

Factors influencing population growth in a bobcat population

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Abstract

Bobcats (*Lynx rufus*) are the most broadly distributed native felid in North America and have substantial ecological and economic importance. Despite this importance, little is known about factors influencing population dynamics of this cryptic carnivore. Given recent apparent declines in abundance, we investigated population growth rate (λ) for a bobcat population in the Black Hills, South Dakota, USA, 2016–2022. We constructed and evaluated a females-only matrix population model. Our estimate of asymptotic λ , derived from estimates of vital rates obtained over 6 years, was 0.85 (95% CI = 0.72, 1.02), which indicates that the vital rates in 2016–2022 were inadequate to sustain the population. Elasticity and sensitivity values were highest for changes in adult survival probability followed by, in order, changes in kitten and juvenile survival and adult reproductive contribution. Life-stage simulation analysis also supported that adult survival was most important; however, the juvenile survival (91 day–1 year) component of a bobcat's first year of life was also important and a stronger influence on population growth than the kitten survival (first 90 days) component. For the combination of survival and reproductive rates we estimated positive population growth required either annual adult survival >0.85 or 275-day juvenile survival >0.35 , regardless of other vital rates. When assuming a baseline harvest rate of 23.5%, reducing the harvest rate to

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9% led to a positive mean growth rate and a >0.50 probability of a growing population. Monitoring juvenile-to-adult harvest ratios can provide an indicator of age structure in the population, and we recommend restricting harvest when that ratio falls below 10%, particularly when managers lack research information on population growth.

KEYWORDS

Black Hills, bobcat, elasticities, female survival, growth rate, life-stage simulation analysis, *Lynx rufus*, matrix modeling

The bobcat (*Lynx rufus*) is the most broadly distributed native felid in North America (Anderson and Lovallo 2003, Lesmeister et al. 2015). This species is important as a predator of herbivores in ecological communities through trophic cascades (Schmitz et al. 1997, Lesmeister et al. 2015) and has economic value as a prized furbearer (Anderson and Lovallo 2003). The adding of bobcats to Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora in 1975 led to increased efforts for data collection and knowledge about how harvest influences the species (Rolley 1987, Woolf and Hubert 1998, Anderson and Lovallo 2003). Even though well-intentioned efforts to produce data and results were formalized, very few coordinated research studies were realized, and this species has received little attention in terms of the collection of vital rates and modeling of demographics (Anderson 1987, Roberts and Crimmins 2010).

Vital rates of importance in bobcat population dynamics include estimates of adult female survival rates and recruitment (Rolley 1985, Knick 1990, Bluett et al. 2001). Annual adult survival varies between harvested and unexploited populations with higher rates of survival in unexploited populations, suggesting that harvest is additive (Knick 1990, Anderson and Lovallo 2003). Annual survival rates in bobcat populations that are harvested range from 53–67%, while adult survival rates in unexploited populations range from 78–97% (Rolley 1985, Knick 1990, Chamberlain et al. 1999, Anderson and Lovallo 2003).

While adult survival has been well studied, few studies have quantified kitten survival (Morrison 2022). Some earlier studies have used harvest data and life tables to reconstruct kitten survival estimates, which varied from 7–71% (Crowe 1975, Blankenship and Swank 1979, Hoppe 1979). Radio-telemetry studies on kitten survival are limited but indicate 0–3-month survival varies from 0.25–0.87 (Lovallo 2007, Moriarty 2007) and annual survival varies from 0.45 to 0.63 (Knick 1990). Unfortunately, these radio-telemetry kitten survival estimates are difficult to compare because they calculated kitten survival over different intervals based on their definition of the age class. Thus, there is a paucity of information on the factors influencing kitten survival, especially during the first several months of life.

Reproductive rates are also an important component of bobcat population dynamics, which can be influenced by pregnancy probability and litter size. Pregnancy probability is a reproductive parameter that can vary depending on age. Female bobcats can become pregnant when they are 9–12 months old, but it is rare; most studies indicate females are more likely to begin breeding when ≥ 1 year of age (Crowe 1975, Knick et al. 1985, Anderson and Lovallo 2003). Pregnancy probabilities range from 0.46–0.69 (Fritts and Sealander 1978, Tycz 2016, Landry 2017), and yearlings have a lower pregnancy rate than adults (Knick et al. 1985, Anderson 1987). Average litter size can vary between 1.7 to 3.6 kittens/litter and typically yearlings have fewer kittens/litter than adults (Anderson 1987, Koehler and Aubry 1994). Both pregnancy and litter size may also be influenced by prey abundance, with pregnancy probability and litter sizes declining when prey populations are low (Knick 1990, Koehler and Aubry 1994).

Limited information exists on population growth rates (λ) of bobcats. Knick (1990) suggested yields of bobcats are more sensitive to changes in adult female survival than kitten survival in Idaho, USA. Increasing the mortality of

productive females was additive and had a greater effect on yield than kitten survival and population growth was declining when prey availability was lower (Knick 1990). Simulations indicated thresholds of importance included harvest not exceeding 20% of the population (Knick 1990) and adult female survival rates ≥ 0.52 (Knick 1990). Bobcat populations likely exhibit substantial inter-annual variation in survival, reproduction, and population growth rates and such thresholds may not hold across space and time.

Bobcats are a valued game animal both recreationally and economically, as fur prices can average over US \$460 per pelt (Lehman et al. 2023). Modern harvest records of bobcats in South Dakota, USA, date back to 1973 and statewide harvest has varied from just over 60 to just under 1,000 bobcats (Lehman et al. 2023). Harvest of bobcats in the Black Hills has ranged from a high of 144 in 2004–2005 down to 29 in 2020–2021 (Lehman et al. 2021). Both harvest and mark-recapture survey data suggest declining abundance in the Black Hills (Lehman et al. 2023). The cause of the apparent decline in bobcat abundance in the Black Hills is unclear. Given recent declines in the Black Hills, 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 mark-recapture survey data, we predicted that the population of bobcats in the Black Hills is in decline ($\lambda < 1$). We hypothesized that survival of adult females and kitten survival would have the greatest influences on the finite rate of population change.

