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Factors influencing rate of decline in a Merriam's wild turkey population

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Abstract

We investigated population growth rate (λ) for a Merriam's wild turkey (*Meleagris gallopavo merriami*) population in the northern Black Hills, South Dakota, USA. We constructed and evaluated a females-only matrix population model. Our estimate of asymptotic λ, derived from estimates of vital rates obtained from 2016–2018 was 0.74 (95% CI = 0.60, 0.88), which indicates that the vital rates were inadequate to sustain the population. Elasticity values were highest for changes in adult survival probability followed by, in order, changes in juvenile survival, yearling survival, and adult reproduction. We could only achieve stable or growing populations (i.e., $\lambda \geq 1$) by increasing the probability of adult and yearling survival (holding all other vital rates constant). Estimated adult survival rate in the work reported here was lower than values reported for other populations in the Black Hills; therefore, managing for increased female survival (≥0.68) may be the most practical strategy for promoting wild turkey population growth in this system. We recommend no female harvest during any open turkey season.

KEYWORDS

Black Hills, elasticities, growth rate, hen survival, matrix modeling, *Meleagris gallopavo merriami*, Merriam's wild turkey

The wild turkey (*Meleagris gallopavo*) is an important game species because of its cultural and economic value (Flake et al. 2006). Since the 1950s, there has been an extensive effort to restore wild turkey populations in the United States; owing to many successful reintroductions, wild turkeys have returned to much of their historical range (Kennamer et al. 1992, Eriksen et al. 2015). Unfortunately, turkey populations in the United States have declined 5–8% from 2004 to 2014 (Eriksen et al. 2015), motivating resource agencies to focus research activities to

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investigate which demographic parameters have the greatest impact on population growth. These broad declines in wild turkey populations are largely unknown, but habitat loss, primarily loss of early successional vegetation, and density-dependent factors have been surmised as potential causes (Eriksen et al. 2015). In montane systems of the West, shifting weather patterns led to altered vegetation responses and decreased survival and reproduction for many bird species (King and Finch 2013).

For populations of wild turkeys, vital rates of interest typically focus on the female segment of the population and include estimates of adult and yearling survival, nesting rate, nest survival, re-nesting rate, clutch size, hatchability, and poult survival (Rumble et al. 2003, Pollentier et al. 2014*a*). Population growth rates of wild turkeys are sensitive to changes in adult female survival (Suchy et al. 1983, Wakeling 1991, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001, Tyl 2019). Wild turkey populations may have negative population growth if fall harvests decrease female survival (Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001). Conservative fall harvest rates of ≤10% have been recommended to make sure wild turkey populations continue to grow; however, in all of these harvested populations, female survival rates were ≥56% (Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001, McGhee et al. 2008). Populations with higher survival rates and reproductive output should have a greater ability to compensate for harvest, whereas harvest mortality is more likely to be additive in low-density or declining populations (Bartmann et al. 1992).

Nest and poult survival may also influence population growth rates (Roberts et al. 1995, Roberts and Porter 1998, Pollentier et al. 2014*a*). Pollentier et al. (2014*a*) suggested that continued restoration and enhancement of high-quality habitat with early successional vegetation have the greatest potential to positively influence population growth by improving nest and poult survival for eastern wild turkeys (*M. g. silvestris*). Such improvements to nesting and brood-rearing areas also could improve female survival by reducing mortality risks while incubating eggs and raising poults (Pollentier et al 2014*a*). Similar habitat manipulations were suggested for Merriam's turkeys (*M. g. merriami*) in the West, and vegetation treatments directed at improving body condition of females through improved abundance and distribution of food would likely improve nesting rates (Wakeling 1991, Wakeling and Rodgers 1995, Hoffman et al. 1996, Rumble et al. 2003).

