MODELING DEMOGRAPHIC PROCESSES IN AN ENDANGERED POPULATION OF BIGHORN SHEEP

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Abstract: We developed a demographic simulation model to explore how population vital rates, initial size, and the addition of animals influenced the viability of an endangered population of bighorn sheep (*Ovis canadensis*) consisting of 8 subpopulations. Perturbation analyses indicated that quasi-extinction risk was more sensitive to changes in adult female survival than to changes in reproduction or survival of young animals. This pattern was similar in 8 subpopulations that had different initial sizes, survival rates, and recruitment rates. Subpopulation viability was related to the initial number of females and to adult female survival, but not reproduction. Management actions that increase adult survival may be most effective when implemented in the largest subpopulations, whereas actions involving the addition of animals may be most effective if implemented in subpopulations with high survival rates. Subpopulation augmentation in yearly increments was more effective at reducing quasi-extinction risk than was adding the same total number of animals at the beginning of the simulation. The level of augmentation needed to substantially reduce quasi-extinction risk exceeded reported levels of female movement among populations or subpopulations. This finding led us to speculate that rescue effects, which are uncommon events for bighorn sheep, may be too rare or of inadequate magnitude under current conditions to effectively reverse bighorn sheep population declines.

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We developed a demographic simulation model to examine the population dynamics of bighorn sheep, and to help guide conservation strategies for this species. We used the population of desert bighorn sheep in the Peninsular Ranges (Sharp 1994) of California as a case study. This population, which was federally listed as endangered in March 1998 (U.S. Fish and Wildlife Service 1998), currently is comprised of at least 8 subpopulations or "ewe groups" (Rubin et al. 1998, Boyce et al. 1999). Overall abundance has declined during the past quarter century (DeForge et al. 1995, Rubin et al. 1998), with the population size estimated as 334 animals in 1998 (U.S. Fish and Wildlife Service 2000). Disease, poor lamb recruitment, habitat loss and modification, human disturbance, and predation by mountain lions (*Puma concolor*) have been implicated in contributing to the decline of this population (U.S. Fish and Wildlife Service 2000).

The overall goal of our study was to improve our understanding of bighorn sheep population dynamics and to refine management strategies by examining the relative importance of vital rates (age-specific survival and reproductive rates) and the addition of animals. We conducted perturbation analyses (Caswell 2001) by comparing risks of quasi-extinction under baseline and altered demographic conditions, with risk of quasi-extinction defined as the probability of a population falling to or below a given threshold number of females during a short time period (Ginzburg et al. 1982, Burgman et al. 1993, Beissinger and Westphal 1998). We refer to population viability in a general sense as the ability of the population to persist through a 10-year period.

Our first objective was to explore the relative importance of 6 vital rates on the short-term viability of subpopulations in the Peninsular Ranges, and our second objective was to assess how the addition of animals (which could occur through natural immigration or artificial augmentation) influenced subpopulation viability. Our third objective was to examine whether the viability of the entire population was influenced by the choice of subpopulation in which key vital rates were altered or to which animals were added. We conducted this analysis at plausible low and high levels of female movement among subpopulations to determine whether the rate of movement influenced quasi-extinction risk and the conservation strategy that might be most effective at reducing this risk.

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METHODS

Natural History and Model Structure

We developed a stage-based matrix projection model (Caswell 2001) for female bighorn sheep, written in TrueBasic (TrueBasic, West Lebanon, New Hampshire, USA). We excluded males because bighorn sheep are a polygynous species and population dynamics are primarily driven by the number of females (Geist 1971). The model included 5 age-based stages (lambs, yearlings, 2-yr-old females, 3-yr-old females, and females ≥4 yr old; Fig. 1), selected because empirical data show that lamb production and lamb survival are lower among 2- and 3-year-old females than in older females (Festa-Bianchet 1988, Rubin et al. 2000). Empirical data suggest that no difference exists in annual survival among age categories of adult (≥2 yr old) females in this population (Hayes et al. 2000). The simulation model used a 1-year time step, and animals remained in the last stage (≥4 yr old) until death.

We chose a 1-year time step because bighorn sheep in the Peninsular Ranges are seasonal breeders with most lambs born during the spring months of February, March, and April (Rubin et al. 2000). Census vectors were modeled as occurring 6 months after the birth of lambs, coinciding with fall helicopter surveys. Reproduction was defined as production of a 6-month-old female lamb, a definition that combines lamb production and lamb survival. Therefore, at each simulated census (as at the time of empirical censuses) yearlings were 1.5 years old, 2-year-old females were 2.5 years old, and so forth.

In the Peninsular Ranges, bighorn sheep are distributed in at least 8 subpopulations or "ewe groups" (Rubin et al. 1998, Boyce et al. 1999) with an approximately south–north geographic orientation as follows: Carrizo Canyon, Vallecito Mountains, San Ysidro Mountains south of road S-22, San Ysidro Mountains north of road S-22, Coyote Canyon, Santa Rosa Mountains southeast of Highway 74, Santa Rosa Mountains northwest of Highway 74, and San Jacinto Mountains. Our model was spatially realistic in that it simulated this arrangement relative to the potential movement among subpopulations.

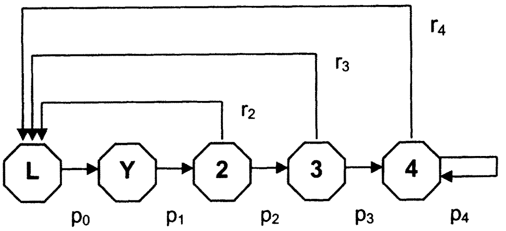

Fig. 1. Structure of population model for female bighorn sheep. Stages L, Y, 2, 3, and 4 correspond to lamb, yearling, 2-yr-old, 3-yr-old, and ≥4-yr-old, respectively. Transition probabilities, p_0 through p_4, represent the proportion of females surviving from 1 stage to the next (or remaining in the last stage, in the case of p_4), and r_2, r_3, and r_4 are the reproduction rates of 2-, 3-, and ≥4-yr-old females, respectively.

Matrix Structure

Within-subpopulation dynamics and between-subpopulation dynamics were both included in 1 large population projection matrix, **A**, with the form:

$$\mathbf{A} = \begin{bmatrix} A_1 & M_{2\to1} & M_{3\to1} & \cdots & M_{8\to1} \\ M_{1\to2} & A_2 & M_{3\to2} & \cdots & M_{8\to2} \\ M_{1\to3} & M_{2\to3} & A_3 & \cdots & M_{8\to3} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ M_{1\to8} & M_{2\to8} & M_{3\to8} & \cdots & A_8 \end{bmatrix}.$$

The diagonal elements, A_i, represented within-subpopulation dynamics (within subpopulation i), while all other elements, $M_{i\to j}$, represented between-subpopulation dynamics (movement from subpopulation i to subpopulation j). Each element in the main matrix was, itself, a 5 × 5 matrix to represent the 5 stages. Diagonal elements (the within-subpopulation matrices) had the form:

$$A_i = \begin{bmatrix} 0 & F_1 & F_2 & F_3 & F_4 \\ P_0 & 0 & 0 & 0 & 0 \\ 0 & P_1 & 0 & 0 & 0 \\ 0 & 0 & P_2 & 0 & 0 \\ 0 & 0 & 0 & P_3 & P_4 \end{bmatrix}$$

where $F_x = P_x r_{x+1}$ (except for F_4, which equals $P_4 r_4$), and r_x equals the per capita reproductive rate (proportion of females producing a 6-mo-old female lamb) for females in stage x (e.g., r_2 represents the proportion of 2-yr-old females producing a 6-mo-old female lamb). The transition probabilities, P_x, were based on the number surviving and the number moving to another subpopulation. Therefore,

$$P_x = p_x - \sum_{j \neq i}^{j=1 \text{ to } 8} m_{x,i,j},$$

where p_x = the proportion of animals surviving from stage x to x + 1 during the year, and $m_{x,i,j}$ = the proportion of animals in stage x moving from subpopulation i to j during the year. Because we assumed that lambs and yearlings do not move among subpopulations, $P_0 = p_0$, and $P_1 = p_1$.