STUDY AREA

The study area was located in the Black Hills physiographic region (Flint 1955; Figure 1); this area ($\sim 4,420 \text{ km}^2$) was in Fall River, Custer, Pennington, Meade, and Lawrence counties in South Dakota, and in Weston County, Wyoming, USA. The study area was primarily Black Hills National Forest, interspersed with private land and areas managed by Custer State Park, Wind Cave National Park, and the Bureau of Land Management. Elevation ranges from 975 m in the southern Black Hills to 2,207 m at Black Elk Peak; topography varied greatly from steep canyon walls to flat meadows. Annual precipitation is approximately 50 cm on average, with most of the precipitation (60–73%) occurring May–October (Hoffman and Alexander 1987). In 2020 and 2021, annual snowfall ranged from 84 cm in the southern end of the study area to 343 cm in the north and temperatures ranged from -36°C in February to 38°C in July and August (National Climatic Data Center 2022). Vegetation varied considerably from north to south, where forests dominated the landscape at higher elevations and grasslands dominated the southern portion of the study area. Ponderosa pine (*Pinus ponderosa*) was the most common tree species, but patches of white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and bur oak (*Quercus macrocarpa*) occurred at local sites. Wildfire, logging, and mountain pine beetle (*Dendroctonus ponderosae*) infestations created natural and man-made openings in the forest throughout the study area. 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).

In the Black Hills, the bobcat harvest season runs from 26 December–15 February with no limit on the number of bobcats an individual trapper can harvest. From 2016 through 2022, a range of 29–53 bobcats were legally harvested annually from the Black Hills, comprising an estimated 15–25% of the population estimated using radio-marked bobcats and mark-recapture estimation (Lehman and Nelson 2017, 2018, Lehman et al. 2019, 2020, 2021, 2022). Potential predators of bobcats in the Black Hills include coyotes (*Canis latrans*) and puma (*Puma concolor*). In the Black Hills, bobcats prey upon lagomorphs (*Sylvilagus* and *Lepus* spp.), deer (*Odocoileus* spp.; adults and fawns), elk (*Cervus canadensis nelsoni*) calves, wild turkeys (*Meleagris gallopavo merriami*), small mammals, porcupines (*Erethizon dorsatum*), weasels (*Mustela* spp.), and passerines (Lehman 2005, 2015; Tycz 2016).

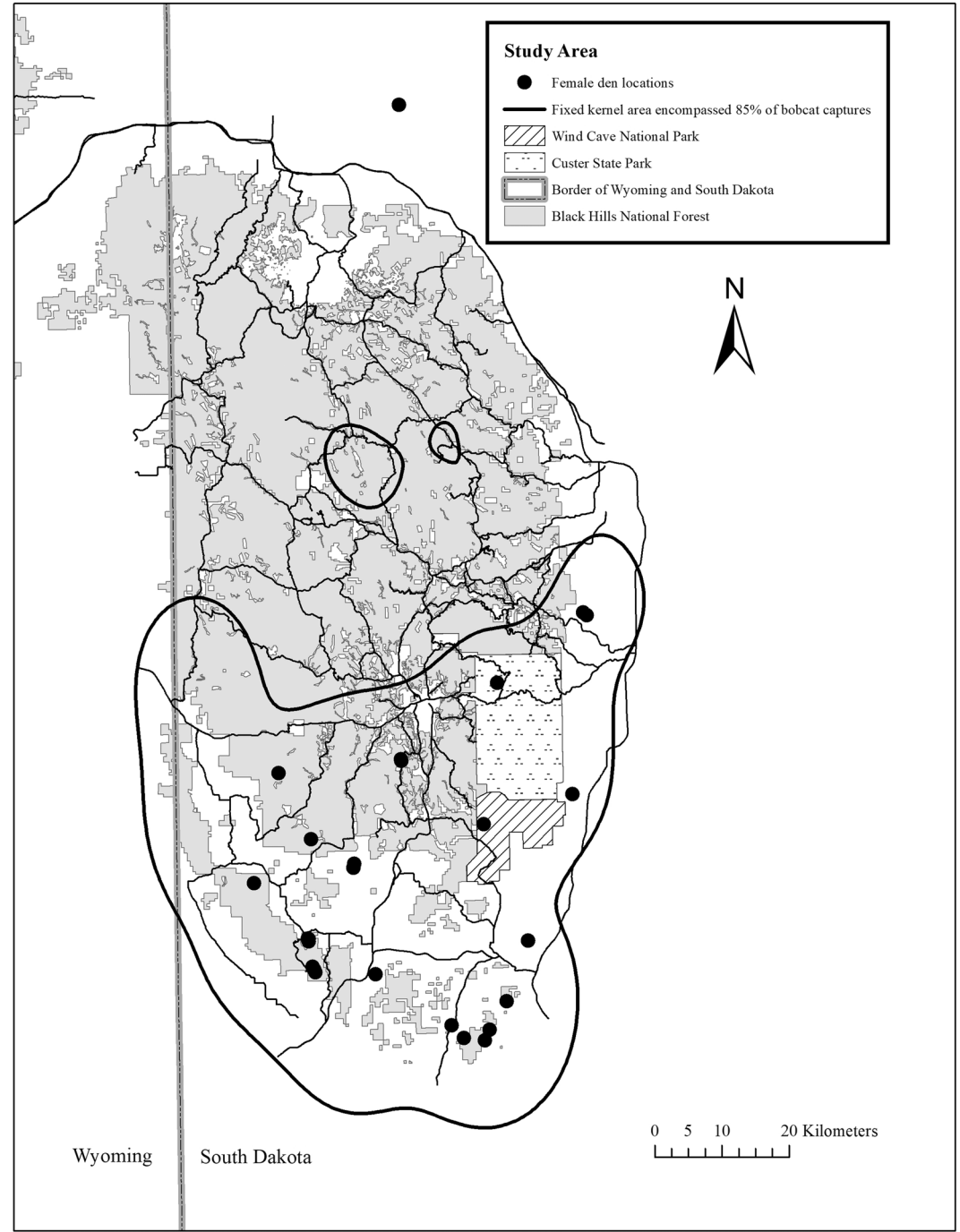


FIGURE 1 Study area for estimating demographic rates of bobcats in the Black Hills, South Dakota, 2016–2022.