In addition to habitat factors that managers can directly manipulate, climatic factors such as temperature, snow depth, and rainfall can influence female survival and other vital rates, and consequently population growth rates (Porter et al. 1980, Rumble et al. 2003, Caudill et al. 2014, Lavoie et al. 2017). Ambient temperature affects metabolism and extreme lows may cause starvation if supplemental foods are not available (Haroldson et al. 1998). Deep snow can reduce wild turkey movement and limit access to food, potentially leading to starvation (Vander Haegen et al. 1989, Lehman 2005). In ground-nesting birds, increased precipitation can increase female and nest predation, perhaps because mammalian predators may be more effective at locating nesting females via olfaction during or immediately following rain events (Roberts et al. 1995, Lehman et al. 2008, Webb et al. 2012). In the Black Hills, South Dakota, USA, climatic conditions vary with a gradient of more moderate weather conditions in the south to more inclement weather in the north (Yarnall 2019). Greater amounts of snowfall and precipitation during winter and spring (Yarnall et al. 2020) could potentially have negative impacts on population growth for turkeys in the northern Black Hills.

The Black Hills is a destination of many turkey hunters from across the nation, making Merriam's wild turkeys an important resource recreationally and economically (Flake et al. 2006, Gigliotti 2009), but harvest and survey data suggest declining abundance in the northern Black Hills (C. M. Huxoll, South Dakota Game, Fish, and Parks, unpublished data). The cause of the apparent decline in wild turkey abundance in the northern Black Hills is unclear. Given recent declines in the region, there is a need to assess the demographic performance of this important game species using current vital rate estimates. The objectives of this study were to incorporate estimates of vital rates into a stage-based matrix projection model, estimate the asymptotic population growth rate (λ), and estimate how λ responds to incremental changes in vital rates (de Kroon et al. 1986, Koons et al. 2006). Given declines in recent survey data, we predicted that the population of Merriam's wild turkeys in the northern Black Hills is in decline ($\lambda < 1$). We hypothesized that survival of adult females and nests would have the greatest influences on the finite rate of population change.

STUDY AREA

The study area was located in the northern part of the Black Hills physiographic region (Flint 1955; Figure 1); this area (~1,400 km^2) was in Lawrence, Meade, and Pennington counties in South Dakota and in Weston and Crook counties in Wyoming, USA (centroid location: 44.269427, −103.713404). We conducted our work during 2016–2018 and the study area was primarily Black Hills National Forest, interspersed with private land and areas managed by the Bureau of Land Management and South Dakota School and Public Lands. Elevations ranged from approximately 1,000 m to 2,175 m above sea level. Mean annual precipitation and temperature (2008–2018) were 83 cm and 7.7°C, respectively (National Climatic Data Center 2022). Seasons included winter (Dec–Mar), spring (Apr–Jun), summer (Jul–Aug), and fall (Sep–Nov). The northern Black Hills can receive considerable winter snowfall

