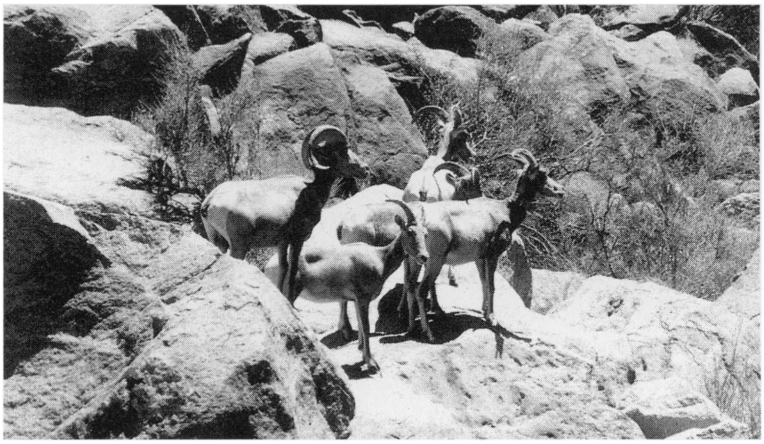

Bighorn sheep in the Peninsular Ranges, California.

Distribution and abundance of bighorn sheep in the Peninsular Ranges, California

Esther S. Rubin, Walter M. Boyce, Mark C. Jorgensen, Steve G. Torres, Charles L. Hayes, Chantal S. O'Brien, and David A. Jessup

Abstract We examined the current population structure and past trends in abundance of endangered bighorn sheep (*Ovis canadensis*) in the Peninsular Ranges of California using a variety of approaches. Direct observations of radiocollared animals (*N* = 90 ewes and 24 rams) during 35 months suggested that bighorn distribution in the Peninsular Ranges was fragmented into ≥8 groups of ewes. These findings were supported by aerial-telemetry locations of radiocollared ewes obtained during 43 fixed–wing flights and observations of uncollared bighorn sheep made during 2 helicopter surveys. Boundaries between ewe groups coincided, in 4 cases, with paved roads, leading us to speculate that some fragmentation was recent and artificial. Abundance estimates derived for 5 of the 8 ewe groups in 1994 and 1996 revealed a recent decline of 28% in this portion of the range. Adult population estimates were generated and combined with existing estimates for the remainder of the range to produce estimates of 347 and 276 bighorn sheep in the Peninsular Ranges north of the United States–Mexico border in 1994 and 1996, respectively. Linear regression analysis of 26 years of waterhole count data, collected at 30 sites representing regions used by 4 ewe groups, indicated that numbers of ewes had declined in 2 of these regions since 1971, but that 2 regions had been inhabited by stable ewe populations during this period. We suggest that groups of bighorn sheep in different portions of the Peninsular Ranges are under local influences and exhibit independent population dynamics.

Key words bighorn sheep, California, distribution, *Ovis canadensis*, Peninsular Ranges, population fragmentation, population trends

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Address for Esther S. Rubin: Department of Veterinary Pathology, Microbiology, and Immunology, University of California, One Shields Avenue, Davis, CA 95616, USA, and California Department of Fish and Game, 1416 Ninth Street, Sacramento, CA 95814, USA. Address for Walter M. Boyce (corresponding author), Charles L. Hayes, and Chantal S. O'Brien: Department of Veterinary Pathology, Microbiology, and Immunology, University of California, One Shields Avenue, Davis, CA 95616, USA. Present address for Charles L. Hayes: New Mexico Department of Game and Fish, P.O. Box 25112, Santa Fe, NM, 87504, USA. Present address for Chantal S. O'Brien: P.O. Box 540, Borrego Springs, CA 92004, USA. Address for Mark C. Jorgensen: Colorado Desert District, California State Parks, 200 Palm Canyon Drive, Borrego Springs, CA 92004, USA. Address for Steve G. Torres: California Department of Fish and Game, 1416 Ninth Street, Sacramento, CA 95814, USA. Address for David A. Jessup: California Department of Fish and Game, 1451 Shaffer Road, Santa Cruz, CA 95060, USA.

Bighorn sheep (*Ovis canadensis*) in the Peninsular Ranges of California are thought to be distributed among 7 mountain ranges (Weaver 1972; Fed. Register, Vol. 57, No. 90, 1992) and to comprise a metapopulation (Torres et al. 1994, Bleich et al. 1996, Boyce et al. 1997). Bighorn sheep in these ranges have been listed as threatened by the state of California since 1971 (Calif. Dep. Fish and Game 1992), and have recently been listed as endangered by the U.S. Fish and Wildlife Service (Fed. Register, Vol. 63, No. 52, 1998). A primary reason for the federal listing was a reported decline in numbers of bighorn sheep during the past 25 years. Population estimates were as high as 971 in 1972 (Weaver 1972) and 1,171 in 1974 (Weaver 1975); more recent estimates were 570 in 1988 (Weaver 1989), 400 in 1992 (Fed. Register, Vol. 57, No. 90, 1992), and 327–524 in 1994 (Torres et al. 1994). Disease, drought, habitat destruction and modification, and resource competition have been hypothesized to have contributed to this decline (DeForge and Scott 1982, DeForge et al. 1982, Turner and Payson 1982, Cunningham and Ohmart 1986, Wehausen et al. 1987, Sanchez 1988, Mullens and Dada 1992). Research addressing these factors has increased our knowledge about Peninsular bighorn sheep; however, their spatial distribution has not been determined, a current population estimate does not exist for the entire range, and past abundance trends in most of the range are poorly understood.

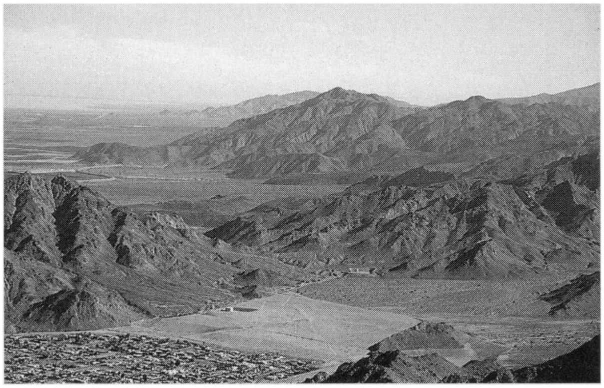
Effective management of a species or population requires accurate knowledge of its spatial distribution (Natl. Res. Counc. 1995). For example, potential fragmentation must be identified and population dynamics in different regions must be understood before risks to population viability can be evaluated and appropriate management strategies identified (Hanski and Gilpin 1991). Fragmentation occurs as a result of natural processes (e.g., habitat heterogeneity, behavioral characteristics [Gilpin 1987, Bleich et al. 1990]) or artificial processes (e.g., habitat loss due to increased human land use, barriers such as fences or roads [Wilcove et al. 1986]). Although bighorn sheep in the Peninsular Ranges have been found to concentrate near water sources during summer months (Jones et al. 1957), their spatial distribution in these ranges has not been examined. Identifying discontinuities in distribution is the first step towards understanding the causes of fragmentation and the resulting spatial structure of bighorn sheep populations in this geographic area.