METHODS

Bobcat captures

We estimated demographic rates of female bobcats through the use of radio-tracking and captured female bobcats from September through April 2016–2022. We captured and fitted bobcats with very high frequency (VHF) collars (M2220B; Advanced Telemetry Systems, Isanti, MN, USA) equipped with a mortality switch set to activate after 12 hours of inactivity and with a life expectancy of 1,598 days. In 2021, 3 bobcats were fitted with global positioning system (GPS) collars (Vertex Lite-1C Iridium; Vectronic, Berlin, Germany). The GPS collars were programmed to obtain a location every 13 hours and were equipped with a mortality switch set to activate after 12 hours of inactivity. The collars had a life expectancy of 533 days with a mean accuracy rate of 8–15 m. We captured bobcats using either guillotine or swing door style cage traps baited with scent lures and other attractants. Once captured, we sedated bobcats using butorphanol, azaperone, and medetomidine (BAM) sedation protocol (Rockhill et al. 2011). Once sedated, we blindfolded and fitted them with collars. We aged female bobcats based on body size, mass, and signs of previous lactation. We classified female bobcats that showed signs of previous lactation as adults (≥ 24 months of age) and bobcats that did not show signs of previous lactation but weighed ≥ 6.0 kg as yearlings (12–23 months of age). We classified bobcats < 6.0 kg with no signs of previous lactation as juveniles (3–12 months of age). The classification of ages we used is based on mass from recaptured kittens ($n = 15$) as they developed through time (South Dakota Game, Fish, and Parks, unpublished data). We located female bobcats once monthly between 1 September and 28 February via homing with aerial radio-telemetry (Morrison 2022). Between 1 March and 31 August, we located female bobcats via ground triangulation 3 days per week to help locate dens and kittens (Morrison 2022). When locating dens using VHF collars, we collected 1,390 triangulations and averaged 3 bearings per location (range = 3–6 bearings). Average time between the first and last bearing was 24 minutes \pm 15.23 (SE) and mean bearing error was 3.81 degrees \pm 6.26.

Females typically begin denning in March and most denning activity occurred throughout summer (Gashwiler et al. 1961, Fritts and Sealander 1978, Moriarty 2007). Female bobcats exhibit strong site fidelity and a reduction in daily movement distance after parturition (Moriarty 2007). Therefore, when 4 consecutive tracking locations for a female were within a 500-m radius, we assumed she inhabited a den and parturition had likely occurred within those days. If the female continued to localize in the same area after 1–4 weeks, investigators with telemetry gear attempted to locate and observe the female as she left the den location. After locating the den, we fitted all kittens with expandable VHF collars (28 grams; SOM2380; Wildlife Materials, Murphysboro, IL, USA), weighed them, determined sex, and aged kittens using dental eruption (Jackson et al. 1988). Collars were $< 5\%$ of body mass (mean kitten mass = 591.13 g \pm 127.30) by the time the kittens were able to walk (Caccamise and Hedin 1985, Gursky 1998). Average kitten age was 2.56 weeks \pm 1.42 when radio-marked.

Estimating vital rates

We estimated survival probability for kitten, juvenile, yearling, and adult females (Table 1). We assumed male and female kitten and juvenile survival were the same. We assumed survival of individual i during day t was a Bernoulli random variable:

$$y_{it} \sim \text{Bernoulli}(y_{i(t-1)} p_{it}),$$

where $y_{it} = 1$ if individual i survived day t , $y_{it} = 0$ if individual i died during day t , and p_{it} represented daily survival probability (Royle and Dorazio 2008, Lehman et al. 2017, Tyl et al. 2023). We assumed daily survival probability was a logit linear function of age (0–3 months [kitten], 3–12 months [juvenile], 12–24 months [yearling], and ≥ 24

TABLE 1 Vital rates used to estimate asymptotic population growth rates ($\bar{\lambda}$) of bobcats in the Black Hills, South Dakota, USA, 2016–2022.

Vital rate	Age ^a	Estimate	95% CI
Annual survival	Adult	0.79	0.68–0.90
Annual survival	Yearling	0.77	0.55–0.93
275-day survival	Juvenile	0.23	0.07–0.50
Reproduction rate	Adult	0.40	0.22–0.61
Reproduction rate	Yearling	0.40	0.07–0.74
Reproduction rate	Juvenile	0.05	0.00–0.50
Litter size	Adult	1.97	1.41–2.62
Litter size	Yearling	2.00	1.31–3.08
90-day survival	Kitten	0.77	0.60–0.92

^aAge classes are adult (≥ 730 days of age), yearling (366–729 days of age), juvenile (91–365 days of age), and kitten (0–90 days of age).

months [adult]). We assumed kittens advanced to juveniles if they survived the first 3 months, and we assumed an individual advanced an age class (i.e., juvenile to yearling, yearling to adult) if they survived past 12 May each year. We accounted for repeated observations on individuals by including a random individual effect.

We estimated the probability that a female bobcat reproduced with a Bayesian logistic regression model. We defined reproduction probability as the probability that a female bobcat alive on 1 April would produce a litter that year. We assumed reproduction probability was a logit-linear function of age of female (juvenile, yearling, or adult) and year of study. We accounted for repeated observations on individuals by including a random individual effect. We estimated litter size by modeling the number of kittens produced by successful females using a truncated Poisson model (David and Johnson 1952, Rota et al. 2014). We assumed the expected number of kittens born to a female that reproduced was a log linear function of age of female (yearling or adult) and year of study. We accounted for repeated observations of individuals by including a random individual effect.

