POPULATION DYNAMICS OF PENINSULAR BIGHORN SHEEP IN THE SANTA ROSA MOUNTAINS, CALIFORNIA, 1983-1994

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Abstract: Fall (1983-1994) helicopter surveys of Peninsular bighorn sheep (Ovis canadensis cremnobates) in the Santa Rosa Mountains (SRM) of Southern California were used to determine annual population estimates and dynamics. Age structure and sex ratio data, as well as maintenance recruitment ratios for population stability, were also examined. During these 12 years, ram:ewe:lamb:yearling ratios averaged 44.9:100:25.2:17.4. Long-term suppressed recruitment following a disease epizootic in the late 1970s caused a 69.1 percent population decline from 374.0 ± 10 adult bighorn in 1984 to 115.5 ± 24 in 1994. Spatial analysis showed that the decline occurred throughout the SRM. The bighorn population decreased at an average annual rate of 17.8 percent from 1984 to 1990, then stabilized at a density of only 0.15 bighorn/km^2.

Key Words: Chapman estimator, demography, helicopter survey, Ovis canadensis cremnobates, Peninsular bighorn, population dynamics, population estimate, recruitment, Santa Rosa Mountains.

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INTRODUCTION

The Santa Rosa Mountains (SRM) of Riverside and San Diego counties once were thought to support the largest and densest desert bighorn sheep (Ovis canadensis) population in California (Weaver and Mensch 1970). This range comprises 48 percent of the current and historic Peninsular bighorn (*O.c.* cremnobates) habitat in the United States (Peninsular Ranges Coordinated Bighorn Sheep Metapopulation Ecosystem Plan, September 22, 1995 Draft). Field studies, waterhole counts, or helicopter surveys (beginning in 1977) provided the basis for subjective bighorn population estimates of 350 in 1953 (Jones et al. 1957), and 500 bighorn in 1967 (Blong 1967), 1970 (Weaver and Mensch 1970), and 1974 (Weaver 1975) in the SRM. In 1970, the Santa Rosa bighorn population was described as stable or possibly increasing, with good recruitment (Weaver and Mensch 1970). However, since 1977, a population decline has occurred in this range, correlated with a disease epizootic causing high lamb mortality (DeForge and Scott 1982, DeForge et al. 1982, Wehausen et al. 1987, Elliott et al. 1994). A fall lamb:ewe ratio of only 11.1:100 was documented for the SRM in 1977, with subsequent years producing similarly low recruitment ratios (DeForge et al. 1982, DeForge and Scott 1982, DeForge 1984, Wehausen et al. 1987). From geographic analysis of pathogen exposure frequencies of bighorn sheep in California, Elliott et al. (1994) found that the southwestern region of the state, occupied by the Peninsular populations, had the highest prevalence values for a majority of the individual pathogens tested for, and the highest level of multiple pathogen exposure.

Peninsular bighorn sheep have been classified as Rare, and then Threatened, by the California Fish and Game Commission since 1972, and were formally proposed for listing as a federally endangered species by the U.S. Fish and Wildlife Service in 1992 (1992 Federal Register, Vol. 57, 90:19837-19843). As part of a comprehensive bighorn demography study and investigation of the population decline documented in the SRM, we conducted annual fall helicopter surveys from 1983-1994 and additional spring surveys from 1983-1986. These surveys were designed to collect demographic and distribution data. Here we examine the dynamics of population size, recruitment, age structure, and sex ratios for the SRM as a whole and spatially from 1983-1994.

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STUDYAREA

The SRM extend 56 km southeast from Palm Springs, California, into Anza-Borrego Desert State Park (Figure 1). Ranging in elevation from 75-2657 m, the SRM are the westernmost extension of the Colorado Desert division of the Sonoran Desert (Ryan 1968). Topography varies from low hills to steep, rocky escarpments and eroded canyons, creating much desirable bighorn habitat. Toro Peak (2657 m) is the highest peak in the SRM; however, bighorn are usually found below 1212 m (Weaver and Mensch 1970). Natural springs are scattered throughout the range, with perennial water most abundant in the central portion. Land ownership in the SRM is in a checkerboard pattern shared by the private sector, the Bureau of Indian Affairs, the Bureau of Land Management, the State of California, the U.S. Forest Service, and city and county governments. Bighorn habitat in the northern SRM (north of Highway 74) is fringed with urban development. Since 1985, a total of 60 (28M, 32F) adult Peninsular bighorn have been released from captivity (Bighorn Institute, Palm Desert, California) into the northern end of the SRM to augment a declining subpopulation in this portion of the range. The southern end of the range, which extends into Anza-Borrego Desert State Park, is more secluded from urbanization, but is frequented by hikers.

Dominant plant species in bighorn habitat include creosote bush (Larrea tridentata), brittle-bush (Encelia farinosa), burro-bush (Ambrosia dumosa), golden cholla (Opuntia echinocarpa), buckhorn cholla (0. acanthocarpa), barrel cactus (Ferocactus acanthodes), agave (Agave deserti), and Mojave yucca (Yucca schidigera) (DeForge and Scott 1982). Annual rainfall is highly variable, with averages for 1983-1994 of 19.8 cmlyr at Anza-Borrego Desert State Park in the southern end of the range, and 15.5 cmlyr at the University of California Boyd Deep Canyon Desert Research Center in the northern portion of the range (Western Regional Climate Center, Reno, Nevada 1994).

METHODS

Annual fall surveys of the SRM were conducted on consecutive days in mid to late October from 1983-1994 with the exception of 1987 and 1994, when due to logistical constraints, a part or all of the surveys were performed in early November. In 1983-1986, additional surveys were conducted in late April to mid-June. Surveys were initiated in the south end of the range and proceeded north, systematically flying all potential bighorn habitat. The range was divided geographically into three main sampling units: 1) southern: Anza-Borrego Desert State Park; 2) central: north of Anza-Borrego Desert State Park, including Dead Indian Canyon; and 3) northern: north of Dead Indian Canyon. This 765 km2 area was flown at 100-150 m contour intervals, up to approximately 1750 m elevation, following the same basic flight pattern each survey. We used a Bell 206B-3 helicopter during 1983-1986 and a Hughes 500-D after 1986. One pilot flew the 1983-1985 surveys, a different pilot was used in 1986, and a third pilot was used for the eight most recent fall surveys. Three observers accompanied the pilot at all times, and the doors of the helicopter were removed to facilitate optimum visibility. Observers were rotated as needed at 1.5-2.0 hour intervals to reduce fatigue. As many of the same, experienced observers as possible were used on the surveys to maximize sighting probabilities and classification accuracy. Survey length varied from 10.0 to 17.5 hours ($\bar{x}$=13.7, SD=2.1), resulting in flight intensities of 0.8 to 1.4 min/km^2.

Data collected included group size, sex and age classification, location, and elevation. When bighorn were sighted, the helicopter was maneuvered to ensure accurate counting and classification. We used a modified version of Geist's (1971) classification system (Class II-IV rams, ewes, yearling males, yearling females, and lambs). Bighorn locations were recorded on topographic maps at the time of the sighting.