If distribution is discontinuous, then abundance estimates and knowledge about the dynamics of each spatial subunit will be required to assess population viability (Gilpin 1987, Boyce 1992). Recent survey efforts have concentrated on 1 portion of the Peninsular Ranges (the Santa Rosa Mountains [DeForge et al. 1995]), but current abundance estimates do not exist for the remainder of the range. In the Santa Rosa Mountains, early (1957–1976) estimation techniques differed from those used more recently, making identification of long-term trends in abundance difficult. Waterhole count data were used for early estimates, whereas annual helicopter surveys were used to generate estimates starting in 1977. Helicopter surveys have indicated a population decline during 1977–1982 (Wehausen et al. 1987) and 1982–1995 (DeForge et al. 1995) and suggest a large decline in numbers relative to earlier estimates (DeForge 1984, DeForge et al. 1995). It is not known, however, if this decline was rangewide or if helicopter survey estimates can be compared to early (pre-1977) estimates.

We used locations and movement patterns of radio-collared bighorn sheep, as well as observations of uncollared bighorn sheep, to describe the spatial pattern of distribution of ewes in the Peninsular Ranges. We generated current abundance estimates for bighorn sheep south of the Santa Rosa Mountains from aerial helicopter survey data. In addition, we analyzed a 26-year data set of annual waterhole counts of bighorn sheep that were conducted in selected portions of the range outside of the Santa Rosa Mountains to assess long-term population trends. Our objectives were to (1) describe the distribution of bighorn ewes in the Peninsular Ranges, (2) generate current abundance estimates for bighorn sheep south of the Santa Rosa Mountains, and (3) assess recent and long-term trends in bighorn sheep numbers in the Peninsular Ranges in regions outside of the Santa Rosa Mountains.

Study area

The Peninsular Ranges are located in southern California and Mexico, in the Colorado Desert division of the Sonoran Desert (Ryan 1968; Fig.1). On the north, the Peninsular Ranges are bordered by the Transverse Ranges. From this point, they extend south approximately 225 km in California and another 1,200 km into Baja California, Mexico. In the United States, the range is from 80 to 225 km wide and the maximum elevation is 3,293 m at San Jacinto Peak. Bighorn sheep inhabit the east-facing side of the Peninsular Ranges in habitat characterized by steep slopes and cliffs, canyons, and washes. On the eastern side, vegetation associations are coniferous forest, primarily ponderosa pine (*Pinus ponderosa*) and white fir (*Abies concolor*), ≥1,800 m; chaparral, ≥1,500 m; and pinyon pine (*P. monophylla*)-juniper (*Juniperus californica*), ≥1,200 m. Lower elevations are dominated by agave (*Agave deserti*)-ocotillo (*Fouquieria splendens*), cholla (*Opun-



Bighorn sheep habitat, Peninsular Ranges, California.

tia spp.)-palo verde (*Cercidium floridum*), and creosote (*Larrea tridentata*)-palo verde-mesquite (*Prosopis* spp.) associations (Ryan 1968). Bighorn sheep most frequently have been found at elevations <1,400 m (Jorgensen and Turner 1975), typically staying below the pinyon pine-juniper vegetation association. Maximum temperature in bighorn sheep habitat often reaches 46°C in the summer months, and winters are mild, with temperatures occasionally reaching freezing. Annual rainfall is variable with maxima of 35-470 mm during the past 36 years. Rainfall exhibits a bimodal distribution pattern with most (approx 70%) occurring in the winter months and a lesser amount in the late summer months (Natl. Oceanic and Atmospheric Adm., 1962-1997). We discuss the portion of the Peninsular Ranges located within the United States.

Methods

Between fall 1992 and fall 1993, we captured and radiocollared 98 bighorn sheep (82 ewes and 16 rams) east of Highway 74 in the Santa Rosa Mountains and north of Interstate 8 (Fig. 1). Radiocollared bighorn sheep were already present in the Peninsular Ranges west of Highway 74 as part of ongoing projects conducted by the California Department of Fish and Game and the Bighorn Institute. Our goal was to place radiocollars on sheep throughout the remainder of the range. Previous ground- and aerial-reconnaissance surveys had identified areas occupied by bighorn sheep, and we attempted to collar animals in each of these areas. We captured bighorn sheep via netgun from a helicopter; each animal was aged and fitted with an identifiable eartag and a radiocollar with a unique frequency (Telonics Inc., Mesa, Ariz.). We processed and released bighorn sheep at capture locations or at a base camp ≤5 km from the capture site.

We attempted to locate and observe every radiocollared animal at least once per month, from the time of capture, at approximately 30-day intervals. On 2 occasions animals were observed from a helicopter, but most (≥98%) observations were made from the ground. Data collected at the time of each sighting included date, time, geographic location (Univ. Transverse Mercator coordinates), group size, group composition, and the presence of other collared animals. Collared bighorn sheep were located through September 1995. From February 1994 through September 1995, bighorn sheep also were monitored in this same manner in the Santa Rosa Mountains west of Highway 74, where we identified all ewes and most rams by the presence of radiocollars and eartags.

Bighorn ewes typically exhibit a greater degree of philopatric behavior than rams (Geist 1971). Therefore, we determined spatial population structure from locations and movement patterns of females. We used the program CALHOME (Kie et al. 1994) to generate a 100% minimum-convex-home-range polygon (MCP) for each radiocollared ewe. Each polygon was based on all observations made of a particular ewe during the study and was used to spatially determine the outline, rather than area, of her home range. We assumed that ewes with overlapping or partially overlapping home ranges were members of the same home-range group (Geist 1971) and that discontinuities between these groups represented a fragmentation in the distribution of

Fig. 1. Peninsular Ranges in southern California. Each ● indicates a waterhole count site in Anza–Borrego Desert State Park. Sites are shown grouped (circled) to correspond to 4 of the ewe groups identified in this study (from north to south): Coyote Canyon, north San Ysidro Mountains, south San Ysidro Mountains, and Carrizo Canyon. Thick gray line depicts Anza–Borrego Desert State Park boundary.

ewes. In some portions of the range, we found clusters of ewes that were connected to each other by the home range of only 1 ewe. In each of these cases we examined the movement of the ewe with respect to number, duration, and frequency of movements between groups to determine whether or not these movements represented infrequent intergroup moves.

In addition to our direct observations, the general locations of radiocollared bighorn sheep were monitored during fixed-wing aircraft flights conducted south of the Santa Rosa Mountains. Flights were conducted 1-2 times per month in a Cessna 185 aircraft. Radiocollared bighorn sheep were located using a telemetry receiver that was installed in the aircraft, and the general location of each animal was recorded by a biologist familiar with the topography of the study area. We placed 5 radiocollars in locations unknown to the flight crew to verify the accuracy of this technique and determined that a maximum error of approximately 1 km existed. We considered this level of accuracy sufficient because we used these data simply to verify the home ranges generated from ground observation.

