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Cost-Benefit Analysis of Mountain Lion Management for the Recovery of Endangered Sierra Nevada Bighorn Sheep

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ABSTRACT: We evaluated the consequences of different predator management strategies and the subsequent effects on time and cost to recovery for federally endangered Sierra Nevada bighorn sheep. Based on data collected during 1995-2009, we used stage based demographic modeling to estimate vital rates in three isolated herds, accounting for sampling error and variance. Using those vital rates we predicted the time and associated cost for the population to meet delisting goals. We found recovery time increased from 17.3 to 28.6 years using a density independent model and from 25.9 to 38.6 years using a density dependent model for different mountain lion management strategies. Commensurate cost increases of over 10 million dollars (unadjusted cost) result in either case. Our study suggests that appropriate levels of predator management will result in shorter recovery times and reduced cost of recovery through ensuring the availability of translocation stock. To be most effective, mountain lion management strategies should be population-specific because of underlying differences in predation rates for different herds.

KEY WORDS: cost benefit, cougar, endangered species, mountain lion management, *Ovis canadensis sierrae*, predator management, recovery, Sierra Nevada bighorn sheep, translocations, ungulate

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INTRODUCTION

Endangered species recovery efforts involve the use of scarce resources that are allocated to maximize success (Shogren et al. 1999). Management actions such as predation-control programs may be used to protect those scarce resources. Predator control, when necessary, may be controversial and require more justification than other management actions (Rominger et al. 2004, McKinney et al. 2006, Boertje et al. 2010). Predator management [e.g., of wolves (*Canis lupus*) and bears (*Ursus americanus*)] has been used to successfully increase prey populations in multiple studies with moose in Alaska (Boertje et al. 2010). In New Mexico, predator management [mountain lions (*Felis concolor*)] in four populations during an eight-year study period resulted in a 13% decrease in mortality rates during the period of maximum protection (Rominger and Goldstein 2009). In protecting the island fox (*Urocyon littoralis*), golden eagles (*Aquila chrysaetos*), also under federal protection, were removed in order to promote successful fox recovery (Courchamp et al. 2003). One method of evaluating the best use of limited resources is to compare the cost of various predator management strategies in terms of both time and money.

We evaluate predator control effects on an endangered species using Sierra Nevada bighorn sheep (SNBS, *Ovis canadensis sierrae*). By the 1970s, SNBS herds were reduced to only three extant herds (US Fish and Wildlife Service 2007). During the early 1980s, in an effort to restore SNBS to more of their historic distribution, 116 animals were captured and translocated to create four additional herds (Bleich et al. 1990). While the translocations successfully expanded the distribution of SNBS, the number of individuals shrank to an all-time low of fewer than 125 animals by 1999. SNBS were federally listed as an endangered subspecies in 2000 (US Fish and Wildlife Service 2007). At the time of listing eight herds ranged in size from 12 to 45 individuals (Stephenson et al. 2012) Predation by mountain lions, played a role in the decline during the period between the successful

translocations and the subsequent decline in population (Wehausen 1996, US Fish and Wildlife Service 2007). The Sierra Nevada Bighorn Sheep Recovery Plan, finalized in 2007, identified both translocation and lion management, as important tools available to ensure the recovery of SNBS and includes specific numerical and distributional goals (US Fish and Wildlife Service 2007).

The SNBS Recovery Plan (2007) identified 12 required herds that are essential for recovery and must be maintained for a period of seven years without management. A total of 305 females of at least one year of age are required, suggesting an average of ~25 ewes per population. In 2010, eight herds were occupied, and a minimum of four additional herds needed to be established. Our analysis was based on achieving these numerical and geographic delisting criteria. Translocation enables the creation of new herds and augments existing herds. Predation control provides relief to small SNBS herds to allow sufficient time for the population to grow large enough to support the normal level of predator-prey dynamics found in a healthy ecosystem, but also provides managers with the ability to “harvest” animals from healthy herds for translocation stock.

Predation by mountain lions can be a significant source of mortality in bighorn herds (Wehausen 1996, Hayes et al. 2000, Kamler et al. 2002, Rominger et al. 2004, Rominger and Goldstein 2009). Predation losses may be a synergistic combination of direct and indirect effects, leading to amplified impacts. If reduced population sizes result in a lack of source stock for translocations, predation effects may further delay achieving recovery goals. Stochastic predation events may result in extirpation of small populations (Festa-Bianchet et al. 2006). Onset of predation is often unrelated to sheep density (Jorgenson et al. 1997, Ross et al. 1997, Portier et al. 2006, Rominger and Goldstein 2009) particularly when predators are subsidized by more abundant prey such as mule deer. Thus, the Recovery Plan recommends that all bighorn herds, regardless of size, must be considered for mountain

lion control with the caveat that larger herds, defined as more than 25 females, could be considered large enough to forgo mountain lion control if they were not going to be used for translocation stock. During the period from 2000-2009, since all larger herds were considered translocation stock sources, mountain lion control was implemented across all herds. The mountain lion control strategy consisted of evaluating for removal any cougar with a known bighorn kill. Some mountain lions were removed with a single kill, while others killed a minimum of five bighorn before being killed (US Fish and Wildlife Service 1999). During this period, the same eight herds increased in size to 15-100 individuals (US Fish and Wildlife Service 2007, Stephenson et al. 2012).

Economic analysis adds another dimension to the question of how to measure and evaluate the effects of predation on threatened or endangered populations (Engeman et al. 2002). We often think about endangered species more from the population dynamics perspective (Morris et al. 2002, US Fish and Wildlife Service 2007) than monetary depending on the species (Rubin et al. 1991). Species where conservation is in direct conflict with human economic activities, either through loss of production or damage, are commonly evaluated economically (Montgomery et al. 1994, Engeman et al. 2004). We suggest that the opportunity cost, or allocation of resources to one species rather than another, should be considered in order to maximize the use of conservation dollars (Shogren et al. 2001). In terms of endangered species, both cost and time to recovery must be considered in this context since every added year to recovery adds cost (Shwiff et al. 2005, Langpap et al. 2018). By looking at the changes to both cost of and time to recovery for an endangered species, we propose to give managers another metric to promote effective management.