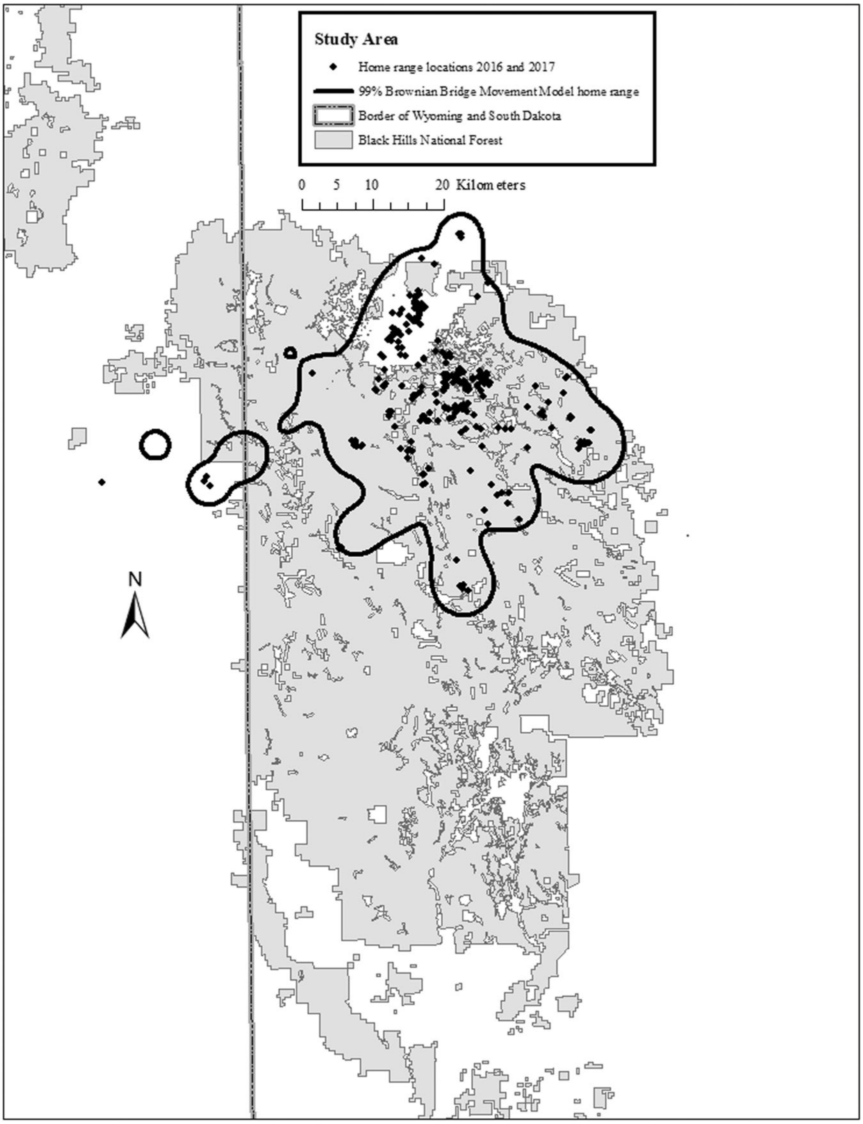

FIGURE 1 Study area for estimating demographic rates of Merriam's wild turkeys in west-central South Dakota and northeast Wyoming, USA, 2016–2018.

with a 10-year average of 264 cm from 2008–2018 (National Climatic Data Center 2022). Potential predators of wild turkeys and their nests included coyote (*Canis latrans*), mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), raccoon (*Procyon lotor*), skunk (*Mephitis mephitis*), red fox (*Vulpes vulpes*), golden eagle (*Aquila chrysaetos*), great horned owl (*Bubo virginianus*), American crow (*Corvus brachyrhynchos*), and northern goshawk (*Accipiter gentilis*). 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 (Larson and Johnson 1999).

METHODS

Turkey captures

We estimated demographic rates of female turkeys by capturing and fitting birds with very high frequency transmitters. We captured female wild turkeys from January through March in 2016 and 2017 using rocket nets (Thompson and Delong 1967). We classified age as juvenile (<1 yr old [juveniles turned to yearlings on 1 Apr after banding]) or adult (>1 yr old) at winter captures based on the presence or absence of barring in the ninth and tenth primary feathers (Williams 1961). We weighed and banded turkeys and instrumented each with a backpack-mounted transmitter (80 g for females) programmed to provide 3 different signals: a moving signal, a short-term non-moving (loafing) signal, and a mortality signal that activated after 8 hours without movement (Advanced Telemetry Systems, Isanti, MN, USA). Yarnall et al. (2020) provide further details of radio-marking and monitoring.

Estimating vital rates

Yarnall et al. (2020) recently estimated annual survival rates for both adult and yearling females in the study population (Table 1). We used the nest survival model for known fate data (Dinsmore et al. 2002, Rotella et al. 2004) to estimate daily survival rates (DSR) of females using Program MARK (White and Burnham 1999) via RMark (Laake 2013) in Program R (R Core Team 2018). We checked the survival status of females ≥4 days/week from January through August, except during nest incubation when we checked females daily; we monitored female survival 1–2 times/month from September through December (Yarnall et al. 2020).

