CATTLE IMPACTS ON MOUNTAIN SHEEP IN THE MOJAVE DESERT: REPORT III

John D. Wehausen
University of California
White Mountain Research Station
Bishop, CA 93514

January 1990

Final Report Completed under Interagency Agreement No. FG 7468-A1
with the California Department of Fish and Game

INTRODUCTION

This report is the third in a series concerning ongoing research on impacts of cattle on mountain sheep (*Ovis canadensis*) populations in the Mojave Desert of California. The first (Wehausen and Hansen 1986) concerned a one-year pilot study directed at the question of competition, and concluded that (1) exploitation competition was not occurring in the areas investigated, (2) interference competition also appeared to be absent, in that minimal range overlap of the two species could be explained more parsimoniously by differences in habitat utilization patterns, rather than avoidance of one species by the other, and (3) there was a high probability that viral diseases introduced to the native sheep from cattle were having a significant effect on population parameters of the sheep through high lamb mortality.

The second report (Wehausen 1988) concerned an initial investigation of the viral disease hypothesis. It concentrated on two closely related gnat-vectored viruses for which cattle can be implicated as the probable long term reservoir: bluetongue (BT) and epizootic hemorrhagic disease (EHD). That study compared population density of one mountain sheep population with high exposure to these viruses (Old Woman Mountains) with a neighboring population of very low exposure (Marble Mountains), and found large differences in the direction expected if these viruses were a significant factor. The observed differences were also in the opposite direction from what would be expected on the basis of nutrient availability in the two ranges. Finally, an apparent improvement in the demographic situation in the Old Woman Mountains was noted to correlate with a drying trend and suggested to be a result of changes in the gnat population.

This third report is an extension of the previous one to a comparison of five populations -- three of high exposure to the viruses in question and two of low exposure. It includes the same two populations discussed in the second report. As such, this report supercedes that one in that most pertinent data from it are included herein.

The Problem

Diseases, particularly pneumonias, have long been noted as playing an apparently significant role in the demography of North American wild sheep (Buechner 1960; Post 1971, 1976). The most serious of these are usually acute pneumonias, which occur in two demographic patterns: (1) all age die-offs, in which a significant portion of a population, including all sex and age classes, dies over a relatively short time period (Foreyt and Jessup 1982, Coggins 1988, Festa-Bianchet 1988), and (2) a high mortality of lambs resulting in a long term population decline as recruitment fails to replace natural adult mortality (DeForge and Scott 1982, DeForge et al. 1982, Wehausen et al. 1987). This study concerns the latter type.

Persistent high lamb mortality has been reported from a number of desert populations of wild sheep (DeForge and Scott 1982, Sanchez et al. 1988, Wallace 1988). Bacterial pneumonia has been the cause of death where investigated, and three viruses, parainfluenza-3 (PI-3), BT, and EHD, frequently have been found associated, either through isolation or serological evidence of exposure (DeForge et al. 1982, Clark et al. 1985, Jessup 1985). One or more of these viruses have been hypothesized as the initial disease factor predisposing the lambs to bacterial infection. Which, if any of these viruses is/are critical to the disease process in lambs is unclear. PI-3 is extremely widespread in wild sheep populations in North America, exposure to which has been found in declining, as well as stable and rapidly increasing populations (DeForge et al. 1982, Clark et al. 1985, Parks et al. 1972). These different demographic settings alone suggest that more than PI-3 is necessary to effect the lamb mortality patterns observed in some populations. However, this may not be true if PI-3 occurs in different strains varying in virulence. Alternatively, PI-3 may be an opportunistic virus that is able to flourish in a population when lambs are weakened by some other stressor, such as poor nutrition or infection by other disease organisms like BT and EHD. PI-3 apparently is transmitted directly from sheep to sheep with the sheep population serving as its own reservoir of infection once introduced, at least for some time.

BT and EHD are quite different viruses from PI-3. They are closely related viruses vectored by arthropods, mostly gnats of the genus *Culicoides* (Thorne 1982a,b, Mullens et al. 1986). The pathology they cause is identical (Thorne 1982a,b); thus from a management standpoint, they can be thought of as simply different strains of the same virus. Here they are treated as such. Wild sheep, like some other North American wild ungulates, appear to contract BT and EHD only as an acute disease, thus carry the virus for only a relatively short time until they die or recover (Robinson et al. 1967, Hoff and Trainer 1981, Thorne 1982a,b). In contrast, cattle are known to contract BT and EHD as a chronic disease with little or no influence on their health (Marsh 1965, Bruner and Gillespie 1966, Hoff and Trainer 1981, Thorne 1982a,b); thus cattle are a likely long term disease reservoir for BT and EHD. This has major management implications: simple removal of cattle from a mountain range suffering persistent high lamb mortality would solve the problem if (1) BT and EHD are major factors in the disease process leading to lamb mortality, and (2) mountain sheep are unable to serve as their own long term reservoir for these viruses. It is the first of these two assumptions that is the central focus of the research reported here. It is important to recognize that the role of BT and EHD in the disease process and the role of cattle as the long term reservoir of the disease are two entirely separate questions. The second of these questions is further complicated by the need of arthropod vectors to transmit the disease. Lacking a sufficient population of vectors, cattle within close proximity of a mountain sheep population may result in little or no exposure of the sheep to these viruses. In fact, the Mojave Desert of California has a number of populations of mountain sheep which show very low levels of exposure to BT and EHD (Clark et al. 1985), yet are in close proximity to cattle.

Study Approach

Carrying capacity is a concept of population ecology that forms a fundamental underpinning of the theory of wildlife management. Ecological carrying capacity can be thought of as the density (animals per area) at which population increase will cease due to environmental resistance (Caughley 1976, McCullough 1979). For an herbivore like mountain sheep, a limited food resource is commonly considered the factor setting carrying capacity; the nutrient intake of females and young at carrying capacity is sufficiently low that the number of young surviving is only equal to the number of adults dying annually. Introducing a disease of clinical importance to such a system can be expected to reduce the ecological carrying capacity because the population will require more nutrients to maintain itself. This would occur through (1) additional nutrients used to combat disease organisms in surviving animals, and (2) extra nutrient wastage in animals (mostly juveniles) dying as a result of the disease organisms. How low this carrying capacity will be relative to a situation free of the disease organisms in question will depend on (1) the influence of population density on disease transmission, (2) the gain in nutrition of individual sheep as population density declines, and (3) the effect of better nutrition in combating the disease. The basic hypothesis of the research reported here is that high exposure to BT/EHD infection in mountain sheep populations will result in reduced density at carrying capacity. A major prediction emanating from this hypothesis is that accurately measured densities of such populations will be lower than healthy control populations having little or no exposure to these viruses, all other factors being equal. Because females are (1) the important reproductive base of wild sheep populations, and (2) behaviorally more conservative than males, thus generally have smaller home ranges, only the female segment of the populations studied was used to test this density prediction.

Popper (1959) considered falsifiability as the fundamental criterion separating empirical science from non-science, and refutation of a hypothesis as the only really clearcut scientific result. This approach is certainly appropriate for studies of the population ecology of diseases of mountain sheep. If we can clearly eliminate one or more disease organisms, such as BT/EHD, as an important factor in a disease complex, we have narrowed the necessary scope of subsequent investigations. That is the study approach followed here. The hypothesis on density of populations exhibiting substantial exposure to BT/EHD is considered a general one. Thus, any population found with a history of high exposure to BT/EHD which also exhibits high density is considered adequate to falsify the entire hypothesis about the role of BT/EHD. Such a finding would imply that factors other than BT/EHD were responsible for low densities that might have been found for other populations showing significant exposure to these viruses.