We used a Population Viability Analysis (PVA) to model the effect of reduced adult survival caused by mountain lion predation. We hypothesized that the model results could be an effective management tool when used as inputs to predict cost and time to recovery. We used post-baseline data to validate the model predictions.

METHODS

Study Area

The Sierra Nevada mountain range forms an eastern boundary for much of California and is approximately 650 km long and ranges from 75 to 125 km wide (Hill 1975). Along the eastern side of the range, topography is largely a result of Pliocene uplifting and Pleistocene glaciers that created U-shaped canyons, steep cirque headwalls, and prominent peaks (Hill 1975). Historical and current distributions of SNBS include only the southern half of the Sierra Nevada (Figure 1), where these geologic processes have created the highest peaks and the most alpine habitat. SNBS spend summers in the alpine along the crest of the Sierra Nevada and winters either in the alpine or at lower elevations typically east of the crest, inhabiting elevations from 1,525 to >4,000m (US Fish and Wildlife Service 2007). Climate in the Sierra Nevada is characterized by relatively dry conditions in summer (May-Sept), with most of the annual precipitation received as snow in winter (Nov-Apr) from northern Pacific storms. There is a typical

strong elevational gradient in temperature as well as a strong rain shadow effect in precipitation east of the Sierra crest. Winter precipitation also declines from north to south and varies considerably depending on year (Major 1977, Wehausen 1992). Low elevations (1,500-2,500 m) are characterized by Great Basin sagebrush-bitterbrush scrub; mid-elevations (2,500-3,300 m) by pinyon-juniper woodland, sub-alpine meadows, and forests; and high elevations (>3,300 m) by sparse alpine vegetation including occasional meadows. Virtually all SNBS habitat is public land, managed primarily by Yosemite and Sequoia-Kings Canyon National Parks, and Inyo and Sierra National Forests. Predators of bighorn sheep in the Sierra Nevada include mountain lions, coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and golden eagles. Mule deer (*Odocoileus hemionus*) are the primary prey of mountain lions and lion distribution is generally associated with mule deer winter ranges.

We assumed that increased mountain lion control could increase adult bighorn survival by decreasing predation events. We acknowledge that yearling and lamb survival might increase as well, but we have limited data on those age classes. Using a stage based demographic model, we defined three different regimes of predator management: the baseline regime (current method, adult survival unchanged), a 1-strike predator control strategy (each detected mountain lion predation results in removal of mountain lion, adult survival increased at Mt. Baxter), and with a preemptive predator control strategy (all detected mountain lion predation results in lion removal and high risk mountain lions removed preemptively, adult survival increases at Mt. Baxter and Wheeler Ridge). Using our model, we quantified the effects of varying levels of predator control on recovery of SNBS in terms of time and cost.

Our models are based on keeping the managed herds at relatively low population sizes to mitigate any potential density dependent effects. While a strong relationship with density dependence has not been detected (Johnson et al. 2010), it may still play a role in these herds. To test how large a role density dependence may play at these low population sizes, we used both a density dependent and exponential growth model for comparison.

Model Parameter Estimation

Parameter estimates for population models were based on data collected 1999-2009 for the Langley and Wheeler herds and 2003-2009 for the Baxter population. From 1999-2002, data from Mt. Baxter is not available. Because bighorn sheep are polygynous (Geist 1971), we restricted the model and its parameters to females (Morris and Doak 2002). Models were parameterized from annual field survey data. Surveys of the Wheeler and Baxter herds were conducted in late March or early April just before lambs were born (pre-birth pulse) and surveys in Langley were conducted in summer, just after lambs were born (post-birth pulse; Johnson et al. 2010, Cahn et al. 2011). The timing of surveys resulted in distinct differences in the data that translate to different parameterizations of population projection matrices, with a pre-birth pulse

