
Captive Breeding and Reintroduction Evaluation Criteria: a Case Study of Peninsular Bighorn Sheep

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Abstract: *Captive breeding and reintroduction programs are rarely evaluated, and assessment criteria vary widely. We used the following criteria to evaluate a bighorn sheep (*Ovis canadensis*) augmentation program: (1) survival and recruitment rates in the captive population, (2) survival of released animals, (3) recruitment of released animals, (4) growth rate of the reintroduced or augmented population, and (5) establishment of a viable wild population. Captive bighorn survival and recruitment was high, averaging 0.98 (SD = 0.05) and 71.0% (SD = 19.4), respectively. Annual survival of free-ranging captive-reared bighorn ($n = 73$, $\bar{x} = 0.80$, SD = 0.11) did not differ ($Z = -0.85$, $p = 0.40$; $n = 14$) from survival of wild-reared bighorn ($n = 43$, $\bar{x} = 0.81$, SD = 0.12). Recruitment was unusually low for both captive-reared ($\bar{x} = 13.7\%$, SD = 0.24) and wild-reared ewes ($\bar{x} = 13.7\%$, SD = 0.20). Although reintroduction did not result in population growth or establishment of a viable population, it helped prevent extirpation of the reinforced deme, preserved metapopulation linkage, and aided habitat preservation. Chronic low recruitment and low adult survivorship precluded achievement of criteria 3-5. Environmental conditions in the release area also appeared to hinder program success. Standard evaluation criteria for ongoing reintroductions allow for informative assessments and facilitate comparisons needed to refine reintroduction science as a recovery tool for threatened or endangered populations.*

Criterios de Evaluación de la Reproducción en Cautiverio y la Reintroducción: un Caso de Estudio del Carnero Peninsular de Montaña

Resumen: *Los programas de reproducción en cautiverio y de reintroducción son ocasionalmente evaluados y los criterios de evaluación varían ampliamente. Utilizamos los siguientes criterios para evaluar un programa de incremento del carnero peninsular de montaña (*Ovis canadensis*): (1) tasas de supervivencia y reclutamiento en la población cautiva, (2) supervivencia de animales liberados, (3) reclutamiento de animales liberados, (4) tasa de crecimiento de la población reintroducida o incrementada y (5) establecimiento de una población silvestre viable. La supervivencia y reclutamiento de los carneros fueron altos, promediando 0.98 (DS = 0.05) y 71% (DS = 19.4), respectivamente. La supervivencia anual de carneros de rango libre obtenidos en cautiverio ($n = 73$, $\bar{x} = 0.80$, DS = 0.11) no difirió ($Z = -0.85$, $p = 0.40$; $n = 14$) de la supervivencia de los carneros silvestres ($n = 43$, $\bar{x} = 0.81$, DS = 0.12). El reclutamiento fue inusualmente bajo tanto para los reproducidos en cautiverio ($\bar{x} = 13.7\%$, DS = 0.24) y las ovejas silvestres ($\bar{x} = 13.7\%$, DS = 0.20). A pesar de que la reintroducción no resultó en un crecimiento poblacional o en el establecimiento de una población viable, ayudó a prevenir la extirpación del deme reforzado, preservó el vínculo metapoblacional y ayudó a la preservación del hábitat. El bajo reclutamiento crónico y la baja supervivencia de adultos imposibilitan el alcanzar los criterios 3-5. Las condiciones ambientales en las áreas de liberación también parecen entorpecer el éxito del programa. Los criterios de evaluación estándar para las reintroducciones en curso permiten evaluaciones informativas y facilitan comparaciones necesarias para refinar la ciencia de la reintroducción como una herramienta de recuperación para poblaciones amenazadas o en peligro.*

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Introduction

We use the term *reintroduction* to refer to the intentional movement of captive-reared animals into a species' historic range to augment or reestablish wild populations. Reintroduction is a widely used conservation tool, having been recommended in 64% of 314 recovery plans for endangered species within the United States (Tear et al. 1993); it is included in recovery efforts for the American bison (*Bison bison*), Arabian oryx (*Oryx leucoryx*), black-footed ferret (*Mustela nigripes*), California Condor (*Gymnogyps californianus*), Mauritius Kestrel (*Falco punctatus*), European wisent (*Bison bonasus*), and red wolf (*Canis rufus*) (Campbell 1980; Conway 1980; Snyder & Snyder 1989; Stanley Price 1989; Phillips 1990; Myers & Miller 1992; Jones et al. 1995). Although guidelines for reintroductions (Griffith et al. 1989; Stanley Price 1991; Kleiman et al. 1994; World Conservation Union/Species Survival Commission Re-introduction Specialist Group 1995) suggest an assessment phase, in which the experiences and results of the program are regularly evaluated, published results of evaluations remain scarce. As recently as 1994, less than half of the projects known to have reintroduced animals had produced assessment information (Beck et al. 1994). Only 29% of 336 bird and mammal translocation programs used marked animals and 16% used radiotelemetry in post-release monitoring (Wolf et al. 1996). The paucity of information on reintroductions is attributed to a failure to monitor released animals, insufficient project duration (Beck et al. 1994), reluctance to report failures, and publications being confined to obscure literature (Sarrazin & Barbault 1996). Because of difficulties with the evaluation and refinement of reintroduction programs, strong arguments exist for improved documentation and development of standard evaluation criteria (Scott & Carpenter 1987; Stanley Price 1991; Beck et al. 1994; Kleiman et al. 1994; Sarrazin & Barbault 1996).

