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RESEARCH ARTICLE

Simulated effects of roadkill and harvest on the viability of a recovering bobcat population

Marissa A. Dyck[1] | Kevin T. Shoemaker[2] | Catherine C. Dennison[3] | Viorel D. Popescu[1,4]

[1]Department of Biological Sciences, Ohio University, 107 Irvine Hall, Athens, OH 45701, USA

[2]Department of Natural Resources and Environmental Science, University of Nevada, 1664 N. Virginia Street, Reno, NV 89557, USA

[3]Ohio Division of Wildlife, 2045 Morse Rd Building G, Columbus, OH 43229, USA

[4]Center for Environmental Research, University of Bucharest, 1 N. Balcescu Boulevard, Bucharest, Romania

Correspondence

Marissa A. Dyck, 57 Oxbow Trail, 107 Irvine Hall, Ohio University, Athens, OH 45701, USA.
Email: marissadyck17@gmail.com

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Abstract

Bobcats (*Lynx rufus*) were extirpated from many midwestern states in the mid-1800s owing to habitat loss and overharvesting. Recently, bobcats have recolonized Ohio, USA, and neighboring states and given their furbearer status elsewhere, there is interest in opening a harvest season; however, demographic factors and viability of this population are currently unknown. We developed a spatial population simulation model to assess the long-term viability of the bobcat population in Ohio in the face of 2 human-induced factors limiting population growth: potential harvest and road mortality. We combined habitat suitability and road mortality risk data with vital rates for bobcats from Ohio and other populations to simulate possible scenarios for Ohio's population. Our baseline scenario simulations showed no risk of extinction for Ohio's bobcat population in the next 40 years, but population trajectories were lower and exhibited greater uncertainty when we modeled the population with a lower maximum density of animals per cell. At low harvest intensity ($\alpha h = 0.05$), the bobcat population also exhibits low risk of extinction. When harvest intensity increases ($\alpha h = 0.1, 0.15$) or when adults (≥2 yr) are targeted by harvest, simulations show declining populations, greater uncertainty in projections, and possible risk of extirpation. Our models indicated that if harvest and road mortality are additive, then the bobcat population could withstand marginal increases in road mortality ($\alpha r = 0.1$) at low harvest intensity

(αh = 0.05). Future increases in road mortality with higher harvest intensity (αh = 0.1, 0.15) were unsustainable. Our results can be used by wildlife managers to assist with decisions on population-level management. This simulation model can easily be adapted for other large mammals and can be modified to assess a variety of ecological and anthropogenic influences to wildlife populations.

KEYWORDS

carnivore, *Lynx rufus*, management scenarios, Ohio, population ecology, population viability analysis, spatial

Species and population risk assessment tools are becoming increasingly pertinent for conservation management. Such assessments can help identify the range of demographic parameters that are important to population persistence, and typically focus on estimating risk of extinction using simulations that incorporate various sources of stochasticity (Lindenmayer et al. 1993, LaRue and Nielsen 2016). In the mid 1800s, bobcats (*Lynx rufus*) were extirpated from a number of states in the midwestern United States owing to overharvesting and habitat loss (Reding et al. 2012). Recently, bobcats have begun recolonizing their former range in the Midwest after a century of absence (Nielsen and Woolf 2002, Roberts and Crimmins 2010, Prange and Rose 2020). In Ohio, USA, bobcat recolonization occurred sequentially with 2 subpopulations that were genetically distinct (as of 2012) in southern and eastern Ohio; the eastern population (with founder animals from WV) was determined to be self-sustaining, whereas the southern population (with founder animals from KY) was thought to be dependent on immigration (Anderson et al. 2015). The 2 populations were approximately 200 km apart and recent genetic analysis of 100 roadkill animals collected in 2019–2020 indicated that admixture has occurred (Heffern 2021).

Broad-scale data collected by management agencies (e.g., roadkill animals) and citizen observations (e.g., motion-sensitive cameras, live sightings) indicate that the bobcat population is increasing, but bobcat expansion may be limited by road mortality (Nielsen and Woolf 2002, Bencin et al. 2019) and intensive agriculture, which dominates this region of the United States (Popescu et al. 2021). As such, understanding the limiting factors affecting the distribution, habitat use, and mortality of expanding bobcat populations at multiple spatial scales can improve the development and implementation of management and conservation plans to ensure long-term population viability (Hurlbert and Jetz 2007, Reed et al. 2017). Given the perceived population trends and the legal harvest of bobcats for fur in most adjacent states, there is interest from trappers and hunters in opening a harvest season for bobcats in Ohio. Therefore, adaptive management of the bobcat population that includes potential harvest decisions would benefit highly from Midwest- and Ohio-specific ecological information, including habitat selection and use, current mortality sources and risk, population density, and demographic parameters.

In this study, we developed a spatial population simulation model to assess the long-term viability of Ohio's bobcat population in the face of human-induced factors limiting population growth, including the effects of proposed harvest and future increase in road mortality. Specifically, we augmented Ohio-based ecological and demographic data with vital rates and dispersal data from other unharvested bobcat populations to test 3 hypotheses regarding the effects of harvest and increased roadkill on the recovering bobcat population in Ohio.

We hypothesized that under current conditions (e.g., habitat suitability, demographics, survival) low levels of harvest would be sustainable (i.e., support non-declining population trajectories; hypothesis 1). While this is intuitive, the bobcat population in Ohio is still recovering and expanding numerically and spatially; therefore, including low levels of harvest (high enough to reflect a realistic state-wide harvest season) in the model could result in unsustainable population trajectories.

When considering different harvest scenarios, we expected that if harvest was applied to only adult animals >2 years old (i.e., young adults and adults), population trajectories would decline more than if harvest was applied to all age groups (i.e., kittens [age 0] and juveniles [age 1] in addition to adults). The importance of adult survival for population growth is often greater for medium to large mammals (Crooks et al. 1998, Heppell et al. 2000, Creel et al. 2004) and has a higher elasticity value for bobcats (Figure S1, available in Supporting Information). Therefore, we hypothesized that when harvest is applied to adults only, the results would exhibit more uncertainty in population trajectories and more trajectories exhibiting population decline (hypothesis 2). As such, harvesting proportionally across all age classes would provide greater harvest opportunity while maintaining population growth.