Since the disease process in question affects populations through inadequate recruitment, population density will drop only slowly over many years once the disease is introduced. Thus, the question must be investigated in the context of dynamics of populations. A population showing high exposure to BT/EHD and a high population density in itself does not refute the hypothesis under investigation unless there is a known history of high exposure for a sufficient length of time. Such a population would need to be studied over at least several years to determine if the population were declining. Recruitment rate is affected by more factors than diseases, and varies from year to year even under the influence of diseases that depress it (Wehausen et al. 1987). Thus, it would be necessary to follow the dynamics of such a population for a sufficient time that a long term population trend could be determined.

Population dynamics can be used further to test the BT/EHD hypothesis. A population with high exposure to these viruses and low population density would normally be considered as evidence supporting the hypothesis. However, if such a population exhibited a clearly increasing trend <u>and</u> evidence of continuing high exposure to the viruses, it would instead be adequate evidence for falsification.

Thus, there are many opportunities to falsify the hypothesis under investigation. The more generalized a hypothesis is, the more such opportunities for falsification there will be, and the greater will be the information content of the hypothesis (Ayala 1975).

As water limited ecosystems, deserts frequently exhibit considerable dynamics due to variation in rainfall alone (Monson 1960, Beatley 1974, Douglas and Leslie 1986, Wehausen et al. 1987, Turner and Randall 1988). The concept of ecological carrying capacity as an upper limit to population density due to food limitations (Caughley 1976, McCullough 1979) loses much of its meaning in such systems, where effects of environmental variation on individual nutrition may far exceed that caused by variation in population density (Caughley 1977, Wehausen et al. 1987). The result of this environmental variation is that the system rarely, if ever, is in a state we can call equilibrium. Caughley (1987:161) recently has introduced the term "centripetality" for such systems as a replacement for "equilibrium". To deal with this problem in testing the primary hypothesis of this study, it has been necessary to compare nearby populations in the same time period, as they will have experienced similar environmental regimes. Of particular importance are patterns of rainfall as they influence forage growth and nutrient availability to sheep. Nevertheless, no two mountain ranges offer identical habitat quality for sheep inhabiting them. Elevation differences alone may result in substantially different plant communities on neighboring ranges. Thus, any demographic differences that might be found and potentially ascribed to disease differences, might equally (and more parsimoniously) be ascribed to habitat differences. Populations inhabiting ranges with inherently greater nutrient availability can be expected to attain higher sheep densities. Consequently, it has been necessary to quantify differences in nutrient availability to sheep in the ranges studied in order to test this alternative hypothesis. Differences in other factors of potential demographic significance, such as predation, also must be considered.

Competition

While this study shifted early on from one focused on traditional concepts of competition concerning cattle to one of demographic impacts of viral diseases for which they serve as a reservoir, competition has not been entirely abandoned. As more populations have been added to the study, any situations having potential for competition have been noted.

Competition in its traditional sense occurs in two forms: (1) interference competition, where one species causes the behavioral displacement of another from an important resource, and (2) exploitation competition, where both are consuming a resource that is in short supply for one of them. As with the question of impacts of viral diseases, to be of significance, competition must have a demographic effect on the population in question. As such, observations during this study have been limited to noting situations having the potential for competition to be occurring.

STUDY POPULATIONS

The five populations reported on here are located in the Old Woman, Marble, Granite, and Cady Mountains, and Old Dad/Kelso Peaks. These ranges lie relatively close to each other in the Mojave Desert of California (Figure 1). This region has a bimodal pattern of precipitation typical of the Sonoran Desert (Figure 2). Precipitation is geographically variable in the study region. The highest mountain ranges, such as the Granite and Old Woman Mountains, tend to pick up more precipitation from winter storms than lower ones. Most winter precipitation comes from cyclonic storms from the west and northwest. Summer precipitation generally emanates from the south, and occurs as localized thunder storms that produce even more variable, but largely unpredictable, geographic variation than winter precipitation. Freiwald (1984) mapped mean annual precipitation isohyets ranging from three to six inches for much of the area under study. However, his six inch isohyet intersects Mitchell Caverns in the Providence Mountains, where average annual precipitation for the past 30 years has been 10.2 inches. Freiwald apparently based his analysis on an earlier much more limited data set. A more likely range for mean annual precipitation in the area is 4-10 inches.

Old Woman Mountains

The Old Woman Mountains are the second highest of the ranges under study, ranging from about 1200 to 5300 ft. The parent material is a mixture of granite and metamorphic rocks. Pinyon pines (*Pinus monophylla*) are found at the highest elevations, but mostly on north-facing slopes; and junipers (*Juniperus* osteosperma) occur on all slopes above about 3000 ft. Otherwise, the perennial vegetation consists of a rather diverse mixture of Mojave desert shrub species, *Yucca shidigera, Nolina bigelovii, Agave deserti*, a variety of cacti, including barrel cactus (*Ferocactus acanthodes*), and an abundance of grass.

Domestic cattle were grazed on the east side of the Old Woman Mountains, mostly away from the range, until the mid-1950's (R. Weaver, pers. comm.). From that time until the recent episode of cattle grazing that began in 1979 (BLM files), no cattle were in the mountain range. After the allotment was reopened in 1979, it was expanded to include portions of the western side of the range, where grazing was absent in the previous episode of cattle use. Apparently, 200 cattle were on the allotment in 1984 for year-round grazing (BLM files). This range contains no feral burros.

For 21 blood samples obtained from mountain sheep in this range during 1984-87, 42.9% were positive for BT, and 76.2% were positive for EHD, and 9.5% were positive for PI-3 (Clark et al. 1985, R. Clark, unpubl.). This population clearly qualifies as one of high exposure to BT and EHD.

Marble Mountains

Sheep range in the Marble Mountains varies in elevation from 1200 ft. at the southeast end to about 3800 ft. near the northwest end. The sheep range is volcanic, except for a steep section of limestone near the southeast end. The perennial vegetation is considerably less diverse and abundant than in the Old Woman Mountains. There are no pinyon or juniper trees, no *Agave or Nolina*, and only very sparse *Yucca shidigera* at the northwest end. The shrub community consists mostly of *Larrea divaricata, Encelia farinosa, Ambrosia dumosa, Krameria grayi, Eriogonum fasciculatum,* and *Ephedra viridis*, with *Acacia greggii, Hyptis emoryi, Hymenoclea salsola, Senecio douglasii*, and a few other shrub species growing in washes Perennial grass is uncommon, occurring mostly in occasional higher shaded gullies. Barrel cactus is very abundant in some areas.

Regular domestic stock grazing is not known to have ever occurred in the Marble Mountains. However, in some recent years, some cattle have wandered over from the east to the north end of the range in winter and spring. A small population of feral burros was present in the early 1980's, but has disappeared.

For 77 blood samples obtained from sheep in the Marble Mountains between 1983 and 1988, 1.3% were positive for BT, 3.9% were positive for EHD, and 5.4% were positive for PI-3 (Clark et al 1985, R. Clark, unpubl.). This population clearly qualifies as one of low exposure to BT/EHD.

Granite Mountains

The Granite Mountains are the highest of those studied, ranging in elevation from 2400 ft. at the west end,,to 6738 ft. at the summit. While the range is mostly granite, it also contains some metamorphic substrate within sheep range. The large elevation range results in what is certainly the highest plant species diversity of the ranges studied. In addition to pinyon and juniper trees, oak trees (*Quercus chrysolepis*) are common on higher cooler slopes, and cottonwoods (*Populus fremontii*) occur at some springs. A number of shrub species absent in the Old Woman Mountains are present in this range. Perennial grass is abundant where cattle have not overgrazed it.

Cattle grazing has occurred in and around the Granite Mountains for many years. Lack of adequate control of this grazing has resulted in a feral cattle population in Bull Canyon. Some of the cattle in Bull Canyon cross back and forth across the pass separating it from the Cottonwood Spring drainage to the east, thus can be considered part of the managed cattle population. However, judging from the lack of brands on many of the cattle in Bull Canyon, it is reasonable to consider it a feral population. Based on actual count a minimum of 40 cattle occupy this drainage year round. Feral burros occupy lower slopes of this range in most areas, and overlap much of the range used by mountain sheep. The Granite Mountains also support a population of deer (*Odocoileus hemionus*) in the upper elevations, and are used regularly by mountain lions (*Felis concolor*).