Creating a viable population is the ultimate goal of most reintroductions (Griffith et al. 1989; Caughley & Gunn 1996), but measurable goals for evaluating the short-term progress of ongoing reintroductions have not been established. Most reintroduction evaluations (Griffith et al. 1989; Beck et al. 1994; Wolf et al. 1996) have used criteria for long-term success to evaluate ongoing reintroductions in various phases. In a review of 145 reintroductions, Beck et al. (1994) concluded that only 16 programs (11%) were successful. Beck et al. (1994) defined success as establishment of a wild population of ≥ 500 individuals free of human support, or population viability as determined by a formal genetic-demographic analysis. Releases were not necessarily the factor that contributed most to population growth; other factors may have been more important in population recovery. Because Beck et al. (1994) included programs in various phases, the reported success rate should increase with

time and probably underestimates the value of reintroductions. Furthermore, Beck et al. (1994) did not necessarily assess the reintroduction programs themselves, and their criterion of 500 individuals may be considered arbitrary given the variance in autecology among species (Sarrazin & Barbault 1996). Standard criteria specifically for evaluating ongoing reintroductions would allow more informative program assessments, facilitate the comparisons needed to detect patterns and test general concepts (Stanley Price 1991; Beck et al. 1994; Wolf et al. 1996), and provide guidance for post-release monitoring and reporting. Evaluations also often generate recommendations for improving program effectiveness (Akakaya 1990; Beck et al. 1991; Black et al. 1997; Biggins et al. 1998).

We propose five criteria for periodic evaluation of reintroduction programs: (1) survival and recruitment rates in the demographically and genetically managed captive population are high; (2) survival and (3) recruitment rates of captive-reared animals released into the wild are within the normal range of values for that or similar species; (4) the reintroduced or augmented population has a positive growth rate; and (5) one or more viable wild populations have been established as a result of the reintroduction. Criteria 1–3 are indices of the released animals' ability to contribute to the population. The fourth criterion may or may not be a direct result of population augmentation, but it is an indicator of conditions for the free-ranging population. The fifth criterion is a measure of long-term success that may require years to achieve and may be considered on spatial scales ranging from isolated populations to metapopulations, depending on the program goals. Because the fifth criterion is the ultimate goal of most reintroductions, in some cases reduced progress toward criteria 1–3 (which may be sensitive to management intensity) may be acceptable in exchange for achieving longer-term measures of success.

We used a captive breeding and augmentation program for the endangered desert bighorn sheep (*Ovis canadensis*) population inhabiting the Peninsular Ranges of southern California as a case study for evaluating ongoing reintroductions. Our assessment included documentation of captive propagation and release methods and the survival and reproduction rates of captive bighorn sheep. We compared survival and reproduction rates of post-release captive-reared and wild-reared bighorn and analyzed factors affecting post-release survival.

Peninsular Bighorn Sheep

Peninsular bighorn sheep inhabit the eastern slopes of the Peninsular Ranges from the San Jacinto Mountains in southern California south to the Sierra San Borjas area of Baja California, Mexico (DeForge et al. 1999). As recently as 1974, there were an estimated 1171 peninsular

bighorn within the United States (Weaver 1975). By 1988 they had declined to 570 (Weaver 1989), and by 1996 only 280 remained, distributed in a metapopulation of eight or more demes (Rubin et al. 1998). Bighorn sheep are polygynous breeders, with females ≥ 2 years old typically producing one offspring per year. The lifespan is 10–12 years for males and 12–14 years for females, although in this study we documented a 16-year-old wild ewe with a lamb. Predators of peninsular bighorn include mountain lions (*Puma concolor*), bobcats (*Felis rufus*), and coyotes (*Canis latrans*).

Bighorn sheep in the Peninsular Ranges were listed as threatened by the state of California in 1971 and as endangered by the U.S. Fish and Wildlife Service in 1998 (USFWS 1998). Reasons for the endangered listing include population declines potentially caused by low recruitment, habitat loss and fragmentation, and high predation rates coinciding with low population numbers. Urban development of bighorn habitat and low adult survivorship are among the greatest threats to the metapopulation (USFWS 2000).