We predicted that additional road mortality would also lead to more uncertainty in population trajectories and more trajectories exhibiting population decline (hypothesis 3) but would have a weaker effect on the population than harvest mortality. Roadkill disproportionately affects juvenile bobcats (age 1) more than young-adult and adult bobcats (ages ≥2; Table S1, available in Supporting Information) and juvenile bobcats represent the main stage for dispersing individuals (Johnson et al. 2010, Hughes et al. 2019). This bias in roadkill susceptibility by age combined with the greater influence of young-adult and adult survival on population growth than juvenile survival (Figure S1) led us to expect that additional roadkill would have a lesser effect on overall population trajectories compared to harvest, which is applied either across all ages equally or only to adults (>2 yr) depending on the harvest scenario.

STUDY AREA

Ohio is located near the northernmost edge of the bobcats' native range in the midwestern United States. Ohio ranks thirty-fifth by geographic size (116,100 km^2), but it is the tenth most densely populated state. It is also home to one of the most extensive transportation systems, with the nation's fifth largest traffic volume, the tenth largest highway network, and fourth largest interstate system. Ohio's land cover is similar to other midwestern states, with a clear partitioning of forested land cover (in the southeast) and agricultural lands interspersed with small forest patches throughout the rest of the state. Land ownership is largely private apart from the Wayne National Forest (managed by the U.S. Department of Agriculture Forest Service) and several large state parks and forests. Ohio contains 5 major ecoregions, though it is primarily composed of the Corn Belt Plains in the west and the Western Allegheny Plateau in the east (Peacefull 1996). Before colonial settlement, Ohio's land cover was up to 95% forest composed mainly of beech (*Fagus* spp.), maple (*Acer* spp.), ash (*Fraxinus* spp.), elm (*Ulmus* spp.), oak (*Quercus* spp.), hickory (*Carya* spp.), and American chestnut (*Castanea dentata*); pre-colonial Ohio's mammalian fauna included large mammals (black bear [*Ursus americanus*], wolf [*Canis lupus*], mountain lion [*Puma concolor*], bison [*Bison bison*], elk [*Cervus elaphus*]), meso-mammals (bobcat, gray fox [*Urocyon cinereoargenteus*], river otter [*Lontra canadensis*], fisher [*Pekania pennanti*], American beaver [*Castor canadensis*]) and numerous small mammal species (Sears 1926). During the nineteenth century, most of Ohio's original forests were cleared for human settlements, industry, and cropland, leaving the state with only 10% forest cover by the early 1900s (https://ohiodnr.gov/discover-and-learn/safety-conservation/about-ODNR/forestry/state-forest-management/state-forest-history, accessed 1 May 2023). The mid-twentieth century saw a push for more recreational lands that brought about reforestation efforts, which shifted to include the reclamation of mining lands in the 1970s. Today, Ohio's land cover is composed of approximately 30% forest (96.3% hardwoods, 3.7% conifers), which is primarily located throughout the unglaciated Western Allegheny Plateau. The mammal fauna is depauperate, with most large mammals being extirpated in mid-1800s; some meso-mammals are witnessing a comeback (bobcat, river otter, American beaver, fisher), while non-native species such as coyote (*Canis latrans*) and red fox (*Vulpes vulpes*) are expanding numerically and spatially (Hody and Kays 2018; https://ohiodnr.gov/discover-and-learn/animals/mammals, accessed 29 May 2023). The elevation in Ohio ranges between 138 m and 472 m. The climate is humid continental with hot and humid summers (Jun–Aug) and generally cool to cold winters (Dec–Feb); summer average temperatures can reach upwards of 32°C,

and winter temperatures can average as low as −2.5°C during nighttime. The average annual precipitation ranges between 800 mm and 1,000 mm, and the northernmost part of Ohio, along Lake Erie, is within the Lake Snowbelt.

METHODS

Our population simulation model explicitly incorporates ecological processes inherent to spatially structured populations, such as movement and dispersal, habitat carrying capacity, and occupancy to improve inference on population trajectories (Possingham and Davies 1995). We evaluated the relative importance of 2 mortality sources by combining potential harvest mortality with additive age-specific mortality from roadkill. Roadkill is the main source of mortality in unharvested bobcat populations (Nielsen and Woolf 2002, Riley et al. 2003, Bencin et al. 2019), as bobcats have few natural predators throughout most of their range and predation by coyotes is rare (Dyck et al. 2022). We investigated the current trajectory of Ohio's bobcat population (baseline scenario) and trajectories with potential harvest (with and without additional road mortality) that focused on either all age groups or adults only (>2 years old). These age-based scenarios are a proxy for how harvest could be managed.

Habitat suitability

We modeled habitat suitability for bobcats (Figure S2, available in Supporting Information) using verified sightings (n = 975) recorded by the Ohio Department of Natural Resources between 2010 and 2019 (Popescu et al. 2021). The dataset included multiple types of verified sightings, such as camera images and videos (84%), incidentally trapped animals (8%), and direct sightings (8%), but it did not include roadkill animals because this would bias results towards areas near roads. Most of the sightings were reported by the public via phone, email, or online (starting in 2018). The Ohio Division of Wildlife used multiple communication methods including press releases, magazine articles, social media posts, presentations to community groups, and informal communication with constituents to encourage the reporting of sightings. Details on the development of the bobcat habitat suitability model are presented in Popescu et al. (2021). Briefly, we used logistic regression with bobcat records as 1s and pseudo-absences as 0s created outside a 5,600-m buffer around all presence records; this distance was equal to the radius of a circle with the same area as the maximum mean bobcat home range in Ohio (99.7 km^2; Prange and Rose 2020). Predictors for this population-level analysis included proportion of land cover types at several scales (3–50 km^2), distance to forest edge (type of edge habitat [e.g., forest-agriculture or forest-urban was not considered]), and distance to high traffic roads (interstate, federal highways, state roads, and county routes with 24% median annual average daily traffic in Ohio of 14,931, 2,346, 785, and 233 vehicles, respectively; https://www.transportation.ohio.gov/programs/data-governance/gis/03-tims, accessed 1 Dec 2021). For the spatial population model simulations, we aggregated the habitat suitability values to a 10-km × 10-km grid cell using a maximum value for habitat suitability and rescaled the resulting grid to a 0–1 range. Lastly, we also reclassified all suitability values > 0.8 as 1.0 and rescaled the 0–0.8 values to a 0–1.0 scale to ensure that bobcat abundance scales were proportional with habitat suitability in our model. Although the relationship between bobcat abundance and habitat suitability is subject to uncertainty (Clare et al. 2015), bobcat habitat requirements are flexible; therefore, we assumed that all high suitability values (>0.8) are likely to support maximum bobcat abundances.