Nondiagonal elements (between-subpopulation movement matrices) had the form:

$$M_{i \to j} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & p_{2,i}m_{2,i,j} & 0 & 0 \\ 0 & 0 & 0 & p_{3,i}m_{3,i,j} & p_{4,i}m_{4,i,j} \end{bmatrix}$$

At each time step, values of vital rates that determined the elements in the projection matrix were defined as explained below. The projection matrix, **A**, was then multiplied by the column vector of the population at time t, $(n_{0,1}, n_{1,1}, \ldots, n_{x,i}, \ldots, n_{5,8})$, to obtain the number of animals in each subpopulation at time t + 1. Here, $n_{x,i}$ = number of animals in stage x in subpopulation i.

Model Parameterization and Incorporation of Stochasticity

Our model required 6 vital rates for each subpopulation, including reproduction (percent of females recruiting a 6-mo-old female lamb) by 2-, 3-, and ≥4-year-old females, and stage-specific transition probabilities (the probability of a lamb surviving to become a yearling, a yearling surviving to become a 2-yr-old female, and the annual survival of females ≥2 yr old). We parameterized our baseline model using empirical data collected in the Peninsular Ranges (Appendix A). These data were generated from extensive field studies, which included helicopter surveys and tracking of radio-collared animals, including the monitoring of 20–40% of the estimated female population during 1993–1998 (Appendices A, B).

We incorporated stochasticity by allowing vital rates to vary. At each time step, t, the value of the vital rate, x_t, was determined using the following equation: $x_t = x + (s \times y_t)$, where x is the mean value of the vital rate for the subpopulation, s is the standard deviation of the vital rate, and y_t is a random variable selected from a normal distribution with a mean of zero and a variance of 1. Stochastic rates of survival and reproduction were calculated at each iteration and were truncated as necessary to remain within the range of 0–1.

We assumed that the empirical data on vital rates incorporated elements of demographic and environmental variation, as well as experimental error of sampling. We were unable to measure experimental error but assumed that it was small relative to demographic and environmental variation. The empirical data were from a short time period and likely underestimated longer-term environmental variation. Our intent was to compare relative quasi-extinction risks rather than to estimate absolute extinction risks.

Vital rates were assumed to be uncorrelated among subpopulations and were, therefore, determined with separate random variables (y_t) among subpopulations. This assumption was supported by the observation of independent long-term abundance trends (Rubin et al. 1998), offspring recruitment patterns (Rubin et al. 2000, Appendix B), and survival patterns (Appendix B) among subpopulations in the Peninsular Ranges. Within a subpopulation, survival and reproduction rates were assumed to be correlated among stages (e.g., a year of poor survival for older females also was a year of poor survival for younger females); however, survival and reproduction were not correlated with each other (survival of adults could be low while reproduction was high). This assumption was supported by the empirical data (Appendix B).

Initial subpopulation sizes and compositions were based on 1994 census data, observed lamb:ewe and yearling:ewe ratios (DeForge et al. 1995, 1997; Rubin et al. 1998), and proportions of adult females estimated to be in each stage during 1992–1994 captures and observations (E. S. Rubin and W. M. Boyce, unpublished data). We did not include density dependence in our model because the effect of density on bighorn sheep (especially at low numbers) is poorly understood.

Model Simulations and Generation of Quasi-extinction Graphs

To address issues important to immediate conservation needs, 10-year projections were simulated with 1,000 replications per simulation. The lowest number of females over the 10 years of each replication was recorded, and the cumulative proportion of replications falling to or below each abundance threshold was used to obtain probabilities and to generate a cumulative quasi-extinction curve for each simulation (Burgman et al. 1993, Akcakaya et al. 1999). Initial baseline simulations run with fewer replications (100, 250, 500) revealed that the quasi-extinction curve was accurately represented by 1,000 replications.

We compared the results of model simulations by examining the relative positions of quasi-extinction curves. We chose this approach because we were primarily interested in quasi-extinction risk rather than population growth rate per se. This approach allowed us to incorporate initial population size in our assessment, and allowed us to assess viability during a short (10-yr) time period without assuming a stable stage distribution (Fox and Gurevitch 2000). Our perturbation analyses were used to evaluate model predictions in response to model inputs. We evaluated both absolute and proportional changes in response to model inputs, similar to analytical sensitivity and elasticity analyses, respectively (de Kroon et al. 1986, Caswell 2001).

Evaluating the Relative Influence of Vital Rates on Population Viability

To examine the relative importance of stage-specific vital rates to quasi-extinction risk, we examined simulations for each subpopulation separately. We ran a baseline model for each subpopulation with the vital rates set at our best approximation of actual values (Appendix A). We noted the threshold number of females in each subpopulation that corresponded to a 50% quasi-extinction probability and chose it as our reference point for perturbation analysis. We refer to this as the 50% threshold number. We conducted perturbation analyses by altering each vital rate incrementally by 5, 10, 15, 20, and 100% and recorded the new probability of quasi-extinction at the 50% threshold number. Because the choice of threshold number of females may have influenced the results, we repeated these perturbation analyses for each subpopulation using the threshold number of ewes defined for quasi-extinction probabilities of 25 and 75%.

For each subpopulation, we also examined the relationship between the 50% threshold number and 3 factors: initial population size (females ≥1 yr old), survival, and reproduction, by plotting values in a scatterplot. For these examinations, we used the mean adult (≥2 yr old) survival and the mean reproduction of females ≥4 years old. The reproduction of younger females and the survival of yearlings would have resulted in the same patterns because these values originally were generated as a proportion of rates for older animals (Appendix A).

Evaluating the Effect of Adding Animals on Subpopulation Viability

To examine the influence of animal additions on subpopulation viability, we evaluated the change in quasi-extinction risk at the 50% threshold number under 2 scenarios: (1) the 1-time addition of animals at year 1, and (2) the addition of animals during each year of the simulation. For the first scenario, we modeled the addition of 1, 2, 5, 10, 20, 30, and 40 animals, and for the second scenario, we evaluated the yearly addition of 1, 2, 3, and 4 animals (resulting in a total of 10, 20, 30, and 40 animals, respectively). We modeled the addition of 2-year-old and ≥4-year-old females separately to determine whether the age of females influenced the effectiveness of animal additions. We assumed that augmented animals had the same survival and reproduction rates as animals already present in the group, and repeated these evaluations separately for each subpopulation in the absence of movement among subpopulations.

Evaluating Conservation Strategies and the Effect of Movement Rates on Choice of Conservation Strategy

We generated a quasi-extinction risk curve for the entire population, using baseline vital rates for each subpopulation (Appendix A). Using the results of the previous perturbation analyses to identify the vital rate having the most influence on quasi-extinction risk, we tested whether the viability of the entire population was influenced by the specific subpopulation in which the key vital rate was improved. We changed this vital rate in each of the 8 subpopulations, 1 subpopulation at a time, and compared the resulting 8 quasi-extinction curves to identify the subpopulation that would have the greatest effect on the viability of the entire population. To compare pairs of quasi-extinction curves, we calculated the mean difference (change in quasi-extinction risk) between the 2 curves across all threshold numbers of females. In addition, we used scatterplots to visually examine the relationship between the rank of a subpopulation (in terms of increased population viability when survival was increased in this subpopulation) and its initial number of females, survival rate, or reproduction rate. In a similar fashion, we evaluated how the addition of animals to individual subpopulations influenced the viability of the entire population. For that evaluation, we modeled the yearly addition of 3 2-year-old females to each subpopulation, 1 subpopulation at a time, and compared the resulting 8 quasi-extinction curves for the entire population.