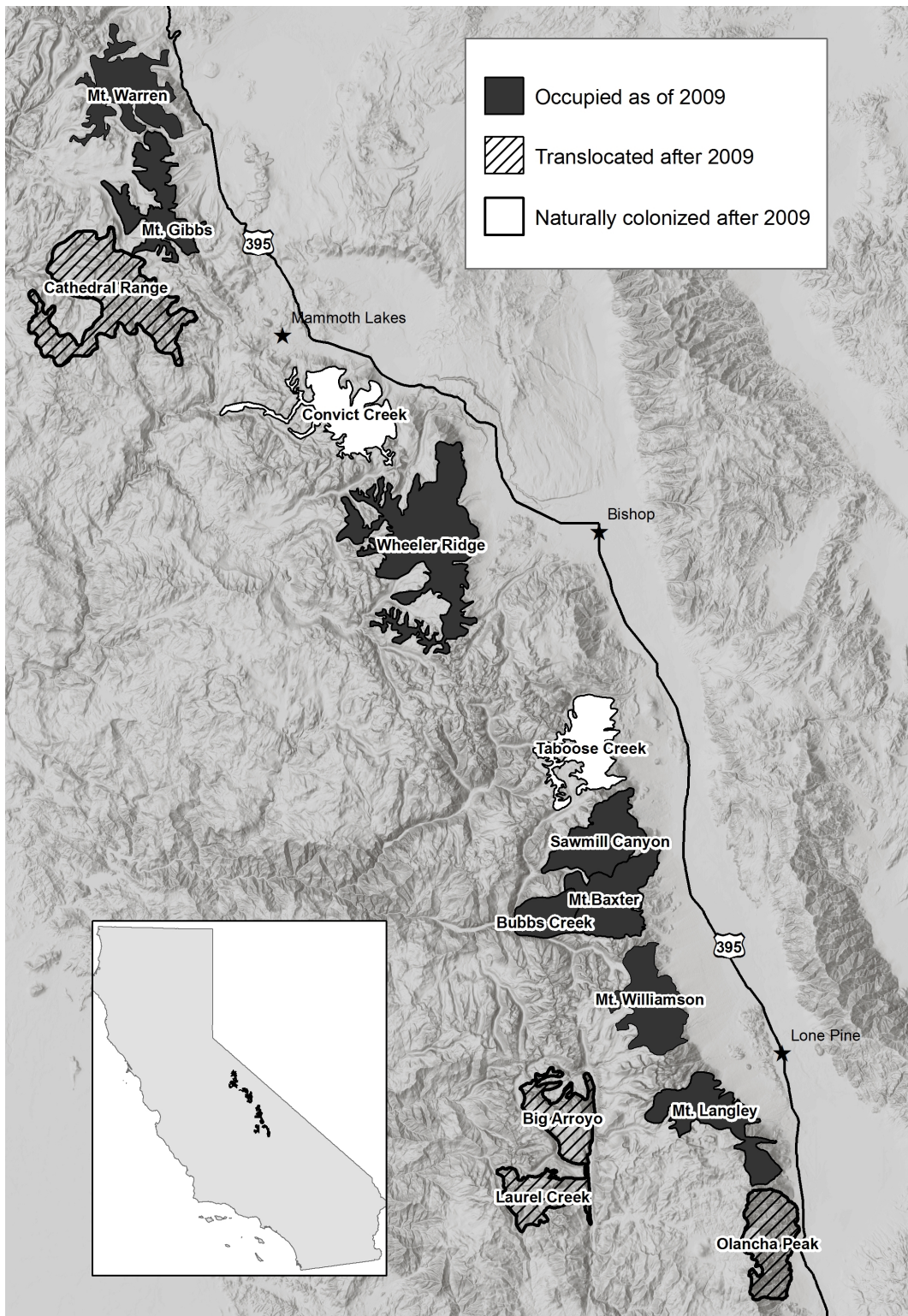


Figure 1. Distribution of occupied Sierra Nevada bighorn sheep (SNBS, *Ovis canadensis sierrae*) herds in the Sierra Nevada Mountain of California under varying mountain lion control strategies. Pre-2009 represents a post listing 1-strike or more control regimen. Post-2009 represents implementation of a pre-emptive strike control regimen.

model used for Wheeler and Baxter and a post-birth pulse model used for Langley (Figure 2).

For Langley and Wheeler, count data of females from successive years was used to estimate fecundity or

recruitment (F_x post-birth pulse or R_x pre-birth pulse) and survival (S_x) values for each life stage on an annual basis (Table 1). For Baxter, we estimated vital rates for a pre-birth pulse model with a mix of telemetry and survey ratio

Pre-Birth Pulse Matrix Model (Wheeler and Baxter) $\begin{bmatrix} 0 & 0 & R_A \\ S_T & 0 & 0 \\ 0 & S_A & S_A \end{bmatrix}$	Post-Birth Pulse Matrix Model (Langley) $\begin{bmatrix} 0 & 0 & F_A * S_A \\ S_Y & 0 & 0 \\ 0 & S_A & S_A \end{bmatrix}$
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Figure 2. Pre- and post-birth pulse matrix models used to simulate female SNBS population dynamics. Vital rates in the pre-birth pulse model are recruitment (RA), 2-year-old female survival (ST), and adult female survival (SA). Vital rates in the post-birth pulse model are fecundity (FA), yearling female survival (SY), and adult female survival (SA).

data because sufficient count data was not available. We used the Kaplan-Meier known-fate estimator to calculate annual adult female survival from radio-collared females from 2007-2009 (Pollock et al. 1989); from these values we calculated average adult female survival (variance discussed below). We estimated annual recruitment the same as for Wheeler based on surveys conducted from 2005-2009. Following Cahn (2011), we assumed that the yearling fecundity was half that of adult females (Figure 2). See Johnson (2010) for a detailed explanation of age classes for post- and pre-birth pulse surveys and calculation of vital rates.

Because we were only interested in the influence of process variance in vital rate parameters on SNBS population performance (White 2000, Mills and Lindberg 2002), we removed sampling (and confounded demographic) variance from our binary vital rate data using the program Kendall.m in MATLAB (Morris and Doak 2002) for count data and Program MARK (White et al. 2001) for radio telemetry data. We report the resulting empirical Bayes estimators (Table 1) (Anderson et al. 1987, Johnson et al. 1989, White et al. 2001) and their process variances. We also estimated correlations (positive and negative) among rates for each population using empirical Bayes estimates (Morris and Doak 2002). Because the Mt. Baxter dataset is smaller than that for Wheeler Ridge (Table 1) and they are similar in seasonal use of habitat, proximity to predators and availability of a large productive winter range, we used the variance estimates and correlations from Wheeler Ridge as surrogates for Mt. Baxter.

Population Model

For the underlying population model, we constructed a stochastic, discrete time, stage-structured matrix model. Reproduction in our study herds occurs once per year in a short birthing season and adults are capable of reproduction in sequential years; therefore, we used a 1-year (May 1-April 30) interval to model population growth. Our model was based on four approximate stages; approximate because animals could be 1-3 months older than stated age for post-birth models and 1-3 months younger for the pre-birth pulse model. For post-birth pulse herds, the stages were newborns (N; 0-1 yr-old), yearlings (Y; 1-2 yr-old), adults (A; 2-16 yr-old), and “senescent”

adults (O; >16 yr-old). For pre-birth pulse herds, the stages were yearlings Y; 1-2 yr-old), 2-yr-olds (T; 2-3 yr-old), adults (A; 3-16 yr-old), and “senescent” adults (O; >16 yr-old). We assumed the survival of animals in the senescent stage class was zero (Byers 1997). We recognize that differences in survival and reproduction may occur among female adult age classes (McCarty and Miller 1998, Berube et al. 1999, Rubin et al. 2002, Festa-Bianchet and King 2007). However, all SNBS field data is collected using the three ages classes (adult, yearling, and lamb) already in the model, so no further resolution in the model is possible (U. S. Fish and Wildlife Service 2007).