We monitored females for signs of incubation based on moving and non-moving signals from transmitters. Once we detected nesting behavior, we marked the nest and then monitored the female's transmitter daily for success or failure (Yarnall 2019). We defined nesting rate as the proportion of females alive on 1 April that attempted to nest at least once during the year (Lehman et al. 2008). 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. We defined female success as the proportion of females that successfully hatched ≥1 poult during ≥1 nesting attempt (Cowardin et al. 1985). Reproduction estimates for adults and yearlings are provided in Yarnall (2019).

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 female via radio telemetry and counting her associated poults. If we were 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 female and count them as they left the roost tree (Lehman et al. 2008).

TABLE 1 Vital rates of females used to estimate asymptotic population growth rates ($\bar{\lambda}$) of Merriam's wild turkeys in the northern Black Hills, South Dakota, USA, 2016–2018.

Vital rate	Age	Estimate	SE
Annual survival[a]	Adult	0.49	0.04
Annual survival[a]	Yearling	0.51	0.05
Nesting rate[b]	Adult	0.83	0.04
Nesting rate[b]	Yearling	0.33	0.05
Clutch size[b]	Adult	9.67	0.31
Clutch size[b]	Yearling	9.43	0.51
Hatch rate[b]	Adult	0.88	0.02
Hatch rate[b]	Yearling	0.86	0.04
Female success[b]	Adult	0.49	0.06
Female success[b]	Yearling	0.13	0.10
Poult survival to 4 weeks[b]	Adult	0.39	0.06
Poult survival to 4 weeks[b]	Yearling	0.39	0.06

[a] Value from Yarnall et al. (2020).

[b] Value from Yarnall (2019).

Estimating asymptotic population growth rates

We combined estimates of survival probability and reproductive rates into a 3-stage female-based, post-breeding matrix projection model (Caswell 2001). We assume the biological year starts 15 July and that the population can be divided into 3 stage classes: juvenile (29 days old on 15 Jul), yearling (1 year and 29 days old on 15 Jul and just reproduced for the first time), and adult (>2 years old on 15 Jul) with the following structure:

$$A = \begin{bmatrix} 0.5 \times F_y \times p_{yf} & 0.5 \times F_a \times p_{yf}^{38/52} p_{af}^{14/52} & 0.5 \times F_a \times p_{af} \\ p_{yf} & 0 & 0 \\ 0 & p_{yf}^{38/52} p_{af}^{14/52} & p_{af} \end{bmatrix},$$

where F_y and F_a are fecundity or the average number of young produced by yearlings and adults, and p_{yf} and p_{af} are annual survival probabilities for yearling and adult females, respectively. We assumed a 50:50 sex ratio at hatching. Adult female annual survival probability (p_{af}) and yearling female annual survival probability (p_{yf}) were estimated for 1 April–31 March of each year (Yarnall et al. 2020). We assumed juvenile survival (time between 29 days post-hatch and 31 March) was equivalent to yearling survival (Roberts et al. 1995, Rolley et al. 1998, Pollentier et al. 2014*b*). Our projection matrix assumes each annual cycle begins when juveniles are 29 days old, which occurs from approximately 15 July each year. Because we assumed yearlings transition to adults on 1 April of each year, we denote this change in survival probability partway through the annual cycle as $p_{yf}^{38/52} p_{af}^{14/52}$, which represents yearlings surviving for 38 weeks from 15 July–30 March and surviving as adults for 14 weeks from 1 April–14 July.

This model assumes the annual cycle ends 4 weeks post-hatching. The average number of young produced at time $t + 1$ by an individual alive at time t is thus:

$$F_y = (nr_y \times fs_y \times cs_y \times hr_y) \times (pfy_{4wks})$$

$$F_a = (nr_a \times fs_a \times cs_a \times hr_a) \times (pfa_{4\text{wks}}).$$

Reproductive parameters included nest rates for adults (nr_a) and yearlings (nr_y), female success for adults (fs_a) and yearlings (fs_y), clutch size for adults (cs_a) and yearlings (cs_y), and hatch rate for adults (hr_a) and yearlings (hr_y). Poult survival for adults ($pfa_{4\text{wks}}$) is the probability a poult will survive from 1 to 4 weeks of age if raised by an adult. Poult survival for yearlings ($pfy_{4\text{wks}}$) is the probability a poult will survive from 1 to 4 weeks of age if raised by a yearling. Poult survival estimates for both adults and yearlings are provided in Yarnall (2019).