To assess whether model results were sensitive to the levels of movement among subpopulations, we first conducted the above analyses without including movement among subpopulations. We then repeated the analyses with a movement

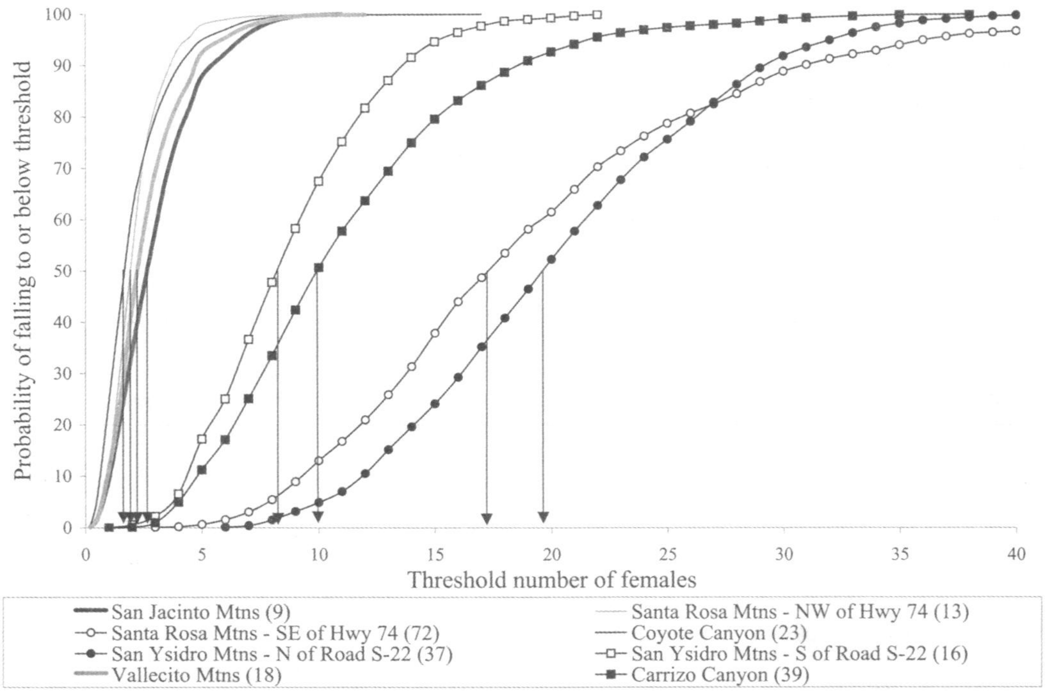

Fig. 2. Cumulative quasi-extinction curves for 8 subpopulations of bighorn sheep in the Peninsular Ranges, California, USA, at baseline vital rates and no female movement among subpopulations. Arrows indicate 50% threshold number for each subpopulation (the threshold number of females at which each subpopulation has a 50% quasi-extinction risk). Initial number of females ≥1 yr old shown in parentheses.

rate of 0.04 moves/sheep-year among neighboring pairs of subpopulations (e.g., 4 females moving from a subpopulation of 100 females every year, or 1 female moving from a subpopulation of 10 females every 2.5 years). Empirical data suggest that the actual frequency of female movement among subpopulations in the Peninsular Ranges would not exceed this level (Rubin et al. 1998) and support 0.04 as a plausible maximum rate. Female movement was assumed to occur only between neighboring subpopulations, an assumption supported by observations of radio-collared females (Rubin et al. 1998). Movement rates were defined as the proportion of the source population emigrating each year, and rates between any pair of subpopulations were assumed to be symmetrical (a small and large subpopulation exchange the same proportion of animals, but a smaller absolute number of females would leave the small subpopulation). Additional assumptions were that females <2 years old did not move, that females did not incur additional risks of mortality while moving between subpopulations, that they maintained the survival rate of the source subpopulation during the year of their move, and that they did not reproduce during the year of their move.

RESULTS

The Relative Influence of Vital Rates on Population Viability

When simulations were run individually for each subpopulation with vital rates set at baseline values (Appendix A), and no movement among subpopulations, the resulting quasi-extinction curves indicated a wide range of risk for the 8 subpopulations (Fig. 2). We found that the 50% threshold number was strongly related to the initial number of females in the subpopulation (Fig. 3a); however, this relationship was not consistent. For example, the subpopulation in the San Ysidro Mountains south of road S-22, which started with 16 females, exhibited a larger 50% threshold number than did the Coyote Canyon subpopulation, which started with 23 females. This relationship likely was influenced by adult survival, which also appeared to be associated with the 50% threshold number (Fig. 3b). No apparent relationship was observed between the 50% threshold number and reproduction.

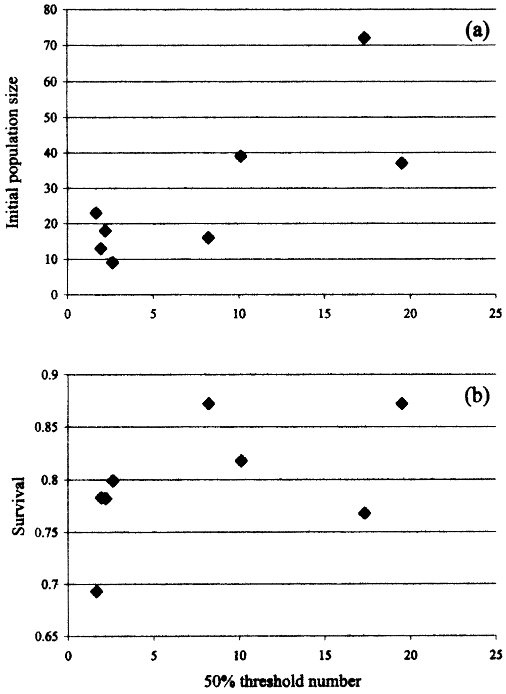

Fig. 3. Relationship between 50% threshold number and (a) initial population size, and (b) adult survival, in 8 subpopulations of bighorn sheep in the Peninsular Ranges, California, USA.

Perturbation analyses, conducted at the 50% threshold number for each subpopulation, indicated that of the 6 vital rates, survival of females ≥2 years of age had the greatest impact on viability for each subpopulation. Reproduction of 2- and 3-year-old females generally had the least effect, while the relative influences of reproduction by older females and the survival of the 2 younger stages depended on the magnitude by which they were increased (Table 1). For example, in Carrizo Canyon, a 5% increase in adult survival resulted in a quasi-extinction risk reduction of 28.1% (Fig. 4). A 5% change in any of the other vital rates, including reproduction of any stage or survival of younger animals, resulted in—at most—a change of 5% in quasi-extinction risk. A benefit equivalent to that gained by increasing survival among ≥2-year-old females by 5% was obtained only by increasing reproduction of ≥4-year-old females (the stage with the highest reproduction) or survival of lambs to the yearling stage by 100%. The increased viability that resulted from increases in vital rates were mirrored by decreases in viability when values of vital rates were decreased (Fig. 4). The relative influence of the 6 vital rates on viability remained the same when this perturbation analysis was repeated using the threshold number of ewes at which the baseline curve indicated 25 and 75% quasi-extinction risk.