Four blood samples were collected from mountain sheep in the Granite Mountains in 1985, and 5 more were collected in 1988. However, the 1988 samples were all lipemic, which precluded their use for determining exposure to the viral diseases in question. Consequently, it has been necessary to base exposure on the 1985 sampling. That sampling produced no positive exposure to BT or PI-3, but 3 of the four (75%) were positive for EHD. The resolution of this limited sample is low. Based on the table provided by Wehausen (1987) one can only state with 95% confidence that the exposure rate in the population was 50% or less for BT and PI-3. Based on the high exposure rate recorded for EHD, I have classified this population as one of high BT/EHD exposure.

<u>Old Dad/Kelso Peaks</u>

Elevations in the Old Dad/Kelso Peaks ecosystem range from 1200 ft. at the base of the Cowhole Mountains, to nearly 4800 ft. at Kelso Peak. As such, elevationally it is somewhat of an intermediate range among those under study. Substrates vary from large limestone masses at Old Dad Peak and the Cowhole Mountains, volcanic material south and east of Old Dad Peak, granite in the Kelso Peaks, to substantial areas of blow sand in the southwestern portion of the sheep range. The vegetation is more like the Marble Mountains than the Granite or Old Woman Mountains; but it is decidedly more diverse in perennial species than the Marble Mountains. For instance, the Old Dad/Kelso Peaks ecosystem contains *Coleogyne ramosissima*, *Penstemon antirrhinoides*, and *Eurotia lanata*, all of which are lacking in the Marble Mountains. Perennial grass is also much more abundant than in the Marble Mountains, occurring both on the limestone (*Stipa speciosa*, *Aristida sp.*), and as substantial stands on blow sand

(*Hilaria rigida* and *Oryzopsis hymenoides*). Also, *Yucca shidigera* is relatively abundant in the Kelso Peaks, and *Yucca brevifolia* is present in the higher, eastern part of the ecosystem.

Cattle graze in or immediately adjacent to sheep range in winter, spring, and fall in the very eastern section of the sheep range (Marl Mountains), and in sandy areas south of Old Dad Peak. A small number of feral burros overlap sheep range north of Old Dad Peak.

Between 1983 and 1988, 165 blood samples were collected from mountain sheep in the Old Dad/Kelso Peaks ecosystem. For this sampling, 1.8% were positive to BT, none were positive to EHD, and 4.0% were positive to PI-3 (Clark et al. 1985, R. Clark, unpubl.). This population clearly qualifies as one of low exposure to BT and EHD.

<u>Cady Mountains</u>

Elevations in the ewe range north of Hidden Valley in the Cady Mountains range from 1300 ft. in Afton Canyon to about 3600 ft near Hidden Valley. South of Hidden Valley, the range peaks out at 4627 ft. The area used by ewes is entirely volcanic, except for the alluvial badlands in Afton Canyon. The area near Hidden Valley is very similar to the Marble Mountains, but between there and Afton Canyon are some substantial areas of blow sand. These sand patches support extensive stands of *Hilaria rigida* and *Oryzopsis hymenoides*. Otherwise, the vegetation is notably sparser and less diverse than in the Marble Mountains.

Cattle graze much of the Cady Mountains, overlapping most of the range used by ewes. Feral burros are lacking, but three feral horses are present in the western part of the ewe range.

Of fourteen blood samples obtained from mountains sheep in the Cady Mountains in 1986 and 1988, 35.7% were positive for BT, 30.8% were positive for EHD, and 7.7% were positive for PI-3 (R. Clark, unpubl.). This is clearly a population of substantial exposure to BT and EHD.

METHODS

Population densities were measured through accurate determination of population sizes and the areas of ranges used by ewes. Total range used by ewes was determined through (1) considerable ground work, (2) helicopter surveys, and (3) fixed-wing telemetry. For the most part, ground work was done without the aid of radio telemetry, because of the biases this would cause for mark-and-sample population estimates. Fixed wing aerial telemetry surveys were carried out by the California Department of Fish and Game and provided longitude and latitude coordinates of each radio collar based on location of strongest signal using a LORAN system. Helicopter surveys during this study have varied greatly in frequency among mountain ranges. The numbers of such surveys by mountain range are as follows: Old Woman Mountains - 3; Marble Mountains - 13; Old Dad Peak - 7; Cady Mountains - 1; Granite Mountains - 1. The area used by ewes was measured using a digitizing table and appropriate software.

Sizes of ewe populations were determined by mark-and-sample (commonly known as mark-recapture) methods. Both radio and marking collars were used. Table 1 is a history of collars installed in the populations under study. With the use of these collars for sequential estimates made over a number of years, an important question has been the number of live collared animals remaining in the population at any time. This has been no problem for radio collars as long as they have functioned, as all but one have had mortality sensors. For marking collars and radio collars that no longer transmit, verification of their persistence in the population has necessarily been based on direct observation of individual collared sheep. In most cases, sampling efforts have been sufficiently intense that every collared ewe was actually observed to be alive. For instance, all of 14 females collared in the Marble Mountains in June of 1986 were known to be alive in 1988. Two ewes in the Old Woman Mountains have been known to have lost collars. One was a rope collar installed in 1984, and the other was an experimental plastic belt-like collar installed in 1985; however, both animals have remained identifiable as marked sheep by their plastic ear tags, and both were still alive in the summer of 1989. Any uncertainties about the number of existing collars will be discussed under individual population estimates in the Results.

Two approaches to sampling for mark-and-sample population estimates are possible: sampling with replacement and sampling without replacement. Most such estimates are made using the latter, in that surveys of entire populations are carried out so as to minimize the probability of sampling any individual more than once per survey. Helicopter counts are commonly of this type. The first ground surveys of this study (in the Old Woman and Marble Mountains) were also of this type. However, there are good reasons to choose a sampling-with-replacement approach instead. What one is basically attempting in mark-and-sample population estimation procedures is to accurately estimate the proportion of the population that is collared. This is a problem involving the binomial distribution, as animals fall into one of two categories: marked or not marked. A basic assumption of such sampling is that it is done with replacement. The statistics worked out for mark-recapture estimates have also often assumed a binomial probability distribution (e.g. Bailey 1951, Overton 1971). Indeed, Bailey (1951:294) opens his analysis of the problem with the statement: "We shall assume that n is sufficiently small compared with x for us to be able to ignore the complications of sampling without replacement". In his terminology, n is the size of the sample, and x is the total population size. This is not necessarily a good assumption, as our samples have sometimes exceeded half the ewe population. Consequently, I have adopted sampling procedures that most approximate sampling with replacement. This has been done by making repeated short visits to each mountain range and slowly building up a sample of adequate size. In so doing, we have also attempted to randomize our sampling of each population by sampling in different geographic areas of the range used by ewes. Any groups of sheep that were located using radio signals from radio-collared ewes were so indicated in notes and were eliminated from the cumulative sample used for population estimates, as were any sheep not seen well enough to determine if they were marked. On a few occasions, telemetered rams have been used to randomly find ewes accompanying them during the rut.

The simple Petersen or Lincoln mark-and-sample estimator (Overton 1971; also known as the maximum likelihood estimator [Bailey 1951]) is Mn/m (where M is the number marked in the population, n is the size of the sample, and m is the number marked in the sample). This can be thought of alternatively as $M/(m/n)$, where m/n is an estimate of the proportion of the population that is marked. This estimator yields an upwardly biased estimate on the average, because m is not independent of n (Pielou 1974). Bailey (1951) and Seber (1970) have each provided modified equations that essentially eliminate this bias. In 1986 and 1987, I used the Marble Mountains population to test these two equations against the simple estimator above for repeated population surveys, as well as against a cumulative sample used to estimate the proportion of the population collared. For 10 surveys of the population (sampling without replacement), the usual Petersen estimator averaged 75.2 ewes, the Bailey and Seber modified estimators respectively averaged 63.5 and 67.4, and the cumulative sample estimator based on the proportion collared yielded 65.6, which is about midway between the Bailey and Seber estimates (Table 2). Consequently, I have adopted the cumulative sample estimator for use in this study.

