DEMOGRAPHY AND MOVEMENTS OF MOUNTAIN SHEEP (*Ovis canadensis nelsoni*) IN THE KINGSTON AND CLARK MOUNTAIN RANGES, CALIFORNIA

By

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ABSTRACT

This thesis consists of three chapters, each written in manuscript form. In the first chapter, the accuracy of Loran-C for determining geographic positions in aerial telemetry studies of mountain sheep (*Ovis canadensis*) was investigated for 2 areas in the eastern Mojave Desert of California. Loran-C error was determined by calculating the difference between geographic coordinates estimated by Loran-C and the actual coordinates of these locations. Before evaluating accuracy, significant biases in the recorded positions were identified and corrected. After these corrections, Loran-C determined positions with 95% probability within circular areas of 1.2 to 1.5 km^2 in one study area, and within 0.8 km^2 in another study area. This low level of resolution suggests that Loran-C has a limited utility for aerial telemetry studies.

The second chapter focuses on the demography of mountain sheep in the area of the Kingston and Clark Mountain ranges in the eastern Mojave Desert of California. Demographic units of mountain sheep were defined by the distribution pattern of radio-collared animals obtained via aerial telemetry. Estimates of population size and trend were made from ground and helicopter surveys. Mountain sheep ewes on Clark Mountain and in the Kingston Range were each defined as separate demographic units; however, substructuring was evident in the Kingston Range population. Because rams were more vagile, they were defined as a single demographic unit throughout the study area. Using mark-recapture methods, the Clark Mountain ewe population was estimated at 58 and the Kingston Range ewe population at 78 animals during the 1991-1992 period. The total ram population was estimated at 130 for this period. The Clark Mountain ewe population may have declined by 21% from 1991 to 1993 due to poor lamb recruitment and mountain lion predation. The Kingston Range ewe population remained relatively stable during this period. Mountain sheep in this area may be better described on a longer term basis by the metapopulation model.

The last chapter describes seasonal intermountain migration of ewe groups in the area of the Kingston and Clark Mountain ranges. Three hypotheses were explored regarding ecological factors underlying migration: (1) ewe migration patterns followed changes in forage quality; (2) hot season migration was driven by water requirements; and (3) migration from hot season ranges were made to reduce predation risk. These hypotheses were not mutually exclusive; however, by testing them in two neighboring populations simultaneously, there was a possibility of rejecting some general explanation for the movement patterns. Percent fecal nitrogen (as a surrogate for forage quality), habitat openness, habitat ruggedness, elevation, and proximity to water were variables used in hypotheses testing. Ewes were found to move to higher, more mesic ranges, nearer to water sources during the hot season. These movements also were likely to have resulted in an increase in forage quality. Migration away from hot season ranges resulted in ewes having higher fecal nitrogen during winter/spring than animals that did not migrate for one population, but not the other population. Ranges moved to after the hot season were not more rugged than hot season ranges, but had significantly less visually obstructing cover than hot season ranges. These results suggest that migration to hot season ranges was influenced by water requirements, forage quality, or both. However, these hot season ranges had decreased visibility which may have increased predation risk. With cooler fall temperatures and relaxed water requirements, ewes moved to more visually open areas with reduced predation risk, even if these movements required the subordination of forage quality.

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CHAPTER ONE

LIMITS IN THE RESOLUTION OF LORAN-C FOR AERIAL TELEMETRY STUDIES

INTRODUCTION

Loran-C is an electronic navigation system that estimates geographic position by measuring time-differences of electronic pulses from a network of land-based transmitters (U. S. Coast Guard 1980). Loran-C is often used in aerial telemetry studies because it reduces flight time from the standard technique of directly mapping positions. Because Loran-C requires little knowledge of study area topography, it also has the potential to reduce error in mapping positions. To analyze Loran-C derived locational data from aerial telemetry of mountain sheep (*Ovis canadensis*) in the eastern Mojave Desert, I required a measure of the error associated with the telemetry positions.

The ability of Loran-C to determine geographic position (accuracy) during aerial telemetry studies is predominately influenced by the position of the aircraft (Loran-C receiver) relative to transmitting stations. In addition, other factors also may influence accuracy including: latitude/longitude solution, elevation above target (i.e., radio-collared animal), and pilot/observer ability. Bias in positions determined by Loran-C may occur because of a study area's location in relation to transmitting stations. In addition, different Loran-C receivers may have functional differences that could produce bias unique to the individual unit. Here, I describe the bias and accuracy of locations determined by Loran-C in 2 areas of the eastern Mojave Desert of California relative to the true position of the aircraft. I test the hypotheses that bias associated with Loran-C varies with individual Loran-C receiver or study area, and that such biases can be mitigated by general correction factors.

STUDY AREA

Research was conducted in 2 separate areas of the eastern Mojave Desert. The northern study area was a string of mountain ranges directly north of Mountain Pass, San Bernardino County, California. This area encompassed the Clark Mountain Range, Kingston Range, and Mesquite Mountains in California, and the southern part of the Spring Range in Clark County, Nevada. The southern study area was approximately 45 km southwest of Mountain Pass and included Old Dad Mountain and the Kelso Mountains in San Bernardino County, California (Figure 1.1). Elevations varied from 805 m to 2,417 m in the northern study area, and from 507 m to 1,452 m in the southern study area.

METHODS

A Cessna 185 fixed-wing aircraft equipped with a R-40 Loran-C (Arnav Systems Inc., Graham, WA) was used in both the northern and southern study areas. A second Cessna 185 with an Apollo II Loran-C (model 612B; II Morrow Inc., Salem, OR) also was used in the northern study area. Therefore, 3 data sets were collected: 2 from the northern area and 1 from the southern area. Data were collected in the southern study area between November 30, 1990 and February 14, 1991 and in the northern study area between September 19, 1991 and January 26, 1993.

Mountain peaks and road intersections were selected as reference points ($n = 9$ or 10/data set). Geographic coordinates determined by Loran-C were recorded as the aircraft passed directly over these reference points. The directions from which the aircraft approached reference points during repeated passes were randomized. Six positions were compiled for each reference point per data set in the northern study area and 16 positions for each reference

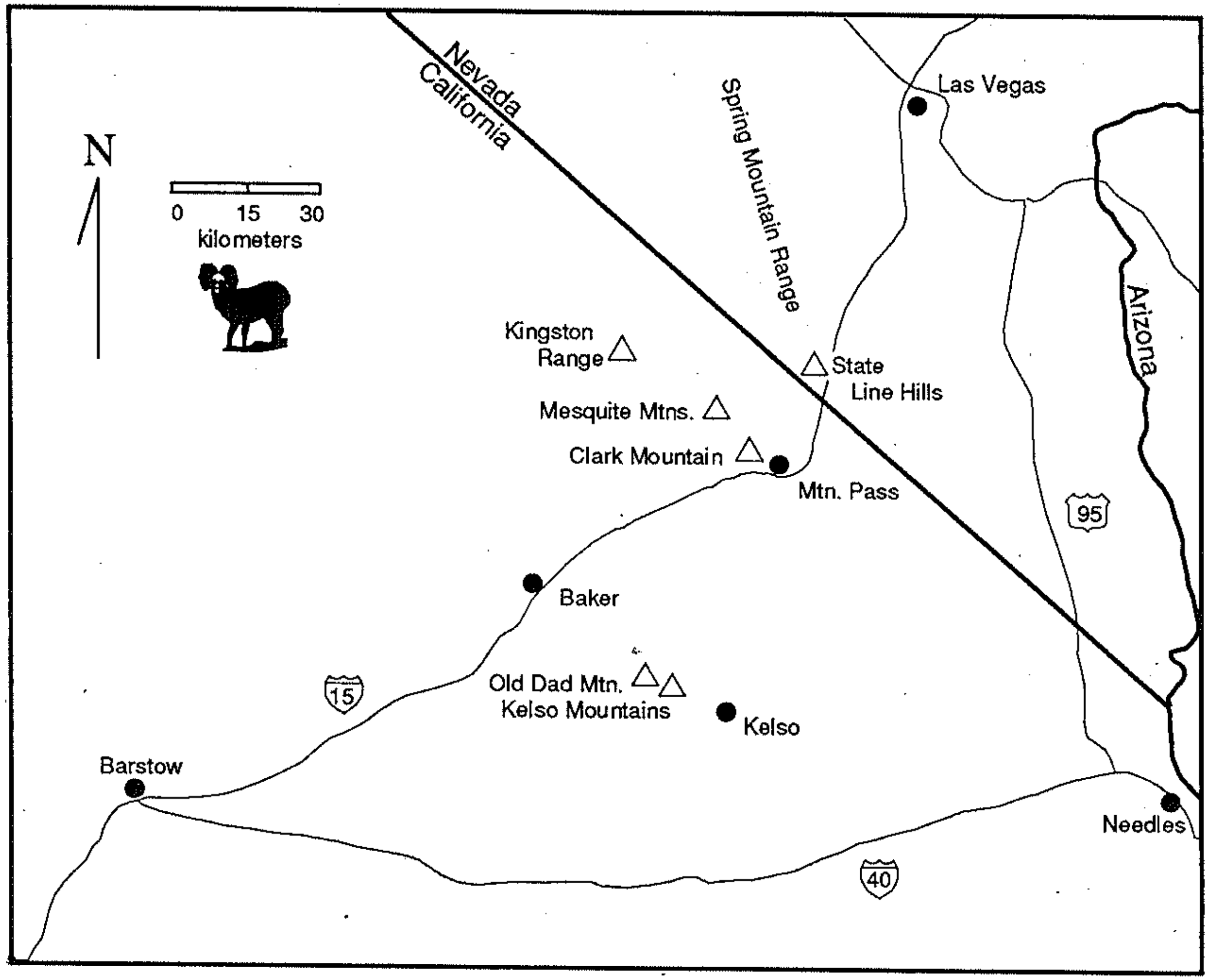

Figure 1.1. General locations for mountain ranges of interest in the eastern Mojave Desert.

point in the southern study area. The geographic coordinates of reference points used for comparisons were determined from 7.5 minute topographic maps.

Latitude and longitude generated by Loran-C were recorded to the nearest 0.10 minute. Based on the general location of the northern study area, this limited the resolution of Loran-C to an area approximately 185 m (N-S) by 151 m (E-W). This represented an accuracy of ≤100 m. I assumed that minor errors in determining reference point coordinates caused by map error or difficulty in determining when the aircraft was directly over the target were within this level of resolution.

Geographic coordinates determined from topographic maps were referenced to the 1927 North American Datum (NAD), and those determined by Loran-C receivers were referenced to datums considered equivalent to the 1983 NAD for conversion purposes. Various measures of latitude and longitude were converted to the 1983 Universal Transverse Mercator Grid (UTM) using the U. S. Army Topographic Engineering Center program CORPSCON V3.01 (beta).

For statistical analyses, data were considered bivariate (Batschelet 1981). Analyses were conducted by combining data within each data set; corresponding reference points were superimposed to form the origin of each combined distribution. These combined distributions were tested for bivariate normality with a goodness of fit test based on the Cramer-Von Mises statistic (Ackerman et al. 1989). Bivariate normality was rejected for 2 of the 3 distributions at the 5% level; therefore, nonparametric statistics were used for further analyses.

To identify potential biases in the distributions, Hodges' bivariate sign test (Batschelet 1981) was used to determine whether the center of error distributions deviated significantly from their origins. Because of the large sample size, critical values presented by Mardia (1972) for the southern study area were used.

Comparisons between the two data sets from the northern study area, and between the first data set from the northern study area and the data set from the southern study area, were conducted to test hypotheses of systematic biases based on study area or Loran-C receiver. Mardia's two-sample test (Batschelet 1981) was used to determine whether centers of the distributions deviated significantly from each other. Since the sample sizes were large, Chi-square tests were used as the final comparison after conversion to circular distributions (Batschelet 1981).

Accuracy of Loran-C was evaluated after adjusting the distributions for significant bias. The adjustment was made by shifting the distribution data toward the origin by an amount equal to the mean vector (mean northing and easting) of the distribution. After this correction, the distribution of points around the origin of each data set was evaluated. The distances these points fell from the origin were tested for normality using the Kolmogorov-Smirnov goodness of fit test (Zar 1984). The null hypothesis of normality for all 3 data sets was not rejected at the 5% level. Since these corrected distributions were normally distributed and generally circular around their origin, the Empirical Rule for mound-shaped distributions (McClave and Dietrich 1988) could be used to interpret the accuracy of the data. The distances the points fell from their origin were used to generate a mean error and standard deviation for each data set from which 68% and 95% error radii were derived.

RESULTS

The null hypothesis that the centers of the distributions determined by Loran-C were the same as their origins was rejected for all 3 data sets (northern data sets $n = 54$, $K = 1$, $P < 0.001$ and $n = 54$, $K = 0$, $P < 0.001$, southern data set $n = 144$, $K = 24$, $P < 0.01$). These significant deviations from the reference points suggested bias in the original distributions determined by Loran-C. The null hypothesis that the 2 distributions from the northern study area, derived using different Loran-C receivers, were from the same population was rejected; these distributions deviated significantly from each other ($X^2 = 53.14$, 6 df, $P \leq 0.001$). Furthermore, the distributions derived from the same Loran-C receiver for the northern and southern study areas also deviated significantly from each other ($X^2 = 32.39$, 7 df, $P \leq 0.001$). Thus, in each of the 3 distributions determined by Loran-C, significant and separate biases were found. Bias in the northern study area was 265 m north and 435 m east for the first data set, and 228 m south and 484 m east for the second data set, while bias for the southern study area was 99 m north and 163 m east. Since no general Loran-C bias pattern was determined based on study area or Loran-C receiver, the correction factors generated from these biases can be simply viewed as after the fact calibrating of the Loran-C receiver to a particular study area.

After correcting for bias, the accuracy of Loran-C varied between data sets; Loran-C was more accurate in the southern than in the northern study area (Table 1.1). In the northern study area, my method determined a position with 95% probability within circular areas of approximately 1.2 km^2 and 1.5 km^2 for the 2 data sets. In the southern study area this value was approximately 0.8 km^2.

Table 1.1. The accuracy of Loran-C after adjusting for bias. Error was calculated as the distance between reference point locations as determined by Loran-C and the actual location of these points. Error radii were calculated after assuming a circular distribution. The two data sets in the northern area were collected using different aircraft and Loran-C units. The northern study area encompassed the Kingston Range, Mesquite Mountains, and Clark Mountain Range in San Bernardino County, California, as well as the southern part of the Spring Range in Clark County, Nevada. The southern study area encompassed Old Dad Mountain and the Kelso Mountains in San Bernardino County, California.