We fit these models using Bayesian methods. We assumed flat prior distributions for all parameters, including slope coefficients of age effects and population-level means and variances for random, individual, and year effects. We fit our model with JAGS via the jagsUI version 1.5.2 interface (Kellner 2021) in program R version 4.3.1 (R Core Team 2023). We ran 3 chains for each model using trace plots to determine an adequate burn-in period and subsequently ran models until we achieved reasonable convergence ($\hat{R} \leq 1.1$; Gelman et al. 2014).

Estimating asymptotic population growth rates

We combined estimates of survival probability and reproductive rates into a 3-stage (kitten and juvenile, yearling, adult), female-based, pre-breeding matrix projection model (Caswell 2001) with the following structure:

$$A = \begin{bmatrix} r_j \times l_y \times 0.45 \times s_k \times s_j & r_y \times l_y \times 0.45 \times s_k \times s_j & r_a \times l_a \times 0.45 \times s_k \times s_j \\ s_y & 0 & 0 \\ 0 & s_a & s_a \end{bmatrix}$$

where r_j , r_y , and r_a are reproduction probabilities of juveniles, yearlings, and adults, respectively; l_y and l_a are expected litter sizes of yearlings and adults, respectively (we assumed juveniles and yearlings have the same

expected litter size); and s_k , s_j , s_y , and s_a are survival probabilities for kittens, juveniles, yearlings, and adults, respectively. We obtained survival probabilities for the matrix projection model from estimates of daily survival probability as follows: daily kitten survival was raised to the power 90; daily juvenile survival probability was raised to the power $365 - 90 = 275$; and daily yearling and adult survival probability was raised to the power 365. We used a 55:45 sex ratio of males to females based on known ratio from sex of radio-marked kittens (Morrison 2022).

We calculated asymptotic population growth rates (λ), sensitivity of population growth rates (S) to very small changes in matrix entries, and elasticity of population growth rates (E) to proportional changes in matrix entries (Caswell 2001). We also calculated the stable age distribution implied by projection matrix A . We accounted for uncertainty in λ , S , E , and stable age distribution by constructing a unique projection matrix A from each posterior draw from our Bayesian analysis. We calculated λ , S , E , and stable age distribution using the popbio version 2.7 package in Program R version 4.3.1 (Stubben and Milligan 2007). Sensitivity and elasticity analyses describe changes in population growth rates as a function of matrix entries, but these entries can be a function of multiple lower-level vital rates. Therefore, we also used life-stage simulation analysis to evaluate how population growth rate varied with each lower-level vital rate (Wisdom et al. 2000). We accomplished this by regressing estimates of λ against corresponding posterior draws for each lower-level vital rate. We calculated r^2 values for each regression, which provided a measure of how much variation in λ was explained by each lower-level vital rate. Similarly, we evaluated how strongly the juvenile and yearling to adult age ratio correlated with λ to evaluate its potential use as an index of population growth.

Finally, given that harvest is the primary tool managers can use to influence bobcat populations, we evaluated how changing harvest rates would influence λ . We made the following key assumptions when evaluating the effects of changing harvest rates on population growth: survival probability was estimated in the presence of harvest, which we call the baseline harvest rate; harvest has a completely additive effect on survival (Knick 1990, Anderson and Lovallo 2003); and the effects of changes to harvest rate are relative to this baseline rate. We evaluated the effects of reducing 2 potential baseline harvest rates on population growth. We evaluated changes to a 23.5% baseline harvest rate, which was the estimated average harvest rate during our study from 2019–2021. We also evaluated changes to a 20% baseline harvest rate, which was considered an important threshold for bobcat management based on the previous study by Knick (1990). By assuming completely additive harvest mortality, we assumed a 1% reduction in harvest rate relative to the baseline harvest rate corresponded to a 1% increase in survival probability for each age class.

RESULTS

We estimated adult survival probability from 66 female bobcats from 2016 through 2022 (Table 2). We estimated kitten and juvenile survival probability from 29 kittens in 2020 and 11 kittens in 2021. Annual adult female survival probability was 0.79 (95% credible intervals [CI] = 0.68–0.90), yearling survival probability was 0.77 (95% CI = 0.55–0.93), and adult and yearling survival probability were not statistically different. The estimated probability that a kitten survived the first 90 days was 0.77 (95% CI = 0.60, 0.92) and that a juvenile survived from 91 days to 1 year was 0.23 (95% CI = 0.07–0.50). Combined, the estimated probability a bobcat survived to its first year was 0.18 (95% CI = 0.05–0.44).

We estimated the probability a female bobcat reproduced from 53 potential reproduction events (i.e., a female bobcat alive on 1 April that was available to reproduce) recorded on 35 radio-marked individuals. The estimated probability an adult reproduced was 0.40 (95% CI = 0.22–0.61), a yearling reproduced was 0.40 (95% CI = 0.07–0.74), and a juvenile reproduced was 0.05 (95% CI = 0.00–0.50). We estimated expected litter size from 19 litters recorded on 17 radio-marked females whose kittens we were able to locate. The expected number of kittens born when an adult reproduced was 1.97 (95% CI = 1.41–2.62) and when a yearling reproduced was 2.00 (95% CI = 1.31–3.08).

TABLE 2 Number of female bobcats captured for this study by year to estimate asymptotic population growth rates ($\bar{\lambda}$) in the Black Hills, South Dakota, USA, 2016–2022.

Year	Age ^a and number
2016	4 adults, 3 yearlings, and 1 juvenile
2017	4 adults, 3 yearlings, and 1 juvenile
2018	5 adults, 5 yearlings, and 1 juvenile
2019	8 adults, 12 yearlings, and 1 juvenile
2020	4 adults, 2 yearlings, and 10 juvenile
2021	2 yearlings

^aAge classes are adult (≥ 730 days of age), yearling (366–729 days of age), and juvenile (91–365 days of age).