Chapman Estimator

We used Chapman's (1951) modification of the Lincoln-Petersen estimator of population size because it assumes sampling without replacement (Seber 1970, 1973) and is recommended for use with two capture occasions (White et al. 1982). Annual adult bighorn population estimates ($\hat{N}$) were determined from fall surveys using Chapman's estimator as:

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

with the following approximately unbiased estimate of variance:

$$var(\hat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2 (m_2 + 2)}$$

where n_1 is the number of adult animals marked, n_2 is the total number of adult animals observed, and m_2 is the number of adult marked animals observed during the survey. We constructed 95 percent confidence intervals as $\hat{N} \pm (1.96)$ SE, where SE = var $(\hat{N})^{0.5}$. Assumptions of the mark-resighting technique are: (1) marked and unmarked animals have equal sighting probabilities; (2) marked and unmarked animals are correctly classified; (3) marked animals are randomly distributed throughout the population, or at least resighting effort is randomly distributed throughout the population; (4) each animal has an equal and independent probability of being resighted; (5) the number of marked animals in the population is known; and (6) the population is geographically and demographically closed (Bear et al. 1989).

From 1983-1992, radio-collared bighorn (Table 1) in only the northern Santa Rosa Mountains (NSRM) were available for use as marked animals (n_1) for determining population estimates. In 1993, four of the collared bighorn were in the southern end of the range, and in 1994, 42 collared bighorn were distributed throughout the SRM. The number of marked bighorn in the study area was confirmed by radiotelemetry prior to surveys.

We used the Chapman estimates for all subsequent analyses requiring population estimates, and 1984 was used as the initial year in long-term trend analysis in an effort to avoid fluctuations caused by sampling variation in the early years of this study. The 1986 estimate was dismissed as an outlier because only 32.3 percent of the collared sheep were observed, which is outside the 99.9 percent confidence interval for the proportion of collared sheep seen in all other years. Density was calculated using the total area surveyed (765 km^2) and catch per unit effort (CPUE) was calculated as the number of adult bighorn seen per hour of helicopter survey time. Population age structure was determined from ram size/age classes. Annual ewe population estimates were determined using the Chapman estimator and the number of collared ewes seen each survey.

Comparison Population Estimates

To create a bound for our Chapman estimates, annual bighorn population estimates were also calculated using three other methods (Table 2). First, to increase the sample size of marked animals in the Chapman estimator, we used the known number of adult bighorn, both marked (collared) and unmarked, in an intensively monitored subpopulation in the NSRM, as the "marked" (n_1) individuals. Second, the cumulative general correction factor (CGCF) of 1.831, determined from the total number of collared animals seen compared to the total number of collared animals present for all 12 years combined, excluding 1986 (183/335), was applied to the total number of adult bighorn seen in each of the surveys. Third, we generated population estimates using the 1994 general correction factor (GCF) of 1826 when sheep were collared throughout the range.

Spatial Analysis

The northern, central, and southern SRM were examined separately to determine the extent of the decline and differences in demography in each geographical sampling unit. These subunits were delineated to separate regions in the farthest southern and northern extensions of the range in which regular ground monitoring of bighorn subpopulations has been conducted, as well as to distinguish the NSRM as the only region where augmentation has occurred within the SRM.

Annual population estimates were calculated for the three sections using the Chapman estimator equation with the number of adult bighorn seen in the Sampling area and the proportion of collared bighorn seen during the entire SRM survey each year. We were unable to determine confidence intervals due to small sample sizes. Densities were determined using the following area estimates: northern, 148.1 km^2; central, 428.6 km^2; and southern, 188.3 km*. The Friedman test (Hollander and Wolfe 1973) was used to test for statistical differences in lamb:ewe ratios among areas.

RESULTS

A total of 1556 bighorn were recorded in 164.3 hours of flight time during the 1983-1994 fall surveys. The number of bighorn observed per survey varied from 209 in 1984 and 1986, to 73 in 1990 (Table 1). Bighorn were seen at elevations between 33-1676 m, in group sizes varying from 1 to 16 ($\bar{x}$=3.3, mode=1). Excluding 1986, an average of 54.4 percent of the collared sheep were observed each survey, (SD=12.2, range=45.8 percent to 69.9 percent). Since 1984, an average of 58.1 percent of all collared ewes and 50.0 percent of all collared rams were observed each year. Coefficients of variation for individual population estimates, excluding 1986, ranged from 10.6 percent to 19.4 percent ($\bar{x}$=14.0, SD=2.8). All four techniques used to estimate the SRM bighorn population produced similar numbers and trends (Table 2).

Population Trend

From 1984-1994, the SRM population showed two phases: the decline phase up to 1990, with an annual decline rate of 17.8 percent, and the stable phase from 1990-1994 (Figure 2). Chapman adult population estimates declined 69.1 percent from 1984 to 1994. Similarly, the total number of adult bighorn observed per survey and CPUE declined 64.2 percent and 53.3 percent (Figure 3), respectively, over the same period and the number of ewes seen per survey dropped 67.9 percent from 131 to 42 (Table 1). The number of ewes seen each survey decreased at a rate of 17.3 percent per year between 1984 and 1990, whereas this number increased at 0.6 percent per year from 1990-1994. The trend of the ewe population estimates corresponds with the trend of the entire adult bighorn population (Figure 2). Estimated bighorn sheep density declined from 0.49 bighorn/km^2 in 1984 to 0.15 bighorn/km^2 for 1990-1994.

Recruitment

Fall lamb:ewe ratios for the SRM ranged from 12.8 to 51.3 lambs:100 ewes ($\bar{x}$=25.2, SD=10.6) for 1983-1994 (Figure 4). Between 1983 and 1990, lamb:ewe ratios varied greatly but were generally low, averaging 21.3:100. Lamb:ewe ratios were considerably higher from 1991-1994, and averaged 32.8:100 (Table 1). Our 1983-1986 fall surveys produced an average lamb:ewe ratio of 25.4:100 (SD=6.9), 39.5 percent lower than the average of 42.0 lambs:100 ewes (SD=6.0) from spring helicopter surveys in those same years. The SRM averaged only 17.4 yearlings:100 ewes (range=5.2 to 33.3, SD=9.6) for 1983-1994 fall surveys, with the trend following the same pattern as fall lamb:ewe ratios (Figure 4). However, the lack of rams classified as yearling age in 1983 or 1984, and the unbalanced cumulative yearling ram:yearling ewe ratio of 150.0:100 implies that classification error may have occurred.

Age Structure

Size/age classes of rams averaged 19.3 percent (SD=14.3) yearling, 24.2 percent (SD=5.8) Class II, 25.8 percent (SD=12.4) Class 111, and 30.8 percent (SD=9.9) Class IV, over the 12 years (Figure 5). In 1985-1989, 40.0 to 47.6 percent of the rams observed during the surveys were yearling or Class II; whereas, in 1990 only 19.2 percent of the rams were in these size classes. The percentage of young rams (yearling or Class II) steadily increased from 36.8 percent in 1991 to 76.2 percent in 1994 (Figure 5).

Sex Ratios

Ram:ewe ratios ranged from 27.8:100 to 61.5:100 ($\bar{x}$=44.9, SD=10.0) for the 1983-1994 fall surveys (Table 1). During the 1983-1990 decline period, ram:ewe ratios averaged 49.7:100, while within the stabilization period they averaged 35.2:100 from 1991-1994. For 1983-1986, fall ram:ewe ratios averaged 44.4:100, while spring surveys averaged 35.8:100. In all fall surveys combined, 61.5 percent of all group sightings contained mixed sexes of adult sheep (31.3 percent of all sightings were single sheep) and 75.8 percent of all rams seen were with ewes.