	Error (m)		Error Radius (m)	
Study Areas	**Mean**	**SD**	**68%**	**95%**
Northern (Data Set 1)	328	179	507	685
Northern (Data Set 2)	308	155	463	618
Southern	248	132	380	511

DISCUSSION

Previous reports suggested that the ability of Loran-C to determine geographic position was comparable to directly mapping positions onto topographic maps. The accuracy of aerial telemetry for mountain sheep using the direct mapping technique is generally reported to be 100 m (Krausman et al. 1984, Miller 1986). However, Miller (1986) discussed an experiment by Witham et al. (1982) in which the resolution of the direct mapping technique was more limited. In Rhode Island and California, ground based Loran-C receivers determined positions within 200 m (Patric et al. 1988, Rhoades et al. 1990). A similar result was reported for the estimated accuracy of a helicopter-based receiver during moose surveys in southeastern New Brunswick (Boer et al. 1989).

The results presented here question the utility of Loran-C for aerial telemetry studies in which highly accurate locational data are desired. After correcting for bias, the method produced linear errors 5.1 to 6.9 times greater than those commonly reported for the direct mapping technique. When viewed as area, this error translates to an increase of 26.1 to 46.9 times that associated with direct mapping.

In the areas included in this study, accuracy of aerial telemetry using Loran-C was adequate for delineating mountain sheep population distribution and long-distance movements. However, Loran-C could distort results if high resolution telemetry data were incorrectly assumed in analyses. For example, geographic information systems (GIS) can be used with aerial telemetry data to analyze habitat selection (Bleich et al. 1992, Bleich 1993, Ebert 1993), but large telemetry errors could result in significant misclassification of habitat use if habitat attribute polygons are small compared to the error associated with the telemetry data. Thus, questions that can be addressed with Loran-C data must be framed in a context that considers the resolution of that technology.

In California, aerial telemetry using Loran-C has been used to track radio-collared mountain sheep in numerous ranges over an extensive geographic area. The results presented here imply that if correction factors are to be applied, Loran-C bias must be determined for each Loran-C receiver used in each range. Furthermore, these results suggest that there is considerable variability in Loran-C accuracy, especially when viewed with earlier Loran-C accuracy studies. Investigators using Loran-C should determine accuracy on a study-area-specific basis. Research objectives should then be evaluated in light of those resolution limits.

CHAPTER TWO

DEMOGRAPHY OF MOUNTAIN SHEEP WITHIN THE AREA OF THE KINGSTON AND CLARK MOUNTAIN RANGES, CALIFORNIA

INTRODUCTION

Management efforts to conserve mountain sheep (*Ovis canadensis*) frequently depend on current estimates of demographic parameters such as size and trend. Fundamental to such parameters is the definition of *population*. Mountain sheep are associated with mountainous, open terrain which results in a naturally fragmented distribution (Bleich et al. 1990). As a consequence of this fragmentation, mountain sheep populations traditionally have been defined by the geographic borders of their preferred habitat. In desert areas, this has meant defining populations by mountain range. Alternatively, mountain sheep distributions have been described recently by the metapopulation model (Schwartz et al. 1986, Bleich et al. 1990). Intermountain movements of rams have been used to suggest genetic connectivity between mountain sheep in distinct ranges (Schwartz et al. 1986). This model describes the dynamics of mountain sheep distribution through the mechanism of extinction and recolonization of populations (demes).

Substructuring within populations may further undermine the traditional perspective of population. Substructuring of ewe populations has been observed in northern mountain sheep (Geist 1971, Festa-Bianchet 1986, Stevens and Goodson 1993) and recently in desert-dwelling mountain sheep (Cunningham and Hanna 1992, Wehausen 1992). For example, a mountain range may contain ewe groups separated by short distances, but exhibiting substantially different population trajectories (Wehausen 1992).

An appropriate definition of population will depend upon the question being addressed. For the purpose of evaluating the current demographic status of a group of mountain sheep, a definition of population should represent a relatively closed demographic unit with little emigration or immigration. In addition, the individuals within the demographic unit should experience similar environmental conditions which might affect their survival and reproduction. Based upon these criteria, differences between rams and ewes may require demographic units to be defined separately by sex in areas where rams move readily between otherwise independent ewe populations. The problem of population definition is exemplified by efforts to monitor populations within the Kingston and Clark Mountain ranges in the eastern Mojave Desert of California.

Two decades ago, Weaver and Hall (1972) suggested the distribution of mountain sheep inhabiting the Kingston Range was restricted to that range, and mountain sheep in the Clark Mountain Range to the south were restricted mainly to Clark Mountain, with a remnant population isolated in the eastern portion of that range. Their survey of these ranges was part of a state-wide inventory (Weaver 1972) and necessarily required subjective determination of population parameters based on a limited amount of field time. For lack of more detailed information, this working hypothesis of mountain sheep distribution in the Kingston and Clark Mountain ranges governed subsequent helicopter surveys to monitor the status of these populations prior to 1990. In October of that year, the suggested distribution of mountain sheep in the area became suspect when several ewes radio-collared in the Kingston Range in September moved to the Mesquite Mountains, located between the Kingston and Clark Mountain ranges. This movement and the proximity of the Mesquite Mountains to the Clark Mountain Range raised questions about the definition of populations in the area and about the meaning of previous population estimates.

Weaver and Hall (1972) subjectively estimated the Clark Mountain population at 40 mountain sheep and the Kingston Range population at 30. Occasional helicopter surveys of these ranges, beginning in 1984, suggested these populations were larger than the previous estimates, with minimum counts over 100 adult animals for the Clark Mountain population in 1984 and for the Kingston Range population in 1986 (California Department of Fish and Game Memoranda). By early 1990, these populations were being considered by the California Department of Fish and Game (CDFG) as a logical choice to expand the limited hunting of mature rams, which at that time was restricted to only 2 populations in the state. Additionally, if the ewes in this area constituted a single large population, these animals would be considered as a potential source of stock for reintroduction efforts. A sound management approach required a better understanding of mountain sheep demography in this area before conducting these extractive activities.

Here, the demography of mountain sheep in the area of the Kingston and Clark Mountain ranges is described. An aerial telemetry study of mountain sheep distribution in the area is used to define demographic units. Estimates of population parameters for these units are presented from ground and helicopter surveys.

STUDY AREA

The study area was a string of mountain ranges in the eastern Mojave Desert directly north of Mountain Pass, San Bernardino County, California. This area encompassed the Kingston Range, the northern portion of which extends into Inyo County, the Mesquite Mountains, and the Clark Mountain Range. The study area also included the State Line Hills area in the extreme southern part of the Spring Range in Clark County, Nevada (Figure 1.1) Descriptions of study area topography, vegetation and weather are given in Chapter 3.

METHODS

Radio-collars equipped with mortality sensors (Telonics Inc., Mesa, Arizona) or marking collars were installed on mountain sheep during several captures conducted over the course of the study by the CDFG (Table 2.1). Mountain sheep were captured individually using a hand-held net-gun fired from a Bell Jet Ranger helicopter. All aspects of animal handling complied with CDFG protocols and were approved by the Institutional Animal Care and Use Committee of the University of Nevada, Las Vegas.

Distribution and movement of mountain sheep were determined by aerial telemetry of radio-collared animals. Aerial telemetry flights began on October 27, 1990 and continued until June 6, 1993. The timing of these flights, which varied throughout the study due to inclement weather and schedule conflicts, was approximately every two weeks. After telemetry flights to determine relocations were terminated, survivorship of radio-collared animals was monitored by monthly flights until December 9, 1993.

During the course of the study, two Cessna 185 airplanes were used for telemetry flights. These aircraft were equipped with telemetry receivers (Telonics Inc., Mesa Arizona) and with directional H-antennae mounted on the wing struts (Krausman et al. 1984). Positions of radio-collared animals were determined by signal strength, and the geographic coordinates for each relocated animal were then estimated by a Loran-C navigation unit as the aircraft passed directly over the animal's position.

Bias and accuracy of positions determined by Loran-C were investigated within the study area (Chapter 1). Analyses using fixed reference points in the study area suggested bias in locations determined by Loran-C and that bias varied between the two aircraft used; each had a different brand of Loran-C receiver. After correcting for bias, analyses of distributions derived using the different Loran-C receivers showed that Loran-C determined positions with 95%

Table 2.1. Capture history of mountain sheep (*Ovis canadensis*) from 09/90 through 12/93 in the area of the Kingston and Clark Mountain ranges, San Bernardino County, California . Animals not collared received ear tags only.

Capture Location	Date Captured	Sex	Birth Year	Collar Freq. or Type	Approx. Date of Death
Clark Mountain					
	12/21/90	F	87	245	11/93
	02/15/91	F	85	265	
	02/15/91	F	84	310	05/93
	02/15/91	F	86-87	420	
	02/15/91	F	83	4365	05/91
	10/11/91*	F	85	3001	11/93
	10/11/91	F	88	3051	
	10/11/91	F	89	4501	
	11/26/91	F	88	43651	
	11/26/91*	M	86	2041	
	02/15/91	M	90	none	
Kingston Range and Mesquite Mountains					
	09/19/90	F	85	225	
	09/19/90	F	<86	240	
	09/19/90	F	85	270	12/90
	09/19/90	F	86	295	
	09/19/90	F	85	300	01/91
	09/19/90	F	88	335	
	09/19/90	F	adult	345	01/91
	09/19/90	F	84	375	
	09/19/90	F	82	455	
	09/19/90	F	86	marker	
	02/15/91	F	87-88	2701	
	02/15/91	F	85	305	02/91
	02/15/91	F	86	329	
	02/15/91	F	84	3451	
	02/15/91	F	adult	355	
	02/15/91	F	86	415	
	02/15/91	F	85	450	02/91
	09/19/90	M	82-83	marker	
	09/19/90	M	89	none	
	12/20/90	M	84	315	
	12/20/90	M	89	406	
	12/20/90	M	88	445	
	12/21/90	M	82	020	09/92
	12/21/90	M	84	204	05/91
	02/15/91	M	84	236	
	02/15/91	M	84	252	
	02/15/91	M	83	395	
	02/15/91	M	82	400	
	02/15/91	M	87-88	441	

* Recaptured animals, marked in capture efforts prior to this study.

probability within circular areas of 1.2 or 1.5 km^2. Locational data used in analyses were corrected for the appropriate bias.

Population estimates were determined by mark-recapture (mark-and-sample) methods. Both radio and marking collars were used. An important assumption of the mark-recapture method is that the number of marked (collared) animals in the population is known during the sampling period. Estimates will be inflated if marked animals die undetected. This was not a problem for ewe estimates since only one of the marked animals was not radio-collared and this animal was seen alive in June 1993. Another potential problem was the presence of mountain sheep that had been captured and collared during disease studies prior to September 1990. Since no information was available on the survival of these animals, they were excluded as marked animals from sampling. All animals marked for this study, and used for population estimation, received an individual letter or number on their collar. In addition, a system of colored ear tags was used to provide further individuality to marked animals.

Over the course of the study, the number of marked mountain sheep in the population varied due to additional captures or mortalities. Occasionally, these changes in marked individuals occurred during sampling periods. When necessary, the number of marked animals used for estimation was a weighted average based on the proportion of sampling that took place in each subperiod in which different numbers of marked animals were present.

Mark-recapture estimation requires that one of two sampling approaches be followed: sampling-with-replacement or sampling-without-replacement. Demographic sampling during this study was conducted using a sampling-with-replacement approach as described by Wehausen (1992). Sampling-with-replacement does not attempt to minimize the probability of sampling an individual more than once during an estimation period as required by sampling-without-replacement. Instead, observations are treated as individual events in which the animal is determined to be marked or unmarked (a binomial probability).

Sampling was conducted by making repeated visits to each mountain range throughout the year to sample ewe groups and, over time, to accumulate a sample large enough for population estimates of meaningful resolution. During any given day, each animal observed was determined to be marked or unmarked. These animals were not counted again during that day. However, if these individuals were seen again at a later date, they could again be counted. Thus, over time, the sum of marked individuals in a sample could outnumber the sum of marked individuals in the population.

Equal sampling probability for every animal in the population is an important assumption of sampling-with-replacement. Random sampling assures equal sampling probability, but due to the difficulty of mountain sheep sampling and a limited amount of sampling time, it was not likely to assure a large enough sample size for reasonable estimates. No random sampling scheme was established prior to sampling, but to approximate random sampling, different geographic areas used by ewes were sampled. Since populations tended to migrate seasonally (Chapter 3), sampling was conducted in the general areas of known mountain sheep concentrations. However, to mitigate potential bias in sampling, other areas of ewe habitat that had been generally abandoned at the time also were sampled. Violations of equal sampling probability may have been further mitigated by the mobility of mountain sheep and by mixing of animals over time. The effect of potential violations of this assumption on the accuracy of population estimates is discussed further in the results. Occasionally, telemetry was used to locate mountain sheep to facilitate fecal sample collection (Chapter 3). Any mountain sheep observed at these times were excluded from mark-recapture estimations.

Demographic sampling also was conducted from a helicopter during capture operations and during helicopter surveys. Surveys were conducted using an experienced pilot and 3 observers, at least 2 of which were experienced in mountain sheep identification and helicopter survey techniques. During surveys, the helicopter flew low-level contours while systematically covering area polygons previously delineated as mountain sheep habitat. In addition to the surveys, opportunistic helicopter sampling was conducted during some capture operations. The proportion of collared animals seen during helicopter surveys of ewe populations were similar to that from ground sampling; therefore, helicopter sampling was combined with ground observations for mark-recapture estimates. Helicopter sampling is generally assumed to be sampling-without-replacement; however, if we treat each sample from the helicopter as an independent event, then the inclusion of helicopter sampling with other independent observations (ground sampling) in a sampling-with-replacement approach seems reasonable. By combining helicopter and ground sampling, sample sizes for demographic estimations were greatly increased.

Population estimates were calculated using Bailey's binomial method (Bailey 1951, Bailey 1952, Seber 1982), which is a modification of the Lincoln-Petersen method. The Lincoln-Petersen method is $N = Mn/m$ (where M is number marked in the population, n is the sample size, and m is the number marked in the sample). The Lincoln-Petersen method tends to upwardly bias estimates, especially for small sample sizes (Seber 1982). The Bailey method is $N = M(n+1)/(m+1)$, which tends to reduce this bias. Because the Bailey method uses the binomial probability distribution, it is appropriate for data collected using a sampling-with-replacement approach (Seber 1982). Confidence intervals were calculated following the recommendations of Jensen (1989). Since confidence intervals for the Bailey method are approximated using the normal distribution, Jensen (1989) suggested that these intervals be developed using the reciprocals of the estimates. This approach has been applied to estimates calculated using other Lincoln-Petersen models, because the distributions of the reciprocals are more nearly normal (Seber 1982). Confidence intervals calculated in this way tend to be relatively wide. Recently, there has been some suggestion that estimates calculated using the sampling-with-replacement approach described above may be more accurate than these types of confidence intervals would suggest (Wehausen, unpublished data). While there may be more powerful and efficient methods for estimating confidence intervals around the data presented here, these were not readily available and so the more conservative approach was adopted.