The Addition of Animals and its Effect on Subpopulation Viability

When the viability of individual subpopulations was considered, the addition of females had the greatest effect on the viability of the smallest subpopulations, regardless of the specific augmentation scenario (Table 2), undoubtedly because a larger proportion of the initial number of females was added. When females were added once, at the beginning of the 10-year simulation, the addition of 5 females reduced quasi-extinction risk of the smallest subpopulation (San Jacinto Mountains) by approximately 25%. However, an addition of ≥20 females was necessary before the quasi-extinction risk of any subpopulation, regardless of size, was reduced by >40%. Viability was increased more when animals were added incrementally over the course of the 10-year simulation than when the same total number of animals was added once during the first year (Table 2). This pattern was found in all subpopulations, despite the range of adult survival rates among the subpopulations, and also was observed when we increased survival to 90%. For example, the addition of 10 2-year-old females during the first year reduced the quasi-extinction risk in the San Jacinto and the Santa Rosa Mountains northwest of Highway 74 subpopulations by 34.1 and 30.2%, respectively. In contrast, the addition of 1 2-year-old female during each of the 10 years reduced the risk of quasi-extinction for these 2 subpopulations by 46.7 and 49.9%, respectively. For all subpopulations, the benefits gained by adding older (≥4 yr old) females were very similar to those resulting from the addition of 2-year-old females (Table 2).

Conservation Strategies and the Effect of Movement Rates on Choice of Conservation Strategy

When subpopulation vital rates were set at baseline values (Appendix A) and no females moved among subpopulations, the overall population had nearly a 100% probability of falling to or below 130 females (from a starting size of 227 females) at least once during the 10 years, but had a low probability (nearly zero) of falling below 40 females (Fig. 5). When female movement rates among subpopulations were increased to 0.04 moves/sheep-year, the viability of the entire

Table 1. Results of perturbation analyses for individual bighorn sheep subpopulations in the Peninsular Ranges. Percent change in probability of quasi-extinction (from baseline at 50%) as a result of incremental changes in vital rates. Reproduction values indicate recruitment of female lambs only.

Vital rate to be increased	Percent increase in vital rate	Carrizo Canyon	Vallecito Mountains	San Ysidro Mountains south of Road S-22	San Ysidro Mountains north of Road S-22	Coyote Canyon	Santa Rosa Mountains southeast of Hwy. 74	Santa Rosa Mountains northwest of Hwy. 74	San Jacinto Mountains
Reproduction by 2-yr-old females	5	1.2	–1.8	1.4	1.7	1.3	–0.3	4.3	2.3
	10	2.7	–1.3	0.9	1.3	0.4	–1.1	4.1	–0.1
	15	–0.4	–1.5	2.0	0.4	1.6	–3.7	4.9	0.3
	20	–1.9	–4.3	–0.3	0.9	–0.3	–2.7	3.6	–1.8
	100	–0.6	–2.6	0.5	1.4	–0.9	–3.7	5.0	–0.5
Reproduction by 3-yr-old females	5	1.3	–3.0	0.3	0.4	–0.7	0.3	3.9	0.6
	10	2.3	–3.6	–0.9	0.7	1.7	–0.7	4.8	–2.9
	15	1.9	–2.5	1.5	–2.2	–0.1	–0.8	5.4	1.1
	20	2.6	–2.8	1.5	–1.2	2.2	–1.4	7.1	–0.9
	100	–2.8	–6.2	–1.4	–1.9	1.7	–1.2	5.7	–2.4
Reproduction by ≥4-yr-old females	5	–1.7	–5.0	–2.9	–0.5	–0.4	–3.8	6.4	–1.3
	10	–3.8	–2.6	–1.5	–4.8	–4.5	–9.0	2.8	–3.6
	15	–4.3	–4.4	–5.2	–6.7	–5.5	–9.2	1.2	–5.8
	20	–7.3	–6.5	–6.5	–11.5	–10.6	–12.9	–2.5	–5.4
	100	–29.8	–24.8	–32.6	–37.2	–27.6[a]	–40.4[a]	–20.6	–28.8[a]
Survival from lamb to yearling	5	–1.7	–2.1	–0.8	–4.4	–2.2	–4.6	1.9	–2.3
	10	–2.8	–5.9	–5.2	–5.3	–4.1	–9.5	2.0	–4.0
	15	–6.1	–8.6	–10.5	–10.2	–4.8	–13.2	1.8	–7.0
	20	–11.2	–7.6	–13.6	–11.9	–8.5	–16.9	–4.3	–10.6
	100	–37.1	–27.6	–41.4	–42.7	–35.8	–46.8	–28.5	–37.6
Survival from yearling to 2 yr	5	–2.3	–5.1	–4.1	–2.1	0.1	–7.1	2.9	–2.5
	10	–5.1	–4.6	–5.9	–7.7	–1.8	–8.6	0.4	–6.9
	15	–4.1	–4.7	–7.5	–9.6	–4.5	–12.9	–3.1	–10.0
	20	–6.7	–8.0	–8.6	–14.5	–9.0	–15.5	–2.3	–10.1
	100	–16.3[b]	–16.0[b]	–17.6[b]	–20.8[b]	–26.0[b]	–31.9[b]	–15.7[b]	–24.5[b]
Survival of animals ≥2 yr old	5	–28.1	–26.9	–27.7	–35.0	–24.2	–30.9	–25.5	–21.9
	10	–45.5	–42.5	–44.1	–48.2	–36.8	–44.7	–43.9	–36.7
	15	–49.4	–48.4	–48.5[b]	–49.8[b]	–46.4	–49.5	–48.6	–46.1
	20	–49.9	–49.8	–49.9[b]	–50.0[b]	–49.4	–49.9	–49.7	–48.4
	100	–50.0[b]	–50.0[b]	–50.0[b]	–50.0[b]	–50.0[b]	–50.0[b]	–50.0[b]	–49.9[b]

[a] Mean exceeded maximum reproduction of 1 lamb per female, assuming 50:50 sex ratio among lambs. Program truncated stochastic value at 1.0.

[b] Mean exceeded maximum survival of 1.0. Program truncated stochastic value at 1.0.

population decreased. However, an increase in adult survival increased population viability more than proportionate improvements in other vital rates, regardless of the level of female movement among subpopulations (Fig. 5).

Because survival of females ≥2 years of age had the greatest influence on quasi-extinction risk for the population and individual subpopulations (Table 1, Fig. 4), we continued our analysis by assessing whether the viability of the entire population was influenced by choice of subpopulation in which adult survival was increased by 10%. With no movement among subpopulations, quasi-extinction risk of the entire population tended to be reduced the most when survival was improved in the largest subpopulations. The greatest benefit was gained when survival was increased in the Santa Rosa Mountains southeast of Highway 74 (mean decrease in quasi-extinction risk = 14.8%, SD = 15.6), the San Ysidro Mountains north of road S-22 (mean = 12.8%, SD = 14.7), and Carrizo Canyon (mean = 9.8%, SD = 9.7). The rank of a subpopulation (in terms of increased population viability when survival was increased in this subpopulation) appeared to be related to its initial number of females, regardless of the level of migration among subpopulations (Table 3, Fig. 6). No apparent relationship was observed between rank and survival or reproduction rates.