Because projected female bighorn population size in the Wheeler and Langley herds grew to unrealistic levels (e.g., >680 females for Langley by year 20) under an exponential growth model, and because recent vital rate data suggest some density dependency as the herds approach 50 females (Johnson et al. 2010), we ran all scenarios (defined below) with and without density dependence. We incorporated density dependence only in the survival of the youngest class (0-1 year or 1-2 year

Table 1. Population-specific vital rate estimates, variances, and years of data included in estimates. Process variance is given for Wheeler and Langley, and total variance for Baxter.

Subpopulation	n	Mean	Variance
Wheeler			
recruitment	10	0.2994	0.0005
2-yr-old survival	10	0.7295	0.0138
adult survival	10	0.9197	0.0083
Langley			
fecundity	10	0.3311	0.0068
yearling survival	9	0.8722	0.0115
adult survival	9	0.9772	0.0001
Baxter			
recruitment	6	0.3185	0.0610
2-yr-old survival	4	0.4566	0.2204
adult survival	3	0.8411	0.0341

Table 2. Sierra Nevada bighorn sheep annual program costs from 2002-2009.

Fiscal Year	Cost (US Dollars*)
02-03	\$840,921.58
03-04	\$809,149.63
04-05	\$799,619.84
05-06	\$775,963.92
06-07	\$789,945.21
07-08	\$734,338.76
08-09	\$713,328.00

*constant 2009 dollars

because bighorn demographic studies have not found density dependence in vital rates of adults (Leslie and Douglas 1979, Wehausen et al. 1987, Mccarty and Miller 1998, Festa-Bianchet 2007). Our translocation strategy is to harvest surplus animals as herds exceed 40 females so that adult survival remains unaffected by any density dependent effects.

For all herds, following Cahn (2011) we used a carrying capacity of 100 adult females and used a discrete (Ricker) logistic model (Caswell 2001, Morris and Doak 2002).

To incorporate environmental variation, the population vector for each year was multiplied by a randomly drawn matrix of vital rate values. We used parametric bootstrapping to select a random value for each vital rate from beta distributions having means, process variances, and a correlation structure specific to each population (Morris and Doak 2002). Because SNBS herds were small, we also included demographic stochasticity in simulations, following Mills and Smouse (1994), for survival and reproduction. For each model scenario, we ran 1,000 iterations. See Johnson (2010) and Cahn (2011) for additional detail about the population model.

We used 30 adult females to initialize our model so that each population had a common basis for comparison. Based on the last field survey for 2009, we estimated the number of yearling females and lambs for the initial population vector by multiplying the observed yearling female:adult female and lamb female:adult female ratios by the 30 adult females. The initial population vector of female yearlings and lambs was six and nine for Wheeler; eight and nine for Langley; and six and eight for Baxter.

Translocation Assumptions

Based on the delisting criteria, each unoccupied population requires an average number of animals of ~25 animals. Using the average number of animals as the minimum, we determined the number of animals needed for translocation source stock. We also included one additional (not required) population and a nominal number of additional animals (25 females) in case one or more herds needed an augmentation to add some conservatism to the projections. This means five new herds are needed.

To have a high probability of producing a viable new population via translocation, we assume that a minimum of 30 females should be translocated (Rubin et al. 2002).

To ensure successful recovery, we modeled 40 females to be translocated into each newly established population (Stevens and Goodson 1993, Singer et al. 2001).

40 females * 5 herds (needing to be established) = 200 animals

Additional 25 for augmentations (as required)

Total Adult Females Needed for Translocation (N_{Total}) = 225
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All currently occupied herds, for the purposes of this analysis, are assumed to grow naturally to reach delisting criteria without supplemental translocations. Unoccupied herds, once established with enough bighorn sheep to meeting delisting criteria, were assumed to continue to persist at or above the required numerical goals. Herds intended to be used as translocation sources were modeled to always remain at or above the average female population size based on the delisting criteria numbers.

Calculations for Time-to-Recovery

The number of females needed for translocation was set equal to the sum of the number of adult females (N_a) produced by each source population.

$$N_{total} = \sum N_a = N_{Langley} + N_{Wheeler} + N_{Baxter}$$

We calculated the number of years (y_a) it took for each source population to reach a population size of 50 adult females (AF) based on a strategy of removing 20 AF for translocation from the total. In the model, these animals were removed at one time once the population reached 50 individuals. In practice, the number removed could be more variable depending on logistic and financial considerations. We then calculated the total number of years ($y_{recovery}$) it would take to reach recovery goals by having 225 AF available for translocations and $y_{recovery} = \text{total years until } N_{Total} = 225$ (needed to meet the recovery goal)

$$N_a = y_{recovery} * AF / y_a$$

combining the two equations and rearranging yields:

$$y_{recovery} = N_{total} / AF * [1 / (1 / y_{Langley} + 1 / y_{Wheeler} + 1 / y_{Baxter})]$$

This calculation is based on an assumed stable population created by growing the population from 30 to 50 ewes and then harvesting them, thus repeating the growth cycle at the higher growth rates predicted by a density dependent model.