History of the Captive Breeding Program

In cooperation with the California Department of Fish and Game (CDFG), the Bureau of Land Management (BLM), and the USFWS, the Bighorn Institute has maintained a captive bighorn population since 1984 (Table 1). Originally, the captive breeding program was a byproduct of disease research on causes of low lamb

survival (DeForge & Scott 1982; DeForge et al. 1982). In 1995 the program was redirected as a formal captive breeding program with the primary goals of safeguarding a sample of the Peninsular bighorn gene pool and producing stock for augmenting and reestablishing wild populations.

Between 1982 and 1998, the Bighorn Institute captured 39 lambs with signs of illness from the Santa Rosa, Jucumba, and In-Ko-Pah mountains for treatment and study. Thirty-three lambs survived: 26 were returned to the wild (some after breeding several years in captivity), and 7 became founders in the captive breeding herd. Healthy wild lambs were captured for breedstock in 1996 (2 females, 1 male) and 1998 (2 females). Two of the four breeding rams were captured as lambs from the northern Santa Rosa Mountains (NSRM), the third ram was captive-born of stock from the NSRM, and the fourth was captured as a lamb from the San Jacinto Mountains. The 18 ewes in the captive breeding program came from several demes and varied in their reproductive success and longevity in the program (Table 2).

Between 1985 and 1998, 74 bighorn were released into the NSRM and three into the San Jacinto Mountains to augment two remnant bighorn demes. Our analysis concerns only bighorn released into the NSRM deme. In 1977 an estimated 90 adult bighorn inhabited the NSRM (Wehausen et al. 1987). By 1982 the population had declined to 60–70 adult bighorn (DeForge & Scott 1982), and in 1985 only 40 remained. Augmentation efforts focused on this subpopulation because of its declining size

Table 1. Adult (≥ 2 years old) bighorn sheep in captivity at Bighorn Institute, sick lambs captured from the wild, and bighorn released into the northern Santa Rosa Mountains, California, 1982–1998.

Year	Adult breeding rams	Adult breeding ewes	Wild sick lambs captured/survived	Captive-reared bighorn released (female, male)
1982	0	0	1/1	0 (0, 0)
1983	0	0	3/3	0 (0, 0)
1984	1	2	4/4	0 (0, 0)
1985	2	5	10/9	1 (0, 1)
1986	3	7	14/12	6 (2, 4)
1987	2	8	3/3	12 (6, 6)
1988	2	9	0/0	5 (2, 3)
1989	2	9	0/0	6 (4, 2)
1990	2	7	1/0	10 (6, 4)
1991	2	6	0/0	6 (4, 2)
1992	2	6	0/0	4 (2, 2)
1993	2	6	0/0	4 (2, 2)
1994	2	6	1/1	6 (4, 2)
1995	2	6	0/0	5 (4, 1)
1996	2	5	1/0	5 (2, 3)
1997	3	6	1/0	3 (1, 2)
1998	3	6	0/0	1 (0, 1)
Total	4 ^a	18 ^a	39/33	74 ^b (39, 35)

^aNumber of different adult breeding bighorn.

^bIncludes a ewe released in 1994 that was excluded from further analyses.

Table 2. Reproductive history of female bighorn sheep bred in captivity at Bighorn Institute, 1985–1998.

Animal	Origin ^a	Year ^b															Total productivity in captivity ^c	Total recruitment in captivity ^d
		1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998			
AME	NSRM	L	L	R												2/2	2/2	
EVE	NSRM	N	N	N	R											0/3	0/3	
AND	NSRM		L	D	L	L	L	D	L	L	L	L	N	R		11/12	9/12	
JUN	BI		N	R												0/1	0/1	
SQU	NSRM	L	L	L												5/4	5/4	
GIM	SSRM			L	LL	L	L	L	L	L	L	L	L	L		13/12	13/12	
MAG	NSRM			L	N	R										1/2	1/2	
CAH	NSRM				L	L	N	L	N	L	N	L	D	N		7/11	8/11	
ENC	NSRM				L	L	R									2/2	2/2	
JAC	JUCM				D	R										1/1	0/1	
CAR	JUCM				D	R										1/1	0/1	
BOR	INKP					L	L	L	N	L	L	N	L	N		7/10	7/10	
INK	INKP					L	L	L	L	L	D	L	L	D	L	10/10	8/10	
HIJ	BI						L	D	R							2/2	1/2	
YAP	BI						D	D	R							2/2	0/2	
ANZ	BI								L	L	D	L	L	R		5/5	4/5	
AZU	CSRM														L	1/1	1/1	
YSI	YSI														L	1/1	1/1	
Production (%)		50	60	80	100	114	86	100	67	100	100	83	83	80	67	84	na	
Recruitment (%)		50	60	60	75	114	71	57	67	100	67	83	83	40	67	na	71	

^a Abbreviations: NSRM, northern Santa Rosa Mountains; SSRM, southern Santa Rosa Mountains; JUCM, Jucumba Mountains; INKP, In-Ko-Pab Mountains; BI, captive born at Bighorn Institute; CSRM, central Santa Rosa Mountains; YSI, San Ysidro Mountains.