We conducted helicopter surveys between the Santa Rosa Mountains and the United States-Mexico border in October 1994 and October 1996 to obtain data on bighorn sheep distribution and abundance. Each survey was conducted during a 4- to 5-day period. Sampling polygons representing potential bighorn sheep habitat (approx 150- to 1,300-m elevation) were delineated prior to the flights. In 1996, 3 sampling polygons were excluded from the survey. We excluded the Fish Creek Mountains and the area between Interstate 8 and the United States-Mexico border because we had observed only 1 ram and no bighorn sheep in these regions, respectively, during the 1994 survey (Fig. 1). In addition, we excluded the Coyote Mountains because we did not observe bighorn sheep during the 1994 survey and our ground observations indicated that bighorn used these mountains primarily in winter and spring. During these surveys, we flew over bighorn sheep habitat at 40-60 km/hour, following topographical contours at 100- to 150-m intervals. Three observers accompanied the pilot in a Bell 206B-III Jet Ranger helicopter. The pilot and observers were not aware of the locations of radiocollared animals and telemetry was not used to locate groups or individuals. As each polygon was systematically surveyed, the location and classification of each bighorn sheep observed were recorded. Bighorn were classified as yearling ewe, adult ewe, yearling ram, Class II ram, Class III ram, Class IV ram, or lamb (classifications modified slightly from those used by Geist 1971). We examined locations of ewes (collared and uncollared) observed during these surveys to determine whether these sightings concurred with home-range polygons derived from ground observations of collared ewes.

Data collected during the helicopter surveys were used to generate population estimates south of the Santa Rosa Mountains. For this analysis, bighorn sheep were classified as ewes and rams (lambs were excluded), and estimates were generated for the ewe population and total population (rams and ewes combined). The number of radiocollared animals present in each sampling polygon was determined just prior to or during each flight, using aerial, fixed-wing or ground monitoring. Collared bighorn sheep were used as marked animals, and population estimates were generated using Chapman's (1951) modification of the Petersen estimator (Seber 1982). The population estimate ($\hat{N}$) was defined as: $\hat{N} = [(n_1 + 1)(n_2 + 1)/(m_2 + 1)] - 1$, where n_1 is the number of collared animals in the sampling area, n_2 is the total number of animals observed, and m_2 is the number of collared animals observed. Estimates were generated for the entire survey area and also for individual ewe groups within this area, using the number of collared bighorn (n_1 and m_2) in the entire survey area or in specific ewe group areas. Confidence intervals (95%) were calculated as $\hat{N} \pm 1.96$ (variance of $\hat{N}$)$^{0.5}$, with the variance (var) defined as var $= [(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)]/[(m_2 + 1)^2(m_2 + 2)]$ (Seber 1982:60). Using the method described by Seber (1982:121), we examined the change in population estimates for 1994 and 1996 by testing the null hypothesis of H_o: $N_{1994} = N_{1996}$, where $Z = [(\hat{N}_{1994} - \hat{N}_{1996})]/[(\text{var}_{1994} + \text{var}_{1996})^{0.5}]$.

Annual waterhole counts of bighorn sheep were conducted at 49 sites during 1971-1996 in selected portions of the Peninsular Ranges (Fig. 1). These counts were conducted in mid-summer (end of Jun-early Aug), which is a hot and dry time of year (since 1962, $\bar{x}$ high temp = 41.7°C and $\bar{x}$ total rainfall = 8.1 mm for Jul) and, thus, an ideal time in which to conduct a waterhole count. The counts were organized by Anza-Borrego Desert State Park staff and carried out by volunteers at sites representing natural springs and 2 man-made drinkers. Counts typically were conducted during daylight hours for 3 consecutive days, during which all observed bighorn sheep were recorded and classified (age and gender).

Nineteen sites which were only counted during a few years were eliminated from the analysis. We grouped the remaining 30 count sites into 4 geographic regions that represented 4 separate ewe groups (as identified in this study) and carried out separate data analyses for each area and combination of areas. Our analyses were restricted to yearling and adult ewes, and count data from each year were converted to number of ewes observed per day. We added a constant of 0.5

to each count because counts of zero existed. We then examined the natural log of the number of ewes counted (per day) each year with linear regression analysis using the program StatMost (DataMost Corp., Sandy, Ut.). Eberhardt and Simmons (1992) advocated the use of linear regression on the log scale for studying long-term population trends, and Hatfield et al. (1996) found that simple linear regression provided a powerful test for detecting long-term trends in raptor counts. We tested the null hypothesis that there was no change in the number of ewes counted per day across years (slope of the regression line = 0) and determined the significance of the regression analysis using a 2-tailed *t*-test (Sokal and Rohlf 1995) and a randomization test (Collins 1990, Manly 1991), using the program RT (Manly 1996). We examined the potential effects of temperature and precipitation as covariates influencing the number of ewes counted each year, using a Spearman rank correlation analysis (Sokal and Rohlf 1995). The highest temperature during the 3 days of the count was used to examine the effect of temperature. We examined the relationship between precipitation and the number of ewes counted using 2 subsets of precipitation data: (1) the cumulative rainfall for the 3 months preceding the count, and (2) the cumulative precipitation during November–February in the winter preceding the year of the count. These 2 subsets were selected because rainfall directly preceding the count may create temporary additional water sources that could influence visitation of sheep to the counted sites, and winter precipitation may have a positive influence on recruitment rate (Douglas and Leslie 1986, Wehausen et al. 1987), thereby increasing the number of (yearling) ewes counted 1.5 years later. Precipitation and temperature data were collected in Borrego Springs, located within 5–55 km of each waterhole count site. Climate data collected at this site were assumed to be representative of climate patterns at all waterhole count sites, because precipitation and temperature were each found to be significantly correlated (product moment correlation $r \geq 0.94$, $P < 0.000$, and $r \geq 0.89$, $P < 0.000$ for monthly high temperature and total precipitation, respectively) among 3 climate data collection sites (Deep Canyon, Borrego Springs, and Ocotillo) located 50–100 km apart in the Peninsular Ranges (Natl. Oceanic and Atmospheric Adm. 1962–1997).

Results

Distribution

We made 3,149 direct observations of 90 radiocollared bighorn ewes (Table 1). Examination of the overlap of 100% MCP home ranges of radiocollared ewes revealed that the distribution of ewes was not continuous in the Peninsular Ranges. Observed discontinuities in overlapping 100% MCP home ranges (fragmentation) resulted in the following provisional assignments of ewe groups south of the San Jacinto Mountains: (1) Carrizo Canyon, (2) south Vallecito Mountains, (3) north Vallecito and San Ysidro Mountains, (4) Coyote Canyon and Santa Rosa Mountains east of Highway 74, and (5) Santa Rosa Mountains west of Highway 74.