We calculated λ and elasticity of population growth rates (E) to proportional changes in vital rates as a function of survival and reproductive rates. Furthermore, we accounted for uncertainty in λ and E by simulating their distributions from random realizations of estimated survival probability and reproductive rates. We simulated 100,000 random draws of vital rates bound between 0 and 1 (e.g., nesting rate, survival probability) from a beta distribution, using moment matching (Hobbs and Hooten 2015) to ensure mean and variance of random realizations were equivalent to estimates reported in Yarnall (2019) and Yarnall et al. (2020). We simulated clutch size as a Poisson random variable. We then constructed a unique projection matrix A from each simulation, from which we calculated λ as the dominant eigenvalue of A and E following Caswell (2001:equation 9.73). We assumed no correlation among vital rates because we were unable to obtain reliable estimates of covariation in vital rates with 2 years of data. Similarly, variation in vital rates is a function of measurement error. Although incorporation of covariation in vital rates and separation of process from sampling variance would be ideal, these assumptions nonetheless allow us to propagate uncertainty in vital rates into estimates of population growth rates. We report $\bar{\lambda}$ and $\bar{E}$ as the mean value of λ and E, respectively, obtained from all simulations.

We evaluated the appropriateness of using λ to evaluate realized population growth rates for our study population comparing observed age distributions with stable age distributions (Gelman et al. 2014, Kéry and Royle 2016). Assuming the number of individuals captured in each of the 2 stage classes (adult and juvenile) was a multinomial random variable with probability vector equal to the stable age distribution and number of trials = 295 (number of individuals captured), we simulated 1,000 capture events.

Finally, we calculated how λ varied as we changed the value of each vital rate across a wide range of possible values (de Kroon et al. 2000). For each vital rate included in the projection matrix, we allowed probabilities to vary between 0 and 1 (or allowed clutch size to vary from 8–11 eggs) while holding all other vital rates constant at their observed levels. We conducted all analyses using custom R scripts (R Core Team 2018).

RESULTS

Turkey captures

We captured 145 female wild turkeys (53 juveniles, 92 adults) and released 97 (46 juveniles, 51 adults) with transmitters in 2016. Twenty-five juvenile females captured in 2016 survived to enter the adult age class on 1 April 2017. In 2017, we captured 150 female wild turkeys (63 juveniles, 87 adults) and released an additional 52 individuals (49 juveniles, 3 adults) with transmitters. Twenty-eight juvenile females captured in 2017 survived to enter the adult age class on 1 April 2018 (Table 1; Yarnall et al. 2020). We marked 45 nests in 2016 (42 first nests, 3 renests) and 59 nests (50 first nests, 9 renests) in 2017; no females abandoned their nest as a result of marking activities (Table 1; Yarnall 2019).

We found that, assuming a stable age distribution, 95% confidence intervals of the number of juveniles captured was 69–120, whereas we captured 116 juveniles during trapping efforts. We therefore conclude that our population's age distribution was close to the stable age distribution and that asymptotic results are a reasonable approximation of the population's dynamics during the time of study.

Population growth

Asymptotic growth rates from a matrix projection model parameterized using point estimates of survival and reproductive rates were well below the value of 1 necessary to sustain the population ($\bar{\lambda}$ = 0.735, 95% CI = 0.604, 0.877; Figure 2). The elasticity value associated with the adult female survival rate was the greatest and values associated with juvenile female survival, yearling female survival, and adult reproduction were each successively lower (Table 2).

Results of changing values of 1 vital rate at a time across a wide, biologically reasonable range of values while holding others at their estimated means, revealed that only increases to adult or yearling survival probability could yield $\lambda \geq 1.0$ (Figure 3). Further, more modest values of adult survival (0.79) than of yearling survival (0.91) could yield $\lambda \geq 1.0$. In a *post hoc* analysis, we also simultaneously increased adult and yearling survival probability because any changes in survival probability as a result of management actions would likely occur for adults and yearlings; increasing the 2 vital rates from their estimated values (0.49 and 0.51, respectively) to values ≥0.68 was necessary to achieve $\lambda \geq 1.0$.