Ewe population estimates for 1991 and 1992 included yearling ewes from the year sampled. Ewe and ram population estimates were calculated for the combined 1991-1992 period by including yearling ewes or yearling rams from 1991, but excluding 1991 lambs that became yearlings when sampling was extended into 1992. Sampling periods varied for other demographic parameters estimated, and included sampling and estimates from 1993. Lamb to ewe ratios were calculated from sampling generally limited to late summer and fall of each year, after periods of potential summer lamb mortality. Yearling ewe to adult ewe ratios were calculated from sampling generally limited to spring and early summer each year, when the potential for misclassification of yearling animals was minimal.

Survivorship of radio collared animals was calculated using the Heisey and Fuller (1985) method. Telemetry months, rounded to the nearest 0.5 month, were used as the sampling unit instead of telemetry days. This was reasonable, since the dates of mortalities were generally accurate to within two weeks. Survivorship was calculated for the entire ram population in the study area and for both ewe populations. Because the Heisey and Fuller (1985) method adjusted to telemetry months appears to be sensitive to sample size, data also were combined for both ewe populations to provide a general survivorship rate for ewes in the entire study area.

RESULTS AND DISCUSSION

Distribution and Population Definition

Ewes in the study area constituted two, and possibly three, major demographic units. Ewes captured in the Clark Mountain Range were not observed in the Kingston Range or Mesquite Mountains, and the reciprocal was true for ewes captured in the Kingston Range and Mesquite Mountains. Radio-collared ewes in the Clark Mountain Range moved seasonally between Clark Mountain and the State Line Hills (Chapter 3). These movements appeared to be made by most of the ewe population. In contrast, radio-collared ewes in the Kingston Range and Mesquite Mountains appeared to consist of two distinct ewe home range groups: those that migrated seasonally between the Kingston Range and the Mesquite Mountains (Chapter 3), and those that remained predominately in the Kingston Range and did not migrate to the Mesquite Mountains. Furthermore, these two groups generally used different areas of the Kingston Range and contact between these groups appeared to be limited (Figure 2.1).

There were other movement patterns within the Kingston Range and Mesquite Mountains suggested by the telemetry data. One radio-collared ewe (Ewe 329; Figure 2.1) stayed mostly on a limestone ridge in the far north portion of the Kingston Range and only occasionally moved to the Mesquite Mountains. This individual did not represent a large group of animals since few mountain sheep were ever observed along this northern ridge during helicopter surveys. Additionally, some Kingston Range ewes moved to a limestone ridge south of the Kingston Range. These movements often occurred during lambing season but did not appear to be consistent from year to year.

For demographic analysis, ewes in the study area were defined as two separate populations: those inhabiting the Clark Mountain Range (Clark Mountain population) and those inhabiting the Kingston Range and Mesquite Mountains (Kingston Range population). While the Clark Mountain population appeared to be reasonably defined, estimates of demographic parameters for the Kingston Range population should be interpreted with caution due to the existence of separate ewe groups. Wehausen (1992) described the ewe population inhabiting the Old Woman Mountains in the eastern Mojave Desert as being comprised of two separate demographic units. These ewe subpopulations had independent recruitment rates and population trajectories. Substructuring of ewe populations can seriously distort estimates of population dynamics if the data used in computations unwittingly come from different ewe groups (Festa-Bianchet 1986) or if sampling is not proportional (random) across ewe groups (Wehausen 1992). By defining ewes in the Kingston Range and Mesquite Mountains as a

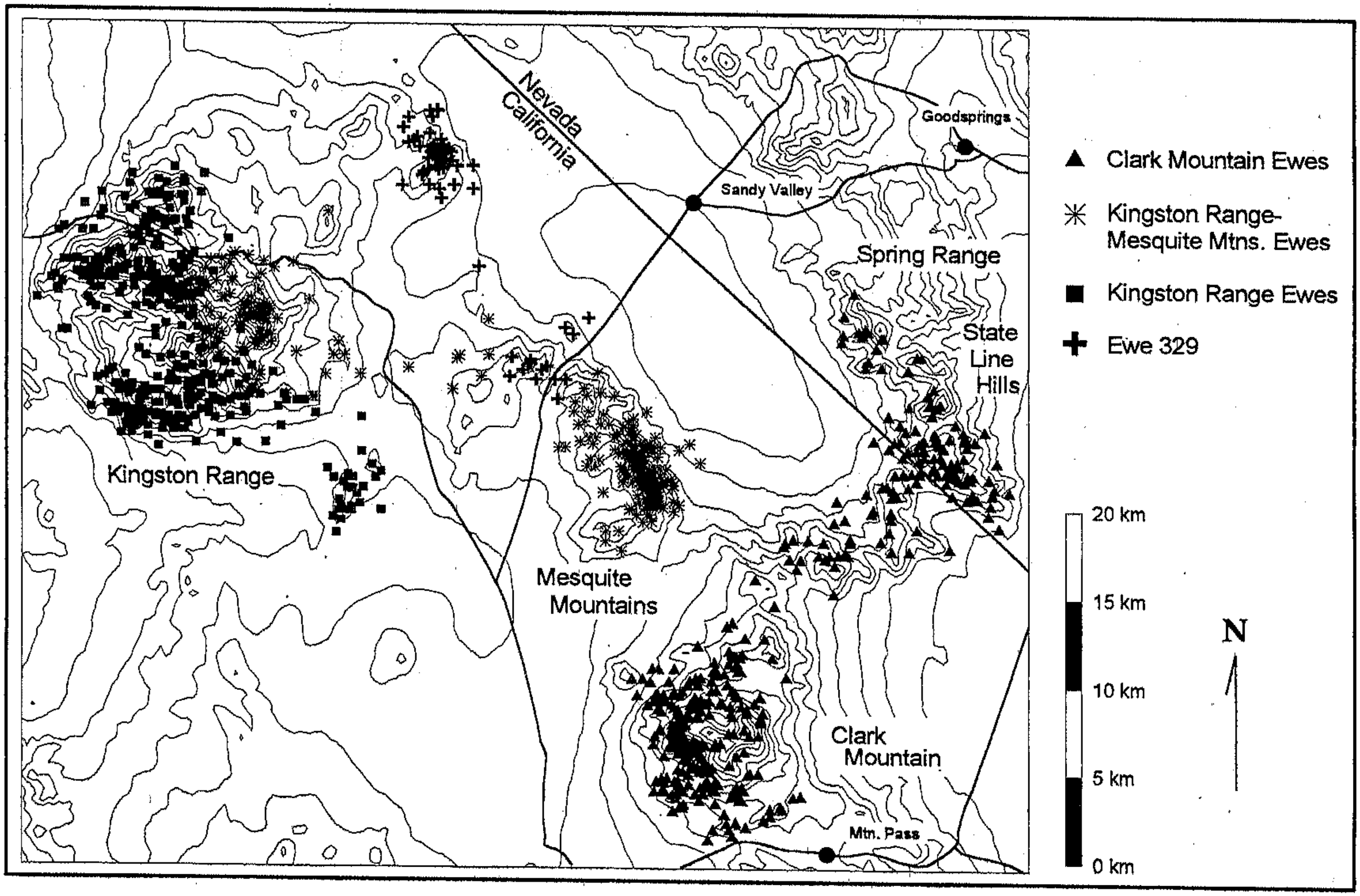

Figure 2.1. Locations of radio-collared mountain sheep (Ovis canadensis) ewes from September 1990 through December 1993 in the area of the Kingston and Clark Mountain ranges, San Bernardino County, California.

single population, demographic sampling and analysis were simplified. However, if these ewe groups had differing demographies, defining them as a single demographic unit may have reduced the meaningfulness of the estimates.

The ram population in the study area appeared to be less substructured by mountain range (Figure 2.2). Rams captured in the Kingston Range were occasionally located in the Mesquite Mountains. Rams captured in the Mesquite Mountains exhibited movements throughout the study area, including the temporary movement of two rams to Potosi Mountain in Nevada during the rut of 1991. Only one adult ram was captured in the Clark Mountain Range, and this animal was located twice in the Mesquite Mountains. While some level of substructuring in the ram population was apparent, for demographic analysis the ram population in the study area was treated as a single unit due to the vagility of these animals.

Population Estimates

Fifty-eight ewes were estimated for the Clark Mountain population during the entire 1991-1992 sampling period. Estimates based on yearly data showed a small increase in the population between the 1991 and 1992 sampling periods, but this difference was minimal (Table 2.2). Because ewes in this range showed little propensity to segregate into groups based on non-overlapping home range patterns, sampling from the ground was not likely to have violated the assumption of equal sampling probability. Helicopter surveys of the population produced rather large samples. For example, during the August 1992 helicopter survey, 50 ewes were counted. This sample represented an unusually large fraction of the population compared with that commonly seen in helicopter surveys of other populations (McQuivey 1978, Wehausen unpublished data). Although unusual, this sample was apparently representative of the population since a ewe estimate from this sampling alone was 58 animals. Thus, the 1991-1992 ewe estimate for this range was likely an accurate reflection of the true population size.

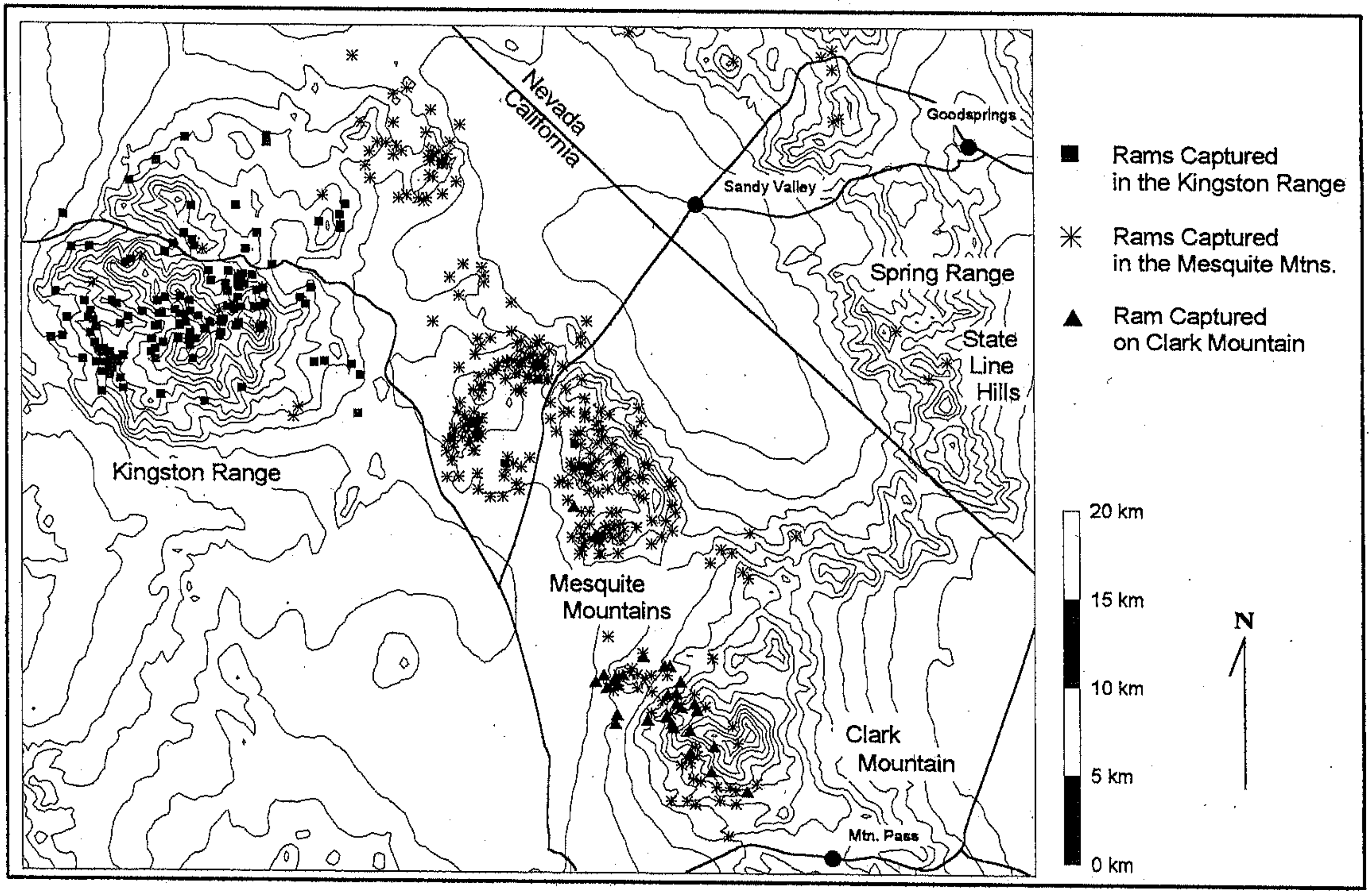

Figure 2.2. Locations of radio-collared mountain sheep (Ovis canadensis) rams from January 1991 through December 1993 in the area of the Kingston and Clark Mountain ranges, San Bernardino County, California.

Table 2.2. Mark-recapture population estimates for mountain sheep (*Ovis canadensis*) in the area of the Kingston and Clark Mountain ranges, San Bernardino County, California. Samples and estimates include yearling ewes or yearling rams from the starting year. Lambs from the first year of sampling, that became yearlings when sampling was extended into a second year, were excluded from estimates. The ram sample and estimate are from data covering the entire study area. When necessary, a weighted mean number of marked animals was used in estimates.

Population	Sex	Sampling Period	No. Marked in Pop.	Sample Size	No. Marked in Sample	Population Estimate	95% C.L.
Clark	Ewe	06/91 - 01/92	5.06	124	11	53	35 - 109
Clark	Ewe	02/92 - 12/92	8	125	16	59	41 - 104
Clark	Ewe	06/91 - 12/92	6.50	249	27	58	43 - 88
Kingston	Ewe	04/91 - 01/92	13	152	23	83	61 - 130
Kingston	Ewe	02/92 - 11/92	13	75	14	66	46 - 118
Kingston	Ewe	04/91 - 11/92	13	227	37	78	61 - 109
Study area	Ram	04/91 - 11/92	11.98	129	11	130	85 - 269

Population estimates for ewes inhabiting the Kingston Range and Mesquite Mountains differed considerably between the 1991 and 1992 sampling periods, although both estimates were well within the other's confidence interval (Table 2.2). These differences were probably an artifact of the sampling method, rather than a real increase in the population. Ground sampling in the Kingston Range was inefficient due to limited access in considerable portions of the range and the expansive amount of mountain sheep habitat. Furthermore, dense vegetation over much of the ewe habitat made the sighting of mountain sheep difficult. Ground sampling in the Kingston Range and Mesquite Mountains tended to favor a certain group of animals, particularly those that migrate seasonally to the Mesquite Mountains, where both access and observations were easier. Other ewe groups and collared individuals were under-represented. This violation of the assumption of equal sampling probability also may have occurred during helicopter sampling. For example, during a helicopter survey in November 1991, only 5 ewes were observed in the Kingston Range in 5.8 hours of survey time. No collared ewes were observed in the Kingston Range during this flight despite the fact that several collared ewes never leave this range. This same survey logged 35 adult and yearling ewes, including 5 collared ewes, in 1.9 hours of survey time in the Mesquite Mountains. Because of these difficulties, the estimate of 78 ewes for the 1991-1992 sampling period should be viewed as a rough approximation. Nevertheless, these data clearly suggest a ewe population of considerable size, in spite of the potential sampling violations.