The connection between ewes in the San Ysidro Mountains and ewes in the north Vallecito Mountains was dependent on the home range of a single ewe, No. T7. Ewe No. T7 was captured in the south San Ysidro Mountains, and her movements out of this area (across county road S-22 into the north San Ysidro Mountains and across Highway 78 into the Vallecito Mountains) were infrequent (n = 1 and 2, respectively) and brief (perhaps <1 day in each case). This ewe had the largest home range of ewes in the San Ysidro Mountains, although she was located fewer times (n = 28) than other ewes in these mountains ($\bar{x}$ = 49.8, n = 19 ewes). We concluded that her movement patterns across these roads were atypical of other ewes and likely represented exploratory movements. When data for this ewe were removed from the analysis, the remaining ewes formed 3 separate groups: 1 group in the northern Vallecito Mountains, 1 in the south San Ysidro Mountains, and 1 in the north San Ysidro Mountains, with road S-22 separating the 2 latter groups. Similarly, the home range of a single ewe, No. X3, was the only observed link between ewes in Coyote Canyon and those in the Santa Rosa Mountains. Ewe No. X3 was first captured near Deep Canyon, just east of Highway 74 in the Santa Rosa Mountains, in the fall of 1993. This ewe was observed outside of this area (in Coyote Canyon and south of Martinez Canyon in the Santa Rosa Mountains) in 3 consecutive sightings during a 3-month period in 1994, representing 6% of our observations of this ewe. She was then observed consistently near Deep Canyon for the next 28 months until she died of unknown causes. Therefore, we regarded this as a possible exploratory movement between ewe groups. When data for ewe No. X3 were removed from the analysis, this group (Coyote and Santa Rosa Mountains, east of Highway 74) separated into 4 groups; 3 groups in the Santa Rosa Mountains east of Highway 74 (in and around Deep Canyon, Martinez Canyon, and the south Santa Rosa Mountains) and 1 group in Coyote Canyon.

Based on these observations, we identified separations among the following groups of ewes south of the San Jacinto Mountains: Carrizo Canyon, south Vallecito Mountains, north Vallecito Mountains, south San Ysidro Mountains, north San Ysidro Mountains,

Table 1. Distribution of radiocollared bighorn ewes and monitoring intensity in the Peninsular Ranges, California, October 1992–September 1995.

Home-range groups of ewes	Home-range overlap[a]	No. of radiocollared ewes	Observations per ewe $\bar{x}$	Observations per ewe SD	Ewe months[b] $\bar{x}$	Ewe months[b] SD
Carrizo Canyon	a	19	39.0	11.9	28.4	7.2
Vallecito Mts.[c]						
South	b	2	7.0	4.2	22.0	0.0
North	c	5	13.2	2.4	19.0	5.2
South San Ysidro Mts.	c	5	50.4	14.0	30.2	7.5
North San Ysidro Mts.	c	14	49.7	19.4	28.4	8.8
Coyote Canyon	d	8	15.0	6.4	17.3	6.3
Santa Rosa Mts.–east of Hwy 74[c]						
south S.R. Mts.	d	3	14.3	1.2	23.3	1.2
Martinez Canyon	d	6	3.8	0.8	21.8	0.5
Deep Canyon	d	13	39.2	16.5	18.9	5.4
Santa Rosa Mts.–west of Hwy 74	e	15	45.6	17.9	18.5	3.6

[a] Shared letters indicate that 100% minimum convex polygon home ranges overlapped.
[b] Number of months each ewe was included in the study.
[c] May represent >1 ewe group.

Coyote Canyon, Santa Rosa Mountains east of Highway 74-south Santa Rosa Mountains, Santa Rosa Mountains east of Highway 74-Martinez Canyon, Santa Rosa Mountains east of Highway 74-Deep Canyon, and Santa Rosa Mountains west of Highway 74 (Table 1; Fig. 2). Our observations of 2 Santa Rosa groups east of Highway 74 (Martinez Canyon and south Santa Rosa Mountains) and the 2 groups in the Vallecito Mountains were based on a small number of ewes and did not represent all months of the year. Delineating separate ewe groups in these regions would be speculative, so we treated ewes in the Santa Rosa Mountains east of Highway 74 as 1 ewe group and all ewes in the Vallecitos as 1 group. We did not observe marked ewes leaving or unknown ewes entering the Santa Rosa Mountains area west of Highway 74; this suggested that movement of ewes between the Santa Rosa Mountains and the San Jacinto Mountains was infrequent. An additional group of ewes, reported to inhabit the San Jacinto Mountains (DeForge et al. 1997), was therefore considered a distinct ewe group.

The locations of ewes observed during the 2 helicopter surveys concurred with our delineation of ewe groups south of the Santa Rosa Mountains. During these flights, 39% (1994) and 74% (1996) of radiocollared ewes were observed, and all ewe sightings (including uncollared animals) fell within home-range polygons of radiocollared ewes. Lack of sightings in portions of the survey area was consistent with separations between: (1) the Carrizo Canyon and Vallecito Mountain ewe groups, and (2) the Coyote Canyon and north San Ysidro Mountains ewe groups. Between March 1993 and December 1996, 43 fixed-wing telemetry flights were conducted and 1,240 locations of radiocollared ewes were recorded ($\bar{x}$ = 22.5 locations/ewe, SD = 14.1, range = 1–40). During these flights, nearly all radiocollared ewes were found to be within their individual 100% MCP home ranges generated from our ground observations. An exception was 1 telemetry location of ewe No. D2, a north San Ysidro Mountain ewe, just south of road S-22. Aerial location data were consistent with our speculation that the Vallecito Mountains may support 2 groups of ewes; again, however, these observations were based on a small number (n = 2) of radiocollared ewes in 1 group.

Direct observations and aerial-telemetry locations revealed 18 occurrences of ram movement between ewe groups. These movements were made by 5 radiocollared rams (among 5 pairs of ewe groups): 1 ram, radiocollared in the San Jacinto Mountains (DeForge et al. 1997), moved in and out of the Santa Rosa Mountains west of Highway 74; a second ram moved between the 2 Santa Rosa Mountains ewe groups (east and west of Highway 74), during the rut in 1994 and 1995; 2 rams each crossed road S-22 between the north and south San Ysidro Mountains ewe groups ≥4 times; and 1 ram was observed in 3 ewe groups (Carrizo Canyon, south San Ysidro Mountains, and the Santa Rosa Mountains east of Highway 74) during our study. Although intergroup movements of some rams occurred during the rut (late summer-fall), other movements occurred outside this period.

Abundance and recent population trends

During the 2 helicopter surveys in 1994 and 1996, we observed 110 bighorn sheep (in 37 groups) and 142 bighorn sheep (in 38 groups), respectively. These observations resulted in a catch-per-unit effort of 4.5 and 6.5 bighorn sheep per hour, respectively. We estimated the ewe population sizes for this portion of the range (Coyote Canyon south through Carrizo Canyon) as 141.3 (± 42.4) and 101.7 (± 20.2) in 1994 and 1996, respectively, and the total population size (excluding lambs) as 214.2 (± 64.4) and 163.0 (± 31.2). We also generated abundance estimates for areas used by individual ewe groups (Table 2). Estimates for 1994 and 1996 were not statistically different when individual ewe group estimates were considered ($P \geq 0.11$ in all cases) or when estimates for the entire adult population were compared (P = 0.16). However, the 1994-1996 change in the ewe population for our entire survey area was significant (P = 0.09) if a significance value of $P = 0.10$ was chosen.