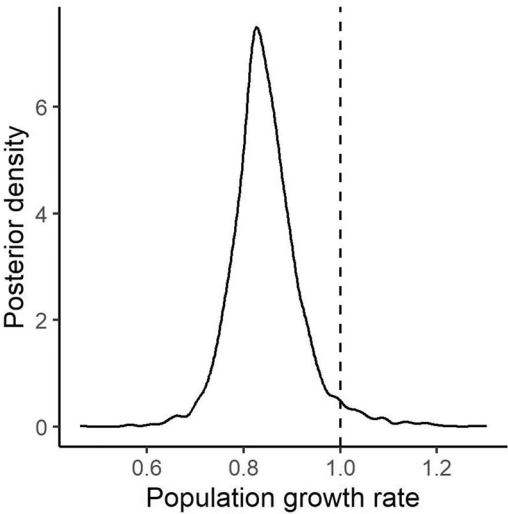


FIGURE 2 Posterior density of estimated population growth rates of female bobcats in the Black Hills, South Dakota, USA, 2016–2022. The vertical line represents the boundary between a growing and declining population.

The asymptotic growth rate from a matrix projection model parameterized using point estimates of survival and reproductive rates was below the value of 1 necessary to sustain the population ($\bar{\lambda} = 0.85$, 95% CI = 0.72, 1.02; Figure 2). Elasticity and sensitivity analysis both indicated that population growth rate was most strongly influenced by adults surviving and remaining adults (matrix element $A_{3,3}$; Table 3). Both analyses also indicated the transition of kittens and juveniles to yearlings (matrix element $A_{2,1}$) and adult reproductive contribution (matrix element $A_{1,3}$) were the second and third most influential variable, though the rank of each matrix element is different between the analyses. Both analyses indicated that the remaining matrix elements had little influence on population growth rates.

Life-stage simulation analysis continued to demonstrate the importance of annual adult survival probability on population growth (Figure 3) but additionally revealed that the juvenile survival (91 days–1 year) and kitten survival (0–3 months) components of a bobcat's first year also strongly influenced population growth rates. This is consistent with elasticity and sensitivity analyses above but identified the kitten and juvenile survival lower-level vital rates as what likely contributed to the relatively high importance of adult reproductive contribution. The life-

TABLE 3 Elasticity (E) and sensitivity (S) of components of a projection matrix for female bobcats in the Black Hills, South Dakota, USA, 2016–2022. Values in each column are the posterior mean, with limits of 95% credible intervals in parentheses.

Matrix entry ^a	E	S
Adult survival	0.82 (0.62–0.95)	0.87 (0.73–0.97)
Kitten and juvenile survival	0.06 (0.02–0.13)	0.07 (0.02–0.16)
Adult reproductive contribution	0.06 (0.01–0.11)	0.81 (0.57–1.06)
Yearling survival	0.06 (0.01–0.11)	0.06 (0.02–0.13)
Yearling reproductive contribution	0.01 (0.00–0.02)	0.06 (0.01–0.12)
Juvenile reproductive contribution	0.00 (0.00–0.01)	0.06 (0.02–0.14)

^aAge classes are adult (≥730 days of age), yearling (366–729 days of age), juvenile (91–365 days of age), and kitten (0–90 days of age).

stage simulation analysis also demonstrated that the ratio of juveniles and yearlings to adults was highly correlated with population growth rate (Figure 4).

We further evaluated which changes in vital rates could lead to the population growing or declining. The population was always declining if either annual adult survival was <0.85 or 275-day juvenile survival was <0.35, regardless of other vital rates. Conversely, the population was always increasing if 275-day juvenile survival was greater than about 0.65, regardless of other vital rates (barring extreme cases of complete reproductive failure; Figure 5). For an annual adult survival probability >0.85 and 275-day juvenile survival probability between 0.35 and 0.65, the population can grow, remain stable, or decline, depending on values of all other vital rates.

Given the importance of adult female survival, we further evaluated the potential influence of harvest rates on population growth. When assuming a baseline harvest rate of 23.5%, reducing the harvest rate to 9% led to a positive mean growth rate (Figure 6) and a >0.50 probability of a growing population (Figure 7). When assuming a baseline harvest rate of 20%, reducing the harvest rate to 7% led to a positive mean growth rate (Figure 6) and a >0.50 probability of a growing population (Figure 7).

DISCUSSION

Adult female bobcat survival in our study (0.79 ± 0.06) was higher than what has been reported in other populations that are harvested, which range from 53–67% and is at the bottom limit of adult survival rates in unexploited populations, which range from 78–97% (Rolley 1985, Knick 1990, Chamberlain et al. 1999, Anderson and Lovallo 2003). Kitten and juvenile survival for the first year of life in our study (0.18 ± 0.07) was much lower than reported annual survival from Idaho, which varied from 0.45 to 0.63 (Knick 1990).

Research on kitten and juvenile felid survival is scarce, but a study on pumas reported support for juvenile female survival explaining most of the variation in λ (Robinson et al. 2014). Certainly, there can be high annual variation in kitten and juvenile survival for felids, as annual Canada lynx (*Lynx canadensis*) kitten survival ranged from 0.05–0.71 (Mowat et al. 1996) and 2 studies on Eurasian lynx (*Lynx lynx*) reported survival rates from 0.33–0.42 (Boutros 2002, Breitenmoser-wursten et al. 2007). If adult survival is steady and kitten and juvenile survival can vary wildly in felid populations, this could be a principal driver of fluctuations in population growth rates.