Road mortality risk

We calculated the risk posed by roads to resident and dispersing bobcats for each 10-km × 10-km grid cell (Figure S3, available in Supporting Information). Road mortality risk for bobcats in Ohio is primarily influenced by

traffic levels, with the highest mortality for busier roads (interstate, U.S., state, and county routes) and lowest for local roads (e.g., township roads; Bencin et al. 2019). Mortality risk is also a function of route type, road density, and surrounding landscape cover (Bencin et al. 2019). We calculated the road mortality risk for each 10-km × 10-km grid cell by summing up the lengths of the 4 road type categories, weighed by the annual risk of mortality for a female crossing the roads for an average of 178 times (based on estimates from global positioning system telemetry of 25 individuals in southeastern Ohio; Bencin et al. 2019) for a median level of traffic for that road type: mortality probability = 0.97, 0.48, 0.29, and 0.19 for interstates, United States highways, state roads, and county routes, respectively. The number of crossings were proportional to each road type in a given cell because bobcats have not shown strong avoidance of various road types in Ohio (Bencin et al. 2019). We selected only females for creating the road mortality map because the telemetry dataset was richer for females and it provides a conservative mortality estimate (i.e., males are at a greater risk of road mortality because of their larger home ranges and movements; Bencin et al. 2019). We then reclassified the resulting map between 0 and 1 using a 10-quantile (or decile) approach. We used this map to calculate additional roadkill to model expected future traffic increases (~half of the scenarios), as baseline roadkill is inherently accounted for in the range of survival estimates used in these simulations (the survival data from unharvested populations include road mortality as the main human-caused mortality source).

Baseline simulation model

We used a lattice framework to model spatial demographic structure (Fordham et al. 2022) and treated each 10-km × 10-km grid cell as a unique subpopulation connected to neighboring cells via dispersal. We used a post-breeding transition matrix (Caswell 2006) structured by stage and sex to simulate bobcat population dynamics within each grid cell. We modeled males and females with a 4-stage life history consisting of kittens (age 0), juveniles (age 1), young adults (age 2–4), and adults (age ≥5). We computed fecundity terms as the product of expected *per capita* offspring production and prior-year survival rates. We assumed a 1:1 sex ratio at birth. Because there is no evidence that male abundance can limit bobcat population growth, we assumed that all females were capable of reproduction even in grid cells with no resident males. We used Poisson distributions to simulate demographic stochasticity in annual births (offspring born at year $t + 1$ to females at year t) and binomial distributions to simulate stochastic variation in survival and sex ratio. We used a ceiling density-dependence process to determine the abundance of each subpopulation (Harris et al. 2012). Density dependence is related to life-history strategy, and using a density-dependence process alone can result in higher population viability and thus overestimation of population growth (Fowler 1981); therefore, we constrained the density-dependent ceiling using estimated habitat suitability to ensure that abundance in each grid cell remained at realistic levels and related to resource availability. Specifically, when the abundance in a grid cell exceeded its maximum value, the baseline transition matrix used to compute population growth in that cell was replaced with a transition matrix with survival of ages 0 and 1 = 0.4, survival of ages 2–4 and ≥5 = 0.6, and low fecundity rates, resulting in below-replacement growth ($\lambda = 0.786$). We determined maximum abundance in each cell by multiplying the relative habitat suitability of each grid cell (values ranging from 0 to 1) by a global maximum density parameter selected based on a density study of bobcats in Virginia, USA (Morin et al. 2018).

Survival and fecundity

We extracted the minimum and maximum reported values vital rates from Ohio (Rose et al. 2020) and unexploited populations only in the Midwest (Hoppe 1979, Nielsen and Woolf 2002, Koehler 2006) and elsewhere within the bobcat range (Crowe 1975, Blankenship and Swank 1979, Knick 1987, Landry 2017; Tables 1 and 2), which allowed

TABLE 1 Fecundity of female bobcats in exploited and unexploited populations in the midwestern United States used in the stage matrix for the simulations in a spatial population model of the bobcat population in Ohio, USA.

Stage	Mean (or range) of fecundity (females per female)[a]	Source
Adults (age ≥5)		
OH	1.625	Rose et al. (2020)
WV	1.425[b]	Landry (2017)
OK	1.35[b]	Rolley (1985)
IA	1.25	Koehler (2006)
Young adults (age 2–4)		
OH	1.5	Rose et al. (2020)
WV	0.93[b]	Landry (2017)
IA	1.34–1.75	Koehler (2006)
Juveniles (age 1)		
OH	0.222	Rose et al. (2020)
WV	0.25[b]	Landry (2017)
OK	1.0[b]	Rolley (1985)
Kittens (age 0)		
OH	0	Rose et al. (2020)
WV	0	Landry (2017)
OK	0	Rolley (1985)
IA	0.06	Koehler (2006)

[a]All fecundity values presented here represent the expected number of female offspring produced by an individual female at the end of the indicated stage class.

[b]Values based on mean placental scars determined in each study, adjusted for pregnancy rates; placental scars were halved to showcase expected number of female offspring produced by an individual female.

us to model harvest mortality separately from other sources of mortality (including baseline road mortality). We built 2 stage-based matrices: a low growth matrix populated with the minimum values, and a high growth matrix populated with the maximum values (Table 3). Reproduction for bobcats typically starts at 1 year, but some younger animals (<12 months old) have been documented as reproducing individuals (Koehler 2006, Rose et al. 2020; Table 1). In our simulations, females started to give birth when they were 1 year old (low growth matrix), while a very small proportion of females started to reproduce at age 0 (high growth matrix; Table 3). Survival data for adults used in our matrices is largely based on telemetry studies in unharvested populations (Table 2); for kittens and juveniles ages 0 and 1, we augmented the best available data using information from unharvested and harvested populations (Table 2). Population growth (λ) varied between 1.06 for the low growth matrix and 1.40 for the high growth matrix. We also calculated a stable stage distribution based on a 1:1 sex ratio. The stable age distribution for the high growth matrix showed that an equilibrium population is mostly composed of kittens representing 0.466 of the population, followed by juveniles and young adults (0.220 and 0.187, respectively), and adult animals making up 0.125 of the population. The low growth matrix yielded a stable stage distribution with similar fractions for juveniles, young adults, and adults (0.200, 0.208, and 0.211, respectively), and slightly lower proportion of kittens

TABLE 2 Survival rates of males and female bobcats in unexploited and exploited (at the time of the study) populations used in a stage matrix for simulations in the spatial population model of the bobcat population in Ohio, USA.