A number of texts offer charts and tables to make rough estimates of confidence intervals around binomial probabilities (Overton 1971, Conover 1980, Rohlf and Sokal 1981). However, these can be calculated exactly using an appropriate computer program (Wenstøp 1988), which I have done. These have, in turn, been converted into confidence limits of population estimates and densities.

For the populations under study longer than one year, I have made yearly estimates of population size. I have defined the population being estimated as the adult and yearling ewes present in that year. However, in most cases, I have extended the sampling for the population estimate into the following year, including only adult ewes in the sample for the second year. This has allowed a larger sample size to be amassed. It assumes that minimal change in the subject population occurs over the period of sampling, or, alternatively, the estimate can be viewed as of the average size of the subject population over the sampling period. This sampling approach also means that many of the ewes sampled in any particular year are used for estimates of the population size in both the year of sampling and the previous year. The critical difference between estimates for consecutive years is the influence of yearling ewe component on the proportion of the ewes collared.

The number of collared sheep in every population has changed at some point due to the addition of collars or known mortalities of collared sheep. In every case, it has been possible to delineate sampling periods for estimates of ewe populations so as to avoid changes in collar numbers during a sampling period. However, for the one mark-and-sample estimate made for a ram population (Old Dad Peak), this was not possible because of the frequency of changes. Instead, it was necessary to determine an average number of collared rams present during the sampling period. This was done as a weighted average on the basis of the proportion of the sampling that took place in each subperiod in which different numbers of collars were present.

One of the important assumptions of mark-and-sample estimation procedures is equal sampling probability for every animal in the population (Pielou 1974, Otis et al. 1978). The sheep in the populations under study have exhibited a high mobility and a constant flux in group composition, providing no reason to expect a violation of this assumption. Nevertheless, the individual markings on collars have allowed a rigorous test for two of the populations of part of this assumption -- whether there was equal probability of being sampled among the collared ewes. This test could not distinguish the patterns of resightings among these ewes from that expected from random sampling. The details are presented in the Appendix. There is no reason to believe that this would be different in the other populations studied.

Essentially all sheep observed have been classified by sex and age. The classes used have been adult ewe, yearling ewe, lamb, yearling ram (also often called a class I ram), and class II, III, and IV rams. These ram classes are based on horn size as defined by Geist (1971) The lamb and yearling classes have been advanced a year at the beginning of the calendar year, before any new lambs have been observed. Proper yearling classification in desert populations of sheep can be difficult because of the long lambing seasons. Large, early born, lambs can be confused with late born lambs of the previous year. The yearling ewe classification has been particularly important to this study in that it has allowed the samples for the population estimates to be developed over more than one year. Also, it has allowed a comparison of lamb recruitment rates one year with yearling:ewe ratios the following year. Consequently, it is worth noting a criterion used as an aid in yearling classification that few investigators seem to be aware of it. Sheep horns begin as a dark gray color and bleach over time in the sun to a much lighter tan color. The patterns of horn color can be used to great advantage in sheep classification. Both sexes put on large amounts of horn growth in the first two years of life. As a result, a lamb is distinguishable in its first year of life because of uniformly dark colored horns. However, by the end of its first winter, the first year's horn grown has bleach to a lighter color. Consequently, in its second year, it will have distinctively two toned horns -- a bleached lamb growth and a darker second year growth. The division is usually near the middle of the horn. Ewe horn growth thereafter is of considerably lesser quantity. In its third year, a ewe no longer exhibits a clearly two toned horn pattern, i.e. the new dark portion will be only a short section near the horn base.

Differences between populations in nutrient availability of the habitats they inhabit was measured by developing seasonal curves of fecal crude protein. Percent fecal crude protein has been considered a useful index of diet quality because of correlations with protein content and digestibility of the diet (Hebert 1973, Hebert *et al.* 1984, Wehausen 1980, Holechek *et al.* 1982, Leslie and Starkey 1985); however, it is more closely an index of digestibility, and secondarily one of protein content through a second correlation between forage protein content and digestibility (Wehausen, unpubl.). As such, it tracks well changes in plant phenology, as affected by such factors as soil moisture content, temperature and species diversity (Wehausen and Hansen 1988). While there are some cautions that should be heeded relative to its use as a diet quality index (Wehausen and Hansen 1988), it is probably ideally suited to investigating annual diet quality patterns for species like mountain sheep that consume considerable amounts of graminoids (Holechek *et al.* 1982, Seip and Bunnell 1985). Fecal samples were collected approximately monthly from each population. Most such samples were collected fresh from sheep observed, and these were almost always from groups containing ewes. On a few occasions in which fresh samples could not be obtained, very recent samples less than a week old were collected instead. Careful attention was given changes in plant phenology in each range and an effort was made to collect fecal samples at what was considered to be the likely peak in spring diet quality, as well as the low point in the winter. Levels at both points were considered important for interpopulation comparisons.

Evidence of exposure to BT and EHD viruses was based on data from blood samples of sheep handled (Clark *et al.* 1985; Clark, unpubl.).

RESULTS

Ewe Ranges

Figures 3-7 contain plottings of direct observations of sheep, aerial telemetry locations, and boundaries of the area used by ewes for the populations under study. The range boundaries for the Marble and Old Woman Mountains have been changed somewhat from the previous report (Wehausen 1988) based on additional information. Most significant is the addition of the entire southern (Surveyor Spring) section of the Old Woman Mountains to the ewe range. This has been added because two of four ewes in this population that have been radio collared have visited this section, one of which was known to traverse the entire southern section on an annual basis to visit the Iron Mountains. One year, she was documented to have borne a lamb in the Iron Mountains, which then returned to the Old Woman Mountains with her later in spring. The inclusion of most of this southern section of the Old Woman Mountains in the ewe range was based on observations of sheep beds throughout it during a helicopter flight. The central section of the Old Woman Mountains around Old Woman Statue continues to be considered rams use only.

With the decline in surface water in the Old Woman Mountains during the 1980's, following the very wet years around the beginning of the decade, only a small number of point water sources remain useful to ewes in the hot season. The sheep concentrate around these in the early summer, but may disperse later in summer if rain and/or cooler weather occur. In the Wilhelm Spr. section, Upper and Lower Craig, and Nursery Springs continue to provide water in summer, with most sheep use at Upper Craig Spring. In the Sheep Camp section, Sheep Camp Spring (next to the guzzler) and Upper Sheep Camp #1 continue to be limited water sources. In 1988, Sheep Camp Spring began running again after tamarisk was removed in the wash above it, and was used heavily by sheep; but in 1989, it was dry until recharged by summer rain. Prior to that rain, the only available water was a limited amount at Upper Sheep Camp #1, which clearly did not quench the thirst of the sheep. Lone Spring and Dripping Spring continue to supply adequate amounts of water in the Dripping Spring section of the range, with the former receiving the majority of sheep use.

For the Marble Mountains, only direct observations are plotted on Figure 4, and many additional observations were not plotted to avoid visual clutter. Figures 8-12 contain aerial telemetry locations and direct observations for the five ewes with radio collars in the Marble Mountains. For these three years of data, the home range of each of these ewes has encompassed a high percentage of the total range used by all ewes; but none of them has encompassed the entire ewe range. Those that cross the pipeline road to use the northern section have not used the very southern section of the ewe range, and, conversely, those that have used the very southern section have not used the northern end. No sheep have been documented to cross Highway 66 to the very southern end of the Marble Mountains. Similarly, no sheep have been known to cross Interstate Highway 40 that cuts off the very north end of the Marble Mountains. Prior to construction of that highway, it is probable that this population had interchange with the Granite Mountains. Ewes occasionally cross Kelbaker Road to visit the Brown Buttes just south of I-40; but I have not included this small area within their range because of the rarity of use.