^b Abbreviations: L, lamb produced and survived; LL, twins produced and survived; R, ewe released into the wild; N, no lamb produced or stillborn lamb; D, lamb died before December of that year.

^c Productivity is the number of lambs per 100 ewes produced per year.

^d Recruitment is the number of lambs per 100 ewes that lived to December.

and its function in linking the small northernmost peninsular bighorn deme (San Jacinto) to the remaining meta-population.

Methods

Study Area

The Santa Rosa Mountains of southern California are within the Colorado Desert division of the Sonoran Desert (Ryan 1968). Our study occurred in a 70-km² area of the Santa Rosa Mountains northwest of Highway 74. Elevations here reach 1160 m, but bighorn are typically found between the valley floor (90 m) and 675 m. Mean annual temperatures for winter and summer range from 6° to 41° C. Annual rainfall during 1985–1998 varied from 3.4 to 28.5 cm and averaged 12.2 cm (Western Regional Climate Center, Reno, Nevada). Vegetation is dominated by brittlebush–white bursage series, creosote bush series, and creosote bush–white bursage series (Sawyer & Keeler-Wolf 1995). Urban development occurs within bighorn habitat in several locations and fringes the entire northern and eastern boundaries of the NSRM. Bighorn sheep have frequented residential communities along the base of the mountains in the study area since the late 1950s.

Captive Rearing and Release

Between January and July of each year, ewes and their offspring were maintained in a 12-ha enclosure encompassing a rugged hilltop with elevations of 290–355 m. Adult rams were maintained in a similar 3-ha enclosure. In addition to the native vegetation in the enclosures, alfalfa, alfalfa pellets, salt and mineral blocks, and water were provided. A 3.1-m chain-link fence that extended 0.8 m underground with 0.5 m of barbed wire on the top prevented mammalian predators from entering the enclosures and bighorn from escaping. The health and behavior of all bighorn were recorded twice daily. Captive animals were not available for public viewing, and a standardized feeding and observation routine was used to limit exposure to humans. Hematology, serum chemistry, parasitology, serology, and virus isolation tests were performed annually on each captive bighorn. Bighorn captured from the wild were screened for common diseases and isolated ≥ 30 days before joining the captive population. Sick animals were tested and temporarily placed in isolation pens if necessary. Veterinary treatment was provided when deemed critical for survival. Necropsies were performed by Bighorn Institute biologists and veterinarians or the California Veterinary Diagnostic Laboratory Service.

Demographic management of the captive population consisted of maintaining the population within the esti-

mated carrying capacity of the enclosures, with a high female:male ratio. Genetic management included controlling matings to avoid inbreeding and minimize mean kinship (Ballou & Lacy 1995) and obtaining healthy breedstock from demographically secure demes near the anticipated release sites. Captive bighorn were selectively combined for the breeding season during August–December. The parentage of all captive-born offspring was recorded in a SPARKS (Single Population Analysis Records Keeping System; International Species Information System) pedigree. Offspring typically were released as yearlings to avoid managing multiple generations in captivity and reduce problems associated with captivity adaptation.

Before release, all bighorn had health evaluations and were ear-tagged and fitted with mortality-sensing radio-collars. Bighorn were transported by truck 20–45 minutes and released directly into the wild. Within the NSRM, bighorn were released in Bradley Canyon ($n = 60$), east Magnesia Canyon ($n = 6$), and west Magnesia Canyon ($n = 8$). Release locations were usually based on the distribution of free-ranging sheep to encourage rapid integration with wild sheep. Water was provided at the release site for 3–20 days following release.

Sheep born at or captured and raised at the Bighorn Institute were considered captive-reared; all other bighorn were considered wild-reared. Of the 74 captive-reared bighorn released into the NSRM, 49 (22 males, 27 females) were captive-born and 25 (12 males, 13 females) were wild-born lambs brought into captivity for research and rehabilitation at 1–5 months of age. Most of these wild-born lambs were bottle-fed and regularly handled for treatment, so they generally were more habituated to humans than healthy captive-born animals. Most bighorn ($n = 62$: 33 males, 29 females) were released as yearlings; 12 (2 males, 10 females) were released as adults (2–6 years old). The 74 sheep were released in 33 groups of 1–6 sheep during all months of the year except March and December. Three bighorn were recaptured after release because of health or integration problems: one ram with a neurological disease was euthanized after recapture and one ram and one ewe were housed in captivity a short time before being released again. The ram integrated with free-ranging bighorn, so only his second release was included in the dataset. The ewe did not integrate with resident bighorn and was eventually transferred to a zoo; she was excluded from our analysis.