Spatial Analysis

A comparison of the 1984 and 1994 fall estimates for each geographic sampling unit revealed population declines of 77.2 percent in the southern end of the SRM, and 71.1 percent in the central portion, but only 35.3 percent in the NSRM where 10 years of population augmentation has occurred (Figure 6). If the augmented bighorn existing in 1994 are excluded, the decline for the NSRM would be at least 81.3 percent, (assuming that no offspring were recruited from augmented sheep). Comparing density from 1984 to 1994, the southern section had the largest decline (76.7 percent) from 0.60 bighorn/km^2 to only 0.14 bighorn/km^2, unless augmented bighorn are excluded from the NSRM resulting in an 82.8 percent decline in density over the 11 years, from 0.29 to only 0.05 bighorn/km^2 in 1994. Bighorn density in the central SRM declined 34.1 percent, from 0.44 in 1984 to 0.15 bighorn/km^2 in 1994. During the stabilization period from 1990-1994, the Southern Santa Rosa Mountains (SSRM) had the lowest mean density of the three regions, at 0.12 bighorn/km^2 (range=0.08 to 0.16).

Density remained the most stable in the central SRM during those 5 years, ranging from 0.13 to 0.16 bighorn/km^2 ($\bar{x}$=0.15). With augmented bighorn included, the NSRM maintained the highest mean density from 1990-1994 of 0.21 bighorn/km^2 (range=0.17 to 0.30).

Lamb:ewe ratios for the central and southern SRM averaged 30.6 (SD=11.3) and 27.6 lambs:100 ewes (SD=13.3), respectively, whereas, the NSRM averaged only 12.0 lambs:100 ewes (SD=11.9) for the 1983-1994 fall surveys (Figure 7). These differences were statistically significant (X^2 = 11.79, P=.003). Yearling:ewe ratios averaged the highest in the central portion of the range at 18.4:100 (SD=13.1), followed by the south end at 15.9:100 (SD=13.2), with the NSRM being lowest at 7.2:100 (SD=8.5) when augmented yearlings are subtracted.

Average ram:ewe ratios for the different geographic subunits increased north to south with 30.5 rams:100 ewes (SD=14.9) in the NSRM, 47.8 rams:100 ewes (SD=12.7) in the central SRM, and 50.4 rams:100 ewes (SD=18.0) in the south. The largest decrease in ram:ewe ratios from 1984-1994 occurred in the SSRM from 51.5:100 down to 9.1:100, when only one adult ram was seen in 1994–the lowest number of rams seen in any one section during our surveys.

DISCUSSION

Population Estimators and Model Assumptions

Any bias caused by violation of mark-resight assumptions (Otis et al. 1978) in this study was considered negligible. Although marked animals were not randomly distributed throughout the population in all years, we attempted to distribute our resighting effort evenly by surveying all potential bighorn habitat, and following the same flight pattern each year. The similarity of habitat, bighorn distribution, and survey intensity in the NSRM compared to the rest of the range, allowed us to make the important assumption that sighting probabilities are the same throughout the SRM. Because we had the largest number of collared animals in 1994 and they were distributed throughout the range, we consider this our most accurate survey. The semblance of the 1994 GCF and the CGCF suggests that having collared animals only in the NSRM from 1983-1992 did not significantly bias our population estimates and further indicates that sighting probabilities were uniform throughout the SRM. If age and sex classes have unequal and dependent resighting probabilities due to different behavioral responses to overflight, then the lack of a random sample of marked animals will affect the bias or precision of the estimator (Bear et al. 1989). Our marked animals were predominantly ewes; however, the average percentage of marked rams and ewes observed each year from 1984-1994 differed by only 8.1 percent.

The precision of mark-resight population estimates relies primarily on three parameters: 1) the number of marked animals in the population, 2) the proportion of marked animals resighted, and 3) the number of resighting flights (Bear et al. 1989, Brower et al. 1990). White et al. (1982) stated that the most effective means of improving the precision of an estimate is to increase the sample size, which we accomplished by using the known number of bighorn in the NSRM as the number of "marked" individuals in the Chapman estimator (Table 2). The CGCF was another technique used to increase sample size, but this method assumes that the survey intensity and sighting probabilities were constant over all years. Although these assumptions were violated, the CGCF population estimates provided a useful comparison that averaged the correction factors associated with our population estimates due to sampling variation. We were able to adequately satisfy the assumptions for the mark-resight technique, and the conformity of the comparison estimates (Table 2) shows the robustness of our Chapman estimates. As White et al. (1982) suggested for reliable scientific studies, all coefficients of variation for individual population estimates, excluding 1986, were <20 percent.

Population Trend

Although oscillations are present, the overall trend of our data from 1983 to 1994 shows that the SRM Peninsular bighorn population declined significantly and then stabilized (Figure 2). Substantial fluctuations in population estimates occurring in 1983-1987 (Table I) may be attributed more to sampling variation due to the new pilots and aircraft used, than to actual changes in the population. The decline indicated by the Chapman estimates from 1989 to 1990 may have been falsely exaggerated due to potentially high estimates in 1988 and 1989. Additionally, the 95 percent confidence limits for the 1989 and 1990 population estimates almost overlap (Table 1), showing that the actual population may have not changed as much as the $\hat{N}$ values alone indicate for those 2 years.

Compared to past SRM estimates and Arizona's average 0.38-0.69 bighorn/km^2 (Remington 1993), the current stabilized bighorn density of 0.15 bighorn/km^2 in the SRM is low. In 1970, when density was approximately 0.66 bighorn/km^2 in the SRM, Weaver and Mensch (1970) referred to this range as some of the best and most important bighorn habitat in California. Potential outcomes of disease(s) causing high lamb mortality are: (1) a reduced carrying capacity; (2) periodic disappearance causing substantial population dynamics; and/or (3) population extirpation (Anderson and May 1979, May and Anderson 1979, Wehausen 1992). Further monitoring will help to determine if the SRM population is capable of increasing to its previous level of approximately 500 animals.

Recruitment

An estimate of the number of lambs surviving to yearling age can aid in predicting population dynamics and determining which segment(s) of a population is/are most susceptible to the active mortality factors (Caughley 1977, Hansen 1980, Remington 1993). The period of depressed recruitment during our study (1983-1990) appears to be a continuation of the low recruitment documented in the SRM since 1977, when an apparent disease epizootic occurred (DeForge and Scott 1982, Wehausen et al. 1987). The SRM fall lamb:ewe ratios obtained through helicopter surveys from 1977-1982 ranged from 8.5 to 28.6:100 and averaged 15.7 lambs:100 ewes (DeForge and Scott 1982). In what may have been the conclusion of a disease epizootic, and/or a density dependent response following 14 years of poor recruitment, the population stabilized and recruitment ratios improved.

Suppressed recruitment is expected following a pneumonia episode in bighorn sheep (Onderka and Wishart 1984, Foreyt 1990). Clinically healthy bighorn can shed pathogens and transmit disease to offspring, but the rate of shedding probably diminishes over time (Foreyt 1990). Additionally, there appear to be host-parasite specific threshold densities, below which the disease cannot persist (Anderson and May 1979, May and Anderson 1979). Serological evidence of viral exposure, as well as isolation of parainfluenza-3 (PI-3), bluetongue (BT), epizootic hemorrhagic disease, and contagious ecthyma viruses from wild-caught, sick lambs from throughout the SRM, has been documented (Bighorn Institute unpublished data). Seemingly healthy, free-ranging adult bighorn in the SRM have yielded serologic titers to these four viruses, as well as isolation of PI-3 virus and BT virus (DeForge et al. 1982; DeForge and Scott 1982; Turner and Payson 1982a, b; Bighorn Institute unpubl. data). The diseases that suppressed recruitment in the SRM may have shown a regulatory function through their abatement at the lower population density maintained from 1990-1994.