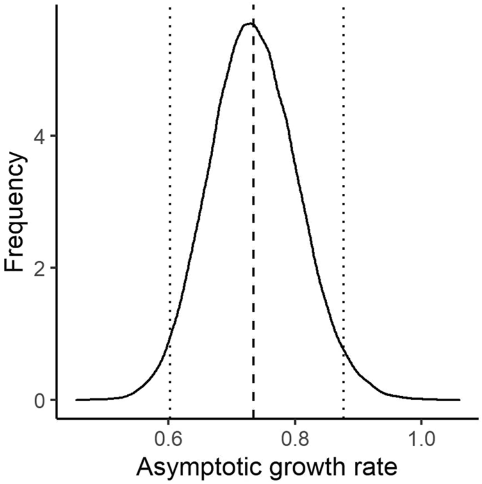

FIGURE 2 Estimated asymptotic growth rate of Merriam's turkeys in our study in the northern Black Hills, South Dakota, USA, 2016–2018. Values <1 indicate declining abundance, whereas values >1 indicate increasing abundance. Mean value is dashed with 95% confidence intervals as dotted lines.

TABLE 2 Mean elasticity ($\overline{E}$) of asymptotic growth rates to proportional changes in vital rates of female Merriam's wild turkeys in the northern Black Hills, South Dakota, USA, 2016–2018. We derived elasticities from a post-breeding projection matrix and stage class names correspond to the stage classes present at the beginning of the annual cycle, which we assume is 15 July.

Vital rate		$\overline{E}$	95% CI
Survival	Adult	0.338	0.209, 0.496
	Juvenile	0.244	0.179, 0.302
	Yearling	0.162	0.140, 0.171
Reproduction	Adult	0.162	0.140, 0.171
	Yearling	0.083	0.039, 0.134
	Juvenile	0.012	0.001, 0.043

