
Incub + age	1,113.11	1.93	0.06	1,101.11	6
Incub \times precip + age	1,113.41	2.23	0.05	1,097.41	8
Incub + precip + yr	1,114.18	3.00	0.03	1,098.18	8
Precip ² + incub	1,114.26	3.08	0.03	1,100.26	7
Incub + age + yr	1,114.27	3.09	0.03	1,098.26	8
Incub \times precip + age + yr	1,114.52	3.35	0.03	1,094.52	10
Incub \times precip + brood	1,114.77	3.59	0.03	1,096.77	9
Incub + precip + age	1,115.03	3.85	0.02	1,101.02	7
Null	1,134.23	23.06	0.00	1,132.23	1

^a Covariates are incubation status (incub), precipitation amount (precip), year (yr), female age (age), and brood rearing status (brood). K is the number of parameters in each model. All models shown in the table include a main effect of season except the null model, which is included for comparison. Daily incubation status (incub) was coded as an incub \times spr.sum interaction without including the main effects of that interaction, where spr.sum is an indicator whether the season is spring or summer (1) or not (0). Models that include another interaction or quadratic relationship include main effects of those terms.

^b Estimates (with 85% CIs) from this model are as follows: $\hat{\beta}_{\text{Intercept}} = 6.24$ (5.98–6.49), $\hat{\beta}_{\text{Spring}} = -0.37$ (–0.73 – –0.00), $\hat{\beta}_{\text{Summer}} = 0.65$ (0.02–1.27), $\hat{\beta}_{\text{Fall}} = 0.91$ (0.23–1.59), $\hat{\beta}_{\text{Incub}} = -0.97$ (–1.43 – –0.50).

^c Estimates (with 85% CIs) from this model are as follows: $\hat{\beta}_{\text{Intercept}} = 6.24$ (5.98–6.49), $\hat{\beta}_{\text{Spring}} = -0.45$ (–0.83 – –0.07), $\hat{\beta}_{\text{Summer}} = 0.55$ (–0.07–1.19), $\hat{\beta}_{\text{Fall}} = 0.90$ (0.22–1.58), $\hat{\beta}_{\text{Incub}} = -0.65$ (–1.19 – –0.11), $\hat{\beta}_{\text{Precip}} = 0.06$ (–0.03–0.15), $\hat{\beta}_{\text{Incub} \times \text{Precip}} = -0.13$ (–0.23 – –0.03).