Unlike the other four populations under study, the sheep in the Marble Mountains show little reliance on surface water in the hot season. There are four sources of surface water in the range: a guzzler toward the south end on the east side, and three springs on the west side near the north end, two of which provide ample water. With the possible exception of ewe #4 (freq. .265), there is no evidence of concentration around water sources in the hot season (Figures 8-12). This population consumes a great deal of barrel cactus (*Ferocactus acanthodes*), which very likely provides sufficient water. In September of 1988, following 5 months of no rain in this mountain range, I collected a sample of barrel cactus flesh from one sheep were eating, and measured the water content at 93%.

The Granite Mountains are a particularly well watered range, with numerous areas of surface water, many of which run for a short distance, even in the hot season. In the summer of 1988, before most of the collars had been installed, these sheep showed a substantial concentration around water sources at the west end of the range. This was not apparent in 1989, when Bull Canyon instead appeared to be the more important center of summer distribution. However, ewes used all areas of their range in the summer of 1989 (Bighorn Basin, Bull Canyon, and the west end). This mountain range is high enough that a slight cooling of summer temperatures causes sheep to disperse from the vicinity of water. In 1989, such cooling already had occurred by mid August, with no return to summer heat thereafter.

Figure 6 contains only the boundary of ewe use for the Old Dad/Kelso Pks. population, which is based on a very large data set. Combined points for aerial and direct observations for this population currently number in the thousands, and will be plotted at a later date by computer using a GIS system. Natural, predictable, surface water in this ecosystem occurs only in the most eastern part, in the Marl Mountains. Four guzzlers provide summer water in the rest of the range, three of which are used very heavily by sheep when they have water.

The Cady Mountains ewe population uses both sides of Afton Canyon, but concentrates on the south side (Figure 7). Afton Canyon is used heavily as a water source during the warmer months, and the many deeply cut gullies of the badlands along its edge are used for shade in summer. Cave Mountain is a large mass of excellent precipitous sheep habitat where lambing might be expected to occur. Such use has not been documented yet. The current light use of Cave Mountain compared with the south side of Afton Canyon may reflect the high amount of human activity in Afton Canyon. It is likely that the range of this population historically extended even further north to the Cronese Mountains, which are now mostly blocked by Interstate Highway 15. So far, no ewes have been documented to use areas south of Hidden Valley, whereas ram use is well-known there. This is explainable on the basis of the central importance of Afton Canyon to this population and the more conservative behavior of ewes compared with rams. However, this is based only on a sample size of four radio-collared ewes, as no attempt has been made on the ground to locate sheep in this southern section; and the only helicopter flight during this study occurred during the hot season, when all sheep were close to Afton Canyon. It is possible that some ewes occasionally wander south of Hidden Valley during the cool season.

Nutrient Intake

Fecal Crude Protein

Figure 13 contains plottings of FCP values for the populations under study for the duration of data for each. A number of comparisons can be made among these curves, but the ultimate measure is an integration of different curves within some specified time period, as this is the best overall measure of nutrient intake within each population. Such a measure can be used for comparisons within a population among years, as well as between populations. The Mojave Desert of California has two potential forage growing seasons: winter-spring and late summer. The winter-spring growing season is the most predictable in occurrence and timing, the latter of which is largely temperature determined (Wehausen and Hansen 1988). The summer growing season is entirely a function of the occurrence and extent of summer rains, which are very unpredictable in timing and location. It is not unusual for just a part of a mountain range to receive summer rains. Thus, it is not surprising that the desert lambing season is coincident with the winter-spring growing season (Wehausen 1990). Consequently, I have concentrated attention on that season.

The value of any integration of FCP will be affected by a number of parameters that visually can be assessed from Figure 13. These are (1) the minimum base values from which the winter rise begins, (2) the maximum values reached in spring, and (3) the length of the growing season, which is mostly affected by how early it begins, but also can be extended somewhat by spring rains. This latter influence is well illustrated by the curves for 1988. In that spring, two unusual late rain storms occurred in the second half of April. The influence on nutrient intake of the sheep is particularly graphic for the Marble and Old Dad populations in the form of an extra, and particularly high, peak in late spring, when the curve normally would be declining (Figure 13).

Comparisons of minimum values suggest that the Marble, Old Dad, and Granite Mountains populations all tend to dip to lower values than the population in the Old Woman Mountains. The notably high minimum FCP value for the Cady Mountains in 1989 is remarkable for a range with such seemingly poor forage resources; but the same can be said for the elevated summer values for this population. This range received no rain in the summer of 1989; yet the FCP values rose substantially that summer. Correlated with this was the good condition of the ewes observed there in late summer, which contrasted with the dished-in rumps of the ewes in the Marble Mountains at the same time, where significant summer rain occurred. Given the poor summer forage resources in the Cady Mountains in 1989, there is only one reasonable explanation for these data -- that the sheep are feeding extensively on green vegetation along the Mojave River in Afton Canyon in addition to drinking there in the hot season. This should be easily tested.

In the first two years of comparison, the Old Woman Mountains exhibited higher spring peak FCP values than the Marble Mountains. The curves suggest that this also would have been the case in 1988 had the unusual April rains not occurred. It is interesting that in the dry year of 1989 this pattern was reversed. In the absence of the April rains, it appears that the 1988 peak value for the Old Dad population also would have been lower than for the Old Woman Mountains. Unlike the Marble Mountains, the 1989 peak Old Dad value was somewhat below the Old Woman Mountains. Only 1989 peak values exist for the Granite and

Cady Mountains. The Granite Mountains had the highest value recorded that year, while the Cady Mountains had a peak value close to that of the Old Dad and Old Woman Mountains populations. At this time of year, the sheep in the Cady Mountains occupy areas away from Afton Canyon, thus these values do not reflect forage resources in Afton Canyon.

Probably the most important parameter influencing total nutrient intake during the winter-spring growing season is its duration. This has been measured as the number of days between the low point in fall or winter, and the point in spring or summer when the curve hits a low point or makes a substantial shift toward horizontal, suggesting a summer low. On the surface, this would appear to be a crude measure, since samples for FCP have been collected only approximately monthly. However, when one looks at the variation that has occurred, between years, this resolution is quite useful. For instance, in the Marble Mountains, the 1988 growing season began with a major tropical storm the last day of October, 1987, causing the FCP curve to begin rising after a data point in the first half of November. The April rains that growing season caused it to extend until late August, when the decline in FCP finally ended. In contrast, the 1989 growing season was not initiated until a storm at the beginning of January; and, because that was the only storm of the season, FCP had already completed its major decline by the end of May (Figure 13). The difference between the lengths of these growing seasons is approximately a factor of two for the Marble Mountains, amounting to somewhat more than five months. Similar differences exist for the other two populations with FCP data in those two years (Table 3).

I have integrated the FCP curves in Figure 13 for the lengths of the winter-spring growing seasons listed in Table 3. In order to correct for the curvilinear relationship between FCP and apparent digestibility, I first used a natural log transformation of the FCP data. This integration provides a measure in units of FCP ln%-days. Thus, since the natural log of 10 is 2.3, a constant value of 10% FCP over a duration of 10 days would yield 23 FCP ln%-days. Since 5% FCP is about a maintenance level for mountain sheep (Hebert 1973), and is a level rarely recorded in wild populations in my experience, I have expressed the integration of the FCP curves as FCP ln%-days above 5%. These integrations exhibit even larger differences between 1988 and 1989 than growing season length. For the Marble Mountains, the difference is nearly a factor of three. 1985 and 1986 were intermediate years (Table 3). The Old Woman Mountains show a consistently higher winter-spring nutrient intake than the Marble Mountains and Old Dad Peak populations. For 1988, the Marble Mountains population was higher than Old Dad, but this was reversed in 1989. 1989 is the only year in which comparisons of all five population can be made. These 1989 values put (1) the Granite and Old Woman Mountains in a class together of highest nutrient intake, (2) Old Dad and Cady Mountains in a second class of intermediate intake, and (3) the Marble Mountains as the lowest (Table 3). This makes sense to the extent that the Granite and Old Woman Mountains (1) are both higher, cooler ranges than the other three, (2) have quite similar plant communities, and (3) have a considerably higher plant species diversity than the other three. Whether the relationships among the other three populations is consistent will require more years of data.