Stage	Mean survival (±SE)	Survival 95% CI	Source
Adults (age ≥5)			
IL unharvested[a]	0.89 ± 0.025	0.84–0.941	Nielsen and Woolf (2002)
IA unharvested[a]	0.82 ± 0.05	0.79–0.92	Koehler (2006)
OH unharvested[a]	0.7	very wide CIs	Ohio Department of Natural Resources
Young adults (age 2–4)			
IA unharvested	0.82 ± 0.05	0.79–0.92	Koehler (2006)
OH unharvested	0.7	wide CIs, small sample size	Ohio Department of Natural Resources
Juveniles (age 1)			
WY harvested	0.67		Crowe (1975)
TX harvested	0.29		Blankenship and Swank (1979)
MI harvested	0.34		Hoppe (1979)
ID harvested	0.45		Knick (1987)
WV harvested	0.5		Landry (2017)
OK harvested	0.45		Rolley (1985)
IA unharvested (1 and 2 years old)	0.61		Koehler (2006)
Kittens (age 0)			
ID harvested	0.45		Knick (1987)
OK harvested	0.66		Rolley (1985)
IA unharvested	0.5		Koehler (2006)

[a]Kaplan-Meier estimates based on telemetry.

(0.387) compared to the high growth matrix. The vital rates with the highest elasticity (whose proportional change has the highest effect on λ) were adult survival and kitten survival to age 1 (Figure S1). Fecundity for all ages and survival of young adults transitioning to adult had the lowest elasticity values; however, most elasticity values were between 0.1–0.2, indicating that while there are differences, vital rates for unexploited bobcat populations have a relatively similar effect on λ.

We estimated the proportion of animals in each stage class killed on roads based on roadkill bobcat carcasses collected during 2008–2014 and 2019–2020 by Ohio wildlife officers. Researchers and state biologists determined sex via necropsy and identification of reproductive organs (uterus, ovaries, testes). Matson's Laboratory (Milltown, MT, USA) aged bobcat teeth via cementum annuli, and we did not include bobcats with unknown ages in the analysis. The overall distribution of road mortalities from 303 animals was 28% kittens (age 0), 40% juveniles (age 1), 27% young adults (age 2–4), and 5% adults (age ≥5; S. Prange, Ohio Division of Wildlife, unpublished data; Heffern 2021; Table S1). Roadkill was biased towards males, which made up 62% of all roadkill across the 2 sampling periods.

TABLE 3 Bobcat high and low stage-based post-breeding matrices built using demographic parameters from unexploited populations. We used the 2 matrices as the upper and lower bounds of parameter space in spatial population trajectory simulations (2020–2060) for the bobcat population in Ohio, USA. Values on the top row of each matrix represent fecundities for each stage and values below represent survival within and between stages for each time step.

	Starting stage (age)			
Ending stage (age)	**0**	**1**	**2–4**	**≥5**
Low projection matrix				
Fecundity	0.00	0.12	1.23	1.30
1	0.55	0.00	0.00	0.00
2–4	0.00	0.55	0.53	0.00
≥5	0.00	0.00	0.27	0.80
High projection matrix				
Fecundity	0.04	0.54	1.83	2.12
1	0.66	0.00	0.00	0.00
2–4	0.00	0.67	0.61	0.00
≥5	0.00	0.00	0.31	0.94

Dispersal

To model the dispersal process, we assumed that only juvenile bobcats engaged in permanent long-distance dispersal, and that dispersal probabilities and distances varied by sex (Johnson et al. 2010, Hughes et al. 2019). We assumed that a fixed fraction of yearling males and females (Table S2, available in Supporting Information) dispersed for each year and subpopulation (grid cell), with the rest remaining in their original subpopulation. For each subpopulation, dispersing males and females were distributed across neighboring grid cells according to a negative exponential dispersal kernel such that mean sex-specific dispersal distances were equal to the values we obtained from the published literature (Table S2). We also constrained dispersal distances to be less than a maximum dispersal distance threshold, which we set at the maximum dispersal distances recorded for males and females, respectively. We used dispersal rates estimated in other midwestern recolonizing bobcat populations in Indiana and Iowa, USA (Johnson et al. 2010, Hughes et al. 2019; Table S2). The majority of dispersing individuals in these populations were 1 year old, and to a lesser extent, 2 years old, and males dispersed at a higher rate than females (65% of males dispersed vs. 26% of females in the population in IA; Hughes et al. 2019). Dispersal distances were greater for males (range = 12.9–203.2 km) compared to females (range = 6.6–53.3 km) in Iowa (Hughes et al. 2019; Table S2). Bobcat dispersers in Indiana showed a similar dispersal pattern but with a lower maximum dispersal distance (64 km; Johnson et al. 2010). For this analysis, we limited the dispersing stage to 1-year-old individuals and considered the absolute minimum and maximum dispersal distances recorded in literature.

Simulation scenarios

Bobcats have a furbearer status and are harvested across most of their range (Roberts and Crimmins 2010) and roadkill is often the greatest source of mortality for bobcats in the absence of harvest (Nielsen and Woolf 2002, Riley et al. 2003, Blankenship et al. 2006, Bencin et al. 2019); therefore, we investigated potential population trajectories using a combination of these 2 direct anthropogenic sources of mortality. We also considered the effect

of a different maximum density in each cell (20 and 30 individuals/100 km^2). We chose 20 individuals/100 km^2 based on a density study of bobcats in Virginia (Morin et al. 2018), but given densities may differ for Ohio, we also referenced the results of the global sensitivity analysis, which provided cut-offs of 28 and 31 individuals/100 km^2 (Analysis S1, available in Supporting Information). We did not consider the effect of different starting population sizes because this was not determined to be an important variable influencing the outcomes in the global sensitivity analysis (Analysis S1).

To test our first hypothesis and investigate the effects of harvest on population trajectories, we considered a baseline scenario and multiple harvest scenarios with a range of harvest intensities (αh = 0.05, 0.1, 0.15). To test our second hypothesis regarding how different forms of implementation may affect population trajectories, we considered 2 types of harvest scenarios based on the population structure of the harvested animals: all-ages, in which all age groups have an equal probability of harvest, and adults-only (ages >2), in which young adults and adults are targeted by harvest (Table 4). The simulated outcome of the latter scenario is higher mortality of adult and young-adult animals, resulting from trapper and hunter bias towards larger animals. Previous research indicates that hunters and trappers are more likely to target larger and thus older bobcats (Landry 2017, Allen et al. 2018). All proposed legally permitted traps would be non-lethal in Ohio; thus, trappers may influence the population structure of harvested animals by releasing smaller and younger bobcats (age 0 and age 1) and pursuing larger and older individuals, with more valuable pelts. Although some researchers have indicated a bias towards male bobcats (Allen et al. 2018), this was primarily with hound-hunters, which are likely to represent a small portion of overall hunters and trappers in Ohio, and data from 2014–2016 bobcat harvest (hunting and trapping) seasons in West Virginia showed no sex bias. Therefore, we included harvest mortality for both sexes. The all-ages scenario simulates a case in which hunters and trappers target all animals proportionally to the age distribution until the harvest limit is reached. To address our third hypothesis on the additive effects of future increases in road mortality with proposed harvest, we modeled additional road mortality using the road mortality risk map (Figure S3) with the harvest scenarios (Table 4).