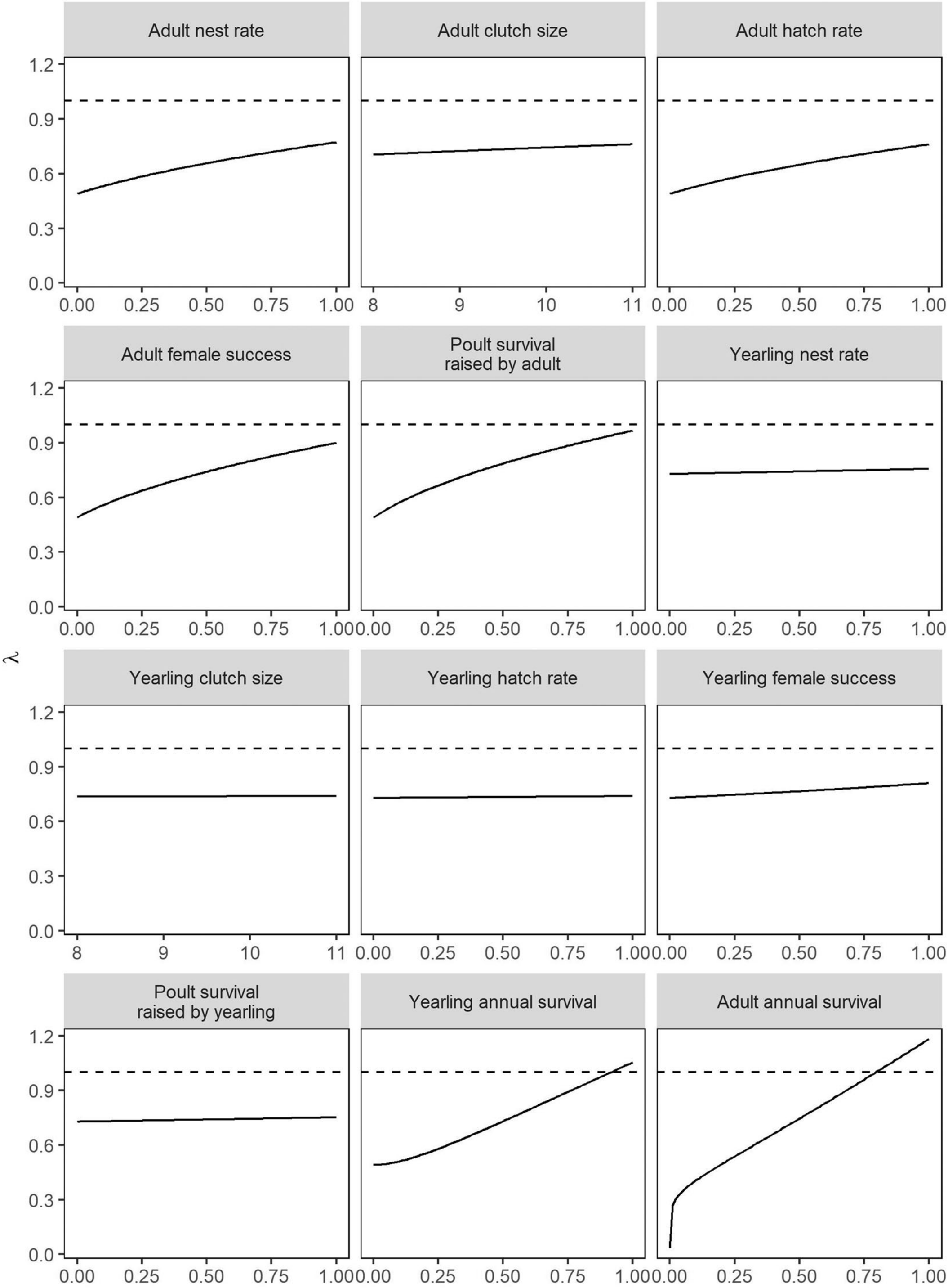

FIGURE 3 Asymptotic population growth rates (λ) of Merriam's wild turkeys in the northern Black Hills, South Dakota, USA, 2016–2018, while altering each vital rate one at a time. The horizontal dashed line represents λ = 1.

DISCUSSION

Dynamics of turkey populations may differ substantially even between nearby locations where turkey populations are in the same county or adjacent counties (Collier et al. 2009; Pollentier et al. 2014*a*, *b*). The northern Black Hills in South Dakota was likely a population sink for Merriam's turkeys, such that this population is not sustainable without immigration. Model projections for the nearby central Black Hills indicate a stable to declining population ($\lambda = 1.03$; 2019–2020) and the southern Black Hills indicate a growing population ($\lambda = 1.26$; 2019–2020; South Dakota Game, Fish, and Parks 2021). Immigration from other areas of the Black Hills will be important for the northern Black Hills to sustain a population into the future.

We estimated that asymptotic growth rates were nearly 1.5 times more sensitive to proportional changes in adult female survival when compared to other vital rates. Moreover, a stable or growing population can only occur if yearling and adult survival increases. Our results support a body of evidence that targeting adult female survival can strongly influence population growth rates (Wakeling 1991, Vangilder and Kurzejeski 1995, Rolley et al. 1998, Alpizar-Jara et al. 2001, Tyl 2019). It has been recommended that fall harvests <10% are conservative and will not cause population declines, but these populations are characterized as having higher survival rates (≥56%) with greater reproductive output and can compensate for some female mortality from a fall harvest (Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001, McGhee et al. 2008). This Merriam's population has a lower survival rate than other populations in the Black Hills and other populations across the West (Rumble et al. 2003, Yarnall et al. 2020) and as a vulnerable population requires a more restrictive approach to fall management (Bartmann et al. 1992). A fall harvest of females or other sources of mortality would be additive and may further decrease female survival (Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001).