Varying Growth Rate Scenarios Analyzed

Using this modeling approach three potential scenarios were evaluated for the time each would take to reach SNBS recovery goals for delisting (US Fish and Wildlife Service 2007). We first ran a baseline model, in which the Langley, Baxter, and Wheeler herds were assigned their

Table 3. Estimated number of years for 3 source herds of female bighorn sheep to produce 20 bighorn sheep females for translocation (y_a), and associated population growth rate (λ), for different levels of predator control. Estimates based on data collected 1995-2009 in Sierra Nevada Mountains, California.

Model Structure	Predator control scenario	Herd units	y_a	λ
Density independent	Baseline	Langley	4	
		Wheeler	7	1.133
		Baxter	Never	1.059
	1 Strike	Langley	4	0.864
		Wheeler	7	1.133
		Baxter	8	1.059
	Preemptive	Langley	4	1.042
		Wheeler	5	1.133
		Baxter	5	1.114
Density dependent	Baseline	Langley	6	1.094
		Wheeler	8	1.058
		Baxter	Never	1.041
	1 Strike	Langley	6	0.864
		Wheeler	8	1.058
		Baxter	8	1.041
	Preemptive	Langley	6	1.025
		Wheeler	7	1.058
		Baxter	8	1.048
			1.038	

^a Density dependence was modeled using a discrete logistic model in which recruitment or fecundity was reduced (Morris and Doak 2002) to meet a carrying capacity of 100 females.

current demographic rates (Table 1) with the idea that mountain lion control would continue as it had for the past decade. In the second case, the 1-strike scenario, we increased adult survival in our model for Baxter (from 0.84 to 0.92) to be equal to those of Wheeler (considered “moderate” rates). This reflects increased population performance that we assume could be achieved by implementing a 1-strike predator control policy, i.e., if a mountain lion kills any SNBS, it will be depredated. In the third case, the preemptive scenario, we increased the adult survival for Baxter and Wheeler to be the same as vital rates at Langley (adult survival 0.98). We assume that Langley vital rates are at roughly maximum values, those that would be expected if cougar predation were largely eliminated. During the period of 1999-2000, only two females were killed by mountain lions in the Mt. Langley population. For all these scenarios, we assumed that once herds grew to 50 adult females, 20 would be removed for translocations and augmentations as outlined in the SNBS Recovery Plan (US Fish and Wildlife Service 2007). In the model, the removal of 20 animals in a particular year were triggered by the population meeting or exceeding 50

animals, this may or may not match the logistical and financial considerations of actual management practices. Using model results, we calculated the number of years it would take to reach recovery goals for each scenario. Calculated times-to-recovery are based on the model population growth rates for both density dependent and non-density dependent assumptions. Given current operating costs of the SNBS Recovery Program, we also calculated the financial implications of enacting each scenario.

Cost Analysis

Benefits of predator management typically are calculated as the number of individual animals spared from predation (Engeman et al. 2002, 2003). Determination of monetary values for individual animals of a specific species is not a straight-forward process (Shwiff et al. 2003). Since predation is in direct competition with producing harvestable animals for translocation, the number of animals saved from predation helps to determine the length of time the program is needed for recovery. We used both the total cost of

achieving recovery and the annual fiscal budget of the program (2000-2009) to estimate additional SNBS program costs incurred with a lack of adequate predator control (Shwiff et al. 2005). Using these two values, we determined the total cost added to the program by delaying recovery.

The cost per additional year of the program is estimated to be \$780,467 per annum (PMT). This is based on the average value of the program cost over the past seven years in constant 2009 dollars (Table 2). The unadjusted cost of recovery was calculated by multiplying the average annual program cost (in 2009 dollars) by the number of years the model predicts as time-to-recovery.

$$\text{Unadjusted Cost} = (\text{PMT})n$$

To evaluate the added cost in terms of constant current dollars, the total cost of the program was calculated as a net present value (NPV) of the unadjusted cost using an ordinary annuity equation with annual compounding. Calculating NPV is based on four variables: annual cost of the program (PMT), discount rate or interest rate per year (i), and time-to-recovery in years (n) (Block 2005).

$$\text{Net Present Value (NPV)} = \text{PMT}[(1 - 1/(1 + i)^n) / i]$$

The discount rate (i) was selected based on a risk-free rate of return. The risk free rate of return is the theoretic interest rate that can be earned on investments without any risk, and thus provides a conservative value for the time value of money in calculating the NPV. For modeling purposes, we used the average yield of US Treasury notes as the risk-free rate of return (Block and Hirt 2005). To get the average yield of US treasuries, we used a 10-year average of US 10-year Treasury note rates for the period of 1998-2008 (Federal Reserve Board 2009). Our model assumed there is no cost change for increased or aggressive predator control over baseline costs because USDA Wildlife Services was under contract to provide such services.

For each scenario, we demonstrated the time required to produce enough females for a single translocation incident (20 females) for each population to compare the relative productivity of each of the herds (Table 3). For each scenario, we also show how long it takes to meet the delisting criteria; the final outputs translate additional years-to-recovery into relative cost-to-recovery (Table 4).

Other management actions identified in the recovery plan, notably, disease prevention and prescribed fire may also have significant effects on the time-to-recovery for SNBS. No attempt was made to include those factors in this analysis. If other herds attain sufficient size, they would also be considered for translocation stock, but are not included in the current analysis.

Model Validation

We evaluated how the model predictions and the underlying assumptions were borne out on the landscape using the field data collected during 2010-2017, when several alternative predation strategies were implemented.

We deployed VHF and GPS collars to monitor bighorn survival and conducted annual ground count to assess population size and demographic rates. Because adult survival was the model input used to predict changes in herd level demographic rates, we used Kaplan-Meier adult survival estimates (White and Garrott 1990) to compare with model inputs. We evaluate the number of animals translocated to augment and create new herds to model predictions over the same period. We note that colonization/emigration, while not predicted in the model, is natural equivalent of additional translocations stock. If the underlying population viability model validates well, the economic predictions based on model outputs are also valid.