For both harvest mortality scenarios, we simulated harvest mortality in any given life stage by applying a multiplier αh, which represents the probability that a given individual will be harvested (Table 4), to a random draw from a binomial distribution (Eq. 1). In all cases, we considered equal mortality risk for males and females. We calculated the number of individuals trapped at time i for stage z in raster grid cell j ($t_{i,z,j}$):

$$t_{i,z,j} \sim \text{binomial}(N_{z,j}, 1 - Harvest_j \times \alpha h \times \beta t), \quad (1)$$

where N_{zj} is the number of individuals in stage z in grid cell j, $Harvest_j$ is the relative harvest intensity within grid cell j based on habitat suitability under the assumption that habitat suitability is proportional to density and thus a proxy for harvest effort, αh is the maximum rate of harvest mortality (0, 0.05, 0.10, or 0.15), and βt is a vector indicating which stage classes are being targeted under the permit-based (vector of 0s for ages 0 and 1, and 2s for ages >2) or quota-based scenario (vector of 1s for each life stage and sex).

For each of the road mortality scenarios, we simulated further increases in mortality from additional roadkill using a similar procedure as for harvest, using a multiplier αr, which represents the fraction of additional bobcats expected to perish in a vehicle collision in areas of highest risk of road mortality (beyond baseline mortality rates described above). The Department of Transportation predicts continuous increases in vehicle traffic nationwide through 2045 (U.S. Department of Transportation, Bureau of Transportation Statistics 2018), thus posing higher risk to bobcats in the absence of mitigation strategies, particularly for high traffic roads (Bencin et al. 2019). Bobcats of age 0 and age 1 have considerably higher mortality (30% and 37% of 303 roadkill carcasses collected were age 0 and age 1, respectively), compared to age 2–4 (28% cumulatively across 3 ages) and age ≥5 (5%; Heffern 2021). We calculated the number of additional individuals killed on roads at time i for stage z in cell j ($r_{i,z,j}$):

$$r_{i,z,j} \sim \text{binomial}(N_{z,j}, 1 - RoadkillMap_j \times \alpha r \times \beta r), \quad (2)$$

TABLE 4 Scenarios ($n = 26$) for simulations in the spatial population model of the bobcat population in Ohio, USA, with baseline conditions based on 2020. Harvest and increases in future road mortality probabilities are simulated with a multiplier that influences the probability of each individual in that stage class (age) being killed by the respective mortality source such that a higher value in the table indicates higher risk and lower survival.

Scenario	Max. abundance/cell	Harvest probability				Cumulative road mortality probability across stages[a]
		Age 0	Age 1	Age 2–4	Age ≥5	
Baseline[b]	20	0.0	0.0	0.0	0.0	0.0
	30	0.0	0.0	0.0	0.0	0.0
Adults-only harvest	20	0.0	0.0	0.05	0.05	0.0
		0.0	0.0	0.1	0.1	0.0
		0.0	0.0	0.15	0.15	0.0
		0.0	0.0	0.05	0.05	0.1
		0.0	0.0	0.1	0.1	0.1
		0.0	0.0	0.15	0.15	0.1
	30	0.0	0.0	0.05	0.05	0.0
		0.0	0.0	0.1	0.1	0.0
		0.0	0.0	0.15	0.15	0.0
		0.0	0.0	0.05	0.05	0.1
		0.0	0.0	0.1	0.1	0.1
		0.0	0.0	0.15	0.15	0.1
All-animals harvest	20	0.05	0.05	0.05	0.05	0.0
		0.1	0.1	0.1	0.1	0.0
		0.15	0.15	0.15	0.15	0.0
		0.05	0.05	0.05	0.05	0.1
		0.1	0.1	0.1	0.1	0.1
		0.15	0.15	0.15	0.15	0.1
	30	0.05	0.05	0.05	0.05	0.0
		0.1	0.1	0.1	0.1	0.0
		0.15	0.15	0.15	0.15	0.0
		0.05	0.05	0.05	0.05	0.1
		0.1	0.1	0.1	0.1	0.1
		0.15	0.15	0.15	0.15	0.1

[a]Probability of road mortality is only considered for future increases because road mortality is inherently considered in survival estimates and was distributed across life stages proportionally to the roadkill data collected by Ohio Division of Wildlife (2008–2013, 2019–2020).

[b]The baseline scenario models population trajectories without harvest mortality or additional road mortality (representing potential future increases in vehicle strikes) but includes current levels of road mortality.

where $N_{z,j}$ is the total number of individuals in stage z in cell j, $RoadkillMap_j$ is a standardized (0–1) value of roadkill risk based on predictions of roadkill at various traffic levels (Figure S3), αr is the road mortality multiplier (0 or 0.1), and βr is a vector indicating the relative roadkill risk by age classes based on of proportions of individuals in the 303 roadkill dataset collected in Ohio (females: 1.08, 1.22, 0.67, 0.21; males: 1.35, 1.84, 1.41, 0.18 for ages 0, 1, 2–4, and ≥5).

We evaluated the outcomes of additive mortality from harvest and increases in road mortality for all stages using a range of harvest intensities (multiplier 0.0, 0.05, 0.1, 0.15) and road mortality intensities (multiplier 0.0 and 0.1) based on the thresholds from the global sensitivity analysis (Figure S9, available in Supporting Information). We do not have data on how harvest and road mortality interact in the Ohio bobcat population, and researchers on carnivores have reported that harvest and road mortality can be additive and compensatory (Moore et al. 2023). Therefore, we chose the more conservative approach (additive; Table 4) to avoid underestimating the effect of increased road mortality on the population. We ran 300 simulation replicates for each scenario. For each simulation replicate, all transition matrix parameters were sampled from within their respective plausible ranges (defined by a minimum [low growth] and a maximum [high growth] matrix; Table 3), on the basis of a single draw from a random uniform (0,1) number generator, such that a low draw (near 0) corresponded to transition rates near their lower bounds and a high draw (near 1) corresponded to transition rates near their upper bounds. In the absence of sufficient data to estimate spatiotemporal process variance in transition rates, we assumed that the parameter ranges (min. and max. values) represented parameter uncertainty and were not a result of annual or site-level variation in environmental conditions. This approach is conservative in that it represents a worst-case scenario that maximizes the resulting estimated risk of extirpation and decline and maximizes the range of uncertainty in population projections. For each year of each simulation replicate, the dispersal process preceded the matrix-multiplication step (representing baseline fecundity and mortality) and the additional direct sources of mortality (road mortality and harvest) followed the matrix-multiplication step.