Subjective recruitment data (gathered through a combination of hiking, waterhole counts, and helicopter surveys) available since 1953 for the SRM (Wehausen et al. 1987), combined with data from this study, suggest a long-term cyclical pattern: at least 9 years of suppressed recruitment from 1953-1961, 15 years of stable or increasing recruitment from 1962-1976, 14 years of low recruitment from 1977-1990, and 4 years of stable or increasing recruitment from 1991-1994.

Witham (1983) suggested lamb mortality in southwestern Arizona is minimal from December-March, highest in April-June and September, and variable in October-November. Our data from spring and fall surveys in 1983-1986 indicate that significant lamb mortality occurs between April and October. High spring and summer lamb mortality make fall helicopter surveys preferable over spring surveys for obtaining accurate recruitment ratios (Russo 1956, McQuivey 1978, DeForge and Scott 1982, DeForge et al. 1993).

Maintenance Recruitment Ratios

Assuming that lamb survival is a driving force for population trends, some investigators have calculated minimum recruitment levels needed to maintain stable bighorn populations (McQuivey 1978, Wehausen et al. 1987, Remington 1993). McQuivey (1978) calculated 26.5 lambs:100 ewes as the requirement for a static population in Nevada by assuming equal sex ratios at birth and estimating annual ram mortality. However, this method depended on accurately aging rams from a helicopter, and the unsupported assumptions of a stationary age distribution with almost no bighorn mortality between fall lamb and yearling age. Maintenance recruitment ratios are dynamic and fluctuate with mortality rates; they should be used with caution, especially when extrapolating to other populations or time periods. Our 12 years of data illustrate this.

Data from the NSRM in 1977-1982 suggested that 17.5 lambs:100 ewes were needed to maintain a stable ewe population (Wehausen et al. 1987). From 1984-1994, the Santa Rosa bighorn population averaged 25.8 lambs:100 ewes, yet the ewe population declined 74.0 percent with a similar decline of 69.1 percent for the entire adult bighorn population. Clearly, a considerably higher recruitment ratio would have been necessary to maintain a stable bighorn population during this time period.

We applied a method used by Wehausen et al. (1987) for estimating the annual recruitment needed to maintain a constant ewe population based on the assumption of equal sex ratios at birth and compensating for change in the ewe population. Our 1984-1994 data indicate a 12.6 percent annual ewe decline rate (Wehausen et al. 1987 found a 3 percent annual decline rate for ewes during the 1977-1982 period). To adjust for the assumed 50 percent male lambs at birth, the 12.6 percent annual decline in the ewe population is doubled, resulting in a 25.2 lambs:100 ewes compensation factor. Adding this to the average lamb:ewe ratio from 1984-1993 of 23.2 lambs:100 ewes shows that an annual fall recruitment ratio of 48.4 lambs:100 ewes was needed to maintain a stable ewe population in the SRM during those years, assuming that all lambs survive to yearling age. Because minimum recruitment levels needed to maintain a population will change as mortality rates change, we found it more accurate to calculate minimum recruitment ratios for three separate time periods. The 18.0 percent annual decline in the ewe population from 1984-1988 resulted in a 62.1 lambs:100 ewes maintenance recruitment ratio, while the 28.0 percent per year ewe population decline in the 1988-1990 period would have required 73.5 lambs:100 ewes to retain stability. The ewe population increased an average of 2.5 percent annually from 1990-1994, producing a maintenance ratio of only 18.2 lambs:100 ewes.

Yearling survival, or more precisely the percentage of fall lambs surviving to the subsequent fall, is also an important factor to be considered for population analysis, since mortality has been shown to be higher for the period from lamb to yearling than after yearling age (Cunningham et al. 1993). Our data from the SRM suggest that yearling mortality is significant and should be considered when determining minimum recruitment levels needed to maintain a stable bighorn population. Actual fall lamb:ewe ratios necessary to balance adult mortality must be higher than those calculated above and by Wehausen et al. (1987). Due to the difficulty of accurately classifying yearlings from a helicopter, we did not determine a correction factor to compensate for yearling mortality.

Age Structure

Prior to 1991, the SRM had an abundance of old animals and a corresponding lack of young, typical of a population declining from poor recruitment. More recently, the population has shown an increasing proportion of young animals, characteristic of a growing population. Yearlings were the largest percentage of rams in 1992-1994, corresponding with increased lamb:ewe ratios for 1991-1993. However, the concurrent marked decrease in Class IV rams after 1991 may have partly caused the increased percentage of yearling rams in 1992-1994. Although the actual number of rams in all age classes continued to decline over the 12-year period, the shift in age structure after 1990 suggests that ram numbers may soon stabilize or increase, matching the recent trend of the ewe population.

Sex Ratios

Bighorn sheep sex ratios vary greatly, ranging from 36-137 rams:100 ewes for 18 studies in 7 localities within the United States (Buechner 1960). During the rut in 1977, the estimated 64 rams:100 ewes in the NSRM was considered consistent with other unhunted bighom populations (Wehausen et al. 1987). Our average ram:ewe ratio (44.9:100) appears low for an unhunted population where poaching is not known to be a substantial problem. The 1989-1990 peak in ram:ewe ratios suggests that the mortality agent(s) in that time period may have more profoundly affected the female segment of the population. The lower average ram:ewe ratio from 1991-1994 (Table I) reflects that while the actual numbers of rams seen during the surveys had continued to decline, the number of ewes seen per survey ceased to decline after 1990.

Assuming equal sex ratios for lambs, variances in sex ratios of adult bighom are a result of differential mortality between rams and ewes, and sheep behavior and movement patterns favor female survivorship (McQuivey 1978). Despite some potential classification error, our 1983-1994 cumulative fall yearling ram:yearling ewe ratio of 150.0:100 is very high compared to the adult ram:ewe ratio of 44.9 for the same time period. This suggests that considerable ram mortality is occumng during the first 2 years of life, when mortality factors typically increase due to changes in social behavior and expanded movements associated with the rut. The fact that rutting movement occurs during periods of high ambient temperatures, low water availability, and reduced forage quality, and that movement renders bighorn more susceptible to disease exposure, predation, and accidents (particularly in areas bordered by urbanization), could partly account for the low ram:ewe ratio in this mountain range. From 1991-1994 alone, four rams and three ewes are known to have been struck and killed by automobiles in the NSRM, and six out of seven of these deaths occurred during the rut (Bighorn Institute unpubl. data). Sampling error in the form of missing ram pastures during the surveys could also potentially contribute to a low ram:ewe ratio, although the high proportion of mixed sex sightings suggests that our surveys were conducted in the height of the rut, when the number of ram bachelor groups would have been minimal. Overall, sex ratios from our survey data (Table 1) suggest that ewes in the SRM have higher adult survivorship than rams.

Spatial Analysis

We recognize that the assumptions for the Chapman estimator were violated when it was used for calculating regional SRM population estimates. However, this estimator provided an annual correction factor to adjust for sampling variation and produced results that could be analyzed for changes in trend, while maintaining consistency with annual estimates for the entire SRM population.