RESULTS

Each scenario exhibited a similar trend; increased predator control leads to shorter recovery times and lower costs. The time to recovery varies from 17.3 to 28.6 years in the density independent model and from 25.9 to 38.6 years in the density dependent model. Cost increases of over 10 million dollars (unadjusted cost) result in both cases.

Without Density Dependence

For the baseline scenario (current level of predator control), the predicted number of years to produce 20 females for translocation is: four for Langley, seven for Wheeler, and zero for Baxter as the population declines based on the model's demographic rates (Table 3). Under the 1-strike scenario, Baxter improves to eight years, but Langley and Wheeler remain the same. Under the preemptive scenario, Langley remains at four years; Baxter is predicted to produce 20 females in five years; and Wheeler in five years. Without density dependence and by using preemptive predator control the time-to-recovery can be decreased by about 40%. Our model predicts 28.6 years' time-to-recovery for the baseline scenario, 21.7 years' time-to-recovery for the 1-strike scenario, and 17.37 years' time-to-recovery for the preemptive scenarios (Table 4).

Without including density dependence, the cost reduction with 1-strike predator control on the basis of NPV using constant 2009 dollars is 25% (unadjusted costs are shown parenthetically). Our model predicts a cost of recovery of 12 (22.3) million dollars for the baseline scenario, 10.4 (17) million dollars for the 1-strike scenario, and 9.1 (13.5) million dollars for preemptive predator control (Table 5).

With Density Dependence

Density dependence reduces the population growth rate because of intra-specific competition for resources. This will slow the pace of translocation efforts and extend the number of years to recovery. For the baseline growth rate scenario (current level of predator control), the predicted number of years to produce 20 females for translocation is: Langley = five years, Wheeler = 10 years; Baxter (declining population) = zero. Under the 1-strike scenario, Baxter improves to: Baxter = 10 years, but Langley and Wheeler remain the same. Under the preemptive scenario, Baxter and Wheeler improve to:

Table 4. Calculated time-to-recovery based on different predator control scenarios.

Scenario	Predator Management Level	Without Density Dependence (n)	With Density Dependence (n)
<u>Baseline:</u>			
Mt. Langley	Current		
Wheeler	Current	28.6 years	38.6 years
Mt. Baxter	Current		
<u>1-Strike:</u>			
Mt. Langley	Current		
Wheeler	Current	21.7 years	27 years
Mt. Baxter	Increased		
<u>Preemptive:</u>			
Mt. Langley	Current		
Wheeler	Aggressive	17.3 years	25.9 years
Mt. Baxter	Aggressive		

Baxter = five years and Wheeler = five years, but Langley remains the same at five years.

With density dependence and by using preemptive predator control the time-to-recovery can be decreased by about 33%. Our model predicts 38.6 years' time-to-recovery for the baseline scenario, 27 years' time-to-recovery for the 1-strike scenario, and 25.9 years' time-to-recovery for the preemptive scenario (Table 5).

Including density dependence, the cost difference based on NPV using constant 2009 dollars is 16% (unadjusted costs are shown parenthetically). Our model predicts a cost of recovery of 13.6 (30.1) million dollars for the baseline scenario, 11.7 (21) million dollars for the 1-strike scenario, and 11.5 (20.2) million dollars preemptive scenario (Table 5).

We used SNBS demography and mountain lion predation data from 2009-2017 for comparison to validate model predictions. During the winter 2009-10 and up through winter 2010-2011, a more aggressive mountain lion predation strategy was implemented, equivalent to the preemptive strategy modelled here. A total of 15 mountain lions were depredated in the 2009-2011 time period as compared to nine mountain lions depredated from 1999-2008. Subsequently, beginning in May 2011 through the winter of 2016-2017, a strategy of no mountain lion control was implemented. No mountain lions were depredated, but SNBS were monitored to detect mountain lion predation. In spring, 2017 a policy of 1-strike was implemented resulting in two mountain lions being depredated. Bighorn population monitoring during 2010-2015 illustrates that low predation rates were observed with an average loss of about one adult female per year for all translocation source herds combined. Adult survival during 2010-2015 remained in excess of 90% in the Mt. Baxter, Wheeler Ridge, and Mt. Langley herds (Runcie et al. 2015), which compares well with the 92% model input for the 1-strike scenario, but is somewhat lower than the 98% rate for the pre-emptive strike scenario. Since

mountain lion control during the period was a mixture of pre-emptive control and no mountain lion control, matching the lower rate seems reasonable. During that same time, 52 ewes were moved creating four new SNBS herds while the translocation herds remained relatively constant in size. We accomplished a significant expansion of bighorn distribution (Figure 2). Two additional herds, Convict Creek and Taboose Creek, were naturally colonized during this period. While these are not translocations, these account for an additional minimum count of 17 ewes (Runcie et al. 2015). In 2016, five adult females were killed by mountain lions in three different herds. In 2017, 18 female SNBS were killed by mountain lions. Of those, 13 were in the Mt. Langley herd. Based on our subsequent summer count data, 47% (27/51) of the total females died that winter, suggesting that we did not detect 13 mortalities.

DISCUSSION

Using the demographic data collected during 1999-2009 when mountain lion control occurred, this analysis is primarily concerned with evaluating the effects of predator management on specific herds of SNBS identified as sources of translocation stock. During this period mountain lion control was the only significant management action implemented that was expected to have demographic effects on the SNBS herds. Three herds were identified as potential source herds for translocation animals based on population sizes: Mt. Langley, Wheeler Ridge, and Mt. Baxter. For females, each of those three herds exhibited different survival rates (adult females = 0.98, 0.92, 0.84) and different levels of predation (max % population known to be killed by mountain lions 3%, 5%, 17%) (Johnson et al. 2010, Stephenson et al. 2012).