We performed all simulation routines and statistical analyses using R version 4.0.3 (R Core Team 2021). We simulated all dispersal and demographic processes in R using the raster package (Hijmans 2022). Code and data for performing all simulations and analyses can be downloaded from the authors' GitHub (https://github.com/marissadyck).

RESULTS

Baseline scenario projections

In the absence of harvest mortality and additional increases in road mortality, simulations predict a bobcat population to grow exponentially until reaching an asymptote (carrying capacity) determined by the simulation parameters. A bobcat population with a starting population size of 2,000 and a density ceiling of 20 individuals/100 km^2 has a median population size of 5,620 (interquartile range [IQR] = 4,868–6,063) after 40 years (Figure 1A), whereas a population with a higher density ceiling (30 individuals/100 km^2) has a median population size of 8,735 (IQR = 7,956–9,296) after 40 years (Figure 1B). No projections from either baseline scenario predict extirpation for the bobcat population, and population trajectories for both scenarios reach an asymptote about 10 years into the simulation.

Effect of potential harvest

The difference in population projections between a density ceiling of 20 and 30 individuals/100 km^2 becomes more pronounced with the addition of harvest mortality. When accounting for low harvest intensity (αh = 0.05)

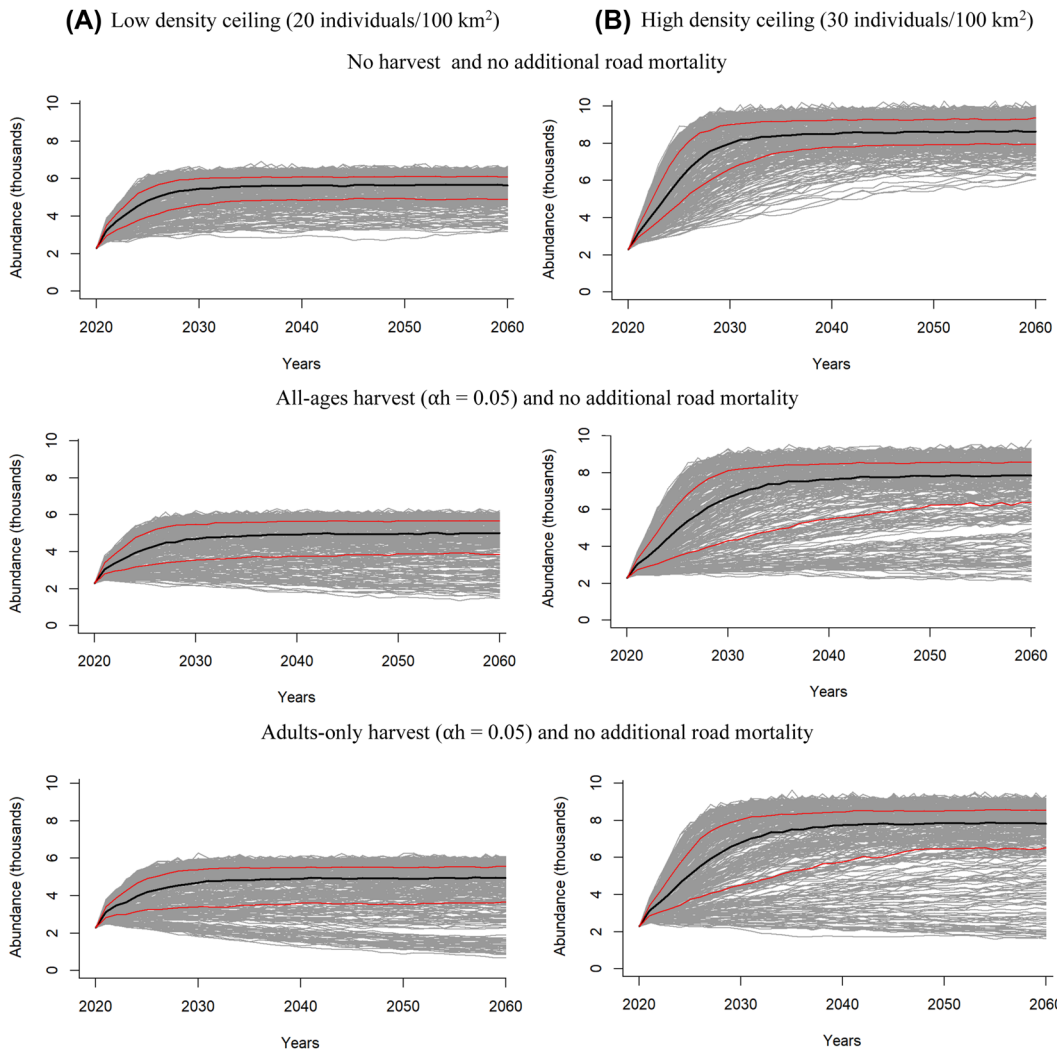

FIGURE 1 Population trajectories for the bobcat population in Ohio, USA, predicted by simulations of a spatial population model with a low (A; 20 bobcats/100 km^2) and high (B; 30 bobcats/100 km^2) density ceiling for a starting population of 12 individuals/grid cell, adjusted by habitat suitability. The top row represents trajectories for the baseline simulation with no harvest or additional road mortality, the middle row represents trajectories for the all-ages low harvest simulation ($\alpha h = 0.05$) with no additional road mortality, and the bottom row represents trajectories for the adults-only low harvest simulation ($\alpha h = 0.05$) with no additional road mortality. Black lines represent the median across 300 simulations, and the red lines are the upper (75%) and lower (25%) quartiles.

distributed evenly across all ages, a bobcat population with a density ceiling of 20 individuals/100 km^2, has a median population size of 5,008 (IQR = 3,500–5,527) after 40 years (Figure 1A). A population with a higher density ceiling (30 individuals/100 km^2) has a median population size of 7,840 (IQR = 4,466–8,298) after 40 years (Figure 1B). For both densities at low levels of harvest, the average abundance and IQR after 40 years were similar to the baseline scenarios regardless of whether harvest was for all ages or restricted to adults (Figure 1).