Ram population estimation was not the focus of sampling efforts, but an estimate of the ram population inhabiting the entire study area was calculated (Table 2.2). Sexual segregation of mountain sheep and the definition of what constitutes a ram population resulted in sampling problems, given the limited amount of sampling time. When not in rut, adult rams tend to use less rugged, more rolling terrain usually avoided by ewes (Bleich 1993). Since ewes were the focus of this study, ground sampling was concentrated in areas primarily used by ewes, thus habitat often used by adult rams was not systematically sampled. Observations of rams usually were made during ewe surveys. Because young rams tend to remain with ewe groups (Bleich 1993, Geist 1971), they were probably over-represented in the sampling. This also was true for helicopter sampling, since large expanses of area potentially used by adult rams were surveyed quickly or simply excluded. The probable bias toward young, unmarked rams may have resulted in an inflated estimate of the ram population. Because of the small sample size and low proportion collared in the sample, the resulting confidence limits for the estimate were extremely wide, and the estimate should be considered a rough approximation.

Ram:Ewe Ratios

A comparison of ram and ewe population estimates can be used to produce a standard sex ratio estimate. By combining the 1991-1992 ewe estimates for both the Kingston Range and Clark Mountain populations and comparing this to the ram estimate from the same time period, the ratio of rams to ewes for the entire study area was 95.6:100. This high ratio undoubtedly resulted from the inflated ram estimate used in the calculation. In contrast, sex ratios from helicopter sampling (Table 2.3) were probably underestimates because of the sampling bias against adult rams. Variation among these ratios probably resulted from inadequate helicopter sampling of adult rams rather than real demographic change. The 1991 ratio was probably the most realistic, but it should still be considered an underestimate because of sampling bias.

Mortality and Survivorship

During the entire study period, a total of 9 radio-collared ewes and 2 radio-collared rams died. One ram died from complications of pneumonia. The cause of death for the other ram could not be determined, but predation was not involved. Two ewes captured in February 1991 in the Mesquite Mountains died within a few weeks of capture. One of these ewes had difficulty controlling its movements when released. Both these deaths were considered capture related and were excluded from survivorship calculations. The cause of death for another ewe could not be determined other than that it was not predation. The remaining 6 ewes died from mountain lion (*Felis concolor*) predation. Three of these ewes were killed in the Kingston Range during January 1991, all within 4.5 months of their capture. Another ewe was killed on Clark Mountain in early May 1991, only 2.5 months after its capture. The remaining 2 lion-kills occurred on Clark Mountain in November 1993. Both of these ewes had been radio collared for over 2 years.

Table 2.3. Ram to ewe ratio estimates for mountain sheep (*Ovis canadensis*) in the area of the Kingston and Clark Mountain ranges, San Bernardino County, California. Data are from 2 helicopter surveys in 1991, 1 helicopter survey in 1992 and 1 helicopter survey in 1993. Sampling includes survey time in the Mesquite Mountains and the State Line Hills. Sampling from the November 1991 survey include data from a double survey of the Mesquite Mountains. Sampling and estimates include yearling animals.

Survey Period	Rams Sampled	Ewes Sampled	Ram: 100 Ewes
October & November 1991	61	145	42.1
August 1992	23	87	26.4
October 1993	27	74	36.5

Table 2.4. Survival rates for mountain sheep (*Ovis canadensis*) in the area of the Kingston and Clark Mountain ranges, San Bernardino County, California. Calculations based on sampling between 09/19/90 through 12/09/93, using the Heisey and Fuller (1985) method.

Sex	Demographic Unit	Number of Mortalities	Telemetry Months	Monthly Survival Rate	Yearly Survival Rate
Ewe	Clark	4	226.5	.982	.807
	Kingston	3	393	.992	.912
	Combined	7	619.5	.989	.873
Ram	Combined	2	274	.993	.916

Wehausen (1992) calculated a yearly survival rate of 0.95 for eastern Mojave Desert ewe populations not suffering from mountain lion predation. The lower annual survivorship of ewes in my study area (Table 2.4) reflected the impact of lion predation. Lion predation on ewes in the study area should be considered moderate in comparison to that reported for ewes inhabiting the Granite Mountains, another Mojave Desert range, where annual survivorship rate was 0.721 due to lion predation (Wehausen 1992). Wehausen (1992) calculated a yearly recruitment rate necessary to balance such predation at 39.3 yearlings ewes per 100 adult ewes (the calculation assumes a fixed recruitment rate for all age classes beginning at 2 years of age and a maximum age of 14 years). Thus, a ratio of 78.6 yearlings per 100 adult ewes would be required for a static ewe population (assuming an even sex ratio for lambs at 1 year of age). To produce static ewe populations in the area of the Kingston and Clark Mountain ranges, the same calculation using the combined survivorship estimate (assuming that this value better reflected true survivorship in the area) would require yearly recruitment of 17.5 yearling ewes per 100 adult ewes, or 35 total yearlings per 100 adult ewes.

Ram survivorship was slightly higher than that for ewes in the study area (Table 2.4), and this reflected the lack of documented mountain lion predation on rams. The only other eastern

Mojave Desert population with which to compare ram survivorship data was the Old Dad Peak - Kelso Mountains population (Wehausen 1992). Ram survivorship in the Kingston and Clark Mountain ranges was higher than that for the Old Dad Peak - Kelso Mountains population. Interestingly, lion predation on rams was documented in the Old Dad Peak - Kelso Mountains area, and the lower ram survivorship in that area was, in part, due to this predation.

Mountain lion predation on ewes in my study area appears to be periodic. An alternative hypothesis presented prior to the documentation of additional predation in November 1993 (Jaeger and Wehausen 1993), suggested the capture event (or some behavior related to capture) may predispose ewes to lion predation. The evidence was the proximity of capture date to the death of the radio-collared ewes from lion predation early in the study. The subsequent deaths of 2 radio-collared ewes 2 years after they had been captured suggests that the earlier correlation may have been spurious. The documentation in January 1991 of an unmarked yearling ram killed by a mountain lion around the same time as the predation on radio-collared ewes also suggests that mountain lion predation was not limited to marked individuals.

Mountain lion density in the eastern Mojave Desert may be low and home ranges may be large, possibly covering multiple mountain ranges. Portions of a mountain lion's home range may remain vacant after its death. If this is the case, the presence of mountain lions in any particular range may be periodic, resulting in periodic lion predation on mountain sheep populations. This hypothesis was supported by the observed colonization of the Old Woman Mountains in the eastern Mojave Desert by a mountain lion. After 5 years of intense field study on mountain sheep in this range in which no evidence of mountain lion was found, Wehausen (1992) described the abrupt appearance of a lion and its subsequent predation on the mountain sheep population. The death of a female lion on Interstate 15 directly south of Clark Mountain in January 1992 could explain the absence of documented predation in the Kingston and Clark Mountain ranges during that year.

Recruitment

The most striking observation on recruitment was the near failure of the Clark Mountain ewe population to recruit any individuals from the 1991 lamb cohort (Table 2.5). No lambs were observed during fall helicopter flights in the range. Ground sampling during summer and fall also found no lambs. However, in February 1992, a single yearling ewe was observed on the lambing range in the State Line Hills. This was the only yearling observed in this population during 1992, and resulted in the recorded yearling ewe to adult ewe ratio for that year (Table 2.6).

The lack of recruitment for 1991 could have resulted from poor lamb production or poor lamb survival. The Mojave Desert suffered a drought during 1989 and 1990. During those years, forage quality was relatively poor for mountain sheep in numerous ranges across the eastern Mojave Desert (based on data from fecal nitrogen curves; Wehausen 1992). However, in desert environments, previous studies have failed to find a correlation that would link

Table 2.5. Lamb to ewe ratios and sampling for mountain sheep (*Ovis canadensis*) populations in the area of the Kingston and Clark Mountain ranges, San Bernardino County, California. Ewe sample sizes include yearling ewes.

Year	Population	Method	Period	Ewes Sampled	Lambs: 100 Ewes
1991	Clark	Helicopter	10/11	23	0
1991	Clark	Helicopter	11/26	29	0
1992	Clark	Helicopter	8/20	50	16.0
1992	Clark	Ground	9/16 -12/21	37	16.2
1993	Clark	Helicopter	10/08	31	12.9
1991	Kingston	Helicopter	10/10	36	33.3
1991	Kingston	Helicopter	11/25	38	10.5
1991	Kingston	Helicopter	10/10 &11/25	74	21.6
1992	Kingston	Helicopter	8/21	37	27.0
1993	Kingston	Helicopter	10/07-10/08	43	27.9

Table 2.6. Yearling ewe to adult ewe ratios and sampling for mountain sheep (*Ovis canadensis*) populations in the area of the Kingston and Clark Mountain ranges, San Bernardino County, California. No estimate was made for the Kingston Range populatin in 1993.

Year	Population	Time Period	No. Ewes Sampled	Yearling Ewe: 100 Adult Ewes
1991	Clark	4/23-9/14	66	1.5
1992	Clark	1/26-7/16	49	2.0
1993	Clark	2/21-6/7	45	6.7
1991	Kingston	4/21-9/21	36	19.4
1992	Kingston	1/24-6/19	43	9.3

preovulation nutrition or precipitation as a surrogate for diet quality, with later recruitment rates (Douglas and Leslie 1986, Wehausen et al. 1987, Wehausen 1992). Wehausen (1992) suggested that the protracted lambing period in desert environments provides ewes with the ability to vary the timing of lambing. This may allow a longer time period to gain the minimum physical condition necessary for ovulation, resulting in fewer lambing seasons being skipped. The environmental conditions present during 1989 and 1990 were unlikely to have resulted in a large percentage of ewes failing to produce lambs during 1991. Therefore, the lack of lambs observed during summer sampling was probably due to high lamb mortality during the spring of 1991.

Precipitation from November 1990 through March 1991 was higher in the region than in the previous two years, and forage quality on Clark Mountain was relatively good (Chapter 3). Lambs born in 1991 were probably not suffering from a lack of nutrition. The likely cause for the lack of lamb survival in the range was a disease process, although there is little direct evidence to support this hypothesis. Diseases that severely increase lamb mortality, but not adult mortality, have been documented or suggested in other desert populations (DeForge and Scott 1982, DeForge et al. 1982, Wehausen et al. 1987). One lamb discovered in the State Line Hills in April 1991, shortly after its death, showed no sign of injuries or predation.

Mountain lion predation offers another possible explanation for the poor recruitment. However, this hypothesis seems less likely. The selection of lambing habitat in this range may be a response to mountain lion predation (Chapter 3). None of the documented lion predation occurred in lambing habitat. Mountain lion undoubtedly kill lambs in the study area, but unless an extreme bias for young animals was present, which was unlikely given the opportunistic nature of mountain lion predation, predation pressure sufficient to eliminate the majority of lambs from the population also would have been expected to greatly reduce ewe survival. While the survival rate of adult ewes was affected by predation, it was not as low as would be expected if predation pressure had been extremely high. That predation alone could have been responsible for the complete lack of lamb survival observed during summer sampling on Clark Mountain seems improbable.

A disease process, or mountain lion predation, also may explain the low 1991 yearling ewe to adult ewe ratio. However, this ratio may be somewhat misleading. Standard yearling to ewe ratios include yearling rams in the calculations. Yearling rams were excluded from calculations of recruitment in an attempt to limit potential sampling bias; young rams may join adult ram groups and as a result be under-represented in sampling that focuses on ewe habitat. An estimate of total yearlings to adult ewes was possible by doubling the yearling ewe to adult ewe ratio (i. e. assuming equal production and survivorship of male and female lambs to yearling age). This produced a total yearling to adult ewe ratio of 3:100 for 1991. However, from ground sampling, the actual observed ratio for total yearlings to adult ewes was 12:100. The observed ratio may have been inflated since there was some question as to whether two young rams observed in August 1991 and recorded as yearlings were not really two-year-olds. Excluding August sampling from calculations eliminated the questionable yearlings and reduced the ewe sample to 51 adults, resulting in an observed ratio of 7.8:100.

Misclassification of yearling ewes as adult ewes was possible, particularly when yearlings were older; thus, sampling may have under-represented yearling ewes. More likely, the sex ratio of surviving yearlings was skewed. If we assume that the yearling to adult ewe ratio was 7.8:100 and a ewe population of 58 animals, the total number of yearlings for 1991 would have been only 4 or 5 animals. A ram biased sex ratio in such a small number of animals was possible. Supporting evidence for a low yearling ewe to adult ewe ratio came from the helicopter surveys in October and November 1991, which recorded only 1 yearling ewe for 51 adult ewes. However, this evidence should be weighed in light of the high potential for misclassifying yearling ewes as adult ewes during late season surveys.

Lamb to ewe ratios in the Clark Mountain Range for 1992 improved somewhat over 1991, but were still low (Table 2.5). This increase was consistent with the 1993 increase in the yearling ewe to adult ewe ratio (Table 2.6). The pattern of low lamb to ewe ratios continued in 1993.

In the Kingston Range and Mesquite Mountains, the substantially different lamb to ewe ratios recorded from two separate fall helicopter surveys during 1991 may have resulted from sampling difficulty (Table 2.5). The early survey did not include the Mesquite Mountains, but the large sample size of ewes in the Kingston Range indicated that most ewes had not yet migrated to the Mesquite Mountains. The second survey included the Mesquite Mountains with all but 5 of the observed ewes being recorded in that range. An alternative hypothesis for the difference in the observed lamb to ewe ratios was that lambs suffered substantial mortality in the 46 days between samplings. Given that a disease process may have devastated lambs in the Clark Mountain population earlier in the year, this was a possibility. However, the 1992 yearling ewe to adult ewe ratio did not support this explanation (Table 2.6). This ratio was higher than would be expected if the lower lamb to ewe ratio were correct. Combining both helicopter samplings produced a lamb to ewe ratio that corresponded to the 1992 yearling ewe to adult ewe ratio. The lamb to ewe ratio for 1992 and 1993 were both substantially higher than those observed for the same years in the Clark Mountain population, which suggested little conformity between lamb mortality in these two populations. However, the processes that govern lamb mortality may be highly stochastic and little can be concluded from 3 years of data.