Population growth was most sensitive to changes in adult female survival probability. Elasticity, sensitivity, and life-stage simulation analyses all indicated that population growth was most sensitive to changes in adult survival probability. Additionally, life-stage simulation analysis identified juvenile survival probability as the component of adult reproductive contribution that was most strongly associated with population growth and as the second

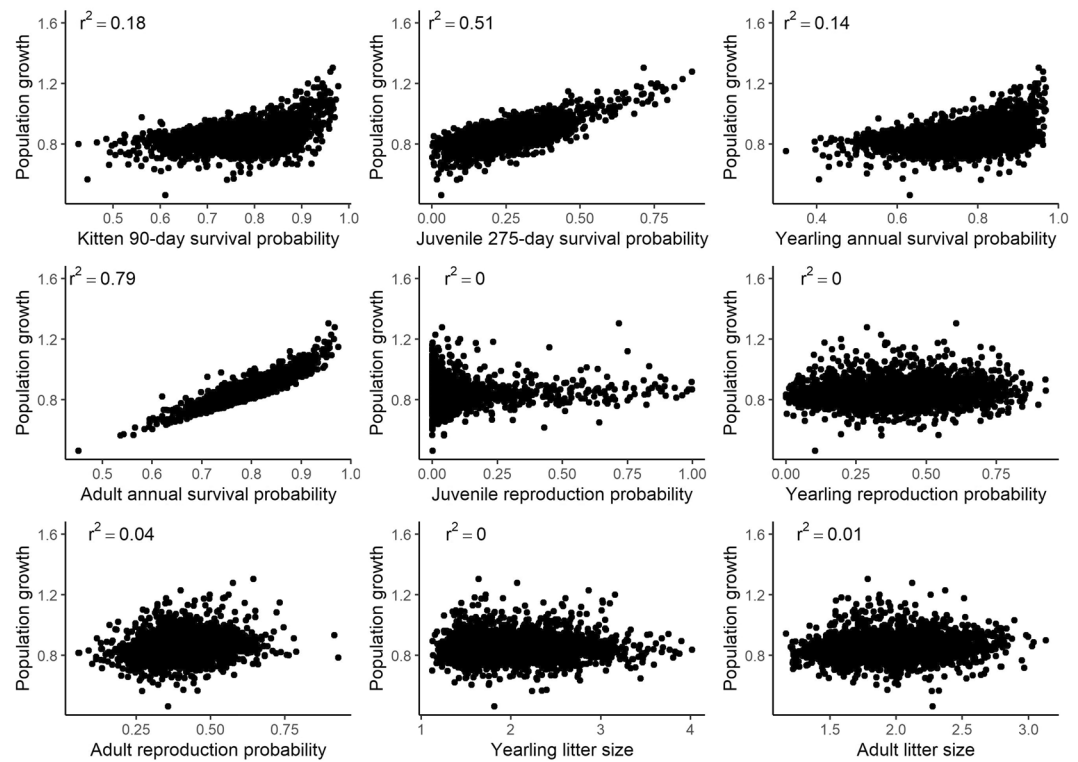


FIGURE 3 Life-stage simulation analysis results for female bobcats in the Black Hills, South Dakota, USA, 2016–2022. Each panel demonstrates how strongly population growth rate is correlated with variation in each lower-level vital rate. Coefficient of determination values (r^2) are obtained by assuming a liner relationship between population growth and lower-level vital rates.

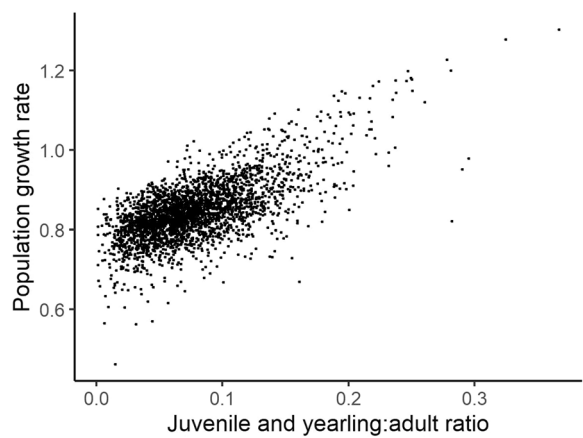


FIGURE 4 Correlation between population growth rate and the ratio of juveniles and yearlings to adults for bobcats in the Black Hills, South Dakota, USA, 2016–2022.

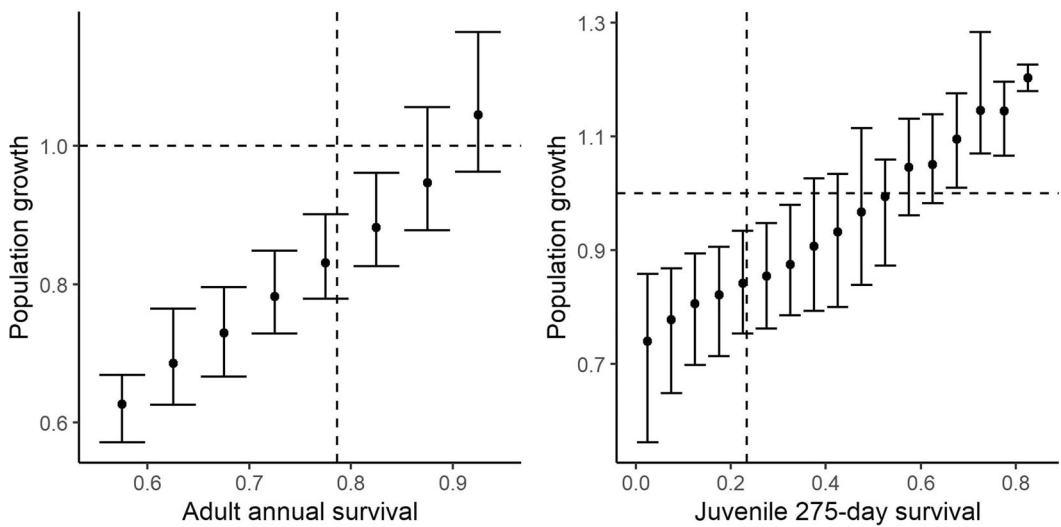


FIGURE 5 Population growth rates as a function of adult and juvenile female bobcat survival probability in the Black Hills, South Dakota, USA, 2016–2022. The x-axis is derived by binning survival probability into equal-length intervals of 0.05 units. The error bars are the limits of the 2.5 and 97.5 percentiles of corresponding population growth rate. The horizontal dashed line represents a stable population growth rate and the vertical dashed line represents the posterior mean adult and juvenile survival probabilities.