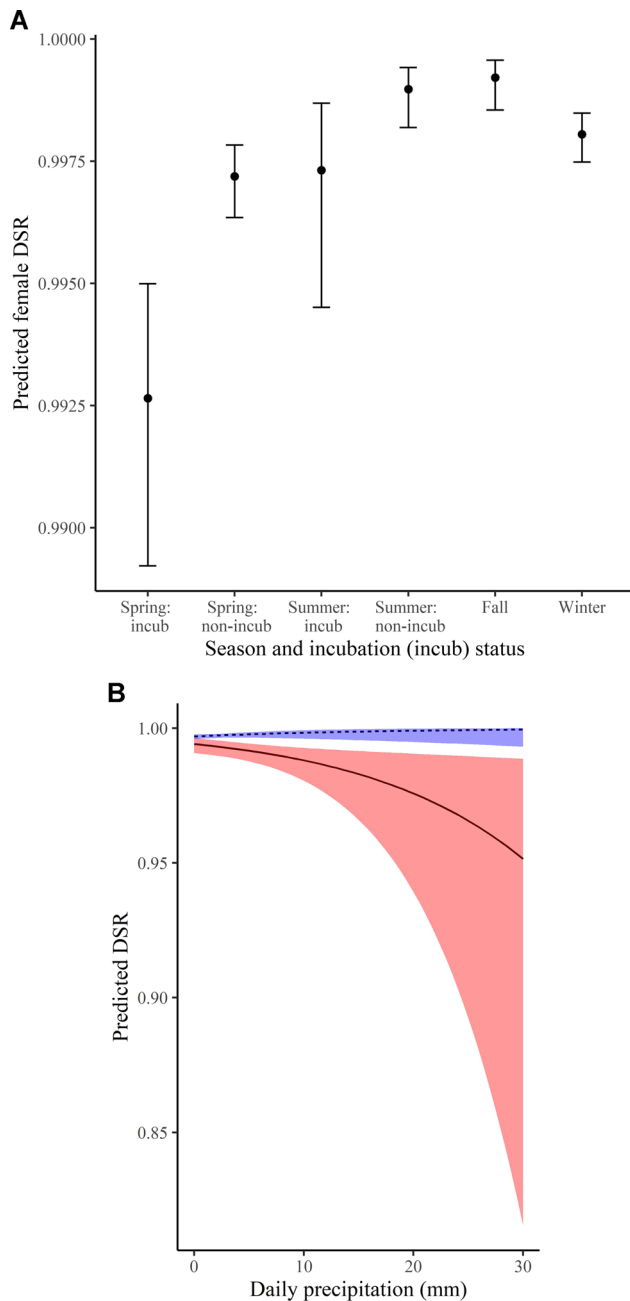


Figure 4. Predicted daily survival rates (DSR) of turkeys and 85% confidence intervals based on A) the season + incubation model during all seasons, and B) the season + incubation \times precipitation model for incubating (solid line, red interval) and non-incubating (dashed line, blue interval) females across a range of precipitation values during spring (observed range of daily precipitation was 0–41 mm). Estimates are based on survival data collected in the northern Black Hills, South Dakota and Wyoming, USA, January 2016–March 2018.

spring and summer depended on a female's incubation status; the second-best-supported model (season + incubation \times precip) had a comparable AIC_c value to that of the top model, despite the addition of a 4-point penalty for 2 additional parameters (Table 1). Precipitation differed notably between spring 2016 and 2017 (Fig. 5), 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 quadratic form for precipitation (Table 1).

Because relationships between female survival and precipitation were consistent among well-supported models, we also present results from the season + incubation \times precipitation model. As predicted, precipitation was associated with reduced daily female survival on days when incubation occurred ($\hat{\beta}_{\text{incubation} \times \text{precip}} = -0.13$; 85% CI = $-0.23 - -0.03$). To visualize combined relationships between female survival, incubation status, and precipitation, we plotted predicted DSRs across a range of precipitation values for incubating and non-incubating females (Fig. 4B).

In addition to predictions based on the top model (season + incubation), we also predicted annual and seasonal survival rates for a female that did not nest and for a female that incubated through a full incubation period (26 days) based on the comparable season + incubation \times precipitation model. Seasonal survival was lowest during spring, particularly for a female that incubated through a full nesting cycle; estimated spring survival was lower for a female that incubated for 26 days than for a female that did not incubate at all (Table 2). Most nesting attempts were completed by the end of June, and seasonal survival was highest during summer, whereas survival during fall was intermediate. Estimated annual survival was lower for females that incubated for 26 days compared to females that did not incubate (Table 2).

To enable managers to make comparisons between this and other studies, we also predicted annual survival for adult and juvenile females regardless of incubation status using the season + female age model. Estimated annual survival rate was 0.49 (85% CI = 0.42–0.56) for adult females and 0.51 (85% CI = 0.43–0.60) for juvenile females.

Cause-Specific Mortality

Predation was the primary cause of female mortality during our study, with predation and probable predation accounting for 44 of 94 mortalities (47%; Table 3). Starvation was the cause of 10 female mortalities (11%). Three of these females 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 females (7%) died of injury or disease. Three females (3%) were killed in car collisions; these mortalities all occurred at the same location where turkeys frequently crossed and congregated near a road near a site where a landowner placed supplemental feed intended for turkeys. A single female 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 29 of mortalities (31%); 16 of these instances occurred when we monitored survival too infrequently to determine cause of death from turkey remains.