Population Estimates, Densities, and Trends

Old Woman Mountains

Of 16 ewes marked in the Old Woman Mountains beginning in the fall of 1984 (Table 1), two are known to have died. One of these died in the spring of 1985 of capture myopathy problems shortly after capture, thus was never used as a marked sheep. Another ewe marked in the spring of 1985 was known to survive through that summer, but ceased to be observed thereafter, and her carcass, including ear tag, was found about a year later. Both of these provided relatively clearcut dates for inclusion in the marked ewe cohort. A third ewe, marked with a rope collar and ear tags in fall 1984, is less clearcut. She has never been observed alive, but appeared on a time-lapse camera photo in the summer of 1985. Consequently, she was considered as a marked animal for the 1984 and 1985 estimates, but not thereafter. All other marked ewes have been observed alive repeatedly; and all are known to have been alive in 1988.

Population estimates for the ewe population in Old Woman Mountains span the years 1984-88. These have exhibited an increasing trend from 31 ewes in 1984 to 54 ewes in 1988 (Table 4). However, confidence limits around these estimates are sufficiently wide that the only statements that can be made with confidence ($P \geq .95$) about trend are that the 1987 and 1988 estimates are significantly higher than the one for 1984, and that the 1988 estimate is significantly higher than that for 1985. Whether there was any real increase during the 1984-86 period is unclear. Recruitment rates for the 1984 and 1985 lamb crops were both in a range that would be expected only to maintain population size (Table 5; Wehausen et al. 1987). 1986 exhibited a notably higher recruitment rate; thus, it is not surprising that the following year was the first one to show a significant increase in population size. With the exception of 1986, the data collected for the Old Woman Mountains have exhibited a significant drop in recruitment ratios from summer lamb:ewe ratios to yearling:ewe ratios the following year (Table 5). Some of this is to be expected simply on the basis of the independence that yearlings, especially males, can show relative to ewes. However, this is not likely to explain the entire magnitude of the drop observed in some years. In part, what this suggests is that the major mortality period for lambs may extend well past their first spring, when high mortality from diseases has been recorded in some populations (DeForge and Scott 1982).

Measurement of the ewe ranges delineated in Figure 3 totaled an area of 58.25 square miles. This translates to ewe densities of 0.53 to 0.92 ewes per square mile for the 1984-88 population estimates (Table 6), and a maximum range of 0.37 to 1.30 ewes per square mile for the 95% confidence limits around these five estimates.

Marble Mountains

Population estimates for the ewe population in the Marble Mountains have been very consistent for 1986-88, exhibiting a sequential decrease from 66 to 62 ewes (Table 5). While the low recruitment rates recorded for this period (Table 4) may give reason to believe that this decrease is real, statistically there is no apparent trend, as the extreme 95% confidence limits for this period range from 50.3 to 83.5 (Table 4). A large sampling during the rut in 1986 yielded a ram:ewe ratio of 109.3:100. This particularly high ratio reflects 1983-85 sex biased removals of sheep from this population for reintroduction that emphasized ewes (Table 7). When this sex ratio is applied to the estimated ewe population for 1986, an estimate of 72 rams results, thus a total population of 138 adults.

Collection of demographic data on the sheep in the Marble Mountains began only in 1983 with helicopter flights. Since only one of these provided a recruitment rate prior to the beginning of this study in 1986 (Table 5), it has been necessary to make inferences about earlier recruitment and population trends from age structure data. These data suggest considerable dynamics since 1978.

The first count to classify rams occurred in 1984, and recorded a predominance of class II rams, followed in importance respectively by class I, and class III+IV rams. All classifications since then have found low percentages of class I and II rams, with class III and IV rams making up approximately 90% of the classification (Figure 14). The sample size in 1984 was small compared with later years, and may not have represented the older ram cohorts accurately. Also, most of the observers were not experienced, thus may not have classified rams properly in all cases. Nevertheless, it is doubtful that these potential problems can completely explain away the virtual disappearance of the I and II classes in subsequent counts. The ram classifications since 1985 suggest a population that has experienced low recruitment for a number of years; thus, the 1984 classification probably caught the last significant cohort to be recruited before it became unidentifiable in the larger III+ size class. The slightly declining trend in the proportion of class III+ rams in the population since 1987 may reflect the influence of a very limited ram harvest in this population beginning in December 1987, probably coupled with some natural mortality in the older age classes.

Data from 49 ewes aged during yearly captures between 1983 and 1986 provide a more accurate picture of recruitment history in the Marble Mountains that corroborates the findings from rams. When the birth years of these ewes are accumulated, a distinctive distribution with a 1980 peak emerges (Figure 15A). Interpretation of this distribution must be cautious because: (1) birth years after 1982 each have respectively more limited opportunities for representation, and (2) interpretation must be made against a background of what would be expected from survivorship curves (e.g. Bradley and Baker 1967, Hansen 1967).

If recruitment numbers were constant, the distribution of birth years would be expected to decline very slowly for a number of years, then drop more rapidly. The pattern for 1978-82 in Figure 15A was derived from ewes aged 1-5 in 1983, 2-6 in 1984, 3-7 in 1985, and 4-8 in 1986. Only 16% of this sampling fell in age classes older than 6; thus, this is largely a sampling of ewes in age classes in which (1) aging is quite accurate, and (2) survivorship is high. Consequently, the resultant 1978-82 pattern in Figure 15A is probably a reasonable parallel to the number of sheep recruited into the population in those years.

Figure 15A cannot be interpreted as the recruitment rate pattern for 1978-82 because there is good reason to believe that the population was not constant. The 1978-80 exponential increase in Figure 15A is probably best interpreted as reflecting a combination of increasing recruitment rate and population size. The apparent high numbers of recruited sheep in 1979 and 1980 would have increased the population base of reproductive ewes up to 1982; thus, if recruitment rate had been only constant during 1980-82 it would have been expected to result in increasing numbers in the 1980-82 cohorts. The exponential decline that occurred instead in 1981-83 consequently can be interpreted as an underestimate of the actual degree to which the recruitment rate declined in that time period. Restricting the analysis to ewes caught only in 1985 and 1986 allows equal representation through 1984, and indicates that recruitment remained low once it dropped (Figure 15B). This is also corroborated by the yearling:ewe ratio of sheep captured during 1983-86. Classification of yearlings from a helicopter is often difficult. During capture operations, what are believed to be ewes, sometimes turn out to be yearling rams when caught. Consequently, the ratio of yearlings of both sexes to adult ewes in a captured sample probably provides a reasonable measure of the composition in the population. For a sample of 47 adult ewes captured between 1983 and 1986 in the Marble Mountains, this ratio was only 17 yearlings:100 ewes. Actual recruitment data collected beginning in 1986 have documented low rates as a continuing trend (Table 5). For 1986 to 1988, fall recruitment rates exhibited a steady decline, but in 1989 jumped to the highest rate recorded (Table 5). Similar to the data from the Old Woman Mountains, there has been a consistent drop in lamb:ewe ratios one year to yearling:ewe ratios the following year. For the three years of data from the Marble Mountains, this drop has ranged from 6.7 to 8.8 lambs per 100 ewes (Table 5).