When possible, we observed bighorn for several hours immediately following release to record their behavior and integration with free-ranging sheep. Post-release monitoring involved daily telemetry readings and observations at least twice weekly for 3–25 weeks. During all years, radio signals were monitored at least weekly, and we attempted to observe collared bighorn at least once per month. Radiocollars were fitted on wild-reared sheep

as well, and failed collars were replaced annually by capturing sheep in a drive net or by using a net gun fired from a helicopter. When mortality signals were detected, we located radiocollared animals as soon as possible to determine the cause of death. Population estimates were obtained by monitoring of radiocollared sheep or recognition of individual sheep and by annual helicopter surveys.

Data Analysis

We defined lamb production as the number of lambs born per adult ewe (≥ 2 years old) per year. Recruitment was defined as the percentage of lambs that survived to December (approximately 7–11 months old) per adult ewe per year (i.e., number of lambs per 100 ewes in December). Recruitment for captive-reared bighorn in the wild was reported beginning in 1987, the first year captive-reared ewes ≥ 2 years of age were free ranging in the study area.

We calculated annual bighorn survival for 1985–1998 using the Kaplan-Meier method (Kaplan & Meier 1958), modified for a staggered entry design (Pollock et al. 1989). Bighorn were considered at risk from the month of collaring for wild-reared sheep and from the month of release for captive-reared sheep, until their death, censoring (removal from the dataset with their fate considered unknown), or the end of the study. Male bighorn have higher dispersal rates than females, and no females in this area were known to emigrate permanently in over 12 years of monitoring. Therefore, because of the small population size and our intensive monitoring, we considered ewes with failed radiocollars that disappeared ≥ 2 years after collaring or release to be dead as of their last sighting. Ewes who disappeared from the study area < 2 years after collaring or release and all rams that disappeared from the study area were censored.

We compared survival and recruitment rates of captive-reared and wild-reared bighorn with a Wilcoxon signed-rank test ($\alpha = 0.05$) (Sokal & Rohlf 1995). We compared the value for survival of the first year after release to other values using a t test with a pooled estimate of the standard deviation (Sokal & Rohlf 1995). We used multiple linear regression ($\alpha = 0.05$) (Wilkinson & Coward 1998) to determine the relationship between survival the first year after release (number of weeks lived) and 11 variables. Categorical variables were gender, captive-born or wild-born, release site, release season (January–April, May–August, September–December), and release group size (1–6). Continuous variables were release age (in months), total rainfall 3 months before release, total rainfall 12 months before release, total rainfall 12 months after release, annual survival of the NSRM population during the release year, and population size of the free-ranging herd at the time of release. Several

variables were log-transformed to improve their distributions. To identify a subset of models for further investigation, we used backwards stepwise variable selection with $p = 0.15$. The final model was the most parsimonious that explained the highest amount of variation in first-year survival. All probability values (p) are two-sided.

Results

Captive Bighorn

Survival for yearling and adult captive bighorn combined ranged from 0.89–1.0 and averaged 0.98 (SD = 0.054). No adult bighorn died from natural causes while in captivity, but one terminally ill 14-year-old ewe was euthanized. Three yearlings died in captivity, two from disease and one during transport for release.

Captive ewes had high lamb production ($\bar{x} = 83.6\%$, SD = 18.1) and recruitment ($\bar{x} = 71.0\%$, SD = 19.4) during 1985–1998 (Table 2). Production and recruitment of individual ewes in captivity ranged from 0 to 108%; twins were produced twice (Table 2). Between 1985 and 1998, 71 lambs (30 males, 41 females) were born to ewes ≥ 2 years of age, resulting in a sex ratio at birth of 0.73:1. Eleven of 71 lambs (15.5%) born in captivity and 6 of 39 lambs (15.4%) captured from the wild died in captivity. Lamb mortalities were attributed to disease (65.0%), trauma or peritonitis (17.5%), and undetermined causes (17.5%).

Reintroduced Bighorn

Age and gender influenced the survival of captive-reared bighorn during their first year in the wild. Survival for released yearling and adult bighorn ($n = 73$) 12 months after release was 0.61 (SD = 0.06). First-year survival for females (0.64, SD = 0.08) was higher ($t = 4.4$, $df = 71$, $p < 0.005$) than for males (0.55, SD = 0.09). First-year survival for bighorn released as adults (0.75, SD = 0.13, $n = 12$) was higher ($t = 7.3$, $df = 71$, $p < 0.01$) than for bighorn released as yearlings (0.57, SD = 0.06, $n = 61$).

After the first year in the wild, survival for captive-reared sheep improved substantially. Average annual survival for captive-reared bighorn excluding the first year after release (0.88, SD = 0.09) was significantly higher than survival during the first year after release ($Z = -3.04$, $p < 0.01$, $n = 13$) and survival for wild-reared bighorn during the same time period ($Z = 1.92$, $p = 0.05$, $n = 14$) (Table 3). Overall, survival of captive-reared and wild-reared sheep was similar. Average annual survival of yearling and adult captive-reared bighorn combined during 1985–1998 (0.80, SD = 0.10) did not differ ($Z = -0.8475$, $p = 0.40$; $n = 14$) from survival of wild-reared bighorn (0.81, SD = 0.12) (95% con-

Table 3. Population estimates, number of captive-reared bighorn sheep, and annual survival^a of yearling and adult bighorn sheep in the northern Santa Rosa Mountains, California, 1985–1998.