As harvest intensity increases ($\alpha h = 0.1, 0.15$), the median population abundance decreases, the interquartile range widens, and more trajectories predict population decline (Figure 2; Figure S4, available in Supporting

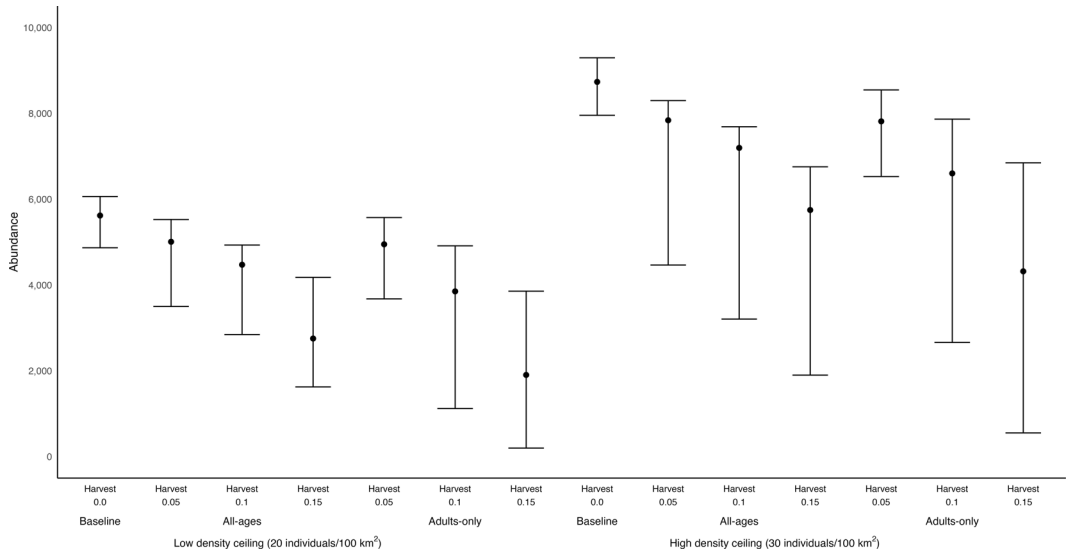

FIGURE 2 Summary of scenario results ($n = 14$) for the bobcat population in Ohio, USA, based on the spatial population model. Predicted median abundance (dot) and interquartile range (bars) for 300 iterations after 40 years (2020–2060) from selected scenarios representing various levels of harvest ($\alpha h = 0.0$–0.15), harvest implementation (e.g., all-ages or adults-only), and for low (20 individuals/100 km^2) and high (30 individuals/100 km^2) density ceilings. All scenarios depicted were modeled without additional road mortality ($\alpha r = 0.0$).

Information). For a population with a density ceiling of 20 individuals/100 km^2 and all ages targeted by harvest, the median abundance after 40 years was 4,473 (IQR = 2,845–4,932) and 2,753 (IQR = 1,625–4,178) for harvest intensity (αh) of 0.1 and 0.15, respectively (Figure 2).

Overall, for any given harvest level, population abundances for the adults-only scenarios are on average lower than the all-ages scenarios, with more projections predicting population decline (Figure S4). Concomitantly, on average fewer animals can be harvested under the adults-only scenario; median = 3.1% of the population for adults only versus median = 4.2% of the population for all ages (values derived from the low harvest [$\alpha h = 0.05$] scenario).

Effect of additional road mortality

When we simulated additional road mortality ($\alpha r = 0.1$), the median population abundance was lower than scenarios without additional road mortality (Figure S5, available in Supporting Information). This relationship becomes more pronounced as harvest intensity increases. For example, for populations with a density ceiling of 20 individuals/100 km^2 when harvest was distributed across all ages at an $\alpha h = 0.05$, the median abundance after 40 years was 4,327 (IQR = 2,708–4,988) and 5,008 (IQR = 3,500–5,527) for simulations with and without additional road mortality, respectively. When higher harvest intensity ($\alpha h = 0.15$) was simulated, the median abundance after 40 years was 1,715 (IQR = 966–3,522) and 2,753 (IQR = 1,625–4,178) for simulations with and without additional road mortality, respectively (Figure S5). Trajectories for populations at a density ceiling of 20 individuals/100 km^2 with additional road mortality have similar median abundances after 40 years as trajectories without additional road mortality (Figure S5). Trajectories at a density ceiling of 30 individuals/100 km^2 with additional road mortality have greater uncertainty (larger IQR) and lower mean abundance after 40 years, particularly at higher levels of harvest ($\alpha h = 0.1$, 0.15; Figure S5).

DISCUSSION

Although bobcat populations have been extirpated in the past, our baseline models indicate that the probability of extirpation for the bobcat population in Ohio, under current conditions, is very low. Simulations without harvest predicted the population to quadruple under a higher density ceiling (30 individuals/100 km^2) and nearly triple under a lower density ceiling (20 individuals/100 km^2) in the first 10 years of the simulation (Figure 1) with no trajectories predicting extirpation. No genetic differences between the 2 initial subpopulations of bobcats in Ohio have been identified (Heffern 2021) and there has been a consistent increase in verified sightings and spatial expansion of bobcats in Ohio (Popescu et al. 2021); thus, the results from our simulations support these observations and our initial hypotheses.

Effects of harvest and additional road mortality

We identified possible sustainable harvest levels for Ohio's bobcat population under specific circumstances, which provides support for our first hypothesis. While the addition of harvest mortality causes greater spread and low population growth for some simulation trajectories, at low levels of harvest ($\alpha h = 0.05$) distributed across all ages and with no additional road mortality, the average trajectories predict similar growth and abundance after 40 years as the baseline scenarios (Figure 1). Furthermore, under specific circumstances (high density ceiling [30 individuals/100 km^2] and all-ages harvest), greater levels of harvest ($\alpha h = 0.1$) were also sustainable (Figure S4 and S5). But when higher harvest intensity ($\alpha h = 0.1, 0.15$) was simulated for a population with a low density ceiling of (20 individuals/100 km^2) or a population with a high density ceiling (30 individuals/100 km^2) and adult-bias harvest results indicated that harvest would not be sustainable (Figure S4 and S5); the interquartile range encompasses declining populations, and some trajectories even approach zero (extirpation) under certain conditions (Figure 2 and S4). Results comparing the all-ages and adults-only scenarios provide support for our second hypothesis. When harvest targets adults only (age >2) instead of all ages, population trajectories are lower (Figure S4), and there are fewer harvest opportunities. Our results indicate that if harvest is to be allowed for Ohio's bobcat population, it should be at low levels ($\alpha h \leq 0.05$) and targeting all ages. This management recommendation is assuming increases in road mortality risk up to 10% for an individual and a density ceiling of 20–30 individuals/100 km^2.