The high yearling ewe to adult ewe ratio of 1991 suggested good recruitment for the Kingston Range population for that year, although the sample size from which this ratio was derived was small. A major discrepancy in the data was that the suggested high recruitment for 1991 corresponded to a drop in the estimated ewe population. Clearly, the demography of this population was not adequately addressed by the sampling method.

Population Trends

The demographic data for the Clark Mountain ewe population from 1991 through 1993 allowed an analysis of population change. Ewe population estimates from 1991 and 1992 indicated an increase of 6 ewes in the Clark Mountain population. This increase was an artifact of sampling, since only one ewe was likely recruited into the population from the 1991 lamb cohort. If we accept a population estimate of 58 ewes for 1991 and a yearly mortality of 0.127 (based on the general survivorship for ewes throughout the study area), then mortality was about 14 ewes for the 2 year period. Recruitment during this period, from observations of yearlings, was only 2 ewes. Based on these calculations, the ewe population declined by approximately 21% during this period. Following the same logic, the expected population at the beginning of 1993 would have been about 46 ewes. Recruitment that year would have been approximately 3 yearling ewes, compared with an expected mortality of about 6 ewes. Thus, the population would have continued to decline during 1993, but at a slower rate.

This calculation of population trend was based predominately on empirical data. Estimates of the beginning population size and yearly recruitment were reasonably good. Small variations in these values will not change the general direction or magnitude of the population decline. The critical factor in this calculation was the mortality value. Here, the value used was considerably lower than that calculated separately for the Clark Mountain population (Table 2.4). Thus, the decline in the ewe population suggested here should be considered a conservative estimate.

The lack of resolution in the demographic data for the Kingston Range ewe population did not allow for a critical evaluation of population trend between 1991 and 1993. However, using the assumptions of ewe life history characteristics suggested by Wehausen (1992; see "Survivorship" above) and assuming the general survivorship value for ewes in the study area, a yearling ewe to adult ewe ratio of 17.5:100 would be necessary for a static Kingston Range ewe population. Yearling ewe to adult ewe ratios in the Kingston Range were a little higher than this value for 1991, but considerably below it for 1992 (Table 2.6). No yearling ewe to adult ewe ratio data were available for 1993. These yearling ewe to adult ewe ratios suggest that the Kingston Range ewe population may have decreased by a small amount during the study period.

CONCLUSION

While a traditional view of population structure may be applicable to the ewes inhabiting Clark Mountain, it does not account for the spatial distribution of the ewes in the Kingston Range and Mesquite Mountains in terms that are clearly meaningful for demographic study. Substructuring is likely in most mountain sheep populations. Identifying populations in which substructuring occurs to a degree that could seriously affect the meaning of population parameters is critical where extractive management actions are to occur (Festa-Bianchet 1986, Stevens and Goodson 1993).

The ewes that migrate to the Mesquite Mountains and those that remain in the Kingston Range may have differing demographies. In this study, potential differences were disregarded and ewes in the Kingston Range and Mesquite Mountains were defined as a single demographic unit. If differences in demographic parameters existed, the result was a possible decrease in the accuracy and meaningfulness of the estimates. Regardless of this sampling limitation, estimates suggested that the overall Kingston Range ewe population was of considerable size. Furthermore, estimates of recruitment and survivorship suggested that the population may have decreased during 1992, but any possible decline during the entire study period was small.

The dynamics of the ewe population in the Clark Mountain Range were well documented. The observed 3 years of poor recruitment, coupled with lowered survivorship of adults due to mountain lion predation, strongly suggested that this population declined considerably during the study period. Whether or not this population is threatened is unclear. Depressed recruitment due to persistent high lamb mortality is common in desert-dwelling mountain sheep populations. Because of their longevity and high survivorship, mountain sheep populations can persist for long periods with limited recruitment. Wehausen (1992) described a mechanism by which long term persistence of populations suffering from disease-related high lamb mortality is possible. He has noted patterns of gradual population declines interspersed with episodes of high recruitment during which populations made large gains. He also hypothesized that these recruitment pulses may occur: (1) within a disease regime because of factors that reduce disease transmission or that increase the survivorship of lambs after the disease is contracted; or (2) through diseases disappearing entirely from populations for periods of time.

Whether or not the Clark Mountain population rebounds through a recruitment pulse could be determined with reasonable sampling effort in this range. However, the presence of mountain lion predation may confound efforts to determine a cause and effect relationship between a possible disease regime and recruitment. If this population is suffering from high lamb mortality due to disease, the added effect of mountain lion predation could produce a recipe for continued population decline by lowering the longevity of adult ewes necessary to maintain a large enough population base between recruitment pulses.

While the current data do not predict the extinction of the Clark Mountain ewe population, an extinction of a local ewe population in the study area would not necessarily be a critical event. The definition of population used in this study was for the expediency of demographic analysis. The vagility of rams in the area and the observed seasonal movement of ewes between mountain ranges, suggests that the mountain sheep in this area may be better described by a metapopulation model. This model predicts the occasional extinction of local ewe groups. Given time, recolonization of the vacated habitat by neighboring ewe groups would follow.

CHAPTER 3

INCENTIVES FOR MIGRATION IN DESERT-DWELLING MOUNTAIN SHEEP EWES

INTRODUCTION

Movements of desert-dwelling mountain sheep (*Ovis canadensis*) often incorporate seasonal shifts in distribution, such as congregation around and dispersal from water sources at the beginning and end of the hot season. Whether seasonal movements constitute migration depends predominately on the extent to which distributions change. Often, these movements simply consist of seasonal reductions or expansion of areas of usage (Leslie and Douglas 1979). True migration (see Dingle 1980) has been well documented in northern mountain sheep populations that inhabit areas with potentially severe winter conditions (Geist 1971, Shannon et al. 1975, Wehausen 1980, Festa-Bianchet 1988). Generally, these are altitudinal migrations during which mountain sheep move to low elevation ranges after heavy winter snows and to high elevation ranges in spring and summer. Migration in desert-dwelling mountain sheep is less common, but has been noted in some populations (McQuivey 1978).

Altitudinal migration in northern mountain sheep populations has been found to follow favorable changes in forage conditions (Wehausen 1980). Altitudinal migration has been shown to increase body weight and body condition of mountain sheep under experimental conditions (Hebert 1973). Even small differences in summer forage quality could positively affect reproduction and survival in northern ungulates (White 1983). However, studies that have investigated migration in northern populations suggested a trade-off may occur between optimization of nutrient intake and predator avoidance for mountain sheep ewes (Wehausen

1980, Festa-Bianchet 1988). Both Wehausen (1980) and Festa-Bianchet (1988) showed that in migratory populations ewes tended to leave their winter ranges when forage conditions there were optimal and move to higher, more rugged terrain where spring plant growth had not yet begun. This was not the case for rams whose movements tended to more closely follow forage quality. Both researchers concluded that ewes were compromising forage quality for presumably safer conditions for their young lambs.

For desert-dwelling mountain sheep, summer water requirement is likely to be an important factor in migration patterns. However, this is only one potential driving force which explains only one side of a migratory pattern. Optimization of forage quality and predator avoidance also may be important factors. These factors are likely to affect the movement of male and female mountain sheep differently because of sexual dimorphism and dissimilar parental responsibilities. Bleich (1993) concluded that sexual segregation of mountain sheep was predominately due to ewes compromising nutrient intake for predator avoidance.

Here, three hypotheses concerning habitat selection that may be driving ewe migration patterns are explored for two neighboring ewe populations in the eastern Mojave Desert that exhibit migratory behavior. The first was that ewe migration patterns simply maximized forage quality. Predictions from this hypothesis were that ewes that migrated during the hot season and again after the hot season should have higher forage quality than those animals that did not migrate. The second hypothesis concerned only hot season migration and suggested that this migration was driven by water requirements. This hypothesis predicted that ewes would select habitats that reduce water requirements or increase access to standing water during the hot season. The third hypothesis concerned migration after the hot season. This hypothesis was developed on the premise that ewes migrating to the hot season ranges for forage quality or water requirements also increased their predation risk. Once the condition restricting ewes to the hot season ranges was no longer operating, ewes should leave these ranges for habitats that reduce predation risk. Predation risk for mountain sheep is integrally tied to two habitat variables: ruggedness and openness (Geist 1971, Wehausen 1980, Risenhoover and Bailey 1985, Bleich 1993). Rugged habitat provides mountain sheep with a means to escape predators, while openness allows for the detection of predators at a distance necessary for mountain sheep to take advantage of escape terrain. This hypothesis predicts that habitat selected after migrating from the hot season range should be more rugged and more visually open than that used in the hot season range. These two variables were evaluated independently.

Evaluation of these hypotheses was fraught with the difficulty that they are not mutually exclusive; thus, more than one may be correct (Quinn and Dunham 1983). Furthermore, they are not necessarily exhaustive in that they may not explain all the possible variation within this system. Nevertheless, by testing these hypotheses simultaneously in two neighboring populations, there was the possibility of rejecting certain general explanations for the movement patterns.

STUDY AREA

The study area was located in a string of mountain ranges in the eastern Mojave Desert directly north of Mountain Pass, San Bernardino County, California. Two migratory ewe populations inhabit this area (see Chapter 2). The Kingston Range ewe population inhabits the Kingston Range, of which the northern portion extends into Inyo County, and the Mesquite Mountains. The Clark Mountain ewe population inhabits Clark Mountain and the State Line Hills area in the extreme southern part of the Spring Range in Clark County, Nevada (Figure 1.1).

The Kingston Range, which reaches an elevation of 2236 m, was located at the northern end of the study area. This large range is composed mostly of steep, rugged, granitic canyons and ridges. The northern and eastern parts of the range are dominated by tilted carbonate formations (limestones and dolomites), surrounded by more gentle, rolling terrain underlain by easily eroded quartzite and shales (Reneau 1983).

The Mesquite Mountains lie to the south of the Kingston Range and to the north of Clark Mountain. The eastern part of this lower elevation range consist of steep, rugged carbonate formations. The northern and western part of the range contain more rolling terrain composed of eroded quartzite and areas with gneiss and granitic substrates (Hewett 1956).

The Clark Mountain Range, at the southern end of the study area, reaches an elevation of 2407 m. Clark Mountain forms the main mass of this range and is composed primarily of steeply sloped carbonate formations with a few slopes of more rolling highly eroded quartzite. The eastern portion of the main mountain consists of gneiss and granitic substrates (Hewett 1956). The Colosseum Mine, a large open-pit gold and silver mine, was located along a fault that separates the main mountain from the eastern and northern portion of the range. The northern part of the Clark Mountain Range forms a series of lower elevation, rugged carbonate ridges that extend east into the State Line Hills area of the Spring Range in Nevada.

Weather conditions have been monitored at the Mountain Pass weather station (elevation 1440 m), and data for 1955 through 1979 have been summarized (see Stone and Sumida 1983). Annual precipitation during this period averaged 197 mm. Summer temperatures commonly reached 32 to 38° C and occasionally 43° C. Convectional storms often produce considerable precipitation during July and August. Winter temperatures averaged 4.5° C during December and January, but often dropped below freezing. Snow was common on higher ridges of both the Kingston and Clark Mountain ranges during winter storms.

Numerous water sources occur in the study area. Springs in the Kingston Range were surveyed by Reneau (1983). The 4 major springs in this range, all of which have been developed, occur along the northern end of the granitic portion of the range near Excelsior Mine Road. Ephemeral springs, seeps and large tinajas occur in the granitic substrate. In addition, 2 artificial water catchments for mountain sheep have been constructed by CDFG.

Perennial springs on Clark Mountain are located mostly on the eastern side of the range, outside areas frequented by mountain sheep. Pachalka Spring, on the west side of the mountain, was within an area commonly visited by mountain sheep, but this spring was overgrown with vegetation and was over-run by cattle. Two artificial water catchments also were present in this range. In addition, a water trough for cattle was located within mountain sheep habitat on the northern side of the range, near the Colosseum Mine. The Colosseum Mine was also the site of a large evaporation pond, which was dry and covered by late 1993. The Mesquite Mountains and the State Line Hills have no known springs or large tinajas. However, the Nevada Department of Wildlife constructed artificial water catchments for mountain sheep north of Devil Peak in the southern Spring Range.

Vegetation in the Kingston Range was described by Castagnoli et al. (1983) and that in the Clark Mountain Range by Prigge (1975). Upper ridges of both ranges are predominately covered by woodlands dominated by pinyon pine (*Pinus monophylla*) and juniper (*Juniperus osteosperma*), with the more mesic canyons also containing white fir (*Abies concolor*). In the Kingston Range, the Pinyon-Juniper Woodlands often intergrade with bitterbrush (*Purshia glandulosa*) and sagebrush (*Artemisia tridentata*) which eventually form a scrub community at lower elevations. Nolina (*Nolina wolfii*) dominates communities on exposed slopes throughout the Kingston Range. On lower elevation slopes in both the Kingston and Clark Mountain ranges, blackbush (*Coleogyne ramosissima*) often forms almost pure stands or dominates scrub communities. Joshua tree (*Yucca brevifolia*) and creosotebush (*Larrea tridentata*) generally dominate communities on the bajadas and lower, dryer slopes throughout the study area. In addition, both Castagnoli et al. (1983) and Prigge (1975) described assemblages of plants that form associations on calcareous substrates. These calcareous communities were described as heterogeneous or anomalous associations of plants lacking unifying indicator species, but containing unique mixtures of calcicolous-rupicolous plants and more common taxa from surrounding communities. These associations are common on slopes in the Mesquite Mountains and State Line Hills.

Potential predators of mountain sheep occurring in the study area included mountain lion (*Felis concolor*), bobcat (*Lynx rufus*) and coyote (*Canis latrans*). Golden Eagles (*Aquila chrysaetos*), potential predators of young lambs, were commonly seen in the area. Mule deer (*Odocoileus hemionus*) occurred in the Kingston Range and on Clark Mountain. Feral asses (*Equus asinus*) and domestic cattle (*Bos spp.*) were commonly seen throughout the study area; although their sympatry with mountain sheep appeared somewhat limited.

METHODS

Telemetry

Radio-collars equipped with mortality sensors (Telonics Inc., Mesa, Arizona) were placed on mountain sheep during several captures conducted by CDFG (see Chapter 2, Table 2.1). Mountain sheep were captured individually using a hand-held net-gun fired from a Bell Jet Ranger helicopter. All aspects of animal handling complied with CDFG protocols and were approved by the Institutional Animal Care and Use Committee of the University of Nevada, Las Vegas.