The large dynamics in recruitment that is apparent for the Marble Mountains since 1978 is worthy of exploration as to possible causes. A reasonable hypothesis would be an environmental cause. November, January, and February precipitation were found to account for much of the recruitment dynamics of a mountain sheep in the Santa Rosa Mountains at the western edge of the southern California deserts (Wehausen et al. 1987). Consequently, precipitation was investigated as a possible cause of the recruitment dynamics in the Marble Mountains, using data from the nearby Mitchell Caverns. These data support the concept that precipitation influencing winter-spring forage growth may have been an important factor in the elevated recruitment in 1979-82. 1978-80 produced notably elevated levels of midwinter precipitation relative to what has occurred since 1960. In fact, one could argue that there was a generally increasing trend beginning in 1976 (Figure 16A). 1980, the year of apparent peak recruitment, produced the highest precipitation in both January and February since 1960. Additionally, March precipitation was elevated throughout the 1978-82 period (Figure 16B). Without an actual quantitative record of recruitment rates during the years in question, it is not possible to make more than such a crude qualitative test of relationships with rainfall. However, January and February precipitation do not explain the apparent elevated recruitment in 1981 and 1982 relative to subsequent years (Figure 16A). If March precipitation was the factor keeping recruitment up in those two years, it fails to explain why it did not stay elevated in 1983, which experienced the highest March rainfall since 1960. Nor can the small variance in recruitment rates measured in recent years (Table 5) be explained by differences in winter spring forage growth determined by precipitation. The year of the longest growing season (1988) yielded the lowest recruitment rate, and the year of worst forage growth (1989) yielded the highest. These data suggest one or more additional factors operating in the system since 1983.

Between July 1983 and July 1985, 57 sheep were removed from the Marble Mountains for reintroductions. Most of these (43) were females, comprised of 35 adults, 2 yearling, and 6 lamb ewes (Table 7). The recruitment rates recorded or inferred suggest that recruitment rates since 1983 have been at a level likely only to replace natural mortality. This is supported by the negligible change in population estimates since 1986. This has two implications. First, there is no evidence of a density-dependent recruitment response to a substantial drop in population density. Second, it is possible to add the sheep removed to the 1986 estimate to arrive at a reasonable estimate of what the population would have been in 1983 before removals began. When this is done, the estimates for 1983 are 109 ewes and 86 rams. This results in an adult sex ratio of 79:100, which is similar to natural sex ratios of other unhunted wild sheep populations (Aldous 1957, Leslie and Douglas 1979, Wehausen 1980, 1983, Wehausen et al. 1987). Including recruited lambs, the total population in 1983 before removals began was probably 210-220 sheep. Thus, the 1983-85 population reduction through removals dropped the density by somewhat more than 25%.

A second approach to the problem of correcting for sheep removed is to apply an annual mortality rate to the ewes removed. Estimates of the size of the ewe population in the Marble Mountains declined 3 percent per year between 1986 and 1988. If we assume that the cohorts of ewes removed from the population at each capture would have declined in number at this same rate if left in the population, the 43 removed would have been 38 in 1988. When added to the estimate for 1988, this results in an estimate of exactly 100 ewes that would have been present if none had been removed.

The total ewe range outlined in Figure 4 measures 28.52 square miles. Thus, the estimated ewe density has varied between 2.30 and 2.17 ewes per square mile between 1986 and 1988, with extreme values for 95% confidence limits of 1.76-2.93. In 1983, this density would have been about 3.8 ewes per square mile; and, in 1988, it would have been about 3.5 if no ewes had been removed from the population.

Granite Mountains

Both ewes that received marking collars in 1985 were observed alive in August of 1988 when additional collaring began. Although neither of these ewes was observed in 1989, both have been included as marked animals in population estimation procedures. Of the five ewes that received radio collars in late summer and early fall of 1988 (Table 1), one was killed by a mountain lion early in 1989, when successful sampling for population estimates was just beginning. Consequently, she was not included as a marked animal for population estimates.

The ewe population in the Granite Mountains has been exceedingly difficult to sample due to (1) very low density, (2) a complex physiographic background, against which it is difficult to see sheep, and (3) difficult access into the middle of their range. This is well illustrated by the sighting record. From October 1988 through November 1989, ground sampling attempts were made on a total of 24 days in all seasons, constituting 43 person days. For this effort, only four groups of sheep containing ewes were seen. Similarly, a two hour helicopter flight in September of 1989 averaged only one sheep per hour, which is only 6% of the sighting rates recorded the following two days in the Old Dad Peak/Kelso Mtns. and Marble Mountain ecosystems. A concerted effort has been made to sample all parts of the ewe range in order to avoid any unknown sampling biases that might occur if ewes were mostly sampled in one portion of the range. Consequently, the sample derived has included ewes seen throughout their range.

The population estimate for the Granite Mountains is based on a sample of only 13 ewes. More than half of these have been collared, with a resultant estimate of 11 ewes in the population and 95% confidence limits of 7-24 (Table 4). The area used by ewes in the Granite Mountains is the least of the five populations under study, at 22.09 square miles. This yields an estimated density of 0.50 ewes per square mile. Even the maximum for the 95% confidence limits is only 1.08 ewes per square mile (Table 6).

The combination of small sample and short study duration make it impossible to say much about recruitment rates and population trend. Some recruitment occurred in 1988, as 3 of the 13 ewes sampled, or 23%, were yearlings. If representative of the population, this is a substantial percentage to be in one age class.

Old Dad Peak\Kelso Mountains

Sampling in the Old Dad Peak/Kelso Mountains ecosystem since the initial completion of collaring early in 1988 has allowed population estimates for each sex present in 1988 and for ewes in 1989. One collared ewe died in July of 1989, so that death was used as a dividing point for the two estimates of ewe populations. For 414 ewes sampled for the 1988 estimate, 13.5% were collared, yielding an estimate of 126 ewes (95% CL: 99-164). For 274 ewes sampled in summer and fall of 1989, the percent collared dropped to 9.8, and the estimate rose to 162 ewes (95% CL: 118-232; Table 4). For a sample of 359 rams sampled, 8.1% were collared, yielding an estimated 1988 population of 186 (95% CL: 132-274; Table 4).

The population increase between 1988 and 1989 is corroborated by a high recruitment rate in 1988 (Table 5). If one takes the recruitment rate from fall 1988, halves it to use only females, and applies this rate to the 1988 population estimate for ewes, the result is 162 ewes expected for 1989 -- exactly the number estimated by mark-and-sample methods. However, this expectation assumes no mortality of recruited lambs, nor of ewes, which is not supported by the drop in the recruitment ratio when measured as the yearling:ewe ratio in 1989 (Table 5). As with such drops recorded for other populations studied, some of this drop may be due to (1) some large yearling ewes being classified as adult ewes, (2) some yearling males dispersing to areas receiving little sampling (twice as many females as males were in the 1989 Old Dad yearling sample when they were distinguished), and (3) a few small, late-born yearlings being classified as lambs. However, some of the drop may be additional mortality of that cohort. This suggests that, while a substantial increase in population was expected, the difference between the 1988 and 1989 estimated ewe populations represents somewhat of an overestimate of the actual change. This could result from an underestimate of the number of ewes in 1988, an overestimate for 1989, or both.

A large number of sheep has been removed from the Old Dad/Kelso Pk. population beginning in 1983 (Table 7). As with the Marble Mountains, these removals have been biased toward females, and allow an assessment of past recruitment patterns based on the age structure of ewes removed. Two such assessments have been made using sheep captured in two time periods: 59 yearling and older ewes caught between 1984 and 1987, and 36 such ewes in December of 1989. The cautions of interpretations of such data for the Marble Mountains also hold for these data. For instance, for the 1984-87 sample, there is less opportunity for representations of the 1984 and 1985 cohorts than previous ones. The results show two years of high recruitment in 1979 and 1980, as in the Marble Mountains, but a very different pattern thereafter (Figure 17). The Old Dad population exhibits regular years of good recruitment mixed with ones of low recruitment throughout the 1980's. Specifically, in addition to 1979 and 1980, 1982, 1983, 1986, and 1988 are well-represented in the plotting of birth years of captured ewes, indicating years of good recruitment (Figure 17). It is noteworthy that for the overlapping years of adequate resolution in these two samplings (1982-85), the pattern is consistent. There exist a few years of measured recruitment data prior to this study (Table 5). Despite limited sample sizes for a couple of these, when coupled with data from 1988, they corroborate the pattern based on ages of ewes: (1) particularly high recruitment in 1988, (2) lesser, but good recruitment in 1982 and 1986, and (3) relative to these, low recruitment in 1987.