If road mortality and harvest mortality have additive effects on this population, as simulated in our models, then the Ohio bobcat population could sustain low levels of harvest ($\alpha h = 0.05$) with a moderate increase in road mortality ($\alpha r = 0.1$). If harvest mortality is higher ($\alpha h = 0.1, 0.15$), however, then the additive effects of harvest and road mortality result in greater uncertainty in simulation trajectories, low to declining population growth, and increased risk of extinction after 40 years (Figure S5). We did not model other levels of additional road mortality because results from the global sensitivity analysis indicated that this variable had less influence on model outcomes than other variables (i.e., survival, fecundity, harvest mortality, and density per cell; Figures S6 and S7, available in Supporting Information), but we expect that further increases in road mortality rates would cause greater declines in population growth and higher risk of extinction.

Model assumptions and limitations

While the density of bobcats in Ohio is currently unknown, the maximum density is likely to be similar to that of nearby states, including Indiana (Jones et al. 2022) and Virginia (Morin et al. 2018). Furthermore, preliminary analyses using eDNA from scat and spatial capture-recapture methods suggest that the bobcat density in a high-suitability area in southeast Ohio (AEP ReCreation Lands) is approximately 20 individuals/100 km^2 (M. A. Dyck, Ohio University, unpublished data). We acknowledge, however, that the relationship between habitat suitability and

bobcat density may be subject to uncertainty. Additionally, in our simulations the relationship between habitat suitability and density is homogenous across our study area. Local differences in this relationship are possible; bobcats in Vinton Furnace State Forest had larger home-range sizes compared to other areas of southeast Ohio (Bencin et al. 2019, Prange and Rose 2020), suggesting a lower density of bobcats even though habitat suitability is similar. Therefore, we recommend that density estimates for representative areas of bobcat range in Ohio be estimated to fine-tune the model. In addition, reliable trend indices such as bowhunter surveys or roadkill surveys would continue to be useful for monitoring population trends.

Lastly, we modeled 2 possible scenarios for harvest implementation, harvest that targets adults only and harvest of all ages equally, and results indicated that harvest across all ages is more sustainable than that of adults only. For this to be accurate, it assumes that hunters and trappers will target all age classes equally; however, previous research indicates that hunters and trappers select larger and thus older bobcats (Landry 2017, Allen et al. 2018). Therefore, population dynamics in Ohio could be similar to the adults-only scenario. Furthermore, misidentification of bobcat sex is common (Hiller et al. 2014, Landry 2017); therefore, even if harvest is focused on male bobcats, we expect harvest to affect larger females as well. A quota-based implementation for harvest, whereby there is pre-defined number of animals that can be harvested in a set period, could reduce harvest bias; however, this is not a guarantee because of uncertainty in a number of factors (e.g., potential for compensatory reproduction due to harvest, additive harvest and roadkill, fluctuating distribution of age classes, environmental conditions, hunter and trapper effort). A quota-based approach can also introduce other concerns such as quota overshoot if there is delay in reporting harvest as seen from recent cases of new hunting and trapping seasons (i.e., for wolves in WI), in which the quotas were rapidly reached and surpassed because of a lag in communication between the hunter and trapper communities and the management agency, and uncertainty in wolf population and underestimation of wolf deaths in the year prior to the 2021 harvest (Gilbert et al. 2022, Treves and Louchouarn 2022). Thus, if a quota is implemented, including an expected overshoot in the initial quota as a precautionary measure would be advised.

We used habitat suitability as a proxy for harvest effort; while this implies that hunters and trappers would focus on the highest density (i.e., most trap per unit effort), harvest pressure is also dependent on ease of access (public vs. private lands, road density, and availability) and hunter and trapper willingness to travel. Ohio has a low proportion of public lands, but it has a dense road network, which facilitates access across the entire geographic distribution of bobcats in Ohio. In addition, a zone-based spatial allocation of effort is likely to be used for fine-tuning harvesting, similar to many other jurisdictions in the eastern and midwestern United States, which could integrate the trapping pressure that accounts for land access and willingness to travel. While our model can easily accommodate zones, we did not implement zones. Delineating harvest zones is an iterative process involving multiple parties and specifying them *a priori* in the model would be seen as prescriptive and potentially lead to conflict among stakeholders. Spatial allocation of harvest effort should be informed by monitoring at the same spatial scale and also highlight sensitive areas for Ohio and regional population connectivity (Popescu et al. 2021) to ensure the continuous expansion and gene exchange across the broader eastern and midwestern United States bobcat population.

MANAGEMENT IMPLICATIONS

Our results suggest that if harvest is allowed, limits should be set conservatively with continued monitoring to ensure the population is sustainable. In addition to continued monitoring, the estimates of habitat suitability and bobcat density should be updated periodically, as this is a recovering population that is expected to expand. In addition, if a harvest season is implemented, collecting carcasses of harvested bobcats to obtain accurate age, sex, and reproductive (e.g., from placental scars) information would be important for managers to assess any hunter or trapper bias in harvest and its potential effect on the population. While we used simulations to assess the effect of

proposed harvest and future increases in road mortality, this model is flexible and could be used to assess other relevant management and environmental scenarios (e.g., changes in land use, variable harvest effort by region, effects of climate change). This spatial population simulation model is useful for managers making decisions about Ohio's bobcat population and can also easily be adapted for other mammalian species with large spatial requirements given data on vital rates and habitat suitability is available.

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CONFLICT OF INTEREST STATEMENT

All authors contributed critically to the drafts and gave final approval for publication. Authors have no conflict of interest to declare.

ETHICS STATEMENT

Our study adhered to relevant regulations and guidelines regarding the ethics of animal welfare (Institutional Animal Care and Use Committee protocol: 17-O-001; Ohio Division of Wildlife Scientific Collection Permit: 20-003).

DATA AVAILABILITY STATEMENT

Data and code will be made available on Github (https://github.com/marissadyck) with a reference to a publicly accessible repository such as DRYAD (https://datadryad.org/stash).

ORCID

Marissa A. Dyck http://orcid.org/0000-0002-6371-0646
Catherine C. Dennison http://orcid.org/0000-0002-6966-7837

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