Year	Fall population estimate of yearling and adult bighorn (ewes)	Number of captive-reared bighorn in the population	Survival of all yearling and adult bighorn (95% CI) ^b	Animal months	Survival of wild-reared bighorn (95% CI) ^b	Animal months	Survival of captive-reared bighorn (95% CI) ^b	Animal months	Survival of released bighorn >12 months after release (95% CI) ^b	Animal months
1985	40 (22)	1	0.70 (0.54–0.86)	313	0.70 (0.54–0.86)	305	1.0 (1.0–1.0)	8	—	—
1986	46 (25)	5	0.87 (0.76–0.99)	335	0.88 (0.76–1.0)	282	0.83 (0.56–1.0)	53	1.0 (1.0–1.0)	12
1987	52 (30)	16	0.90 (0.80–0.99)	439	0.91 (0.80–1.0)	264	0.86 (0.70–1.0)	175	1.0 (1.0–1.0)	44
1988	52 (33)	19	0.90 (0.81–1.0)	451	0.90 (0.77–1.0)	234	0.90 (0.76–1.0)	217	0.93 (0.80–1.0)	145
1989	50 (32)	20	0.72 (0.58–0.86)	406	0.78 (0.59–0.97)	203	0.67 (0.47–0.87)	203	0.87 (0.69–1.0)	152
1990	41 (24)	26	0.77 (0.63–0.90)	357	0.79 (0.57–1.0)	145	0.76 (0.58–0.94)	212	0.92 (0.78–1.0)	152
1991	30 (21)	17	0.75 (0.61–0.90)	296	0.80 (0.55–1.0)	105	0.73 (0.55–0.91)	191	0.86 (0.68–1.0)	154
1992	35 (24)	20	0.89 (0.78–1.0)	309	0.88 (0.65–1.0)	86	0.90 (0.78–1.0)	223	1.0 (1.0–1.0)	165
1993	27 (17)	16	0.64 (0.47–0.81)	270	0.86 (0.60–1.0)	73	0.57 (0.37–0.77)	197	0.70 (0.49–0.91)	165
1994	23 (11)	16	0.64 (0.45–0.82)	218	0.50 (0.10–0.90)	45	0.71 (0.51–0.91)	173	0.70 (0.46–0.94)	134
1995	24 (10)	16	0.82 (0.67–0.97)	238	0.83 (0.54–1.0)	61	0.81 (0.63–0.98)	177	0.90 (0.74–1.0)	127
1996	21 (10)	16	0.75 (0.58–0.91)	248	0.80 (0.45–1.0)	52	0.74 (0.55–0.92)	196	0.77 (0.58–0.97)	148
1997	22 (11)	16	0.78 (0.59–0.97)	237	0.75 (0.33–1.0)	42	0.82 (0.66–0.99)	195	0.85 (0.67–1.0)	156
1998	22 (10)	15	0.89 (0.76–1.0)	222	1.0 (1.0–1.0)	42	0.88 (0.72–1.0)	180	0.93 (0.80–1.0)	166
Mean	—	—	0.79	—	0.81	—	0.80	—	0.88	—

^aSurvival was calculated by the Kaplan-Meier method, modified for a staggered-entry design (Pollock et al. 1989).

^bConfidence interval.

Table 4. Population estimates and recruitment (lambs per 100 ewes in December) for captive-reared and wild-reared female bighorn sheep in the northern Santa Rosa Mountains, California.

Year	No. of ewes ≥ 2 years old			Lambs recruited (percent recruitment)		
	wild reared	captive reared	total	wild reared ewes	captive reared ewes	total
1985	22	0	22	—	—	—
1986	25	0	25	—	—	—
1987	25	5	30	0 (0)	0 (0)	0 (0)
1988	24	9	33	2 (8)	0 (0)	2 (6)
1989	21	11	32	0 (0)	1 (9)	1 (3)
1990	12	12	24	0 (0)	0 (0)	0 (0)
1991	11	10	21	0 (0)	1 (10)	1 (5)
1992	11	13	24	1 (9)	1 (8)	2 (8)
1993	7	10	17	1 (14)	0 (0)	1 (6)
1994	3	8	11	1 (33)	2 (25)	3 (27)
1995	3	7	10	0 (0)	0 (0)	0 (0)
1996	3	7	10	0 (0)	2 (29)	2 (20)
1997	2	7	9	1 (50)	0 (0)	1 (11)
1998	4	6	10	2 (50)	5 (83)	7 (70)
Mean				0.7 (13.7)	1.0 (13.7)	1.7 (13.0)

fidence interval for the difference between means = $-0.07 - 0.10$) (Table 3).