Viability of the entire population was increased when a few animals (3 2-yr-old females) were added to any 1 subpopulation on a yearly basis,

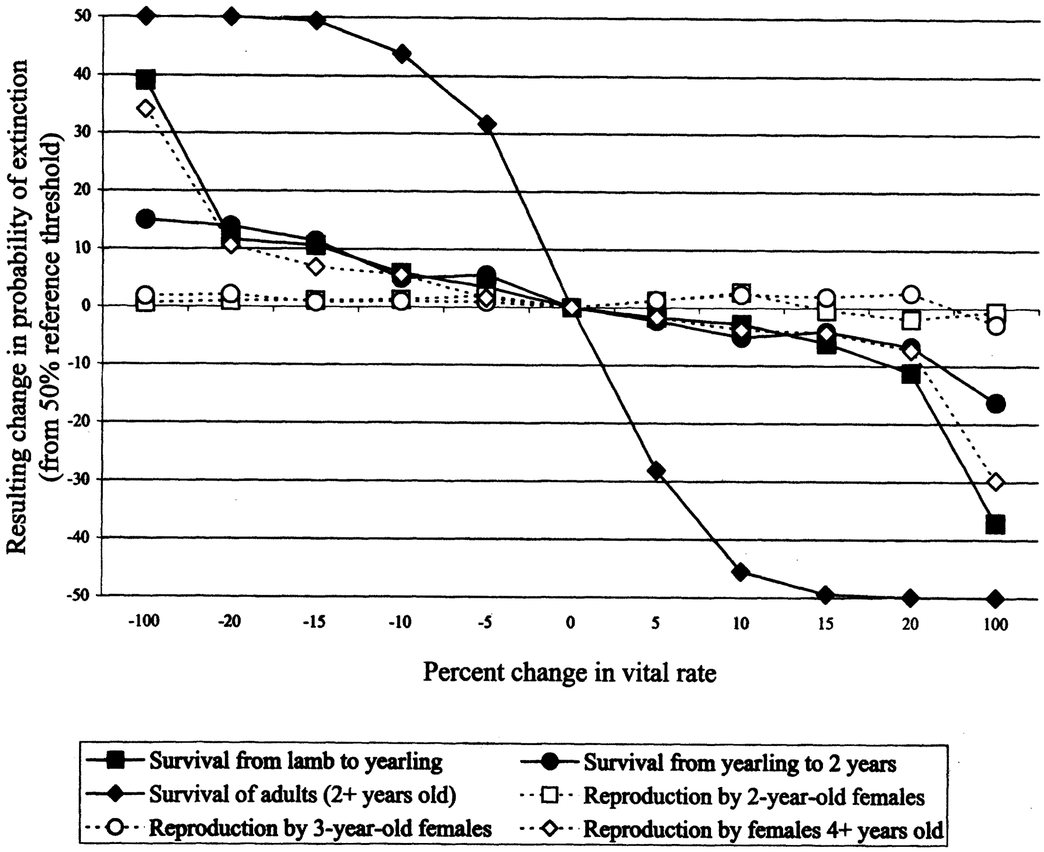

Fig. 4. Results of perturbation analysis for bighorn sheep in the Carrizo Canyon subpopulation, Peninsular Ranges, California, USA.

and the greatest benefit was gained when animals were added to the San Ysidro Mountains north of road S-22 (mean decrease in quasi-extinction risk = 16.5%, SD = 16.2), the San Ysidro Mountains south of road S-22 (mean = 15.5%, SD = 15.7) and the San Jacinto Mountains (mean = 13.7%, SD = 12.5). The rank of a subpopulation (in terms of increased population viability when animals were added to this subpopulation) was strongly related to its survival rate (Fig. 7), and this pattern was observed at both levels of migration among subpopulations. We did not observe an apparent relationship between rank and the initial number of females or reproduction rates.

DISCUSSION

Population modeling and perturbation analyses over a 10-year projection indicated that the viability of the Peninsular Ranges bighorn sheep population is more sensitive to changes in adult female survival than to proportionately similar changes in reproduction or survival of younger animals. This pattern was observed in simulations for each of the 8 subpopulations, even though they had different initial starting sizes, and had exhibited a wide range of recruitment levels and independent long-term trends in abundance (Rubin et al. 1998). The risk of quasi-extinction for individual subpopulations was inversely related to the initial number of females, in agreement with the general conservation principle that smaller populations have greater extinction risk (Gilpin and Soulé 1986). However, this relationship was not consistent and likely was influenced by adult survival rates, which also were inversely related to the risk of quasi-extinction.

At the population level, the risk of quasi-extinction increased as migration rate was increased. This likely occurred because more animals were being moved into subpopulations with poor vital rates. Burgman et al. (1993:213) made a similar observation in 1 of their population models and concluded that increased dispersal may move individuals

Table 2. Percent change in probability of quasi-extinction (from baseline at 50%), for individual bighorn sheep subpopulations in the Peninsular Ranges, as a result of adding 2-yr-old or ≥4-yr-old females under 2 augmentation scenarios. Numbers in parentheses indicate proportion of initial subpopulation added.

Type of augmentation	Total no. of animals added	Carrizo Canyon	Vallecito Mountains	San Ysidro Mountains south of Road S-22	San Ysidro Mountains north of Road S-22	Coyote Canyon	Santa Rosa Mountains southeast of Hwy. 74	Santa Rosa Mountains northwest of Hwy. 74	San Jacinto Mountains
One-time addition of 2-yr-old females in first year of simulation	1	−2.0 (0.03)	−5.3 (0.06)	−4.4 (0.06)	−0.6 (0.03)	−1.7 (0.04)	−1.3 (0.01)	−1.2 (0.08)	−5.4 (0.11)
	2	−2.7 (0.05)	−8.9 (0.11)	−10.0 (0.13)	−2.8 (0.05)	−3.3 (0.09)	−4.4 (0.03)	−5.1 (0.15)	−11.7 (0.22)
	5	−8.2 (0.13)	−16.5 (0.28)	−16.1 (0.31)	−10.8 (0.14)	−8.4 (0.22)	−4.2 (0.07)	−18.8 (0.39)	−25.7 (0.56)
	10	−11.5 (0.26)	−24.7 (0.56)	−29.9 (0.63)	−21.8 (0.27)	−17.4 (0.44)	−10.8 (0.14)	−30.2 (0.77)	−34.1 (1.11)
	20	−26.7 (0.51)	−35.7 (1.11)	−42.4 (1.25)	−35.0 (0.54)	−28.2 (0.87)	−17.7 (0.28)	−43.2 (1.54)	−44.9 (2.22)
	30	−31.8 (0.77)	−43.4 (1.67)	−47.3 (1.88)	−42.6 (0.81)	−32.7 (1.30)	−24.4 (0.42)	−47.2 (2.31)	−47.7 (3.33)
	40	−37.6 (1.03)	−45.3 (2.22)	−48.7 (2.50)	−46.3 (1.08)	−39.2 (1.74)	−30.7 (0.56)	−48.2 (3.08)	−49.9 (4.44)
Yearly addition of 2-yr-old females[a]	10	−30.6	−48.3	−40.3	−24.8	−47.5	−21.3	−49.9	−46.7
	20	−44.1	−50.0	−48.5	−43.2	−50.0	−31.5	−50.0	−50.0
	30	−48.4	−50.0	−49.8	−48.7	−50.0	−43.0	−50.0	−50.0
	40	−49.7	−50.0	−50.0	−49.8	−50.0	−45.9	−50.0	−50.0
One-time addition of ≥4-yr-old females in first year of simulation	1	+2.5	−4.9	−1.9	−0.7	−1.7	−1.1	−0.8	−5.8
	2	−0.9	−7.6	−7.5	−4.2	−1.1	−3.1	−4.6	−10.4
	5	−9.4	−18.0	−16.7	−12.4	−7.5	−4.8	−16.2	−24.7
	10	−12.7	−25.5	−32.2	−22.3	−18.2	−10.3	−32.6	−35.3
	20	−24.7	−35.6	−44.5	−36.7	−27.6	−19.1	−44.2	−46.2
	30	−35.4	−44.1	−46.0	−43.5	−35.9	−25.7	−47.4	−48.0
	40	−39.1	−46.3	−48.3	−47.1	−39.4	−31.5	−49.2	−48.9
Yearly addition of ≥4-yr-old females[a]	10	−28.9	−48.3	−37.3	−28.5	−47.8	−20.3	−49.6	−47.7
	20	−44.1	−50.0	−48.5	−43.1	−50.0	−32.5	−50.0	−49.8
	30	−49.3	−50.0	−49.8	−48.3	−50.0	−43.4	−50.0	−50.0
	40	−49.7	−50.0	−50.0	−49.8	−50.0	−47.0	−50.0	−50.0

[a] Equal number added in each of 10 years.