strongest influence on population growth. This suggests that management actions targeting survival are most likely to influence population growth rates (Knick 1990). Our life-stage simulation analysis further demonstrated that a low kitten and juvenile survival probability is reflected in juvenile-to-adult harvest ratios (Newell and Podruzny 2018), which can be a useful index of recruitment and population growth rates. In Montana, USA, the best predictor of population growth was the ratio of number of juveniles per adults harvested, with higher ratios indicating positive growth rates (Newell and Podruzny 2018). The percentage of harvest that was juveniles in the Black Hills population was 4% in 2020 and 0% in 2021 (Lehman et al. 2020, 2021), reflecting low kitten and juvenile survival probabilities estimated during those years. A portion of South Dakota trapping and hunting methods such as snaring and shooting are a random method of take (35–37% of harvest; Lehman et al. 2020, 2021) and juvenile-to-adult harvest ratios calculated from individuals harvested using these methods can provide an indicator of age structure in the population and can be used as a tool to determine when to make harvest limits more conservative.

Annual survival rates in growing populations that are harvested range from 53–67% (Rolley 1985, Knick 1990, Chamberlain et al. 1999, Anderson and Lavallo 2003) and previous simulations indicated that adult female survival should be ≥ 0.52 (Knick 1990) to ensure a stable or growing population. These values may not hold true for all populations, as our calculations revealed the population will always be declining if either annual adult survival is < 0.85 or 275-day juvenile survival is < 0.35 , regardless of other vital rates. We suspect the primary difference between previous studies (Litvaitis et al. 1987, Knick 1990) and our study is that bobcats in our study had poor survival for their first of year of life (18%). This highlights the importance of evaluating bobcat demographic rates across a range of conditions.

Our elasticity analysis indicated that reproductive contribution also was important but to a much lesser extent than adult survival. Adult reproductive contribution was only important because of the contribution of kitten and juvenile survival. Yearling and juvenile reproductive contribution were not important in our analysis. Reproduction rates in our study (0.40) were below rates reported in other areas (0.46–0.69; Fritts and Sealander 1978, Tycz 2016, Landry 2017). Average litter size was on the lower limit of the range of what was reported in other populations

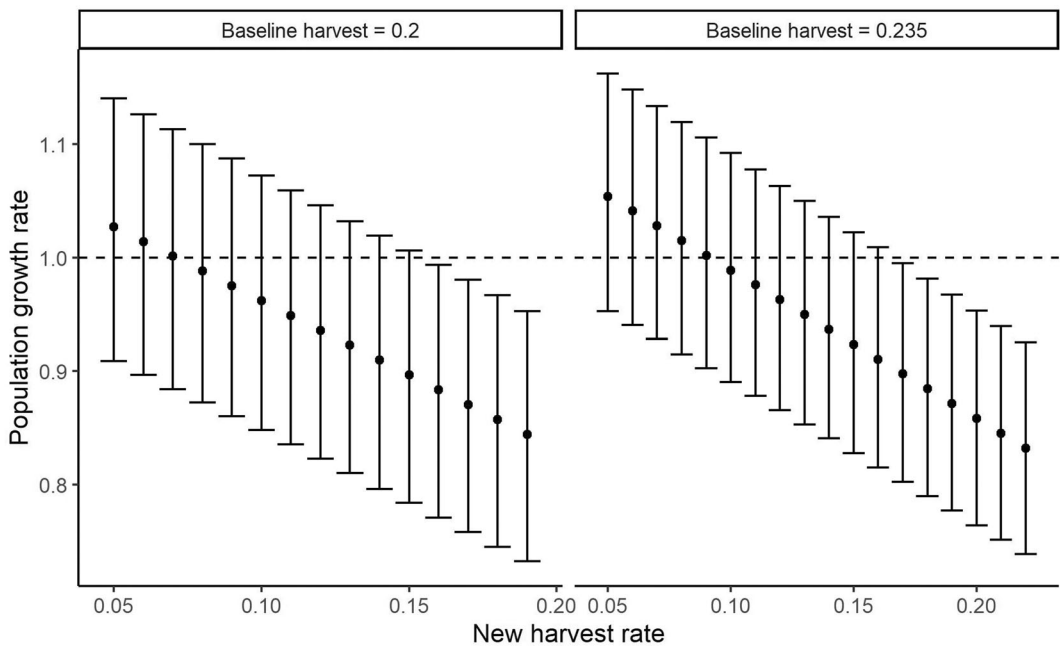


FIGURE 6 Population growth rates as a function of harvest rates of adult and juvenile female bobcats in the Black Hills, South Dakota, USA, 2016–2022. Each plot assumes survival was estimated in the presence of the harvest rate listed in the panel title (harvest rates of 0.20 and 0.235, respectively). The x-axis represents a new harvest rate relative to the baseline harvest rate listed in the panel title. Each point is the posterior mean population growth rate and the error bars are the limits of the 2.5 and 97.5 percentiles of the corresponding population growth rate. The horizontal line separates a growing population from a declining population.

(Fritts and Sealander 1978, Anderson 1987, Koehler and Aubry 1994, Tycz 2016, Landry 2017). Researchers have hypothesized that prey availability, and particularly lagomorph populations, influence pregnancy and litter size for adult and yearling females (Knick 1990, Koehler and Aubry 1994), and Knick (1990) hypothesized that during jackrabbit (*Lepus californicus*) declines population growth rates of bobcats were much lower.