Long-term abundance trends

We grouped waterhole count sites (n = 30) to represent 4 of the 8 ewe groups that we identified in this study: Carrizo Canyon, south San Ysidro Mountains, north San Ysidro Mountains, and Coyote Canyon (Fig. 1; Table 3; Appendix A). North San Ysidro Mountains and Coyote Canyon were each further subdivided into distinct canyons or sets of canyons. The number of sites counted within a geographic area was not consistent throughout years, but Spearman rank correlation analysis indicated no significant relationship ($-0.29 \leq r_s \leq 0.17$, $P \geq 0.17$ for each area) between the number of sites and number of ewes counted. The number of ewes counted in Coyote Canyon declined significantly (t-test: $P = 0.03$, randomization test: $P = 0.02$) at a rate of 2.6% per year during 1971-1996. When the 3 subunits within Coyote Canyon were examined individually, however, only sites in Cougar Canyon and Sheep Canyon exhibited a significant decline ($P < 0.001$), at a rate of 13.1% per year. Sites in the north and south San Ysidro Mountains exhibited nonsignificant (P = 0.55 and 0.46, respectively) changes in the number of ewes counted during 1971-1996. The shorter (10-yr) data set for the Carrizo Canyon area showed a significant (P = 0.03) decline of 9.9% per year in the number of ewes counted per year from 1973 to 1982.

A significant correlation (r_s = 0.61, P = 0.002) existed between the number of ewes counted and the high temperature recorded during the count for the south San Ysidro region only. We found no significant ($P \geq 0.23$) association between the number of ewes counted and winter precipitation during the preceding year, or between the number of ewes counted and rainfall in the 3 months preceding the count, for any region or subunit.

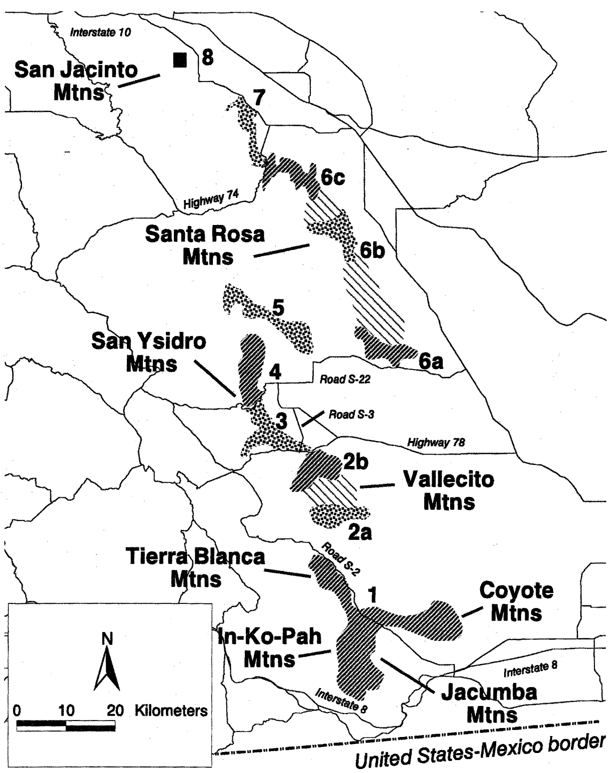


Fig. 2. Distribution of bighorn ewe groups in the Peninsular Ranges, California 1992-1995. Stippled and shaded areas indicate regions used by home-range groups of ewes identified in this study: 1-Carrizo Canyon, 2a-south Vallecito Mountains, 2b-north Vallecito Mountains, 3-south San Ysidro Mountains, 4-north San Ysidro Mountains, 5-Coyote Canyon, 6a-Santa Rosa Mountains east of Highway 74 (south), 6b-Santa Rosa Mountains east of Highway 74 (Martinez Canyon), 6c-Santa Rosa Mountains east of Highway 74 (Deep Canyon), 7-Santa Rosa Mountains west of Highway 74, 8-San Jacinto Mountains (■ indicates general location of this group, DeForge et al 1997). Wide hatch marks indicate possible connectivity between ewe groups in the Vallecito Mountains and the Santa Rosa Mountains.

Discussion

Distribution

We concluded that bighorn ewes in the Peninsular Ranges exhibited a fragmented distribution and that ≥8 ewe groups existed as a result of this fragmentation (Table 1; Fig. 2). We believe that radiocollared ewes were representative of the entire ewe population, because ≥23-30% of the ewes south of the Santa Rosa Mountains were radiocollared (based on 1994 and 1996 ewe population estimates for this region), and all observations of uncollared ewes were within areas used by collared ewes during helicopter surveys of potential bighorn sheep habitat. Our observations indicated that the Carrizo Canyon ewe group occurred north of Interstate 8 in the In-Ko-Pah, Jacumba, Tierra Blanca, and Coyote Mountains. We did not document any movement by ewes between these mountains and the Vallecito Mountains, which were occupied by the next closest group of ewes. The Vallecito Mountains may be inhabited by >1 ewe group, but this needs to be confirmed by additional

Table 2. Population structure and abundance estimates for bighorn sheep in the Peninsular Ranges, California, in 1994 and 1996.

Current ewe group delineations[a]	Ewe population (95%CI)		Adult population (95%CI)		Previous distribution delineations[b]	Previous estimates[b]
	1994	1996	1994	1996		
Carrizo Canyon	39.0 (20.9–57.2)	23.5 (17.7–29.3)	58.5 (28.5–88.5)	34.4 (26.8–42.1)	Carrizo Gorge	25
					Pinto and In-Ko-Pah Mts.	10
Vallecito Mts.	17.7 (6.7–28.6)	19.0 (19.0–19.0)	29.0 (12.4–45.6)	28.0 (28.0–28.0)	Vallecito Mts.	20
South San Ysidro Mts.	15.3 (9.9–20.6)	12.3 (6.9–17.8)	19.0 (12.2–25.8)	25.7 (13.6–37.7)	Palm and Tubb Canyons and Pinyon Ridge	90
North San Ysidro Mts.	32.0 (9.5–54.5)	22.1 (16.2–28.1)	68.3 (14.6–122.1)	39.0 (25.9–52.2)	Palm and Tubb Canyons and Pinyon Ridge	90
Coyote Canyon	21.8 (15.4–28.2)	23.0 (5.5–40.5)	29.3 (21.9–36.8)	37.0 (8.2–65.8)	Coyote Canyon	100
Santa Rosa Mts.–east of Hwy 74			115.5 (91.5–139.5) all Santa Rosa Mts.[c]	93.8 (71.8–115.8) all Santa Rosa Mts.[d]	Santa Rosa Mts.	120
Santa Rosa Mts.–west of Hwy 74			115.5 (91.5–139.5) all Santa Rosa Mts.[c]	93.8 (71.8–115.8) all Santa Rosa Mts.[d]	Santa Rosa Mts.	120
San Jacinto Mts.			approx 17[e]	approx 19[e]	San Jacinto Mts.	15