Our SNBS cause-specific mortality data for all collared animals, both male and female, showed that mountain lion predation is a major source of mortality. Johnson et al. (2013) demonstrated a link in predation rates and

Table 5. Projected Net Present Value (NPV) costs based on varying levels of predator control.

Scenario	Without Density Dependence			With Density Dependence		
	Unadjusted Cost	NPV cost	Percent of Minimum Cost	Unadjusted Cost	NPV cost	Percent of Baseline Cost
Baseline	\$22,349,728	\$12,040,029	100%	\$30,103,716	\$13,631,507	100%
1-Strike	\$16,954,966	\$10,406,745	86%	\$21,072,601	\$11,699,580	86%
Preemptive	\$13,508,078	\$9,050,723	75%	\$20,206,604	\$11,453,475	84%

demographic rates particularly in the Mt. Baxter and Wheeler Ridge herds. Habitat does not appear to be a limiting factor in these herds. Resource selection modeling indicated that abundant habitat exists for SNBS in each herds (Johnson et al. 2005). Density dependence does not appear to be a strong effect during this period (Johnson et al. 2011). Although the absolute number of mortalities from predation in any SNBS population is not large, the number of adult females is small, ranging from as few as 11 to as many as 37 during the years 1999-2009 (Stephenson et al. 2012). SNBS are especially susceptible to the effects of stochastic predation events because of the small population sizes. During the study period, most herds experienced low rates of predation, because under the mountain lion control plan in place, offending mountain lions were removed (Figure 1). In 2009, for the Mt. Baxter population, the annual mortality rate for females was 20%, 85% of which was attributed to cougar predation. Mt. Baxter was the only translocation source population that experienced a large stochastic predation event during 2000-2010 (Stephenson et al. 2012). During the 1970s the Mt. Baxter population had more than 100 ewes, suggesting that this population has high growth potential and is not limited by habitat quality (Wehausen 1980).

Typical adult survival at Wheeler Ridge (0.92 CI = 0.008) and Mt. Langley (0.98 CI = 0.0001) indicated that a more typical mortality rate should be less than 10% (Johnson et al. 2010). Increased rates of mortality in such small herds may involve the deaths of only two or three individual animals, seemingly very small numbers but very important in the context of an endangered species. Depressed demographic rates, particularly adult survival in ungulates may result in lower population growth rates. Lower population growth rates, in turn, can have a measurable effect on the time-to-delisting since animal consumed by predators reduce the population base for both translocation and reproduction.

Predation limits the number of animals available for translocation as predators consume potential candidates for translocation and limit growth rates. In the Mt. Baxter and Wheeler Ridge herds, predation shows a strong relationship with adult survival (Johnson et al. 2013), the primary factor driving the population trend in those herds (Johnson et al. 2010).

Translocations of SNBS are required to reintroduce herds into geographically disparate areas where natural colonization is unlikely. These herds are necessary to

achieve downlisting and delisting goals identified in the Recovery Plan. During the 1980s similar management actions created the Wheeler Ridge, Mount Warren, Mount Gibbs, and Mount Langley herds (US Fish and Wildlife Service 2007). In order for translocations to occur, bighorn herds must be of sufficient size to allow removals to occur without adverse effects on the source herds. During the period of the study, 1999-2009, only 11 ewes were translocated (Stephenson et al. 2012). This was primarily because of a lack of sufficient translocation stock. Population sizes during that period reflected the initial recovery upon listing as an endangered subspecies from extremely low population numbers. Eleven ewes per decade is inadequate to create the four new herds necessary to meet recovery goals (Rubin 2002). In order to achieve recovery in a reasonable time more translocation stock was needed.

We recognize that some authors suggest that predation control may not be effective as a long-term strategy (Van Ballenberghe 2006, Bergstrom 2017). However, short-term predation control can be effective. In a mule deer population, it was concluded that cougar removal may have only a short-term positive effect (Hurley et al. 2011). Such an effect would supply needed translocation stock for the bighorn recovery program.

Models allow prediction of relative effects of different rates of adult female survival regimes (and thus predation) on time to recovery (Shwiff 2005). These predictions are based on the assumption that reduced predation results in higher adult female survival. We evaluate this assumption below.

Two of the three scenarios modeled (“baseline” and “1-strike”) show similar results; a significant increase in time-to-recovery (Table 4) and significant additional costs (Table 5) relative to the preemptive scenario. Our analysis demonstrated the temporal and financial impacts of the negative effects of predation on long-term growth rates. We modeled results based on both including and excluding density dependence and under a range of predator management scenarios (Figure 2). The intent of this analysis was not to predict the precise number of years that delisting will take, but to give a relative measure of the potential effect that different predator management strategies could have on meeting recovery goals.

Our model predictions are consistent with measured population trends observed in bighorn sheep in New Mexico (Rominger and Goldstein 2008) and Alberta (Festa-Bianchet et al. 2006) when mountain lion control

methods were analyzed. We also compared our model results and population data following seven years of monitoring the implementation to assess our assumption of predation affecting adult female survival and ultimately population growth rates for SNBS. Recognizing that correlation does not imply causation, we can still attempt to evaluate if our modelling exercise provided insight. During the period of low predation, as the model predicted, the source herds produced a significant surplus of animals for translocation. While the rate of production did not precisely match the model, that is to be expected as the model was intended as a guide to trends rather than an absolute predictor. The model suggested that over a period of five years (density independent model) to seven years (density dependent model) the program source herds should produce 60 surplus animals for translocation compared to the 52 actually moved in five years. However, if we were to take credit for the additional animals that colonized, it would bring the total to 69, and production would exceed the predictions of the model by 15%.