Distribution and movements of mountain sheep were determined by aerial monitoring of radio-collared animals. Aerial telemetry flights began on October 27, 1990 and continued until June 6, 1993. The timing of these flights, which varied throughout the study due to inclement weather and schedule conflicts, averaged every two weeks. Independence of telemetry data was assumed in statistical analyses. Ebert (1993), using a formula from Swihart et al. (1988), calculated that for mountain sheep habitat analysis, approximately 16 hours between flights was necessary for independence of successive observations. The critical assumption was that the probability of observing an animal in any portion of its home range was equal (Swihart and Slade

1985). The minimum time between flights was 4 days, which was considered sufficient to meet this requirement.

During the course of the study, two Cessna 185 airplanes were used for telemetry flights. These aircraft were equipped with telemetry receivers (Telonics Inc., Mesa Arizona) and with directional H-antennae mounted on the wing struts (Krausman et al. 1984). Positions of radio-collared animals were determined by signal strength, and the geographic coordinates for each located animal were then estimated by a Loran-C navigation unit as the aircraft passed directly over the animal's position.

Bias and accuracy of positions determined by Loran-C were investigated within the study area (Chapter 1). Analysis of fixed reference points in the study area suggested bias in locations determined by Loran-C and that bias varied between the two aircraft used; each had a different brand of Loran-C receiver. After correcting for bias, analysis of distributions derived using the different Loran-C receivers showed that Loran-C determined positions with 95% probability within circular areas of 1.2 or 1.5 km^2. Locational data used in analyses were corrected for the appropriate bias.

Analyses of telemetry locations were conducted using the geographic information system pMAP (Professional Map Analysis Package, SIS 1986). Within this raster-based GIS, the study area was reconfigured as a grid consisting of one ha cells (100 m x 100 m). Commercially available 3 arc seconds digital elevation data (SoftWright, Aurora, Colorado) were used as the basis for a digital elevation model (DEM) of the study area. To assign a single elevation to each grid cell from the more densely and unevenly spaced 3 arc seconds data, the GIS program ARC/INFO (Environmental Systems Research Institute, Redlands, California) was used to create a triangulated irregular network (TIN). A single elevation for the center of each cell was then interpolated from the TIN, and these data were used to construct the DEM within pMap.

Determination of Seasonal Ranges

Telemetry data from individual radio-collared ewes were combined by mountain range to form population distributions. To increase sample size, telemetry data were combined between years. Seasonal ranges for each of the two populations were defined by spatial segregation of telemetry data rather than by a strict temporal evaluation; telemetry locations within each of the seasonal ranges were considered representative of that range regardless of when the observations were made. Radio-collared ewes inhabiting the Kingston Range were comprised of 2 subpopulations, those that migrated to the Mesquite Mountains and those that did not. Because there was only a small overlap in the area of the Kingston Range used by these 2 groups (Chapter 2), telemetry data from only those animals that migrated to the Mesquite Mountains were used to determine seasonal range in the Kingston Range.

Telemetry locations on the fringe of major distributions were considered migratory movements, exploratory movements, or the result of extremely large Loran-C errors (Chapter 1). To reduce the number of erroneous telemetry locations and eliminate telemetry locations within movement corridors, the GIS was used to weight each location by the density of surrounding locations. This was done by establishing a 500 m buffer around each telemetry location, which was approximately equal to the 68% error radii calculated for locations determined by Loran-C within the study area (Chapter 1). Each telemetry location was then weighted by the total number of locations recorded within its 500 m buffer (range 1 - 26). Telemetry locations separated by more than 500 m from other locations (weighted value = 1) were discarded. A few remaining telemetry locations within migratory corridors ($n = 5$, weighted values = 2) also were discarded. The final data set used in analyses contained approximately 85 % of the original data; these were the more densely spaced telemetry positions. This process produced two seasonal ranges for each of the two populations. These seasonal ranges were simply called Clark Mountain and the State Line Hills for the Clark Mountain ewe population, and the Kingston Range and Mesquite Mountains for the Kingston Range ewe population (Figure 3.1).

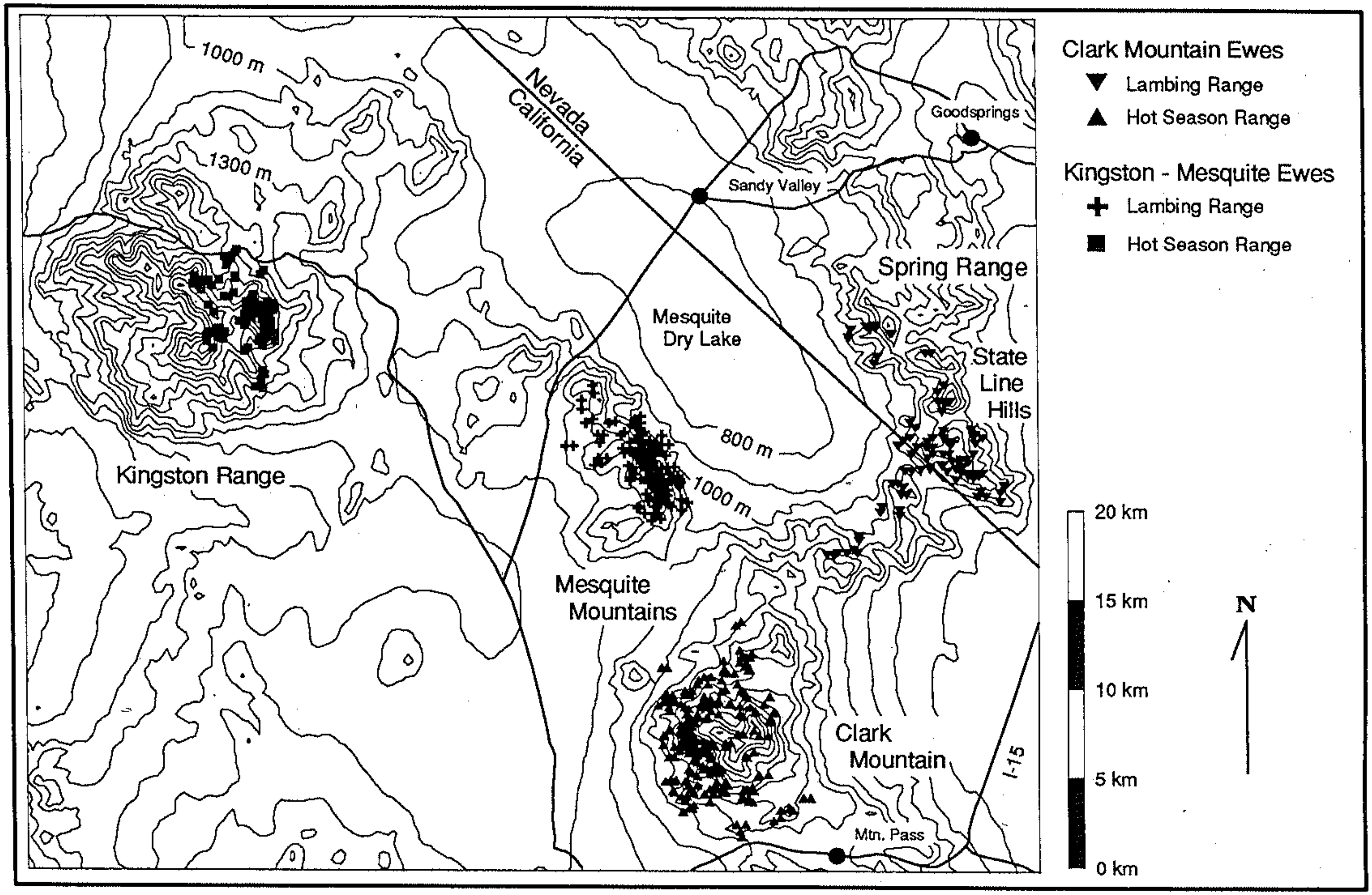

Figure 3.1. Seasonal ranges of mountain sheep (Ovis canadensis) ewes in the area of the Kingston and Clark Mountain Ranges, San Bernardino County, California.

Land Surface Ruggedness and Elevation

To test differences in land surface ruggedness between seasonal ranges, a land surface ruggedness index (LSRI) was developed within the GIS using a method described by Ebert (1993). The maximum percent slope of each cell in the study area was computed by comparing the elevation of a target cell to that of its 8 neighboring cells. A LSRI value for each cell was then computed by totaling the maximum percent slope of a target cell with those from its 8 neighbors.

Two approaches were used for statistical comparison of LSRI values between seasonal ranges. The first approach disregarded any further error in telemetry locations and evaluated the LSRI values assigned to each 1 ha cell in which telemetry locations were recorded. This seemed a reasonable approach since these locations were "best guesses" of the true positions. However, because of potential error in the telemetry data, a second evaluation incorporating a conservative measure of telemetry error (Chapter 1) was conducted in which LSRI values were averaged for all cells within a 500 m buffer around each telemetry location (area = 81 ha/observation). These average LSRI values were then assigned to telemetry locations for statistical evaluation. The results from these two approaches were qualitatively the same, and only the latter is discussed in further detail.

LSRI data sets were tested for normality using the Kolmogorov-Smirnov goodness of fit test (Zar 1984); none of the data sets permitted the rejection of the null hypothesis of normality ($P > 0.05$). However, data from Clark Mountain and the State Line Hills had unequal variances ($F = 1.70$, $P < 0.05$). Therefore, Mann-Whitney tests were used in statistical comparisons (Zar 1984). Since the areas selected after the hot season were predicted to be more rugged than those selected during the hot season, one-tailed testing was used in each of the two populations to evaluate the null hypothesis that the area moved to after the hot season was not more rugged than that selected during the hot season.

Elevation data also were analyzed by first averaging elevation within 500 m of a telemetry location and assigning this as the location's value. These average elevation values also were tested for normality, and the data set from the Mesquite Mountains permitted the rejection of the null hypothesis of normality ($P < 0.05$). Therefore, Mann-Whitney tests were used for statistical comparisons (Zar 1984).

Visual Openness

To test differences in the visual openness between the seasonal ranges, random points ($n = 78$) were selected from 1 ha cells within the GIS that contained mountain sheep telemetry locations. Visual openness at these locations was estimated in the field using a cover-pole analysis similar to that described by Griffith and Youtie (1988) for assessing deer hiding cover and by Bleich (1993) for assessing horizontal cover within mountain sheep habitat. The approximate center of the chosen cell was located and an observation point established on the nearest mountain sheep sign (tracks, beds, or pellets); when no sign was obvious, a point was chosen. The observer crouched at a height of approximately 1 m (mountain sheep height) and viewed the cover-pole at a distance of 20 m. Cover-poles were 2 m in height and divided into 8 segments, each 25 cm in length. The percent of each segment obscured was then estimated to the nearest 10%, and the type of cover causing the obstruction, if any, was recorded as either vegetation or geomorphic feature (rock or slope). To provide a general measure of horizontal cover at each location, the cover-pole was viewed at 90 degree intervals around the observer, with the initial direction chosen randomly. The observer then moved 60 m in a random direction and repeated the process. Maximum cover, expressed as the mean percent of the entire cover-pole not visible, was then calculated by averaging the percent of all measurements taken for both observation points at each location ($n = 64$ pole segments). The type of cover also was averaged and expressed as the mean percent of the pole covered by either vegetation or geomorphic feature.

Cover-pole data sets were produced for each range and comparisons were made between Clark Mountain ($n = 17$) and the State Line Hills ($n = 15$) and between the Kingston Range ($n = 23$) and Mesquite Mountains (n = 23). These data sets were found to be normally distributed ($P > 0.05$) using the Kolmogorov-Smirnov goodness of fit test (Zar 1984). Variances between data set pairs also were tested, and found to be unequal between Clark Mountain and the State Line Hills ($P < 0.05$). Therefore, the Mann-Whitney Test (Zar 1984) was used to evaluate differences between the seasonal ranges. Since areas selected after the hot season were predicted to be more visually open than those used during the hot season, one-tailed testing was used in each of the two populations to assess the null hypothesis that cover in the area used after the hot season was not less than that on the hot season range.

Cover-pole data also were separated and evaluated at >1 m and < 1 m above the ground. This was done to explore potential differences caused by the lower meter having generally greater cover than the upper meter. The results of these analyses were qualitatively the same as those for data using the entire cover-pole, and only analyses using the entire cover-pole are discussed in further detail.

Diet Quality

Percent fecal nitrogen (FN) was used to investigate differences in diet quality (nutrient availability) between seasonal ranges. Fecal samples were collected approximately monthly from 1991 through 1993 in the Kingston Range, Mesquite Mountains and on Clark Mountain. This was possible because some mountain sheep were present in each of these ranges throughout the year. Fecal samples also were collected from the State Line Hills during the spring of 1992 and during the late fall and spring of 1993. Fecal sampling in this area was limited to periods when mountain sheep were present; essentially no fresh sign was found during surveys in summer after most mountain sheep had migrated to Clark Mountain. To facilitate data analysis, the time between fecal sample collections on Clark Mountain and the State Line Hills and between the Kingston Range and Mesquite Mountains was minimized, usually occurring within a few days of each other. This time period was short enough to minimize the effect of changes in forage quality on statistical comparisons. Most samples were collected fresh from observed ewe groups. When fresh samples could not be obtained, samples found along recent tracks or beds (usually not more than a few days old) were collected.

Monthly samples were combined by mountain range to form composites before analysis. Percent fecal nitrogen was determined by Micro-Kjeldahl digestion (Wildlife Habitat Laboratory, Washington State University). Fecal nitrogen is considered a useful index of diet quality because of correlations with forage protein content and digestibility (see, Leslie and Starkey 1985, 1987). Differences in diet quality of mountain sheep have been investigated using FN (Hebert 1973, Wehausen 1980, Wehausen 1992, Bleich 1993, Irwin et al. 1993). Wehausen (unpublished data) has shown that FN is predominately an indicator of digestibility and only secondarily of forage protein content through a second correlation between forage protein content and digestibility. He also found that the relationship between digestibility and FN was somewhat better when FN was analyzed on an ash-free basis. Additionally, Wehausen (unpublished data) showed that the relationship between digestibility and fecal crude protein is curvilinear and reciprocal. Following his recommendations, FN was calculated on an ash-free basis (fecal organic matter nitrogen; FOMN) and analyses of diet quality were performed after linearizing the data using a natural log transformation. Because FOMN is correlated with season and sampling was conducted in pairs, pair-sample *t* tests (Zar 1984) were used. Only questions concerning whether FOMN was higher in one area than another were of interest; consequently, one-tailed testing was used. Since sample sizes within any particular season were small, tests based on only 1 year of sampling would have a high probability of Type II error. To avoid this, data were combined across years for each season before testing.

RESULTS

Seasonal Movements

Radio-collared ewes captured in the Clark Mountain Range moved seasonally between Clark Mountain and the State Line Hills area of the Spring Range (Figure 3.2). Analysis of telemetry data suggested that the ewes tended to leave Clark Mountain for the State Line Hills in late January and returned to Clark Mountain by early June. Field surveys confirmed this general trend; although, winter movements from Clark Mountain to the State Line Hills occurred over an extended period of time, with some ewes moving as early as November. Return movements appeared to occur over a shorter time period, generally coinciding with the onset of hot weather.