Our elasticity analysis indicated that adult reproduction also was important, but to a lesser extent than adult survival. Yearling reproduction was not important in our analysis and nesting rates and female success were lower than what was reported in the southern and central Black Hills for yearling females (Rumble and Hodorff 1993, Lehman 2005, Lehman et al. 2008). Nesting rates and female success of yearling females vary considerably across the range of Merriam's turkeys (Rumble et al. 2003). Researchers hypothesized that quality of habitat or winter nutrition influences nesting by yearling females (Rumble and Hodorff 1993, Hoffman et al. 1996) and Wakeling and Rogers (1995) hypothesized that managers could increase nesting rates of females through habitat manipulation versus management aimed at controlling predators. Body condition may be important, given that mass of adult and yearling females in the northern Black Hills ($\bar{x}$ adult mass = 4.4 kg; $\bar{x}$ yearling mass = 3.6 kg) were significantly lower than females from the southern Black Hills ($\bar{x}$ adult mass = 4.7 kg; $\bar{x}$ yearling mass = 3.8 kg; Lehman 2005, Yarnall 2019). Several researchers studying the relationship between nesting and nutrition or food availability suggested that habitat manipulation directed at improving body condition of females through increased abundance and distribution of food would likely improve nesting rates of Merriam's turkeys (Wakeling 1991, Wakeling and Rodgers 1995, Hoffman et al. 1996, Rumble et al. 2003). For example, timber harvest manipulations that manage for large trees (>30 cm diameter at breast height) with a basal area of 22–28 m^2/ha will increase abundance of pine seeds and provide more food resources (Hoffman et al. 1993, Lehman et al. 2007).

Estimates of annual survival for incubating and non-incubating females were lower in the northern Black Hills (Yarnall et al. 2020) than survival in the central (Rumble et al. 2003) and southern (Lehman 2005) Black Hills. Lower annual survival in the northern Black Hills is driven mainly by lower rates of survival during winter and spring, as female survival in summer and fall were comparable between the northern and southern Black Hills (Lehman 2005, Yarnall et al. 2020). We believe these seasonal differences are likely related to the distinctly different climatic conditions females experience in the northern and southern Black Hills, namely increased precipitation during the winter and spring months in the northern Black Hills (Yarnall et al. 2020). We necropsied multiple females that died of starvation during winter and the spring nesting period and 1 that died of starvation during summer following incubation (Yarnall et al. 2020), providing additional evidence of poor body condition. We are unaware of any other turkey studies that documented female starvation during nesting or summer.

Previous demographic modeling of Merriam's turkeys suggested that greater survival of subadult and adult females and increased reproduction through habitat manipulation could increase population growth (Wakeling 1991, Wakeling and Rogers 1998, Rumble et al. 2003). Unfortunately, this previous work did not provide how λ would change based on incremental changes in these important vital rates. Our work adds to the understanding of how important adult female survival is to Merriam's turkey population growth, particularly in an environment that receives inclement weather. Future research could evaluate hypotheses concerning habitat manipulation through a control and treatment design and determine if such habitat treatments increase female survival, weights, nesting rates, and other reproductive parameters.

MANAGEMENT IMPLICATIONS

Merriam's wild turkeys in the northern Black Hills are more vulnerable to decline when compared to other populations in the Black Hills and the most important vital rate influencing the population growth rate is adult female survival. Management activities should aim to minimize mortality for females and increase survival rates by ≥40% (survival ≥ 0.68). Therefore, we recommend no female harvest during any open turkey season. Based on research data, 11% of females have beards in the northern Black Hills (M. J. Yarnall, Montana State University, unpublished data) and could potentially be harvested during spring. Leg-banded females with beards were reported harvested in 2018–2019 (C. P. Lehman, South Dakota Game, Fish, and Parks, unpublished data). Although current spring harvest regulations allow for harvest of bearded females, we recommend that the definition of a legal wild turkey be changed to male only during spring seasons. Education and outreach programs designed to highlight these sex-based differences also would be important to implement or maintain.

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CONFLICTS OF INTEREST

We declare no conflicts of interest.

ETHICS STATEMENT

All procedures were reviewed and approved by the Institutional Animal Care and Use Committee at Montana State University (protocol 2015-25).

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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