Recruitment was also similar between wild-reared and captive-reared animals. From 1987 to 1998, recruitment for the two groups did not differ ($Z = -0.18$, $p = 0.86$, $n = 12$), averaging 13.7 lambs per 100 ewes ($SD = 0.24$) for captive-reared ewes and 13.7 lambs per 100 ewes ($SD = 0.20$) for wild-reared ewes (Table 4). The release program did not result in growth of the augmented population. Between 1985 and 1998, the NSRM bighorn population declined significantly ($p < 0.01$) from an estimated 40 bighorn to 22 bighorn (Table 3), despite augmentation with 73 bighorn.

Of the 43 wild-reared bighorn monitored during 1985–1998, 21 died, 12 were considered dead, 5 were censored, and 5 were alive at the end of the study period. Cause of death for wild-reared sheep will be reported elsewhere. Of 73 released bighorn, 51 died dur-

ing the study, 7 were censored, and 15 were alive at the end of the study. Twenty-three (45%) of the released bighorn deaths occurred ≤ 6 months after release. Mountain lion predation was the primary cause of death for released bighorn, followed by urbanization (Table 5). Deaths attributed to urbanization included ingestion of toxic, exotic plants (*Oleander* spp. and *Prunus* spp.; $n = 5$) and automobile collisions ($n = 4$). All 4 bighorn that died from urban-related causes ≤ 6 months after release had been released in Bradley Canyon (Table 5). Survival during the first year after release was associated ($F = 3.4$, $df = 2$, $p = 0.01$, $R^2 = 0.17$) with release site and season of release. Releases in Bradley Canyon and east Magnesia Canyon resulted in higher first-year survival than releases in west Magnesia Canyon. Bighorn released in January–April survived better during the first year than those released at other times of the year. We found a weak association ($p = 0.08$) between release-

Table 5. Causes of mortality for captive-reared bighorn sheep released into the northern Santa Rosa Mountains, California, 1985–1998.

Source of mortality	All released bighorn mortalities (%)*	Mortalities occurring ≤ 6 months after release (%)*	Causes of mortality during the first 6 months after release, by release site		
			Bradley	East Magnesia	West Magnesia
Mountain lion predation	29.4	30.4	3	0	4
Other predation	7.8	8.7	2	0	0
Urbanization	17.6	17.4	4	0	0
Possibly urbanization	7.8	17.4	4	0	0
Disease	3.9	4.3	1	0	0
Unknown	33.3	21.7	3	2	0
Mortalities ≤ 6 months after release	NA	NA	17	2	4
Total number of bighorn released	NA	NA	59	6	8

*NA, not applicable.

group size and post-release survival, with a group size of one resulting in the highest survival.

Discussion

Peninsular Bighorn Reintroduction

The peninsular bighorn sheep reintroduction program met two of the five criteria we proposed for assessing ongoing reintroduction programs. High rates of survival and recruitment for captive bighorn compared to free-ranging populations (Wehausen 1992; DeForge et al. 1995, 1997; Hayes et al. 2000) indicated that the program attained the first criterion of success. Similar recruitment rates have been reported for other captive bighorn populations (Calkins 1993; Rominger & Fisher 1997).

Because survivorship for captive-reared, released sheep was within the lower range of reported values for other desert bighorn populations, the second criterion for program success was also met. Annual survival for desert bighorn sheep is typically ≥ 0.80 (Cunningham & deVos 1992; Wehausen 1992); in recent years, however, survivorship of bighorn sheep in the Peninsular Ranges has been lower than that of other bighorn populations, primarily because of high predation rates (DeForge et al. 1997; Hayes et al. 2000). Our data show that urbanization is an additional factor contributing to adult mortality in the NSRM and is therefore hindering program success. Other reintroduction studies have also found substantial human-related mortality in released animals; the primary cause of mortality in reintroduced red wolves (*Canis rufus*) (Phillips 1990) and golden lion tamarins (*Leontopithecus rosalia*) (Beck et al. 1991) was human activity (i.e., automobile collisions, accidental trapping, or theft).

The third criterion of reintroduction success—high recruitment—was not achieved. Perhaps the most striking result of this assessment was the chronic low recruitment of both captive-reared and wild-reared bighorn sheep in the NSRM. Our data on lamb production by free-ranging ewes corroborate the findings of other studies of bighorn sheep (DeForge & Scott 1982; Borjesson et al. 1996), which suggest that low recruitment is caused by neonatal mortality rather than low production. Although in the 1980s disease was common among lambs (DeForge et al. 1982), signs of disease abated during the early 1990s, and the direct and indirect effects of urbanization on bighorn currently appear more important. Predator populations along the urban interface, high and prolonged concentrations of bighorn feeding on lawns (which may facilitate disease transmission), altered maternal behavior of ewes browsing in urban areas, and other urban-related factors appear to have contributed to high lamb mortality. The NSRM is the only

location in the Peninsular Ranges where bighorn frequent urban areas, and recruitment data from neighboring demes (DeForge et al. 1995, 1997; Rubin et al. 2000) suggests that local factors are reducing lamb survival in the NSRM. Achieving the next criteria for reintroduction-program success requires minimizing the effects of urbanization on bighorn and reducing both juvenile and adult bighorn mortality rates.