DISCUSSION

Our results provide strong support that variation in DSR of female Merriam's turkeys during spring and summer is related to whether the female was currently incubating eggs,

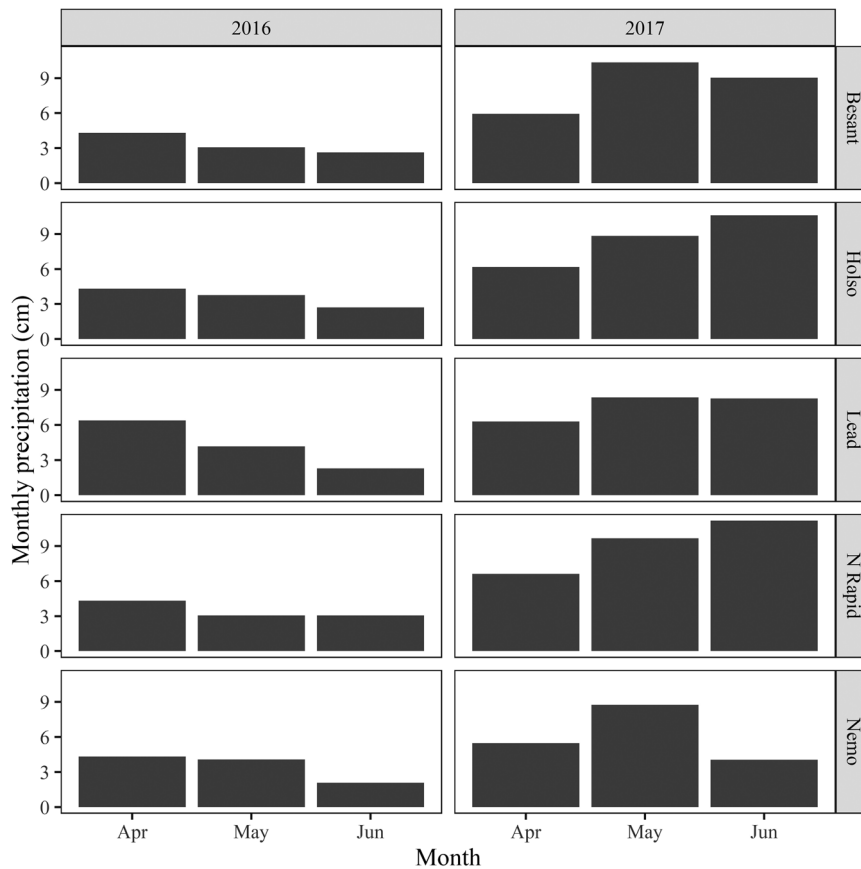


Figure 5. Spring precipitation by month at 5 locations in west-central South Dakota and northeast Wyoming, USA, April–June 2016 and 2017.

Table 2. Estimates of turkey female survival (\hat{S} ; annual and seasonal) for the northern, central, and southern Black Hills, South Dakota and Wyoming, USA. Estimates for the northern Black Hills come from the current study (by yr, based on the season + incubation \times precipitation 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 are shown when available.

	North						
	2015–2016 ^a		2016–2017		South ^b		Central ^c
	\hat{S}	SE	\hat{S}	SE	\hat{S}	SE	
Annual	0.48 ^c	0.04	0.44 ^c	0.05	0.67	0.02	0.68
1 Dec–30 Nov	0.53 ^f	0.04	0.54 ^f	0.04			
Winter ^d	0.79	0.03	0.79	0.03	0.93	0.02	
1 Dec–31 Mar							
Spring	0.70 ^c	0.04	0.64 ^c	0.07	0.83	0.04	
1 Apr–30 Jun	0.77 ^f	0.04	0.78 ^f	0.04			
Summer	0.94	0.02	0.94	0.02	0.96	0.02	
1 Jul–31 Aug							
Fall ^d	0.87	0.03	0.87	0.03	0.86	0.05	
1 Sep–30 Nov							

^a Based on data collected from January 2016–November 2016.

^b Estimate for adult females.

^c Estimate for adult and juvenile ages combined.

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

^e Estimate for a female that incubates for 26 days starting on the median date of incubation initiation that year.

^f Estimate for a female that does not incubate a nest.

consistent with a cost of reproduction predicted by life-history theory (Stearns 1992) and with previous studies indicating that nesting females 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 effect of any such discrepancies was insufficient to mask the influence of precipitation on female survival.