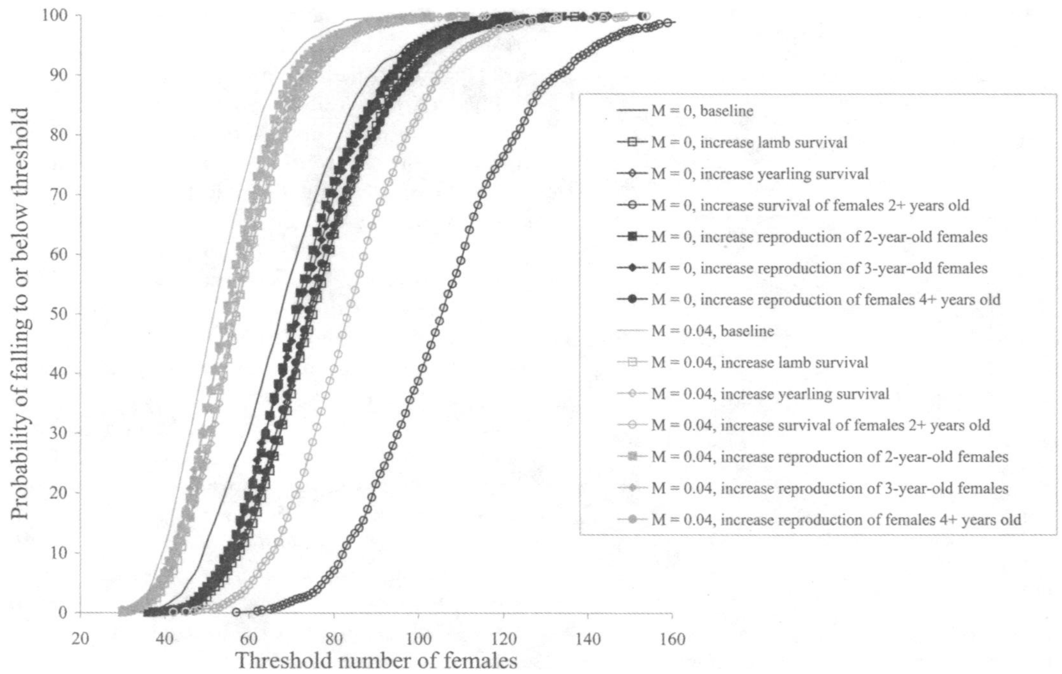

Fig. 5. Cumulative quasi-extinction curve for the entire population of bighorn sheep in the Peninsular Ranges, California, USA, with female movement among subpopulations (M) set at zero and 0.04 moves/sheep-year, showing vital rates at baseline values and at 5% above baseline.

into population sinks. However, the risk of quasi-extinction was more sensitive to changes in adult survival than to similar changes in other vital rates, regardless of movement rate among subpopulations. Leslie and Douglas (1986) suggested that the management utility of their bighorn sheep population model may have been limited by unknown female survival rates, and the importance of adult survival also has been established for other long-lived species (Crouse et al. 1987, Wootton and Bell 1992, Doak et al. 1994, Heppell et al. 1996).

The survival of adult bighorn sheep in the Peninsular Ranges has been low relative to other populations (Hayes et al. 2000), and substantial increases may be biologically realistic. For example, a 5% increase in adult survival in the 2 subpopulations with the highest observed survival rates (both San Ysidro Mountains subpopulations) resulted in a mean survival of 0.92 and a >25% reduction in the risk of quasi-extinction. In Coyote Canyon (the subpopulation with the lowest baseline survival rate), increasing adult survival by 20% resulted in a mean survival of 0.75 and reduced quasi-extinction risk by 50%. These increases in survival are realistic in that they are similar to, or less than, rates documented in other bighorn sheep populations (Andrew et al. 1997, McCarty and Miller 1998). Since predation by mountain lions recently has been the primary cause of adult mortality in the Peninsular Ranges (Hayes et al. 2000), adult survival might be increased in this region by removing mountain lions (Ernest et al. 2002), or by managing habitat or prey species such as mule deer (*Odocoileus hemionus*). Our analyses suggest that the viability of the entire population tended to be most sensitive to changes in adult survival in the larger subpopulations (Santa Rosa Mountains southeast of Highway 74, San Ysidro Mountains north of road S-22, and Carrizo Canyon), presumably because increased survival was experienced by numerous females. Based on our model results, a 10% increase in adult survival in just 1 of these subpopulations potentially could reduce the risk of quasi-extinction of the entire population by 27–43%.

The viability of individual subpopulations also may be improved by increasing reproduction. However, our model suggests that substantial increases are necessary to produce results equal to those seen when adult survival is increased. It was necessary to increase reproduction of the oldest (≥4 yr old) females by ≥20% before the quasi-

Table 3. Relative ranking (1 through 8) of bighorn sheep subpopulations, in terms of effectiveness in improving viability of the entire population, when adult (≥2 years old) survival was increased by 10% in 1 subpopulation at a time, and when 3 2-year-old females were added to 1 subpopulation at a time. Rankings shown at 2 rates of female movement among subpopulations (M moves/sheep-year). Highest ranking (1) indicates that a change in this subpopulation resulted in the greatest improvement in viability for the entire population. Asterisks (*) indicate tied rankings.

Subpopulation (initial no. females present)	Ranking when adult survival was increased		Ranking when animals were added	
	M = 0	M = 0.04	M = 0	M = 0.04
Carrizo Canyon (39)	3	3	4.5*	4
Vallecito Mountains (18)	5	5	6.5*	6
San Ysidro Mountains S of Road S-22 (16)	4	4	2	2
San Ysidro Mountains N of Road S-22 (37)	2	1	1	1
Coyote Canyon (23)	8	6	8	8
Santa Rosa Mountains SE of Hwy 74 (72)	1	2	4.5*	5
Santa Rosa Mountains NW of Hwy 74 (13)	7	7	6.5*	7
San Jacinto Mountains (9)	6	8	3	3