The seasonal shift in distribution of Clark Mountain ewes represented a migration of approximately 19 km. Ewes migrated along the northern part of the Clark Mountain Range which forms a series of rugged carbonate ridges that extend east into the State Line Hills. While one radio-collared ewe showed an affinity for this set of ridges, most of the Clark Mountain ewes moved through this area and into the southern portion of the Spring Range.

The radio-collared ewes inhabiting the Kingston Range were comprised predominately of two major subpopulations which demonstrated little overlap in their respective distributions (see Chapter 2, Figure 2.1). One of these subpopulations remained in the Kingston Range throughout the year; although, some of these animals occasionally moved for short periods to a limestone ridge directly south of the range. The other subpopulation exhibited a seasonal pattern to movements between the Kingston Range and the Mesquite Mountains (Figure 3.3). Analysis of telemetry data suggested that these migrating ewes tended to move from the Kingston Range to the Mesquite Mountains in October. The return trip was generally made in late June. Field surveys confirmed the general pattern of these movements, but also suggested that a few ewes remained in the Mesquite Mountains during summer months. These animals may have been individuals that did not migrate, or possibly animals that simply moved

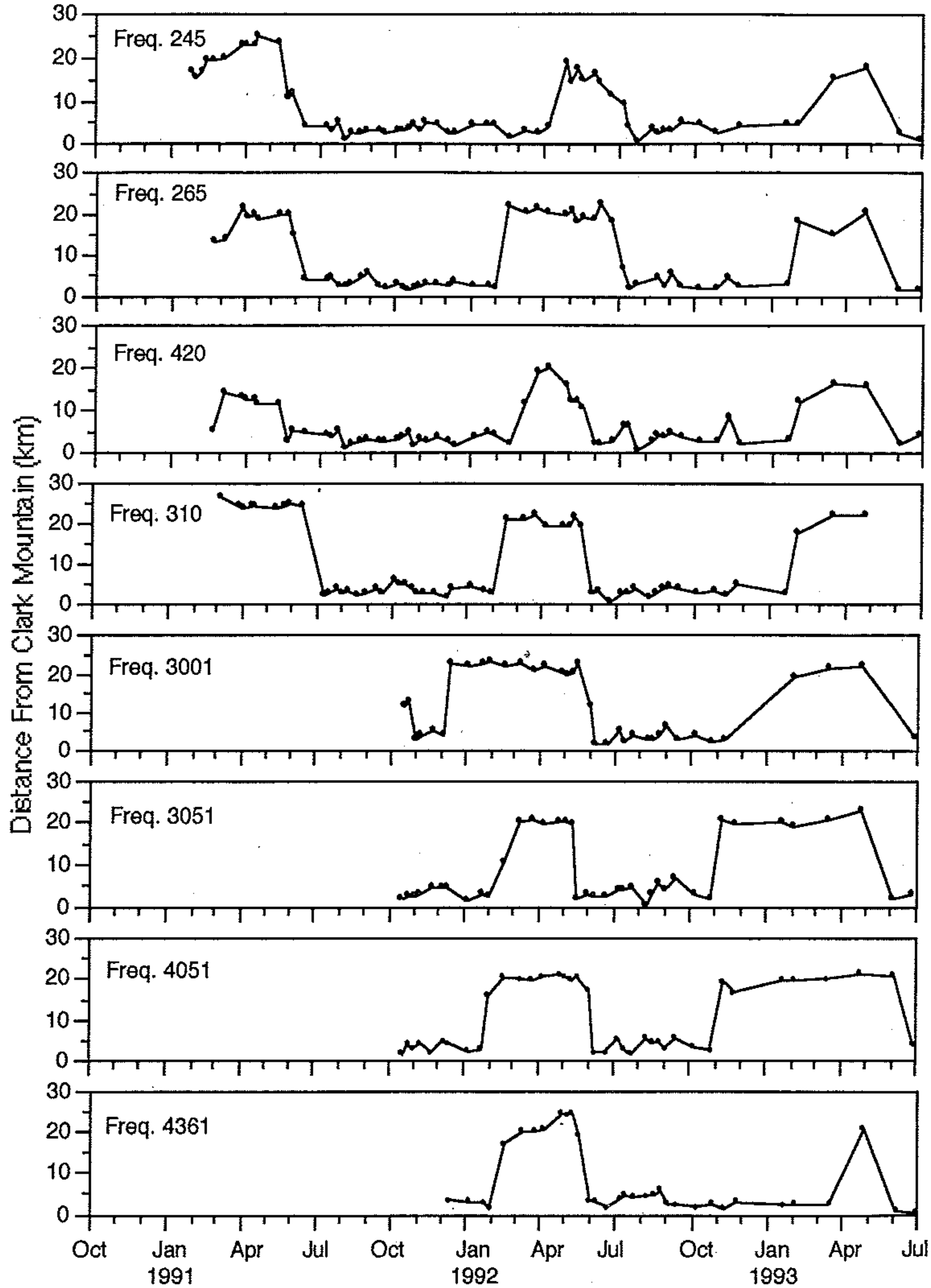

Figure 3.2. Seasonal movement of radio-collared mountain sheep (*Ovis canadensis*) ewes between Clark Mountain, San Bernardino County, California and the State Line Hills, Clark County, Nevada. Radio-collared ewes with limited relocations excluded.

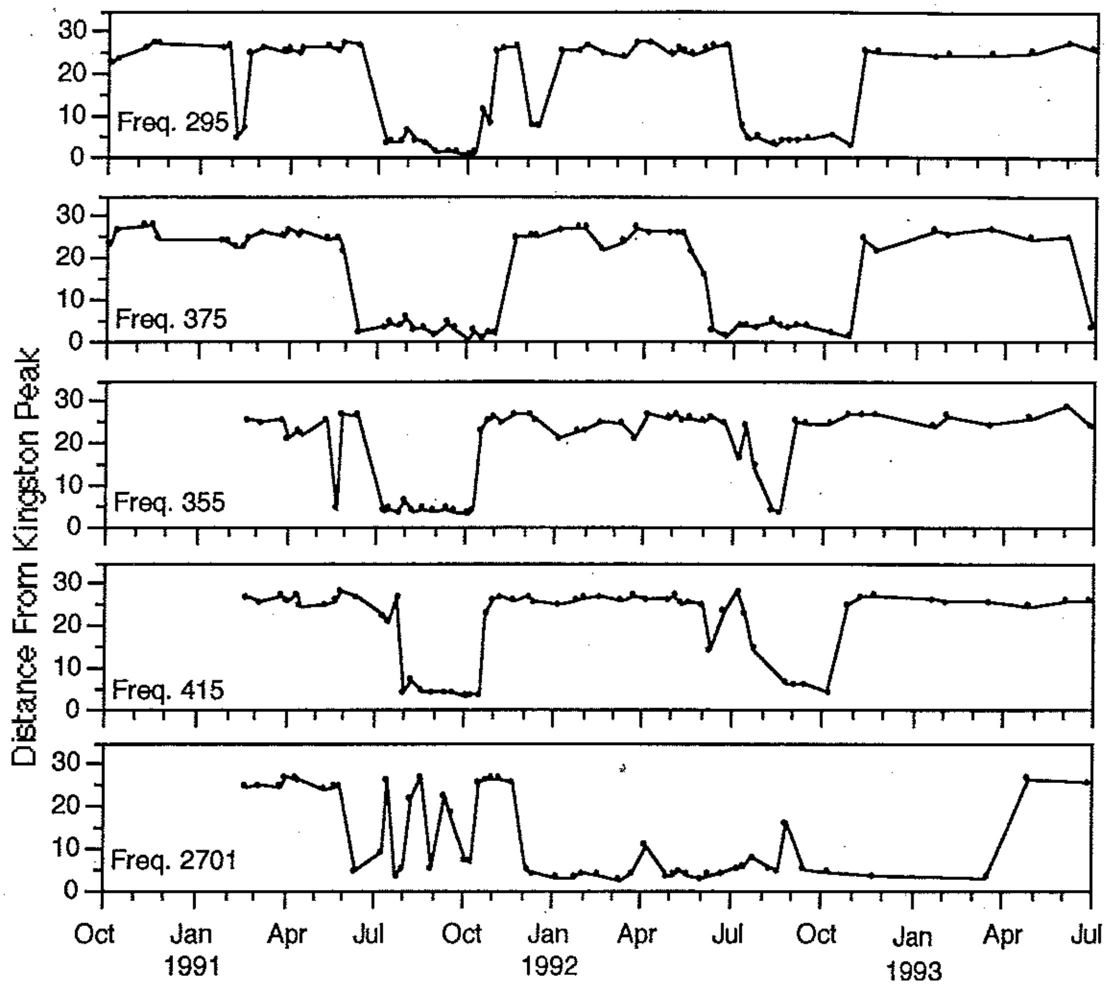

Figure 3.3. Seasonal movement of radio-collared mountain sheep (*Ovis canadensis*) ewes from the Kingston Range to Mesquite Mountains, San Bernardino County, Califronia.

back from the Kingston Range for periods during the summer. They also could have been individuals from a small ewe group, represented by the movements of one radio-collared ewe, that demonstrated a different distribution pattern. This radio-collared ewe remained mostly along a limestone ridge in the north of the Kingston Range, but occasionally moved to western portions of the Mesquite Mountains. Helicopter surveys confirmed that this animal represented only a small number of mountain sheep.

Ewes migrating from the Kingston Range to the Mesquite Mountains were required to move across several areas of flat bajada and two rural roads. Movement appeared to follow a set of hills and ridges forming a series of "stepping-stone" habitats connecting these ranges. This represented a linear shift in distribution of approximately 22 km, although the actual distance traveled by these animals was somewhat longer.

Movement in Relation to Water

Migrating ewes clearly moved toward water sources during the hot season. No natural water sources are known to exist in the Mesquite Mountains or the State Line Hills. Springs and natural water catchments were present in areas used by ewes during the hot season on Clark Mountain and in the Kingston Range. Artificial water catchments also have been constructed in these ranges. The artificial water catchments in the southern portions of the Spring Range, one of which is near the areas commonly used by Clark Mountain ewes, did not appear to influence movements by most of this population.

The affinity of ewes for areas near water sources on Clark Mountain during summer months is potentially misleading. Ewes in this range did not habitually use known permanent water sources; most water sources in this range are not located in habitat favored by ewes. Water sources within areas commonly used by ewes received some use, but this did not appear to be regular. In the Kingston Range, hot season ewe distribution corresponded with the general area in which major water sources occurred; although, use of these waters also appeared to be occasional. For both ewe populations, environmental factors related to altitudinal shifts in habitat may mitigate the need for standing water.

Clark Mountain and the Kingston Range are more massive mountain ranges with greater altitudinal relief than the State Line Hills and the Mesquite Mountains. Elevations at which ewes were located differed significantly between Clark Mountain and the State Line Hills ($Z = -13.701$, $P = 0$) and between the Kingston Range and Mesquite Mountains ($Z = -12.788$, $P = 0$). Ewes occurred at higher elevations on Clark Mountain (median elevation = 1738 m) than in the State Line Hills (median elevation = 1313 m) and at higher elevations in the Kingston Range (median elevation = 1846 m) than in the Mesquite Mountains (median elevation = 1369). While the State Line Hills and Mesquite Mountains support desert vegetation, cooler temperatures and more precipitation on the higher slopes of Clark Mountain and the Kingston Range support Pinyon-Juniper Woodlands and stands of white fir. Vegetation in the higher ranges is likely to retain higher moisture levels in the hot season (Hebert 1973). Convectional storms also tend to produce more precipitation on the higher ranges during summer months. These cooler, more mesic conditions on Clark Mountain and the Kingston Range probably allow mountain sheep to balance water requirements without necessitating the extensive use of surface water.

Land Surface Ruggedness

Analysis of Land surface ruggedness failed to reject the null hypothesis that LSRI values from the State Line Hills were not higher than those from Clark Mountain ($Z = -0.037$, 1-Tail test $P > 0.50$). The median LSRI value on Clark Mountain was 285 while that in the State Line Hills was 293, suggesting little difference between the ruggedness of these areas. Similarly, LSRI values in the Mesquite Mountains were not significantly higher than those in the Kingston Range ($Z = -7.973$, 1-Tail test $P > 0.50$). Indeed, the median LSRI value in the Kingston Range was 379 while that in the Mesquite Mountains was 288, indicating that the area used in the Kingston Range was more rugged than that in the Mesquite Mountains.

Visual Openness

The null hypothesis that maximum cover in the State Line Hills was not lower than that on Clark Mountain was rejected ($U = 242$, 1-Tail test $P < 0.0005$). Similarly, when data were analyzed for vegetation cover only, the null hypothesis was rejected and vegetation cover was found to be significantly less in the State Line Hills than on Clark Mountain ($U = 244$, 1-Tail test $P < 0.0005$). The null hypothesis that cover caused by geomorphic features was not significantly different between these ranges could not be rejected ($U = 167$, 2-Tail test, $0.20 > P > 0.10$).

These same results were found between the Kingston Range and Mesquite Mountains. The null hypothesis that maximum cover in the Mesquite Mountains was not lower than that in the Kingston Range was rejected ($Z = 3.405$, 1-Tail test $P < 0.01$). Also rejected was the null hypothesis that vegetation cover was not lower in the Mesquite Mountains than in the Kingston Range ($Z = 4.064$, 1-Tail test $P < 0.01$). The null hypothesis that cover from geomorphic features was not significantly different between the Kingston Range and Mesquite Mountains could not be rejected ($Z = -1.212$, 2-Tail test $P > 0.20$).

These results suggest that the disparities in maximum cover between habitats were predominately a consequence of differences in vegetation structure. Any potential differences caused by geomorphic dissimilarities between habitats either did not exist, or were overwhelmed by vegetation differences (Figure 3.4). Because cover is a measure of visual openness, these results suggest that visibility in the State Line Hills was less obscured than on Clark Mountain and that the same was true between the Mesquite Mountains and the Kingston Range.