[a] Based on observations of ewes made between October 1992 and September 1995.
[b] Anza–Borrego Desert State Park, unpubl. data, 1990; Bighorn Inst., unpubl. data; as cited in Federal Register, Vol. 57, No. 90, 1992.
[c] DeForge et al. 1995.
[d] J. R. DeForge and S. D. Ostermann, unpubl. data, Bighorn Inst., Palm Desert, Calif., 1996.
[e] DeForge et al. 1997.

observations. Ewes in the San Ysidro Mountains appeared to be distinct from groups in both the Vallecito Mountains and Coyote Canyon and formed 2 ewe groups, 1 on each side of road S-22. The movements of ewes No. T7 and No. D2 revealed that ewe groups in the San Ysidro Mountains and the Vallecito Mountains were linked by infrequent, exploratory movements of ewes. However, ewe movement between these groups was clearly limited, and we did not document any permanent emigration. Coyote Canyon apparently was inhabited by a distinct group of ewes. Excluding 1 temporary movement by ewe No. X3, we did not observe bighorn sheep moving between Coyote Canyon and the Santa Rosa Mountains. In the Santa Rosa Mountains, our data revealed a division between ewes on the west side of Highway 74 and those on the east side. Bighorn sheep in the Santa Rosa Mountains east of this highway may comprise >1 ewe group, but additional observations would be needed to delineate other ewe groups in this area. Movement of ewes between the Santa Rosa Mountains and the San Jacinto Mountains was not observed in our study or that of DeForge et al. (1997).

Although population structure can be described at several hierarchical scales (Hanski and Gilpin 1991), we selected groups of ewes with overlapping home ranges as a meaningful unit with which to examine the distribution of bighorn sheep in the Peninsular Ranges. Young ewes typically learn their home ranges by following their mothers and other older females and show a high degree of philopatry to their home ranges throughout their lives (Geist 1971). Consequently, ewes with overlapping (or partially overlapping) home ranges may be more closely related to each other than to other ewes (Festa-Bianchet 1991). The natal philopatry exhibited by ewes also reduces the likelihood that ewes will colonize new areas. We therefore assumed that groups of ewes with overlapping home ranges form units that have ecological and evolutionary significance with respect to the genetic and distributional structure of bighorn sheep. This view has been supported by a recent mitochondrial-DNA analysis of the genetic structure of ewe groups in the Peninsular Ranges (Boyce et al. 1999).

The spatial structure of populations is formed by discontinuities in distribution that result from habitat heterogeneity and biological characteris-

Table 3. Summary of bighorn sheep waterhole-count analysis, Peninsular Ranges, California. Annual counts were conducted during 1971–1996 (Carrizo Canyon counts were conducted 1973–1982).

Count region	No. sites counted	No. yr counted	Regression coefficient (SE)[a]	Annual percent change	*P*-value[b]
Carrizo Canyon	4–6	10	– 0.0996 (0.038)	– 9.9	0.03
South San Ysidro Mts.	1–4	26	– 0.0191 (0.025)	– 1.9	0.46
North San Ysidro Mts.			+ 0.0105 (0.017)	+ 1.1	0.55
Palm Canyon	1–5	25	+ 0.0036 (0.019)	+ 0.4	0.86
Hellhole Canyon	1–4	23	+ 0.0076 (0.024)	+ 0.8	0.75
Coyote Canyon			– 0.0262 (0.011)	– 2.6	0.02
Lower Willows–Box Canyon	1–2	25	+ 0.0294 (0.021)	+ 2.9	0.17
Middle Willows–Salvador Canyon	2–5	26	– 0.0233 (0.015)	– 2.3	0.14
Cougar Canyon–Sheep Canyon	1–4	26	– 0.1305 (0.019)	–13.1	0.0002
All San Ysidro Mts.			+ 0.0007 (0.016)	+ 0.1	0.97
San Ysidro Mts. + Coyote Canyon			– 0.0169 (0.007)	– 1.7	0.03

[a] Linear regression of number of ewes counted each year (data were transformed to natural log after constant of 0.5 was added).
[b] Null hypothesis: regression coefficient = 0. *P*-values shown are based on randomization test, *t*-test values were nearly identical.

tics of the species (Gilpin 1987). Fragmentation is typically seen as detrimental to population viability, but a certain degree of fragmentation is an inherent component of population structure. Although bighorn sheep are able to cross large tracts of land, the philopatric behavior of ewes and their association with mountainous, open terrain results in a distribution that could be considered naturally fragmented (Bleich et al. 1990). We propose, however, that construction and use of roads may have increased the fragmentation of ewe distribution in the Peninsular Ranges. Four of the boundaries between ewe groups that we defined coincided with paved roads (Highway 74 in the Santa Rosa Mountains, road S-22 in the San Ysidro Mountains, Highway 78 between the San Ysidro Mountains and the Vallecito Mountains, and road S-2 between Carrizo Canyon and the Vallecito Mountains; Fig. 2).

It is possible that the section of road S-2 that separates ewe groups in Carrizo Canyon and the Vallecito Mountains coincides with a natural topographical break, which may promote discontinuity in ewe distribution (Fig. 2). In contrast, a more southern stretch of this road, located in continuous, rugged terrain, was crossed seasonally by Carrizo Canyon ewes. Similarly, road S-3, which was crossed occasionally by ewes in the south San Ysidro group, passed through continuous, rugged terrain. However, other roads that separated ewe groups (Highway 78, road S-22, and Highway 74) also traversed continuous, rugged terrain. We only observed radiocollared ewes crossing Highway 78 and road S-22 on 1 and 2 occasions, respectively, and never documented ewes crossing Highway 74, although we observed ewes within 50–100 m of these roads on numerous occasions. Ewes were observed crossing Highway 74 during the 1970s (V. Bleich, Calif. Dep. Fish and Game, pers. commun.). Vehicular traffic has been found to be associated with decreased habitat use (Krausman and Leopold 1986) and increased mortality (Cunningham and deVos 1992) in other mountain ranges. The apparent lack of movement across Highway 74 during our study may have resulted from increased traffic (Calif. Dep. of Transportation records [unpubl. data] indicate that traffic has approx tripled on this road since 1970), a decline in the number of ewes west of this highway (DeForge et al. 1995), or a combination of these factors.

The other ewe group boundaries that we identified may have resulted from breaks in suitable habitat or loss of ewe groups due to disease, habitat modification, or predation. For example, at the north end of the Peninsular Ranges, reduced numbers of bighorn sheep (DeForge et al. 1995) and the loss of habitat to urban development may have contributed to the apparent lack of connectivity between ewes in the San Jacinto Mountains and those in the Santa Rosa Mountains. The boundary between the Coyote Canyon ewe group and the north San Ysidro Mountains ewe group coincides with the loss of bighorn sheep in Cougar Canyon and Sheep Canyon revealed in our analysis of waterhole count data (Table 3; Appendix A). The use of off-road vehicles and livestock grazing (currently restricted activities) may have contributed to this fragmentation and the current absence of bighorn sheep in Cougar Canyon and Sheep Canyon.