When mountain lions began targeting SNBS again, beginning in 2016, one of our source herds lost 50% of the reproductive base delaying time to recovery. Again, the model was not completely accurate in the sense that the model was based on an annual incremental increase in predation rates rather than a sudden catastrophic stochastic predation event, but the result appears to be similar. The model would suggest a loss due to predation of $3\text{-}5 \text{ ewes/year} * 5 \text{ years} = 15/18 \text{ ewes}$ for a given population as compared to actual documented losses to mountain lion predation at Mt. Langley of 13 ewes with up to 24 potential losses.

Economic analysis provides an additional tool to quantify and understand the cost and temporal effects of changes in predation rates. Economic modeling is based on the concept of economic growth, which means that the value of a fixed amount of money declines over time (Block 2005). This adjustment called discounting is fundamental in time value of money calculations. There is an inherent conflict in the economic growth model, based on discounting future costs, and conservation (Czech 2008, Sterner 2009). This conflict raises the question of whether discounting future costs in the context of an economic analysis for conservation purposes is a sufficient approach to guide policy decisions. Discounting suggests that costs in the future do not have much value today. Thus, when adjusted costs (discounted costs) are reviewed in our results, the effects appear diminished as compared to the unadjusted costs. For the density dependent case a cost of 30 million dollars when discounted becomes only 13.6 million in present dollars and the cost decrease from baseline to aggressive predator control is only 16%. When reviewing time or unadjusted costs as a measure of cost, such potential distortion does not occur. Using either of these methods for measuring differences results in an approximate 30% decrease in the time to or cost of recovery. This suggests that care must be taken when interpreting the results of an economic analysis performed solely on the basis of adjusted costs. Both adjusted and unadjusted costs as well as time should be considered in the comparison while recognizing that inflation is real and

that discounting does provide some additional insight about true costs.

With this in mind, we suggest that appropriate levels of predator management will result in shorter recovery times and reduced cost of recovery. During the time of lower predation significant progress toward the Recovery goals was achieved (Vucetich et al. 2006, US Fish and Wildlife Service 2007) while maintaining healthy herds in the source herds as predicted.

We did not address compensatory versus additive mortality in this analysis. The underlying analysis is predicated on the idea that Mt. Baxter, with the highest historically recorded population in the Sierra Nevada (Wehausen 1980), has the capability to be as productive as Mt. Langley. Mt. Baxter, during the 1999-2009 decade, had more adult females killed by mountain lions than any other population and the commensurate lowest growth rates (Stephenson et al. 2012). Program data does not support determining how much of this mortality was additive versus compensatory or how much unrecorded mountain lion predation may have occurred, but it does suggest that significantly higher productivity may be possible as noted in the results above. When this is taken together with the effects of mountain lion predation documented at Mt. Baxter in the 1980s (Wehausen 1996) the evidence supports the model assumptions of mountain lion predation effects on adult female survival. Finally, the model provided good agreement with the data collected during the following seven years as noted earlier.

One additional factor, not considered in this analysis, is a potential for increased lamb:ewe ratios with more aggressive mountain lion control. Mountain lion predation may be an important mortality factor in bighorn lamb mortality (Parsons 2007) as well as an indirect effect, meaning affecting downstream population growth by reducing the reproductive base (Bourbeau-Lemieux et al. 2011). While increased cougar control did not consistently increase lamb:ewe ratios in New Mexico, some improvements did result (Rominger and Goldstein 2009). While not modeled here, should lamb:ewe ratios increase, the effect would be additive to the predicted positive influence on population trajectories and subsequent translocation opportunities. As we continue to collect and analyze data to verify our model predictions, our predator management could be adapted to incorporate the most effective strategy as demonstrated through demographic response, while recognizing that other considerations may also affect management decisions. Predation is only one of the explanatory variables for population growth rates, so a demonstrated sensitivity to mountain lion management will allow for effective adaptive strategies.

Recovery and delisting for the SNBS requires growing into a functioning metapopulation that can withstand periodic episodes of predation and foster subsequent recovery without management intervention (US Fish and Wildlife Service 2007). If, during recovery and certainly post recovery, mountain lion predation leads to the extirpation of SNBS herds, then metapopulation dynamics involving local extinctions and recolonizations will become important. Natural recovery processes (i.e., in the absence of translocation efforts) for these herds would require a very long time-scale because bighorn ewes are

extremely philopatric (Festa-Bianchet 1991). This could lead to significant delays to recovery in the absence of predator control.

Other effects not covered in this study, but potentially detrimental to the recovery of bighorn sheep are highlighted in the Recovery Plan (US Fish and Wildlife Service 2007). Loss of genetic diversity will not likely cause problems in the short-term (Johnson et al. 2010), but with delayed recovery could become significant. Metapopulation dynamics because of more geographically separate herds will afford some protection from stochastic events (US Fish and Wildlife Service 2007). The sooner those additional herds can become occupied, the sooner such protection can be afforded.

While objective analysis demonstrates the benefits of a more aggressive mountain lion control policy, arguments over commonly undefined values and preferences may still shape policy decisions (Lackey 2007, Rominger 2007). For example, California has legislation in place (Proposition 117 passed in 1990) protecting mountain lions from sport hunting. Yet further California legislation in 1999 directed that mountain lions be managed to prevent predation on bighorn sheep. Mountain lions are not endangered and more aggressive predator control for a limited time is not expected to have any significant long-term effects on mountain lion populations in the eastern Sierra Nevada (US Fish and Wildlife Service 1999). However, both human values and scientific analysis have and deserve to be part of the discussion (Mitchell et al. 2018), as the two sections of California law clearly demonstrate. While it is tempting to say that policy needs to be shaped solely by objective science, a Structured Decision Making (SDM; Robinson et al. 2016) framework could better allow managers to appropriately weigh the values of different stakeholders to reach a consensus decision. Economic analysis can be one important tool to assist in making these decisions. These analytic results and data are but one of the inputs to the Stakeholders Group of the SNBS Recovery Implementation Team.

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