extinction risk of any subpopulations was reduced by 10% (from 50% to 40% at the 50% threshold number). A 20% increase in reproduction may be biologically feasible as it would require every 100 females in this stage to recruit 30–87 lambs to 6 months of age, depending on the subpopulation and assuming an even sex ratio among lambs (Simmons et al. 1984). Such an increase may be most achievable in subpopulations with lower baseline reproduction rates, such as the 1 in the Santa Rosa Mountains northwest of Hwy 74. In any subpopulation, however, mean reproduction values for this stage had to be increased by 100% (doubled) to reduce quasi-extinction risk by 20–40%. In the subpopulations with lower baseline reproduction rates (Santa Rosa Mountains northwest of Hwy 74, Vallecito Mountains, Carrizo Canyon, and north and south San Ysidro Mountains), every 100 females in this stage would then have to recruit 50–89 lambs to 6 months of age, depending on the subpopulation. In the remaining 3 subpopulations (San Jacinto Mountains, Santa Rosa Mountains southeast of Highway 74, and Coyote Canyon), a 100% increase would have exceeded 1 lamb per female, an unrealistic situation. Since the model truncated reproduction at 1.0, the actual increases in mean reproduction for these subpopulations were 38, 44, and 77%, respectively. Gaillard et al. (1998) reported that populations of large ungulates typically exhibited much variation in recruitment, often in response to population density, while adult survival typically remained more constant and was less influenced by density. That finding suggests that although management actions may be able to increase overall reproduction, more variation could be expected in this rate than in adult survival. It has been suggested that organisms with delayed sexual maturity and long lifespans are less resilient to low adult survival than to periods of low reproduction (Congdon et al. 1993), and that iteroparity may allow members of a long-lived species numerous opportunities to replace themselves (Heppell et al. 1996). Our results suggest that this generality can be applied to bighorn sheep, and that changes in survival of adult bighorn sheep will have more influence on population viability than similar changes in recruitment. Although simulations of vital rates to estimate life-stage importance have previously been conducted for other species (e.g., McCarthy et al. 1995, Wisdom and Mills 1997, Crooks et al. 1998), none have focused on bighorn sheep. Our findings, therefore, have implications for management decisions and may be used to refine future population models (Emlen and Pikitch 1989).

For a number of species, computer simulations have indicated that a small number of migrants from neighboring populations can prevent the extirpation of a population through a rescue effect (Brown and Kodric-Brown 1977, Fahrig and Merriam 1985, Beier 1993, Stacey et al. 1997).

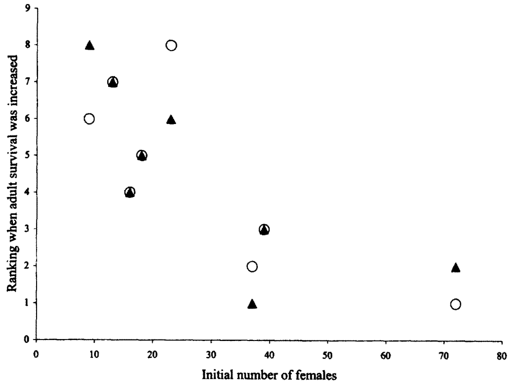

Fig. 6. Relationship between initial number of females present and ranking of individual subpopulations of bighorn sheep in the Peninsular Ranges, California, USA. Rank indicates the relative effectiveness in improving viability of the entire population when adult survival was increased by 10% in 1 subpopulation at a time, with the highest rank (1) signifying the greatest effectiveness. Open circles indicate no migration among subpopulations, and closed triangles indicate migration rate of 0.04 moves/sheep-yr.

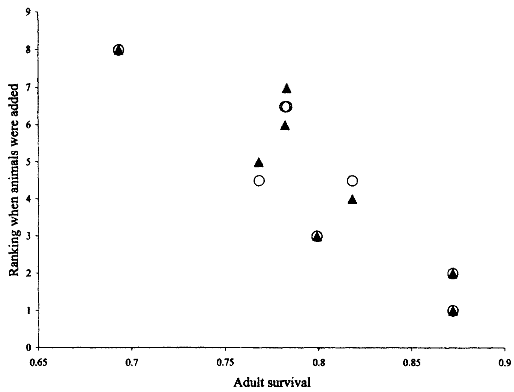

Fig. 7. Relationship between adult survival and ranking of individual subpopulations of bighorn sheep in the Peninsular Ranges, California, USA. Rank indicates the relative effectiveness in improving viability of the entire population when 3 2-yr-old females were added to 1 subpopulation at a time, with the highest rank (1) signifying the greatest effectiveness. Open circles indicate no migration among subpopulations, and closed triangles indicate migration rate of 0.04 moves/sheep-yr.

Bighorn sheep are poor dispersers (Geist 1971) that live, at a broad landscape scale, in naturally fragmented habitats (Schwartz et al. 1986, Bleich et al. 1990), and it is likely that rescue effects and recolonizations occur slowly over long time periods in this species (Bleich et al. 1996). Today, the chance of these events occurring is further reduced because habitat has been lost to development, and habitat fragmentation has reduced the ability of bighorn sheep to move through remaining habitat (Bleich et al. 1996). We found that even for the smallest subpopulation (in the San Jacinto Mountains), 5 females had to be added in year 1 to reduce the risk of quasi-extinction by 25%, while a 1-time addition of 20 females was necessary to reduce this risk by 40%. We compared these numbers with published accounts of movement by female bighorn sheep in the Peninsular Ranges and in other populations (Geist 1971, Ough and deVos 1984, Krausman and Leopold 1986, Rubin et al. 1998) and concluded that rescue effects, which are uncommon events for bighorn sheep, may be too rare or of inadequate magnitude to effectively reverse bighorn sheep population declines. The ultimate conservation goal should be a self-sustaining population (U.S. Fish and Wildlife Service 2000), and habitat connectivity should be maintained to allow for gene flow mediated by the more frequent moves by males (Bleich et al. 1990, Boyce et al. 1997). In addition, unoccupied habitat should be protected because it may provide sites for future subpopulations (Bleich et al. 1996), and it may provide existing subpopulations with resource options during long-term environmental changes. However, it is likely that an artificial rescue effect, via augmentation, could pull a subpopulation through a time period when its demographic dynamics would otherwise drive it to extinction.

Our model results provide insight and some general guidelines for augmentation of subpopulations in the Peninsular Ranges. We found that the effectiveness of augmentation was not influenced by the age of added females (2 yr old vs. ≥4 yr old). Quasi-extinction risk was reduced more effectively when animals were added yearly for 10 years, rather than all together at the beginning of the 10-year simulation. This is likely because animals that were added at the beginning of the simulation were exposed to mortality during each year, while animals that were added sequentially were essentially protected from mortality until they were added to the subpopulation. The additional reproduction of animals added once at the beginning of the simulation apparently did not compensate for the additional mortality. This suggests that the viability of subpopulations may be dependent on either an improvement in vital rates (either through human intervention or by natural processes) or the repeated addition of animals. The goal of self-sustaining subpopulations may not, therefore, be met by augmentation alone and will only be met if the underlying causes of the decline are ameliorated. A similar conclusion was drawn by Wootton and Bell (1992) in their assessment of peregrine falcon (*Falco peregrinus*) population dynamics. An additional finding, which is intuitive, is that the smallest subpopulations showed the greatest response per individual female added. In addition to promoting the conservation of individual subpopulations of bighorn sheep in the Peninsular Ranges, the Federal Recovery Plan for this population recommends that the size and viability of the entire population be increased (U.S. Fish and Wildlife Service 2000). Our results show that viability of the entire population was increased most effectively when animals were added to subpopulations with high adult survival.

MANAGEMENT IMPLICATIONS

When faced with declining subpopulations, managers may need to decide between investing in efforts to improve vital rates or to augment animal numbers. Both strategies have been used by managers of bighorn sheep populations, but it has been difficult to compare their levels of effectiveness quantitatively. Using results such as those presented here, managers can cautiously weigh the cost and benefits of various strategies. For example, to improve subpopulation viability in the Santa Rosa Mountains southeast of Highway 74, the model suggested that similar results could be obtained by (1) adding 40 females at 1 time, (2) adding 2 females every year during 10 years, or (3) increasing survival of adults by 5%. The final decision likely would be influenced by factors such as the availability of animals and fiscal and logistical restraints, and should be reevaluated as additional demographic data become available. In addition, assumptions of our model, such as the assumption that augmented animals have the same survival and reproductive rates as existing animals in the subpopulation, should be further tested. It also is possible that the effect of density dependence could alter our results or conclusions. We did not include density dependence in our model because little is known about its effect on bighorn sheep; however, this assumption should be further tested. Management decisions should be based on the consideration that the ultimate conservation goal is to have self-sustaining populations. This will be facilitated by a better understanding of factors that influence the survival of adult bighorn sheep. Future research at an ecosystem level, including research on the relationships between bighorn sheep, habitat, mountain lions, and deer likely will contribute valuable information that will assist conservation efforts for this species.