The declining trend from 1984 through 1990 and the following stabilization are apparent in all three regions, but the changes occurred in varying degrees in each area (Figure 6). The augmented NSRM population remained substantially more stable over the years than the other regions, although it gradually declined despite the addition of 60 adult bighorn. The two major highways bordering this portion of the range, and the urbanization at its northernmost extension, create a higher potential for human-related bighorn mortalities than in the other regions. While the NSRM were maintained at a higher density, the southern and central portions of the range both stabilized at densities near 0.15 bighorn/km^2. Lamb:ewe ratios were the highest for all survey years in all three areas in 1994, perhaps indicating an increasing population trend for the entire SRM if recruitment can more than replace adult mortality.

CONCLUSION

We have shown the dynamics of a bighorn population exhibiting low recruitment for a prolonged period following a disease epizootic, which resulted in a 69.1 percent decrease in the adult population. Long-term depressed recruitment (1977-1990) led to an old age population with characteristic high adult mortality. Improved recruitment after 1990 caused the age structure to gradually shift to one dominated by younger animals, and allowed the population to stabilize at low numbers. The SRM bighorn population required approximately 13 years to stabilize following the disease outbreak in the late 1970s. Spatial analysis indicated that this trend was experienced throughout the range.

It is important to note that maintenance recruitment ratios cannot be generally applied to other populations or time periods; from 1983-1994 the SRM bighorn population averaged 25.2 lambs:100 ewes (which is higher than the maintenance recruitment ratio suggested by Wehausen et al. [1987], and near that suggested by McQuivey [1978]), yet the population declined 69.1 percent from 1984-1994. Considering the SRM 1990-1994 estimated maintenance recruitment ratio and the present recruitment rates, this bighorn population should remain stable or increase if adult survival remains fairly constant.

The compounded effects of disease and low recruitment, 4 years of drought beginning in 1987, and a high incidence of mountain lion predation in recent years (Bighorn Institute, unpubl. data; Steve Torres, CDFG, personal comm.), presumably had a cumulative influence on the SRM bighorn population. The decline response to disease or density dependent factors may have subsided with the lower population density attained in 1990, thus the resulting leveling trend. However, even after the original causes of a decline are eliminated, small, isolated populations are vulnerable to demographic, genetic, and environmental stochastic forces intrinsic to the dynamics of small populations, which may drive them to extinction (Lacy 1993, Caughley and Gunn 1996).

There is a need for further research to identify pathogen sources and pathways, the extent of infectious disease, implications of urbanization in and adjacent to bighorn habitat, and specific characteristics of this subspecies and the region they inhabit that may make bighorn in the Peninsular ranges particularly susceptible to decline. Continued surveys of the SRM bighorn population are needed to monitor the dynamics of this now precarious population and to' maintain the long-term database already established on these bighorn.

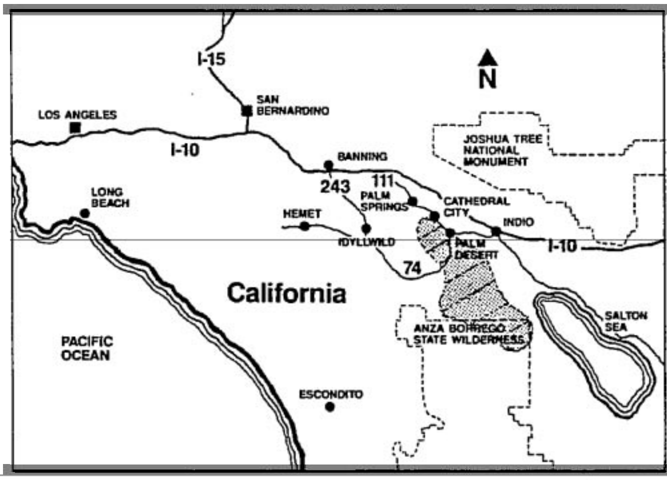

Figure 1. *Location of the Santa Rosa Mountains, California (stippled area).*

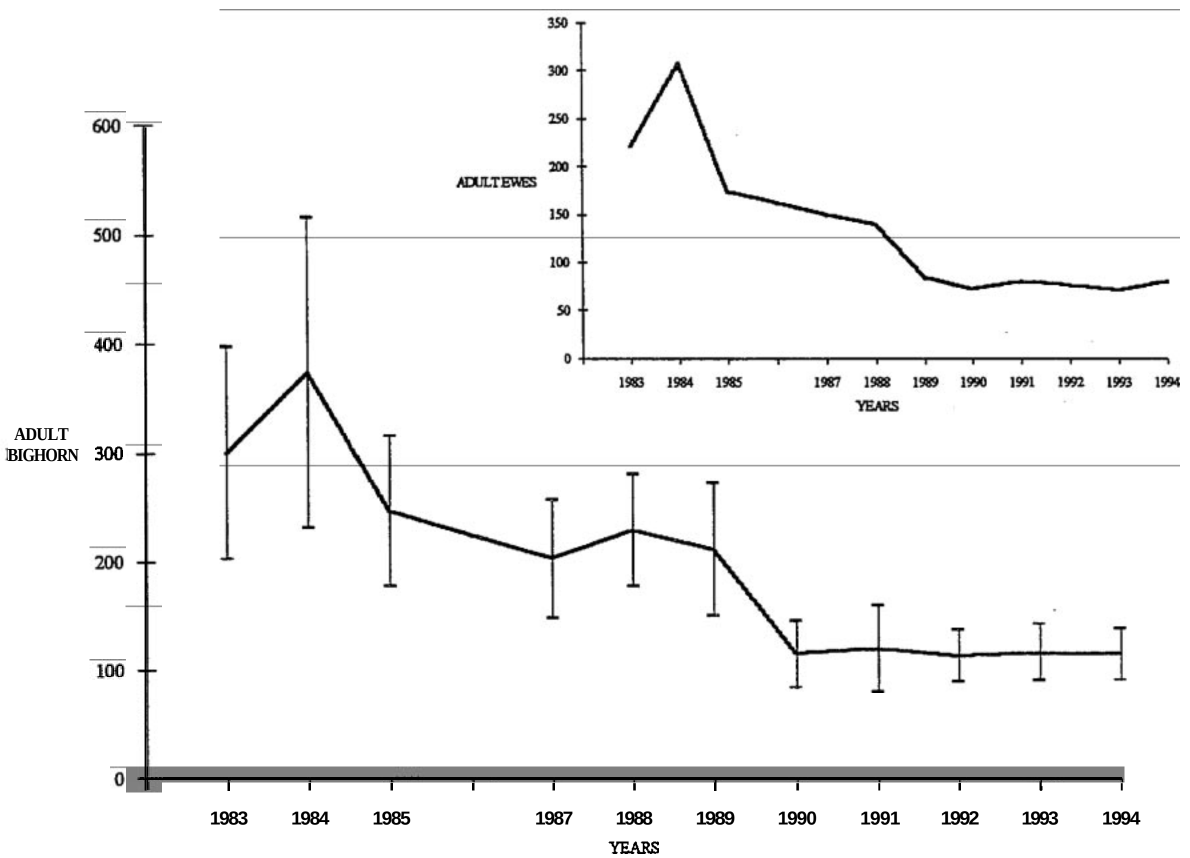

Figure 2. *Adult population estimates with 95% confidence intervals from 1983-1994 fall helicopter surveys of Peninsular bighorn sheep in the Santa Rosa Mountains, California. Inset graph shows annual adult ewe population estimates. The Chapman estimator was used to determine population estimates, excluding 1986 as an outlier*