In this study, juvenile survival dropped considerably from 91–365 days and starvation (41%) and predation (38%) were the primary causes of mortality (Morrison 2022). In the Black Hills and throughout their range, lagomorphs are a primary prey source for bobcats (Anderson and Lovallo 2003, Tycz 2016). In 2016, Tycz (2016) observed lower rates of pregnancy coincided with decreased occurrence of lagomorphs in the diet of bobcats in the Black Hills. Reproduction often declines during seasons of reduced food abundance for a variety of species including lynx (Brand and Keith 1979), marbled murrelet (*Brachyramphus marmoratus*; Becker et al. 2007), primates (Fedigan 1983), and Eurasian otter (*Lutra lutra*; Ruiz-Olmo et al. 2001). We hypothesize that lower lagomorph abundance between 2020 and 2021 could have contributed to lowered pregnancy rates and the high number of kitten mortalities caused by starvation. Based on previous studies on young felid survival, most mortalities were observed to occur during the first 3 months of life with predation as the leading cause of mortality (Logan and Sweanor 2001, Boutros 2002, Lovallo 2007, Moriarty 2007). Our results suggested higher survival for the first 90 days (0.77), and the majority of the mortalities occurred between 91–365 days. At this stage bobcat kittens are no longer protected by a den and therefore may be more susceptible to predation. Moreover, juveniles are spending greater amounts of time independent from the female between 91–365 days of age and are likely hunting on their own (Moriarty 2007), which, coupled with hypothetically lower prey abundance, could have resulted in the high number of starvations observed during this time.

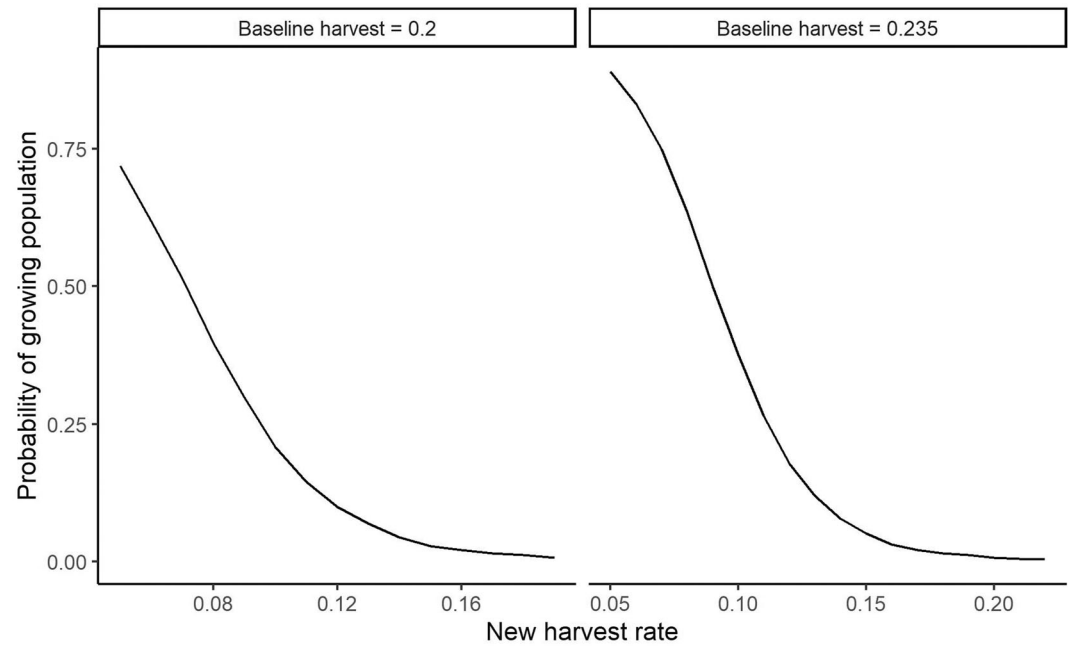


FIGURE 7 The posterior probability of a growing population (i.e., population growth rate >1) as a function of harvest rates of adult and juvenile female bobcats in the Black Hills, South Dakota, USA, 2016–2022. Each plot assumes survival was estimated in the presence of the harvest rate listed in the panel title (harvest rates of 0.20 and 0.235, respectively). The x-axis represents a new harvest rate relative to the baseline harvest rate listed in the panel title.

Our matrix analyses reveal a bobcat population undergoing a precipitous decline but perhaps this population could have some compensatory immigration, or net movement of individuals from adjacent areas to the Black Hills to replenish this population (Turgeon and Kramer 2012). Some puma populations in heavily hunted or sink areas have recovered because of compensatory immigration from neighboring areas with higher densities (Robinson et al. 2008, Stoner et al. 2013). We documented movement of radio-collared bobcats leaving the Black Hills and immigrating to new areas elsewhere in South Dakota, Wyoming, and Nebraska. Other bobcat studies from areas in central South Dakota have not documented immigration of radio-collared individuals from their study areas to the Black Hills (Mosby 2011, Tycz 2016).

Previous demographic modeling of bobcats suggested that greater survival of adult females and increased reproduction during periods of higher prey abundance could increase population growth (Knick 1990). Our work adds to the understanding of how important juvenile survival is to bobcat population growth, and just managing for higher adult female survival may not necessarily lead to a positive population growth rate. Future research could evaluate hypotheses related to factors influencing juvenile survival such as prey availability, starvation, and interspecific predator interactions.

MANAGEMENT IMPLICATIONS

After accounting for uncertainty in the harvest rate of bobcats in our population, it was necessary to reduce the harvest rate to 7–9% to allow for a positive mean growth rate. Even though our results indicate a healthy adult female survival rate, this bobcat population has a lower kitten and juvenile survival rate and our results support a

more restrictive approach to harvest management. Our research highlights the importance of juvenile survival (91 days to 1 year) in bobcat population growth, and our reduced juvenile survival rate was mirrored in harvest data in the form of low juvenile-to-adult harvest ratios. These ratios can provide an indicator of age structure and could be a useful indicator of periods of low recruitment and population growth. Managers could monitor these age ratios from harvest data and identify thresholds for determining when harvest regulations should be more restrictive. For example, based on our population model, when the juvenile-to-adult ratio falls below 10%, populations are predicted to decline. Therefore, enacting more restrictive harvest regulations when juvenile-to-adult ratios fall below this threshold could be a management action aimed at increasing population growth. Trapper education and outreach programs designed to highlight the importance of protecting females would be important to implement, and if protected at an adequate level may allow for a positive growth rate.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All kitten handling, marking, and monitoring procedures were approved by the West Virginia University Research Committee (Animal Care and Use Committee approval number 1909028979).

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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