The reintroduction program did not meet our last three criteria for success because the original cause of decline had not been alleviated and/or an additional limiting factor (urbanization) was operating. Understanding or eliminating the original or existing causes of population decline is imperative for successful reintroductions. As Caughley (1994) pointed out, the Hawaiian Goose (*Nesochen sandvicensis*) reintroduction was unsuccessful because it lacked the diagnostic steps to determine why the population declined originally. Successful conservation entails merging the “declining population paradigm” that involves the cause of population reduction and its cure with the “small population paradigm” that deals with the effect of smallness on population persistence. Reintroduction is a small population paradigm tool that can only help restore populations if the limiting factors have been addressed.

Another benefit of reintroduction-program assessments is the development of specific recommendations for program revisions. For example, survival patterns for released bighorn suggest that first-year survival could be improved. Higher rates of survival in animals released in January–April probably reflect the better forage quality and water availability in the winter and spring seasons. The significance of the release site to first-year survival may be a function of several factors, including the amount of escape terrain near the release site and proximity to free-ranging sheep. Our observations and the gregarious nature of bighorn sheep suggest that integration is key to survival for released animals. The importance of knowledge transfer from experienced to naïve animals has been recognized (May 1991; Tear et al. 1997); other studies have found that releases to augment populations were more successful than releases into vacant habitat (Black et al. 1997; Maxwell & Jamieson 1997; Sanz & Grajal 1998). Bradley Canyon had the most escape terrain near the release site and almost always contained free-ranging sheep, but it was also within 200 m of the urban-mountain interface where at least four sheep later died from urban-related causes. Releases were least successful in west Magnesia Canyon, an area that provided high-quality forage but little escape terrain and was infrequently used by free-ranging sheep in recent years. Our results suggest that releasing bighorn near the urban interface may increase their vulnerability to urban-related mortality factors, and releasing bighorn in habitat with little escape terrain or few conspecifics may increase their risk of predation (Table 5).

Predation strongly influenced the survival of released animals; during 1992–1998, however, predation was also the most frequent cause of death for six other bighorn demes in the Peninsular Ranges (Hayes et al. 2000). While in captivity, bighorn reacted to coyotes near the enclosure, but they had no known experience with mountain lions, and translocated animals probably have less knowledge of escape terrain. Wolf et al. (1996) found that predation on released animals was not significantly greater among captive-reared animals than among wild-reared, translocated animals. This perhaps indicates that habitat familiarity is more important than experience with predators. High rates of predation on translocated bighorn (Rowland & Schmidt 1981) further support this hypothesis. For captive-reared bighorn, the occurrence of most first-year mortalities (82%) within 6 months after release and the high rates of survival of released animals beginning the second year after release indicate that animals gain critical survival knowledge during the first year in the wild. Accordingly, even temporary predator control before and during the first year of a release may improve post-release survival.

Although rates of survival of bighorn released as adults were significantly higher than those of bighorn released as yearlings, release age was not a significant factor in our regression analysis of first-year survival. Releasing captive-reared bighorn at ≥ 2 years of age would likely increase first-year survival, but release age may influence whether released bighorn establish their own home range, as found by Roy and Irby (1994), or adopt that of the existing population. We suggest that releasing yearling bighorn promotes the transfer of traditional knowledge of home-range use, which presumably aids population persistence.

When reintroductions are evaluated, indirect benefits of the project also warrant discussion (Kleiman 1989). By 1996, >70% of the NSRM population was captive-reared (Table 3), so we assume that the population would have been extirpated without augmentation. Maintaining bighorn in the NSRM has provided a stepping stone for ram movements through the metapopulation (DeForge et al. 1997), time to research the cause of decline, and opportunities for public education. Because NSRM bighorn are often visible to the public and frequently have been featured in the media, they have served as an important flagship species for habitat conservation.

Assessing Ongoing Reintroduction Programs

We presented five criteria for evaluating ongoing reintroduction programs, which also provide a guide for post-release monitoring and reporting of results. Although few reintroductions have established viable populations (Beck et al. 1994), in most cases reasons for program failure are unknown: are captive animals not re-

producing, are released animals not surviving, or is the original cause of decline still suppressing the population? The criteria we present allow assessment of ongoing programs and identification of the causes of reintroduction failure, and they promote adaptive management. Case studies and reviews thus far suggest that local community involvement and public education are associated with successful projects (Beck et al. 1994) and that successful reintroductions often require many years (Griffith et al. 1989, Beck et al. 1994). Further comparative analyses will allow additional generalizations regarding successes and failures of reintroductions, resulting in a more refined and useful tool for preserving biodiversity.

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