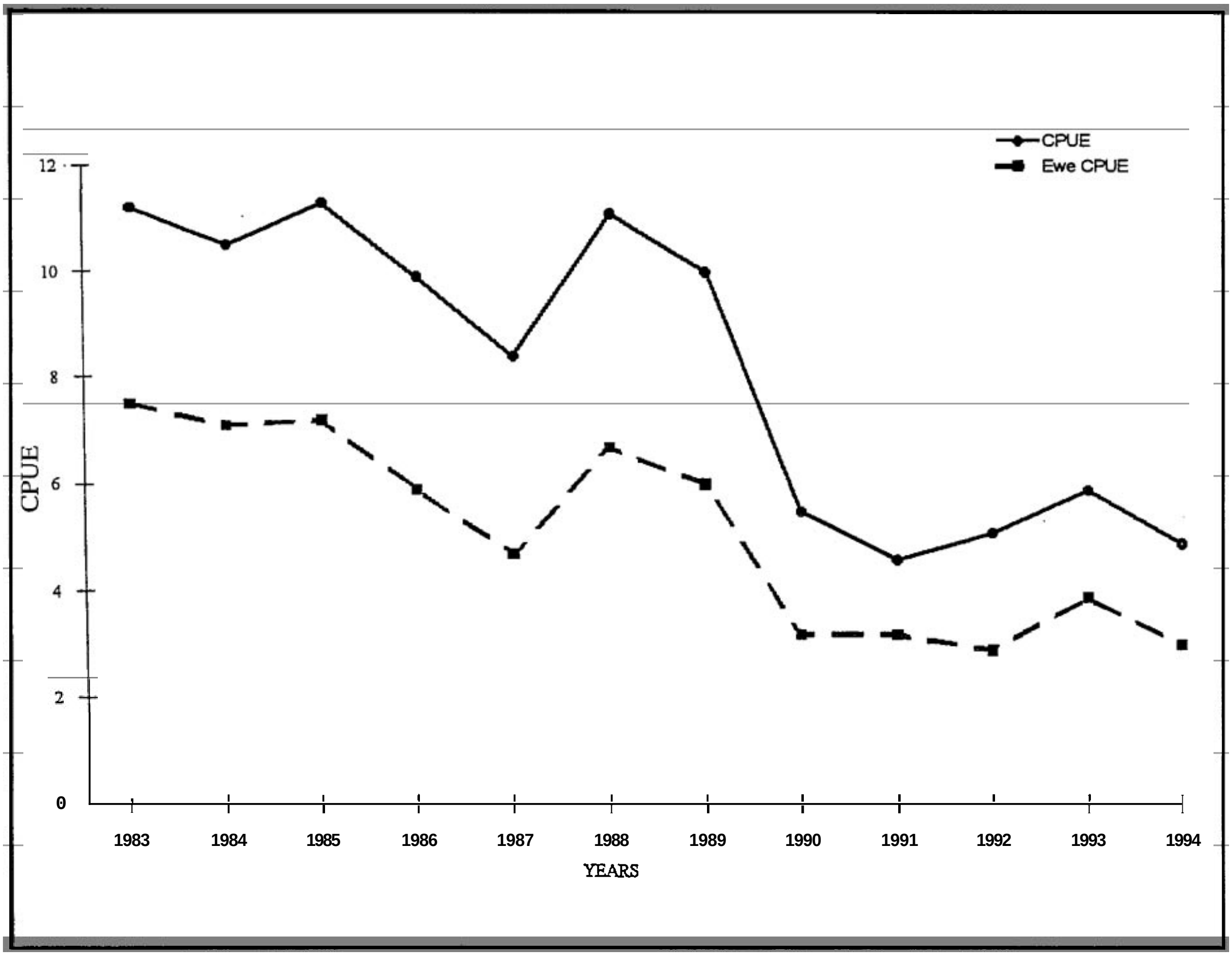

***Figure* 3.** *Adult bighorn seen per helicopter hour, or catch per unit effort (CPUE), along with ewes seen per helicopter hour during 1983-1994 helicopter surveys of Peninsular bighorn sheep in the Santa Rosa Mountains, California.*

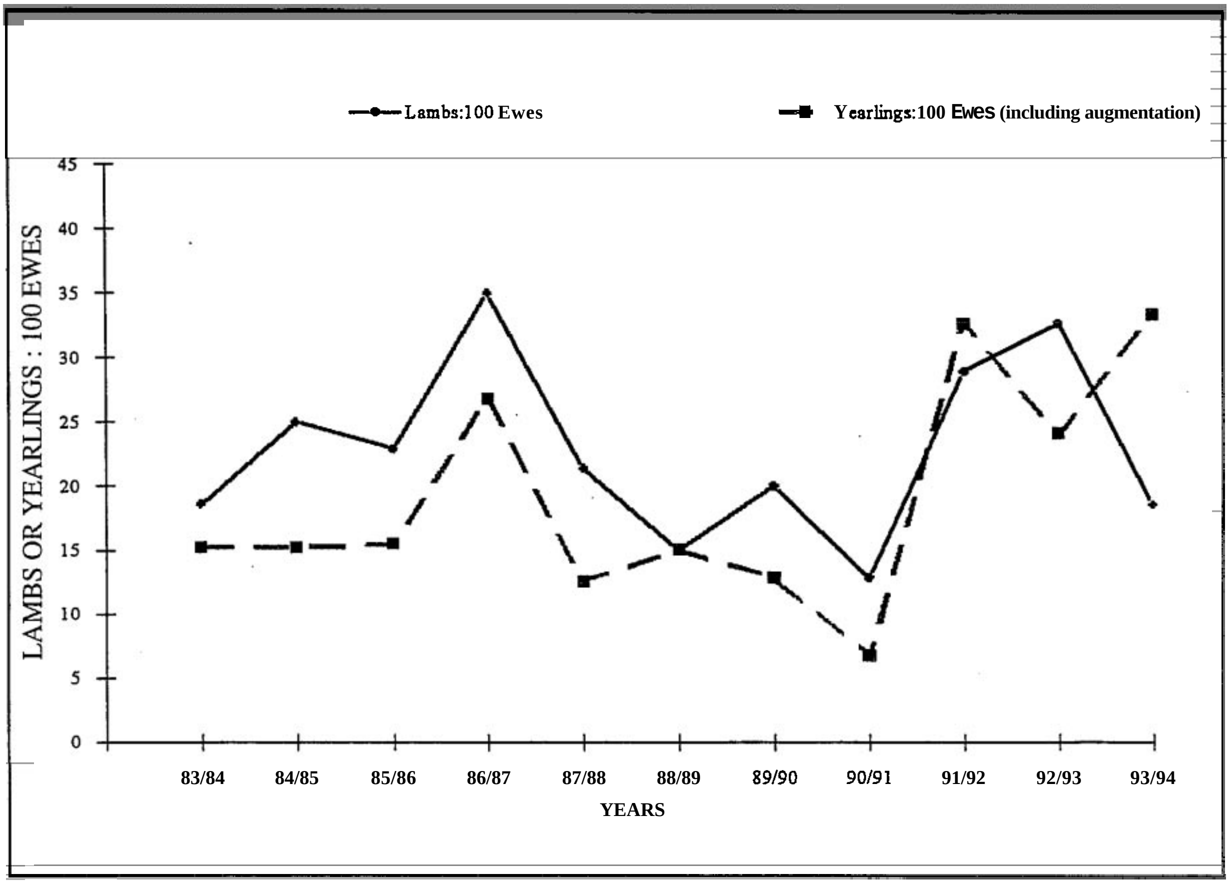

Figure 4. *Lamb:ewe ratios with the subsequent year's yearling:ewe ratios, from 1983-1994 fall helicopter surveys of Peninsular bighorn sheep in the Santa Rosa Mountains, California.*