Diet Quality

Fecal nitrogen curves suggested that movement by mountain sheep from Clark Mountain to the State Line Hills during spring months may have resulted in improved nutrient

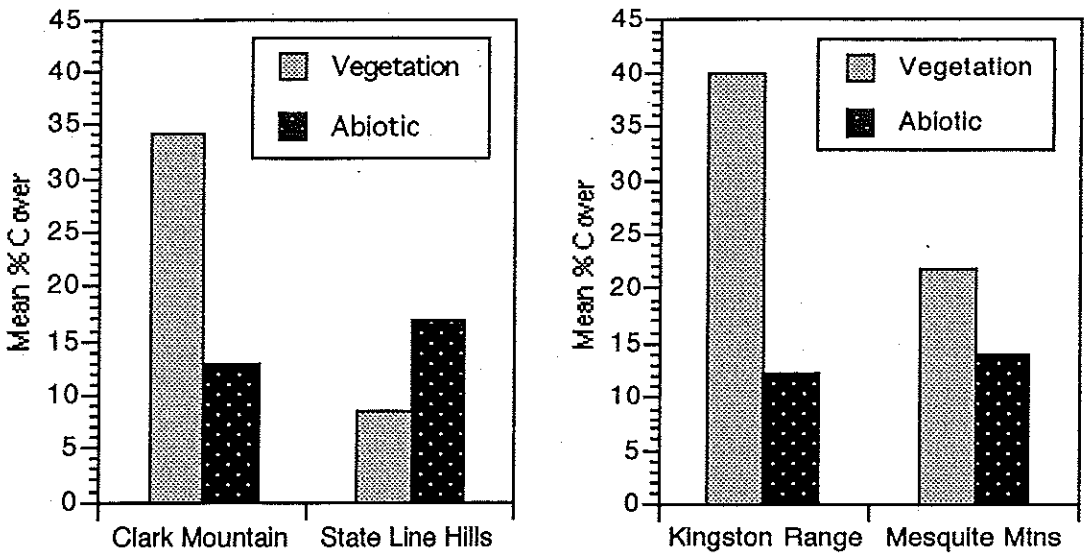

Figure 3.4. Mean percent of vertical cover by covertype on Clark Mountain, San Bernardino County, California and State Line Hills, Clark County, Nevada; and in the Kingston Range and Mesquite Mountains, San Bernardino County, California. Abiotic cover includes topographic features such as boulders or slopes.

intake (Figure 3.5). When analyzed for the period of mid-February to early June, the null hypothesis that FOMN from the State Line Hills was not higher than that from Clark Mountain was rejected, and FOMN was determined to be significantly higher in the State Line Hills (Paired t value = 2.295, 1-tail $P = 0.0237$). In contrast, assessment of diet quality curves from the Kingston Range and Mesquite Mountains suggested that diet quality did not improve with movements after the hot season (Figure 3.6). When FOMN was analyzed for early November to early June, when mountain sheep were abundant in the Mesquite Mountains, the null hypothesis that FOMN from the Mesquite Mountains was not higher than that in the Kingston Range could not be rejected (Paired t value = -2.283, 1-tail $P = 0.9833$). Similarly, analysis of FOMN for only the spring months, February to early June, also failed to reject this null hypothesis (Paired t value = -0.360, 1-tail $P = 0.3685$).

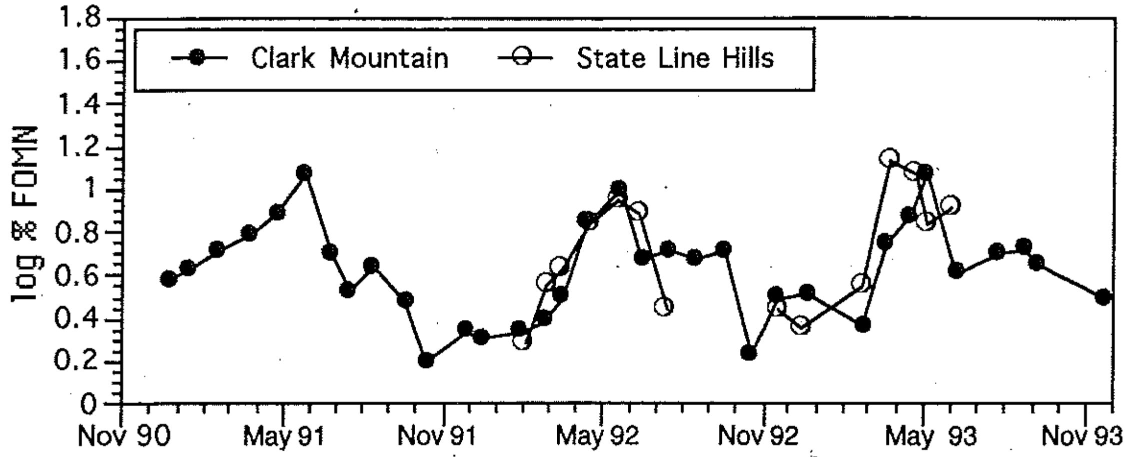

Figure 3.5. Diet quality curves for mountain sheep (*Ovis canadensis*) on Clark Mountain, San Bernardino County, California and in the State Line Hills, Clark County, Nevada. Values are expressed as the natural log of percent fecal nitrogen on an ash-free basis (fecal organic matter nitrogen).

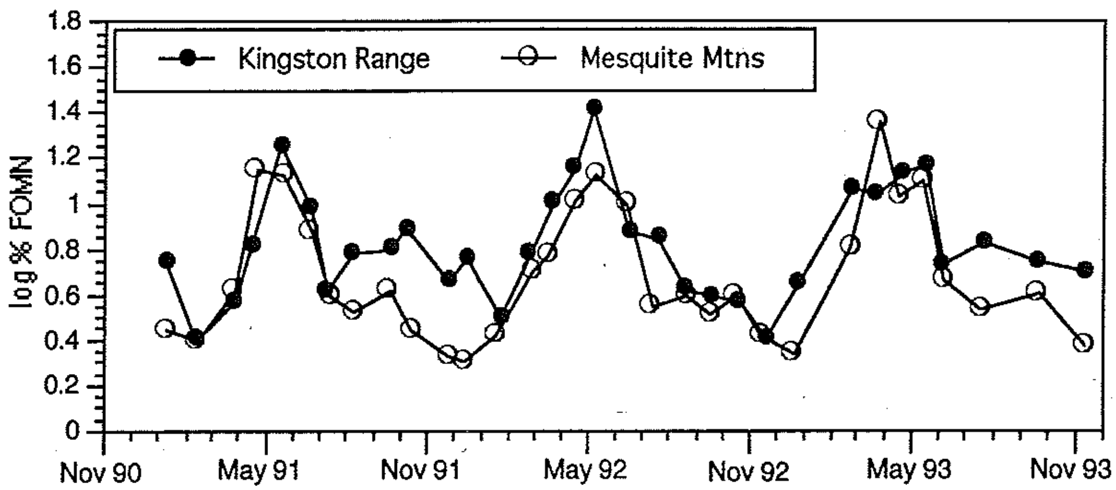

Figure 3.6. Diet quality curves for mountain sheep (*Ovis canadensis*) in the Kingston Range and Mesquite Mountains, San Bernardino County, California. Values are expressed as the natural log of percent fecal nitrogen on an ash-free basis (fecal organic matter nitrogen; FOMN).

When FOMN was analyzed for June through October, when most mountain sheep from the Mesquite Mountains were in the Kingston Range, the null hypothesis that FOMN from the Kingston Range was not higher than that from the Mesquite Mountains was rejected, and FOMN in the Kingston Range was determined to be significantly higher (Paired t value = 4.117, 1-tail P = 0.0011). The relationship between diet quality in the Kingston Range and Mesquite Mountains was evident when FOMN was integrated between data points representing the beginning and ending of migration periods (Wehausen 1992). These integrations measured only the area under the curves above 1% FOMN. Because sampling days varied somewhat between ranges, integrated values were divided by the number of days in each period, thus providing an index expressed as an average daily value. This index provided an illustration of the average diet quality for specific periods in the Kingston and Mesquite Mountains, which suggested diet quality in the Kingston Range was higher than that in the Mesquite Mountains during all periods (Figure 3.7).

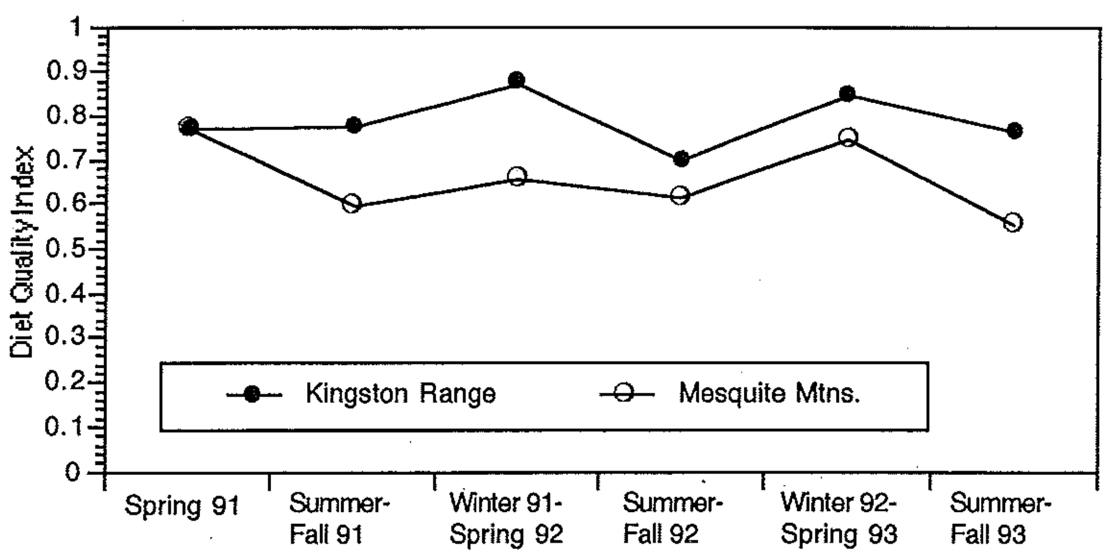

Figure 3.7 Diet quality index for mountain sheep (*Ovis canadensis*) in the Kingston Range and Mesquite Mountains, San Bernardino County, California. Index values were calculated by integrating the natural log of fecal organic matter nitrogen above 1 % for periods representing times between migrations. Values are expressed as an average daily value for each period.

DISCUSSION

The distribution of mountain sheep, particularly ewes, in some desert mountain ranges has been shown to be restricted to areas near water sources during the hot season (Blong and Pollard 1968, Leslie and Douglas 1979, Cunningham and Ohmart 1986). Hot season water requirement also has been suggested as influencing migration patterns of at least one desert-dwelling mountain sheep population (see Leslie and Douglas 1979). In the area of the Kingston and Clark Mountain ranges, ewes left ranges on which they reared lambs that contained no natural standing water at the beginning of the hot season and moved to ranges with numerous water sources.

While the need for standing water could not be rejected as the driving force behind hot season migration, these same movements occurred over an altitudinal gradient that caused other environmental changes between habitats that may have mitigated the importance of surface water. These changes included: cooler temperatures, an increased likelihood of summer precipitation, and potentially higher moisture content of forage plants. Turner (1973) suggested that during hot summer months when ambient temperatures frequently rise above mountain sheep body temperature and forage moisture diminishes, desert-dwelling mountain sheep are unable to balance water requirements without drinking water. However, Krausman et al. (1985) have shown that ewes can exist in desert mountain ranges devoid of standing water even when daily temperatures exceed body temperature. Mountain sheep on the higher slopes of the Kingston and Clark Mountain ranges were probably able to avoid prolonged exposure to temperatures well above their body temperature, which may have reduced their need to frequently drink water. Nevertheless, availability of water sources could not be rejected as influencing hot season migration.

The selection of higher elevation ranges on Clark Mountain and the Kingston Range during the hot season also likely resulted in an increase in forage quality. Where it was possible to compare summer FN values, the higher elevation range had significantly higher values than the low elevation range. Field observations of some forage species suggested that flowering continued well into the hot season on high elevation ranges when the same forage plants on lower elevation ranges had ceased flowering. The altitudinal variation in the high elevation ranges also provided mountain sheep with access to an increased number of vegetation communities, increasing the diversity of forage species.

Migration of desert-dwelling ewes in winter from high elevation ranges to low elevation ranges did not appear to be solely a response to forage quality. While spring FN was significantly higher for ewes that migrated to lower elevations in the State Line Hills than for those that remained on Clark Mountain, the exact opposite was true for the neighboring Kingston Range population. Unfortunately, a confounding factor in this analysis was the presence in the Kingston Range of a second subpopulation of ewes that remained in this range year-round. While these two subpopulations showed only a small overlap in distribution (Chapter 2), some fecal samples collected in the Kingston Range during winter months undoubtedly came from animals of the non-migrating subpopulation. FN from these ewes was possibly influenced by forage conditions outside the areas of the Kingston Range used by migrating ewes. Whether migrating individuals would choose similar habitats were they to remain in the Kingston Range during winter months is unknown, but they would have the potential to access better forage. The implication of this analysis was that some factor other than forage quality may have influenced winter migratory behavior of these ewes. In a similar situation, spring migrating ewes in northern populations reduced forage quality in exchange for areas with presumably lower predation risk for their young lambs (Wehausen 1980, Festa-Bianchet 1988).

Migration of desert-dwelling ewes from hot season ranges to the ranges used for lambing was expected to correspond with an increase in habitat ruggedness and visual openness. However, the ranges in which lambing occurred did not have higher LSRI values than the corresponding hot season ranges. This suggested that selection for more rugged habitat was not a factor contributing to the movement of ewes from the hot season ranges. However, there is a possibility that the selection for ruggedness may have a component at a finer scale than that used to conduct this analysis. Ewes may select ruggedness not only as a characteristic of larger scale changes in slope and elevation, but also for characteristics dependent on the geologic substrate of an area. Nevertheless, the hypothesis that ewes moved from hot season ranges to more rugged lambing habitat was not supported. Conversely, visual openness was significantly greater on the ranges used for lambing than on the corresponding hot season ranges. This increase in openness on the lambing ranges was due to less horizontal vegetation cover on these lower, drier ranges. Thus, the reduction of predation risk may have been the primary factor in ewe movements from hot season ranges.

Predation risk may have been substantial in the Kingston Range and on Clark Mountain. Of 7 radio-collared ewes that died from natural causes during the study, 6 were attributed to mountain lion predation (Chapter 2). Mountain lion predation occurred only on Clark Mountain and in the Kingston Range; no predation deaths were documented in the State Line Hills or Mesquite Mountains. This suggests that predation risk may have been higher for ewes while in the habitats with greater visual obstruction. Deer inhabit Clark Mountain and the Kingston Range, but their distribution does not extend into the State Line Hills or Mesquite Mountains. Mountain lions probably range throughout the study area, but their activity is likely to center around deer habitat. Predation risk for mountain sheep may be higher when near, or within, these habitats. Predator avoidance may explain the movement of adult ewes from the Kingston Range to the Mesquite Mountains well before the lambing season, even though the Kingston Range had better forage quality.

In summary, the results of this study suggested that a combination of environmental factors influenced migratory behavior in desert-dwelling ewes. During the hot season, ewes moved to higher, cooler, more mesic ranges near natural water sources, with increased access to more nutritious forage. However, these hot season ranges had decreased visibility which may have increased predation risk. With cooler fall temperatures and relaxed water requirements, ewes moved to areas of lower predation risk, even if these movements required the subordination of forage quality.

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