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Appendix A. Baseline vital rates for individual bighorn sheep subpopulations in the Peninsular Ranges, California, USA.

Vital rate	Carrizo Canyon	Vallecito Mountains	San Ysidro Mountains south of Road S-22	San Ysidro Mountains north of Road S-22	Coyote Canyon	Santa Rosa Mountains southeast of Hwy. 74	Santa Rosa Mountains northwest of Hwy. 74	San Jacinto Mountains
Lamb to yearling survival								
Mean	0.500[a]	0.500[a]	0.500[a]	0.500[a]	0.500[a]	0.500[a]	0.500[a]	0.500[a]
SD	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200

Yearling to 2 yr old survival								
Mean	0.736[b]	0.704[b]	0.785[b]	0.785[b]	0.623[b]	0.691[b]	0.705[b]	0.719[b]
SD	0.103	0.129	0.107	0.077	0.121	0.085	0.106	0.128
Annual survival of females ≥2 yr old								
Mean	0.818[c]	0.782[c]	0.872[c]	0.872[c]	0.693[c]	0.768[c]	0.783[d]	0.799[e]
SD	0.115	0.143	0.119	0.085	0.135	0.094	0.118	0.142
Percent of 2-yr-old females recruiting a female lamb to 6 mo								
Mean	0.039[f]	0.028[f]	0.046[f]	0.049[f]	0.063[f]	0.077[f]	0.029[f]	0.081[f]
SD	0.022	0.011	0.014	0.029	0.021	0.009	0.014	0.069
Percent of 3-yr-old females recruiting a female lamb to 6 mo								
Mean	0.055[f]	0.039[f]	0.066[f]	0.071[f]	0.090[f]	0.110[f]	0.041[f]	0.115[f]
SD	0.031	0.016	0.020	0.041	0.031	0.013	0.021	0.098
Percent of ≥4-yr-old females recruiting a female lamb to 6 mo								
Mean	0.174[g]	0.125[h]	0.208[g]	0.224[g]	0.283[h]	0.346[g]	0.129[g]	0.362[i]
SD	0.097	0.049	0.063	0.128	0.096	0.040	0.064	0.309
Initial subpopulation composition[j] (L,Y,2,3,4+)								
	7,0,0,4,35	2,0,0,0,18	6,1,0,0,15	5,5,0,0,32	4,1,5,0,17	17,10,5,0,57	2,2,1,1,9	2,3,0,0,6

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[a] Survival from lamb (6 mo) to yearling (18 mo) stage. Mean estimated from comparisons of lamb:female ratios and following year's yearling:female ratios observed during fall helicopter surveys and field observations (DeForge et al. 1995; E. S. Rubin and W. M. Boyce, unpublished data). Because the calculated survival estimates showed great variation and adequate data were not available for some subpopulations, we used the approximate rangewide mean of 0.50 and chose a standard deviation of 0.20. Therefore, in about 67% of years, survival of this stage fell between 0.30 and 0.70.

[b] Survival from yearling (18 mo) to 2-yr (2.5 yr) stage. In the absence of empirical survival data for this stage, we assumed that survival would be slightly (10%) lower than survival of ≥2-yr-old females in each subpopulation. Standard deviation (SD) was calculated by keeping the coefficient of variation (CV; Sokal and Rohlf 1995) equal to the CV for survival among ≥2-yr-old females (Appendix B).

[c] Mean and SD generated from data on radiocollared females (Appendix B).

[d] In the absence of empirical survival data for this stage in this subpopulation, we estimated the mean and SD by taking the average of values reported in the 2 neighboring groups (San Jacinto Mountains and Santa Rosa Mountains southeast of Highway 74).

[e] Mean and SD calculated from data shown in DeForge et al. 1997.

[f] Reproduction data on young (2- and 3-yr-old) females were not available for all subpopulations (because not all subpopulations included young radiocollared females) so we compared the reproduction of young (2- and 3-yr-old) females with that of older (≥4-yr-old) females on a rangewide basis, and then used this relationship to estimate the mean reproduction of young females in each subpopulation, based on the reproduction of older females in that subpopulation. Rangewide, reproduction by 3-yr-old females was approximately 32% that of ≥4-yr-old females, while reproduction by 2-yr-old females was approximately 22% that of ≥4-yr-old females. Standard deviations were calculated by keeping the CV equal to the CV generated from empirical data on older females (Appendix B).

[g] Mean and SD calculated from data on radiocollared females (Appendix B). Observed reproduction data were divided by 2, to obtain an estimate for female lambs only, assuming an equal sex ratio for lambs (Simmons et al. 1984).

[h] Mean and SD generated from data on radiocollared females and lamb:ewe ratios observed during fall helicopter surveys. Observed reproduction data were divided by 2, to obtain an estimate for female lambs only, assuming an equal sex ratio for lambs (Simmons et al. 1984).

[i] Mean and SD generated from data shown in DeForge et al. (1997), using data from fall surveys only. Observed reproduction data were divided by 2, to obtain an estimate for female lambs only, assuming an equal sex ratio for lambs (Simmons et al. 1984).

[j] Initial population compositions. We used 1994 female population estimates for each subpopulation (DeForge et al. 1995, 1997; Rubin et al. 1998) for the total number of females >1 yr old, and used observed age categories of females to determine the number of females in each age category. In the absence of age composition data for the San Jacinto Mountains, we assumed that all females were ≥4 yr old. We used observed lamb:ewe and yearling:ewe ratios from 1994 surveys to estimate the number of female lambs and yearlings in initial subpopulations.

Appendix B. Survival and reproduction of radiocollared bighorn sheep in the Peninsular Ranges, California, USA, 1993–1998.

Vital rate	Year	Carrizo Canyon	Vallecito Mountains	San Ysidro Mountains S of Rd. S-22	San Ysidro Mountains N of Rd. S-22	Coyote Canyon	Santa Rosa Mountains SE of Hwy. 74	Santa Rosa Mountains NW of Hwy. 74
Annual survival of females ≥2 yr old[a] (animal mo)	1993–1994	0.80 (218)	0.84 (70)	0.82 (59)	0.81 (180)			
	1994–1995	0.75 (171)	0.65 (86)	0.76 (45)	0.92 (140)	0.52 (76)	0.88 (290)	
	1995–1996	0.70 (135)	0.75 (43)	1.00 (36)	0.82 (123)	0.74 (40)	0.65 (228)	
	1996–1997	0.84 (67)	1.00 (36)	1.00 (36)	0.81 (57)	0.67 (30)	0.77 (142)	
	1997–1998	1.00 (47)	0.67 (61)	0.78 (50)	1.00 (66)	0.84 (68)	0.77 (92)	
Reproduction of females ≥4 yr old[b] (no. of females)	1993	0.555 (18)		0.400 (5)	0.692 (13)			
	1994	0.467 (15)		0.600 (5)	0.100 (10)		0.727 (11)	0.333 (9)
	1995	0.200 (10)		0.333 (3)	0.429 (7)		0.750 (8)	0.111 (9)
	1996	0.167 (6)		0.333 (3)	0.571 (7)		0.600 (5)	0.333 (6)

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[a] Methods described in Hayes et al. (2000).

[b] Percentage of females recruiting a lamb to 6 mo of age; methods described in Rubin et al. (2000).