During this study, we did not observe bighorn sheep in the mountains directly west of the Vallecito Mountains (the Sawtooth Range, Oriflamme Mountains, and lower elevations of the Laguna Mountains), and we observed only 1 ram during our survey of the Fish Creek Mountains. Early studies suggested that both of these areas may have supported "transient" populations (Weaver et al. 1968, Weaver 1972), and single rams have been sighted occasionally over the past 25 years

(M. Jorgensen, unpubl. data). Although recent observations suggest that these areas are used by only a small number of rams, ewe groups were observed at the edge of these mountains (southeast edge of the Vallecito Mountains and northwest extent of the Tierra Blanca Mountains), suggesting that both of these areas may be used by ewes under different climate conditions or population sizes. Bighorn sheep use of mountains west of the Vallecito Mountains also may have been restricted by livestock grazing and fire suppression.

We did not observe bighorn sheep between Interstate 8 and the Mexican border, an area that was estimated to be inhabited by ≥20 bighorn sheep in 1968 (Weaver et al. 1968) and 30 bighorn sheep in 1979 (Cunningham 1982). Helicopter surveys of this area detected only 2 rams in the early 1980s (D. A. Jessup, unpubl. data) and no bighorn sheep in the mid-1980s (M. Jorgensen, unpubl. data). It is likely that the construction of Interstate 8 (a 4-lane freeway) in the mid-1960s, in combination with railroad activity, livestock grazing, poaching, and fire suppression, contributed to the disappearance of sheep in this area. Thus, Interstate 8 and Interstate 10, at the north end of the range, effectively isolate bighorn sheep in the United States Peninsular Ranges. Bighorn sheep movement into the San Bernardino Mountains to the north and into Mexico to the south may have been limited even before freeway construction. However, it is likely that these freeways and associated habitat modification (e.g., fencing and urban development) have further restricted any such movements.

Abundance and recent population trends

Increased fragmentation can reduce population size (Burgman et al. 1993) and effective population size (Gilpin 1987), thereby increasing the risk of extinction (Gilpin and Soule 1986). From our 1994 survey data, we estimated that the population size (rams and ewes combined) in the United States Peninsular Ranges, excluding the Santa Rosa and San Jacinto Mountains, was 214.2 ± 64.4, with the largest single group consisting of approximately 68 individuals (Table 2). A survey of the Santa Rosa Mountains conducted in 1994, using techniques similar to ours, generated an estimate of 115.5 ± 24 adult bighorn sheep (DeForge et al. 1995). The San Jacinto Mountains were believed to support an additional 17 bighorn sheep (DeForge et al. 1997). The estimated population of bighorn sheep in the United States Peninsular Ranges was, therefore, 347 in 1994. Surveys conducted in 1996 produced bighorn sheep population estimates of 163.0 ± 31.2 south of the Santa Rosa Mountains, 93.8 ± 22 in the Santa Rosa Mountains (J. R. DeForge and S. D. Ostermann, unpubl. data, Bighorn Inst., Palm Desert, Calif., 1996), and 19 in the San Jacinto Mountains (DeForge et al. 1997), thus generating a combined estimate of 276 bighorn sheep in the United States Peninsular Ranges in 1996. South of the Santa Rosa Mountains, our data suggested a short-term (2-yr) decline of 24% ($P = 0.16$) and 28% ($P = 0.09$) among adults and ewes, respectively. Given the endangered status of bighorn sheep in the Peninsular Ranges, we believe the use of a significance value of $P \leq 0.10$ is appropriate. Thus, we concluded that the number of ewes had declined significantly during this 2-year (1994-1996) period. Earlier estimates that were generated for this portion of the Peninsular Ranges could not be directly compared with our estimates because different techniques were used (i.e., waterhole counts or surveys conducted on foot; Weaver 1972, Jorgensen and Turner 1973, Jorgensen and Turner 1975, Weaver 1975).

Long-term abundance trends

Our analysis of waterhole count data supported the conclusion that bighorn sheep numbers have declined in selected regions of the Peninsular Ranges outside of the Santa Rosa Mountains (Table 3; Figs. 1 and 2). However, not all areas covered by the waterhole counts exhibited a decline. For example, our analysis suggested that the number of bighorn sheep has declined in Coyote Canyon, but remained relatively stable in the north and south San Ysidro Mountains during the past 26 years. Furthermore, the decline in Coyote Canyon was caused largely by the loss of sheep in one portion (Cougar and Sheep Canyons) of this large canyon (Table 3; Appendix A).

These results emphasize the importance of scale and resolution when assessing population parameters such as abundance and trends. For instance, if data from the 2 San Ysidro regions were combined with data from Coyote Canyon, it would appear that a significant ($P = 0.03$) decline had occurred throughout this region (Table 3). This effect, however, would be primarily due to the data from Cougar and Sheep Canyons. The decline in the number of ewes counted in Cougar and Sheep Canyons was accompanied by a positive, but statistically nonsignificant ($P = 0.17$), trend in the number of ewes counted in the Lower Willows-Box Canyon area. This could be the result of a shift in habitat-use patterns; however, the loss of bighorn sheep in 1 portion of Coyote Canyon was accompanied by an overall significant decline in numbers in this canyon. Cougar and Sheep Canyons are located between the north San Ysidro and Coyote Canyon ewe populations, and we could have assigned waterhole count data from this area to the San Ysidro Mountains region rather than to Coyote Canyon. Although we do not know what pattern of home-range connectivity existed between ewes in Coyote Canyon and ewes in the north San Ysidro Mountains in the past, we treated Cougar and Sheep Canyons as a part of Coyote Canyon because these sites are geographically closer to areas currently used by ewes in Coyote Canyon, and the canyons drain into Coyote Canyon.

The analysis of waterhole count data collected in Coyote Canyon and in Carrizo Canyon provides evidence that local declines in numbers of bighorn sheep have occurred. In the Santa Rosa Mountains, DeForge et al. (1995) documented an adult population decline of 69% during a 12-year period (1983-1994). When these authors divided their survey area into 3 geographical sampling units, it was found that a decline was evident in all 3 areas, with similar declining trends in 2 sampling units and a slower decline in the third sampling unit (Santa Rosa Mountains-west of Highway 74), the only location in the Peninsular Ranges where the population has been augmented with captive-born animals (DeForge et al. 1995). Additional analysis of their survey data, incorporating ewe group boundaries suggested in our study, would be especially valuable in understanding these regional trends.

The analysis of waterhole count data revealed variation in trends among ewe groups, suggesting that the demographic dynamics in these groups were independent and that ewe groups may be influenced by local as well as landscape-scale factors. Winter precipitation has been found to be associated with lamb recruitment in the following year (Douglas and Leslie 1986, Wehausen et al. 1987) and thereby has the potential to influence the number of ewes counted 1.5 years later. However, we found no relationship between the number of ewes counted and precipitation during winter months in the year preceding the count, nor with precipitation during the 3-month period preceding the count. We also found that the number of ewes counted was not consistently correlated with the high temperature during each count. These findings suggested that other, local influences (specific to ewe groups), e.g., habitat quality, predation, or disease, may be more important than the effects of climate. During our study we found that predation by mountain lions was common and appeared to fluctuate among ewe groups and among years. Predation may have been responsible, in part, for variation in the dynamics of individual ewe groups.