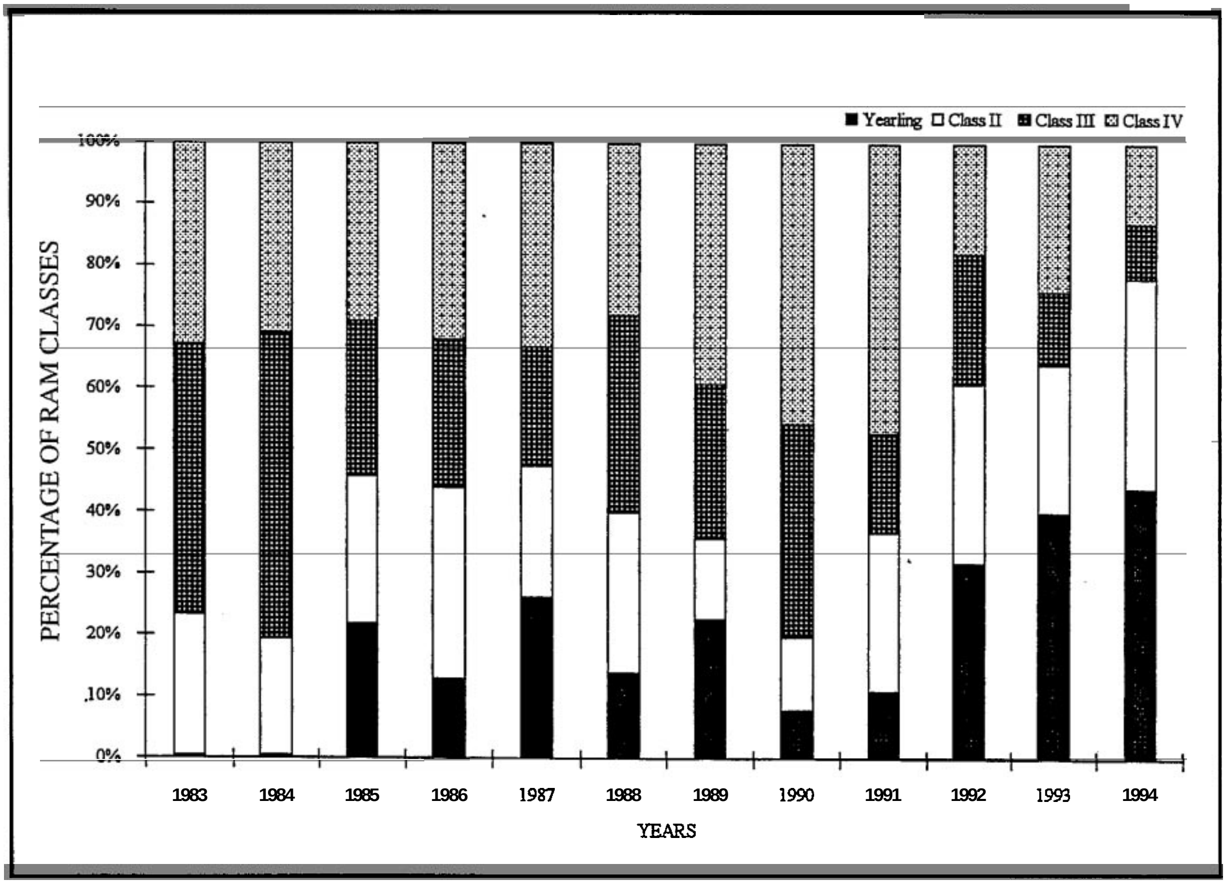

Figure 5. *Percentages of ram classes obtained from 1983-1994 fall helicopter surveys of Peninsular bighorn sheep in the Santa Rosa Mountains, California. Approximate ages were assigned to rain classes as follows: Class II, 2-4 years; Class 111, 5-7years; Class III, ≥8 years.*

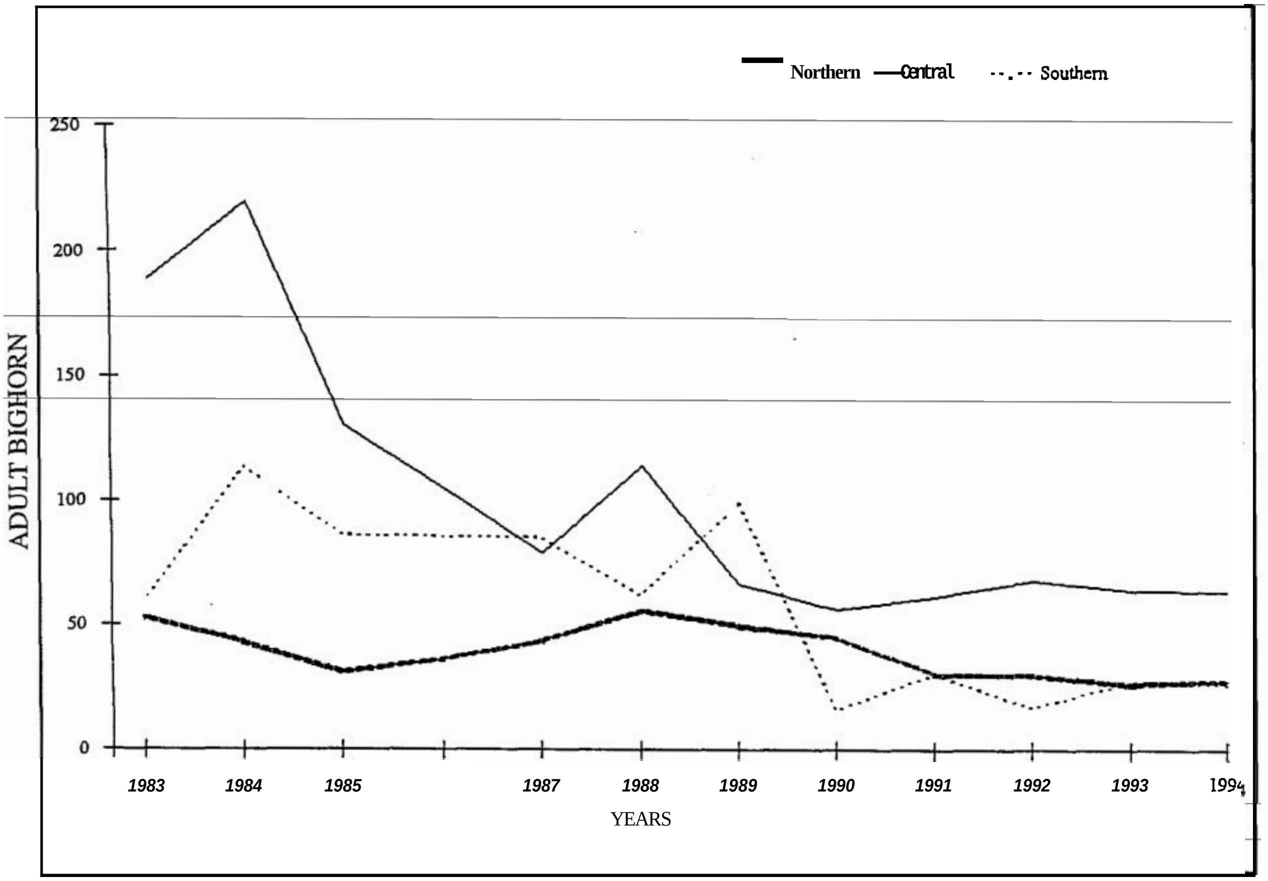

Figure 6. *Adult population estimates for Peninsular bighorn sheep in the northern, central, and southern Santa Rosa Mountains from 1983-1994 helicopter surveys, excluding 1986 as an outlier Since 1985, a total of 60 adult bighorn have been released into the northern Santa Rosa Mountains to augment a declining subpopulation.*