Merriam's turkeys in Arizona experienced higher rates of predation during brood rearing than during incubation (Wakeling 1991). Yet in contrast to this study and our expectation, we did not find evidence for a reproductive cost of brood-rearing behavior. Two factors may have prevented us from detecting an association between brood rearing and female survival. First, relatively low rates of nesting and nest survival (Yarnall 2019) resulted in a modest sample of hatched nests (50 successful nests in 2016 and 2017). Second, we rarely knew the exact date of brood loss, forcing us to approximate the number of days a female spent brood rearing based on the midpoint between the last day she was

Table 3. Percentage (%) and number (*n*) of turkey female mortalities by cause in the northern Black Hills, South Dakota and Wyoming, USA, 2016–2018 by season (winter = 1 Dec–31 Mar, spring = 1 Apr–30 Jun, summer = 1 Jul–31 Aug, fall = 1 Sep–30 Nov).

	Winter		Spring		Summer		Fall		Total	
	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
Mammalian	12	4	20	9					14	13
Mammalian ^a	6	2	11	5					7	7
Avian	9	3	18	8					12	11
Undetermined predator	9	3	7	3					6	6
Undetermined predator ^a	9	3	9	4					7	7
Starvation	9	3	14	6	14	1			11	10
Unknown	33	11	11	5	43	3	100	10	31	29
Injury or disease			9	4	43	3			7	7
Roadkill	9	3							3	3
Transmitter ^b	3	1							1	1
Total	100	33	100	44	100	7	100	10	100	94

^a Probable cause of death.

^b Mortality caused by transmitter snagging on barbed wire fence. Female was right censored in the survival analysis.

observed with poults and the first day she was observed without a brood. Future investigations focused on cost of reproduction would benefit from methods that provide more robust encounter histories (e.g., more frequent counts or young marked with radio-transmitters), but researchers must carefully consider how these alternatives might affect the survival of young.

Contrary to our expectation and results from other studies of this species (Rumble et al. 2003), we did not find evidence that female age was associated with survival. We expected smaller-bodied juvenile females 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 (Fig. 3) to affect adult and juvenile survival differently. Juvenile females nested at lower rates than adult females (Yarnall 2019), 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. Vital rates that are current and region-specific (Pollentier et al. 2014a, b) are important in turkey management. Although previous research focused on survival of Merriam's turkeys in the Black Hills did not explore quantitative effects of precipitation or individual reproductive status, our estimates of annual survival for incubating and non-incubating females are lower than survival in the central (Rumble et al. 2003) and southern (Lehman 2005) Black Hills (Table 2). Lower annual survival in the northern Black Hills is influenced mainly by lower rates of survival during winter and spring; female survival in summer and fall were comparable between the northern and southern Black Hills (Table 2). These seasonal differences are related to the distinctly different climatic conditions females experience in the northern and southern Black Hills (Fig. 1). Additionally, survival of an incubating female through spring (Apr–Jun) was lower than survival through winter (Dec–Mar), despite the winter period lasting a month longer than spring (Table 2); this seasonal difference emphasizes the cost nesting imposes on female survival.

Although we did not have appropriate data to explore the effects of snow depth and temperature on female 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 and in ponderosa pine forest, which represent areas with and without supplemental food, respectively. But Lehman (2005) did not detect differences in winter survival between these 2 groups of females. 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 (Fig. 3), we observed lower winter survival in the northern Black Hills compared to farther south (Table 2). Additionally, we observed multiple females that died of starvation during winter and the spring nesting period, and 1 female that died of starvation during summer (Table 3). Necropsies of females killed accidentally during capture revealed limited energy reserves. We are unaware of any other turkey studies that have documented female starvation during nesting or summer. The prevalence of starvation and comparatively low winter survival during the mild conditions encountered during our study suggests that female survival may be lower when future winter conditions are average or harsh.

MANAGEMENT IMPLICATIONS

Female survival in the northern Black Hills is lower than in the central and southern Black Hills, emphasizing the need for locally relevant data on vital rates for turkey management. 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, South Dakota could provide a reasonable approximation of daily precipitation in the northern Black Hills. Future investigations of female turkey survival in the Black Hills should quantify the effect of winter conditions to help managers predict population-level effects of weather events.

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