We conclude that bighorn sheep in the Peninsular Ranges are currently distributed in multiple ewe groups. This distributional pattern may be influenced by the abundance of bighorn sheep and may, therefore, be altered if population size increases or decreases. Furthermore, the distribution of ewe groups may shift slightly over time, in response to habitat and resource availability. We identified a recent decline in the number of ewes in areas outside of the Santa Rosa and San Jacinto Mountains. Within our study area, some, but not all, ewe groups exhibited long-term declines. This suggests that ewe groups may have been influenced by different factors and, thus, face different extinction risks. Recently, a regional approach to bighorn sheep management has been promoted (Torres et al. 1994, Bleich et al. 1996), emphasizing the concept of bighorn sheep metapopulations, first proposed by Schwartz et al. (1986). We suggest that the most effective conservation tactics will be those that make use of this regional approach, while simultaneously considering the identity and dynamics of the individual ewe groups. Comparisons of individual ewe groups may provide valuable insight into the apparent differences in local abundance trends, because different influences may be acting on different ewe groups. Trends should be monitored (via helicopter surveys and waterhole counts) throughout the Peninsular Ranges to assess and direct management efforts. At a regional level, potential connectivity between ewe groups must be maintained through habitat protection (Schwartz et al. 1986, Bleich et al. 1990). A multi-scale approach such as this may provide the greatest insight into the factors that influence the viability of bighorn sheep in the Peninsular Ranges; such insight will enhance the development of effective management decisions.

Acknowledgments. This study was funded by the California Department of Fish and Game, the California Department of Parks and Recreation, the Pew Charitable Trusts, the Educational Foundation of America, the Zoological Society of San Diego, and the Anza-Borrego Desert Natural History Association. We thank J. Allen, V. Bleich, R. Botta, R. Clark, T. Evans, R. Mouton, J. Wehausen, and all those who helped with field data collection and waterhole count surveys. In addition, we are grateful for the assistance and cooperation of the Bureau of Land Management, the Bighorn Institute, Landell's Aviation, the Zoological Society of San Diego, and the University of California Boyd Deep Canyon Desert Research Center during various phases of this study.

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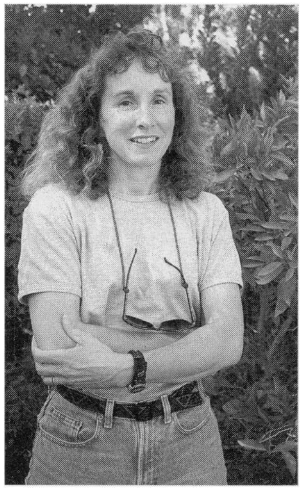

Esther S. Rubin (photo) is a Ph.D. candidate in the Graduate Group in Ecology at the University of California, Davis. Her dissertation focuses on Peninsular bighorn sheep, and she is currently helping to develop a recovery plan for this federally endangered population. ***Walter M. Boyce*** is a professor and wildlife veterinarian at the Wildlife Health Center at the University of California, Davis. ***Mark C. Jorgensen*** is a resource ecologist for the Colorado Desert District of California State Parks, which includes Anza-Borrego Desert State Park. ***Steve G. Torres*** is a senior wildlife biologist with the California Department of Fish and Game and is responsible for the management of bighorn sheep and mountain lions in the state. ***Charles L. Hayes*** is now a biologist with the New Mexico Department of Game and Fish and is heavily involved with the management of mountain lions and black bears in New Mexico. ***Chantal S. O'Brien*** is working on wildlife projects in Arizona and is considering advanced graduate work in wildlife biology. ***David A. Jessup*** is a wildlife veterinarian with the California Department of Fish and Game and is now working extensively with marine species.

Appendix A. Mean number of bighorn ewes counted per day ($\bar{x}$) during annual waterhole counts and number of count sites (n) in the Peninsular Ranges, California, 1971–1996.

	Coyote Canyon						North San Ysidro Mts.							
	Cougar–Sheep Canyons		Lower Willows–Box Canyon		Middle Willows–Salvador Canyon		Palm Canyon		Hellhole Canyon		South San Ysidro Mts.		Carrizo Canyon	
Yr	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n
1971	5.67	3	3.33	2	4.33	2			0.00	1	1.67	2		
1972	6.67	2	3.33	2	7.50	2	10.33	4			3.33	1		
1973	3.67	1			15.00	2	6.33	1			7.33	1	15.83	6
1974	3.83	3	6.33	1	9.83	3	7.00	2	3.00	2	4.17	2	18.17	6
1975	8.00	3	0.00	1	6.33	3	15.67	4	2.00	1	1.33	2	26.50	6
1976	10.83	3	2.17	1	7.83	3	2.67	3			1.67	2	31.83	6
1977	10.67	3	2.00	1	5.17	2	0.50	3	1.67	1	0.50	2	20.00	6
1978	2.33	3	1.67	1	8.33	3	3.00	2	1.67	1	5.00	2	15.33	4
1979	11.00	4	3.83	2	14.83	5	8.33	4	1.00	2	5.50	2	15.33	6
1980	3.00	2	0.00	2	23.00	3	1.33	4	0.00	3	5.67	2	6.83	6
1981	0.00	3	1.83	1	2.50	2	9.33	3	0.00	1	6.33	3	11.00	6
1982	0.33	4	0.67	2	10.67	4	5.67	3	0.33	4	0.00	2	9.83	6
1983	0.17	4	3.83	2	4.67	4	9.67	4	0.00	1	1.83	3		
1984	0.33	4	3.83	2	2.83	4	7.00	4	0.33	3	6.83	3		
1985	0.67	4	1.33	2	6.33	5	14.00	4	0.00	2	8.50	4		
1986	0.00	4	1.67	2	6.67	3	7.00	4	0.00	2	6.17	3		
1987	0.00	4	0.67	2	12.00	4	5.50	5	1.50	2	0.00	3		
1988	0.00	3	4.67	2	1.00	4	10.67	4	1.33	1	6.33	3		
1989	1.33	3	1.67	2	8.33	4	11.00	4	0.67	2	7.67	3		
1990	0.00	3	1.67	2	5.67	4	8.00	4	1.33	2	8.00	3		
1991	0.00	3	7.67	2	7.00	2	9.67	4	0.00	1	0.33	3		
1992	0.33	3	6.67	2	5.67	4	9.33	4	0.00	2	0.33	3		
1993	0.00	3	9.33	2	2.00	4	7.33	5	0.00	1	0.33	3		
1994	0.00	3	7.00	2	3.67	4	6.67	4	2.33	2	3.33	2		
1995	0.00	4	3.67	2	9.00	5	4.67	5	1.67	1	0.67	3		
1996	0.00	3	1.33	2	6.00	3	1.00	4	4.67	2	4.67	3		

Associate Editor: Jacobson