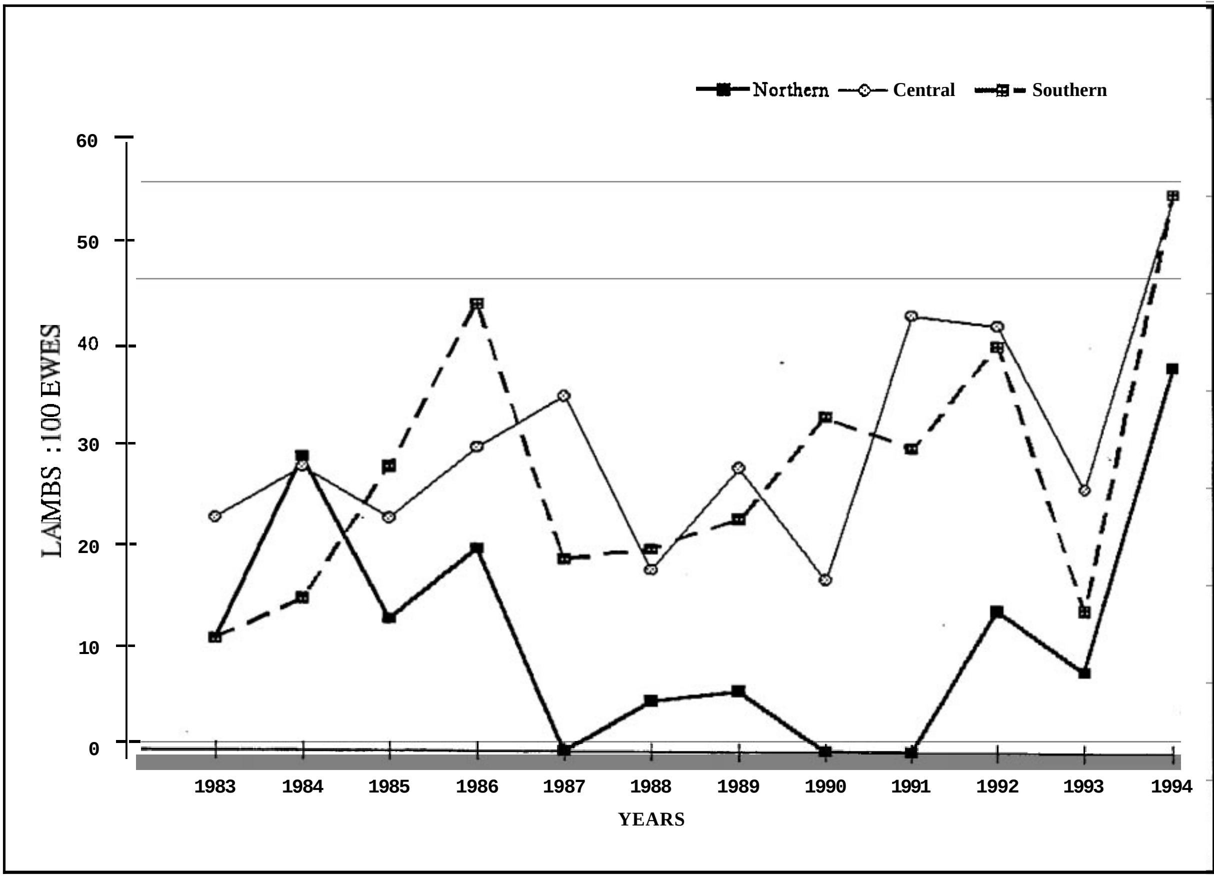

Figure 7. *Lamb:ewe ratios for Peninsular bighorn sheep in the northern, central, and southern Santa Rosa Mountains from 1983-1994 helicopter surveys.*

Table 1. Results from 1983-1994 fall helicopter surveys of Peninsular bighorn sheep in the Santa Rosa Mountains, California.

Year	Flight time (hours)	Total adults seen during helicopter survey	Rams	Ewes	Lambs	Yearling males	Yearling females	Rams/100 Ewes	Lambs/ 100 Ewes	Yearlings/ 100 Ewes	Collared seen/Total collared	Total adults seen in NSRM/ [a]Adult bighorn in NSRM	Adult bighorn seen per helicopter hour (CPUE)
1983	13.0	145	43	97	18	0	5	44.3	18.6	5.2	15/32	25/NA	11.2
1984	17.0	179	48	120	30	0	11	40.0	25.0	9.2	11/24	20/NA	10.5
1985	14.5	164	43	105	24	12	4	41.0	22.9	15.2	13/20	20/31	11.3
1986	17.5	173	54	103	36	8	8	52.4	35.0	15.5	10/31	14/43	9.9
1987	12.0	101	30	56	12	11	4	53.6	21.4	26.8	19/39	21/52	8.4
1988	12.0	133	43	80	12	7	3	53.8	15.0	12.5	24/42	32/51	11.1
1989	10.0	100	31	60	12	8	1	51.7	20.0	15.0	18/39	23/46	10.0
1990	12.3	68	24	39	5	2	3	61.5	12.8	12.8	15/26	26/41	5.5
1991	14.0	65	17	45	13	2	1	37.8	28.9	6.7	11/21	16/30	4.6
1992	15.0	76	19	43	14	9	5	44.2	32.6	32.6	18/27	20/35	5.1
1993	14.0	82	15	54	10	10	3	27.8	18.5	24.1	16/23	18/26	5.9
1994	13.0	64	12	39	20	9	4	30.8	51.3	33.3	23/42	15/20	4.9

[a]Minimum number of adult bighorn confirmed in the NSRM through ground fieldwork prior to helicopter surveys.

NSRM = Northern Santa Rosa Mountains; CPUE = catch per unit effort; NA = not available, adequate data are not available to determine reliable population estimates for the NSRM in 1983 and 1984.

Table 2. *1983-1994 Chapman and comparison population estimates of adult Peninsular bighorn sheep in the Santa Rosa Mountains, California.*

Year,	[a]Chapman estimate ± (1.96) SE using collared bighorn	Chapman estimate ± (1.96) SE using NSRM subpopulation	Population estimate using the CGCF (1.896)
1983	300.1 ± 97	NA	274.9
1984	374.0 ± 142	NA	339.4
1985	246.5 ± 69	250.4 ± 61	310.9
1986	[b]505.2 ± 225	509.4 ± 194	328.0
1987	203.0 ± 55	244.7 ± 68	191.5
1988	229.5 ± 52	210.2 ± 37	252.2
1989	211.6 ± 61	197.8 ± 47	189.6
1990	115.4 ± 31	106.3 ± 19	128.9
1991	120.0 ± 40	119.4 ± 32	123.2
1992	113.5 ± 24	131.0 ± 30	144.1
1993	117.2 ± 26	116.9 ± 25	155.5
1994	115.5 ± 24	85.3 ± 17	121.3

[a]Population estimates used for analysis of population trends.

[b]Not applicable, coeffiecient of variation exceeded 20.0%.

NSRM = Northern Santa Rosa Mountains; CGCF = cumulative general correction factor; NA = not available, adequate data are not available to determine reliable population estimates for the NSRM in 1983 and 1984.

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