Of the 172 sheep removed from the Old Dad/Kelso Pk. population in the past 6.5 years, 126 have been females (Table 7); and of these, the 37 removed in December of 1989 only approximately equaled the population increase brought about by the high recruitment in 1988 (the difference between the population estimates was 36). The question remains to what extent the 89 ewes removed prior to 1989 influenced the size of the 1989 pre-removal population size. Because of the dynamics of recruitment in this population, this question is not as simple as for the Marble Mountains. Between the beginning of removals in 1983 and the 1989 population estimate, there were two years of significant recruitment in which removals might have been replaced: 1986 and 1988. If Figure 17 accurately represents relative numbers recruited in recent years, combined recruitment for 1984-87 did not quite equal that of 1988. Given that the 1988 recruitment increased the ewe population by an (over) estimated 36 ewes, this suggests that total recruitment since removals began in 1983 has probably totaled less than twice that, or approximately 65 ewes, which is 24 less than has been removed in that period. In other words, the population probably did not replace all the ewes removed prior to the 1989 removal. Additionally, to estimate what the population size might have been prior to removals in 1983, it is necessary also to consider natural mortality of ewes between 1983 and 1989. There is no good quantitative basis to do this, but one can make a rough estimate. Adding the approximately 24 ewes not replaced between 1983 and 1989 to the 1989 estimate yields 186 ewes. Unaccounted natural mortality probably would bring the estimated 1983 population size to about 200 ewes. As a program to keep population density in this ecosystem from becoming excessive, the 1983-89 removals apparently have been successful. It is also safe to assume that the population would have been considerably higher in 1989 had the earlier removals not taken place; but how much higher would be a function of the influence of density dependent factors.

The Old Dad/Kelso Pk. sheep range is the largest of those studied, with the area used by ewes totaling 66.36 square miles. This results in estimated ewe densities of 1.89 and 2.45 ewes per square mile for 1988 and 1989 respectively, the latter being the more useful for this study in that it contains more replacement of ewes removed from the population. Confidence limits for the 1989 density estimate are 1.77-3.49 (Table 6). In the absence of removals, the 1989 density probably would have been at or higher than the upper of these confidence limits.

Cady Mountains

Of the six ewes collared in the Cady Mountains in 1988, one died within a month of capture -- presumably a capture related mortality. The others all have been documented to be alive in 1989. Of the three females collared in 1986, two have been observed to be alive in 1989. Population estimates have been made on the assumption that the third one is also alive. In the event that this is incorrect, all population estimation and density values presented would be 12.5% high. Qualitatively, this would have no effect on the results of this study, since the Cady Mountains populations has the lowest density of those studied.

In spite of its low density, the Cady Mountains population has proved to be one of the easiest to sample, due to good access and a background against which the sheep are easily observed. For 44 ewes sampled in 1989, 31.8% were collared, which yielded a population estimate of 25 ewes (95% CL: 17-43; Table 4). This population had the second largest ewe range of the populations studied at 55.13 square miles, resulting in an estimated density of 0.46 ewes per square mile (95% CL: 0.30-0.78; Table 6).

Nine percent of the ewes sampled were yearlings, representing recruitment of 1988 lambs. This is a level that will approximately hold the population constant. Recruitment in 1989 was virtually nonexistent. For 28 ewes sampled in May 1989 or later, no lambs were seen. Fecal pellets from a lamb were observed during the summer, suggesting that at least one 1989 lamb may be present in the population.

Competition

Three situations have found during this study that are noteworthy relative to the question of competition. The first of these occurred in the Old Woman Mountains. In the first report in this series (Wehausen and Hansen 1986), it was suggested that any competition between cattle and mountain sheep that might occur in the Old Woman Mountains probably would involve displacement of sheep from water, i.e. would be interference competition. This apparently occurred in the Wilhelm Spring subpopulation in 1986 and 1987. In the fall of 1985, two adjacent springs were discovered on the west side of this arm of the mountain range and given the names upper and lower Marvin Wood Springs. At that time, the lower of the two held about 200 gallons of water, had sheep fecal pellets on the immediate slopes around it from the previous season, and had no evidence of cattle use. Included were small lamb pellets that were interpreted as dating from late spring. The following winter this spring was colonized by cattle, which continued to use it into July of 1987, when it dried up. Those cattle converted this clear water into a cesspool. At the end of the hot season in both 1986 and 1987, I could find no sign of sheep use at this spring. In both years, the sheep had alternative water sources to use; thus it is unlikely that this apparent displacement had any demographic effect. As such, it cannot be construed as competition in the strict definition of the term. However, this natural experiment suggests the potential for such displacement, which under different circumstances might be more significant. Dunn and Douglas (1982) reported similar displacement of sheep from water due to feral burros.

The second situation with potential for competition concerns Afton Canyon in the Cady Mountains. It was previously noted that (1) forage resources in the Cady Mountains are relatively poor, (2) during the hot season the distribution of this population centers around Afton Canyon, and (3) the most likely explanation for the elevated FCP values in summer was that the sheep were supplementing their diet significantly with lush forage growing along the Mojave River. Cattle also frequently feed on this forage in summer; and therein lies the potential for competition to be occurring. Judging from early reports by railroad workers of sheep groups as large as 40 in Afton Canyon (R. A. Weaver, pers. comm.), the sheep population was probably previously larger than it is today. This competition potential warrants collection of more detailed data on the nature of sheep use of Afton Canyon.

The third situation with potential for competition is Bull Canyon in the Granite Mountains. This is a large north-facing, relatively inaccessible drainage, which has sections with water running on the surface during the heat of summer. While many of these watered sections of the canyon would be adequate for sheep to drink and feed on green forage along the water, their sign near water is essentially absent except along one short stretch that is too rocky for cattle. Perhaps more important is the habitat degradation these cattle are causing. They have so altered the perennial grass (mostly *Stipa speciosa*) and other forage availability on the lower slopes of the canyon that the cattle themselves are forced to climb high up the slopes in the heat summer to find enough forage. Both these observations represent situations with potential for competition with the native sheep.

DISCUSSION

Population Density

The ordering by density (lowest to highest) of the five populations under study for the most recent estimates in Table 6 is: Cady, Granite, Old Woman, Marble, and Old Dad. The three lower density populations fall out as a group distinct from the upper two, with no overlap in confidence limits between the two groups (Figure 18). Had densities not been reduced through removals of sheep from the Marble and Old Dad populations beginning in 1983, the density spread between these two groups of populations would have been considerably greater.

The density pattern in Figure 18 does not match the differences among populations in nutrient availability of habitats, which would produce expectations of the Marble, Cady, and Old Dad populations as a lower group, and the Granite and Old Woman populations as an upper group. However, the observed pattern does fit the expectations based on differences in exposure to BT/EHD. As such, it supports the basic hypothesis of this study -- that significant exposure to BT/EHD leads to depressed population densities.

Population Dynamics

While population density data lend support to the BT/EHD hypothesis, data on population dynamics do not. The increasing trend of the Old Woman Mountains population goes counter to predictions of that hypothesis. One possible explanation is that exposure to BT/EHD has decreased. The Old Woman Mountains have undergone a major drying trend throughout the 1980's. High precipitation input in 1978-80 apparently recharged aquifers, resulting in high availability of surface water for a number of years, including some streams that ran on the surface through the summer. In the second half of the 1980's, the surface water declined to the more normal situation of a small number of point sources (Wehausen 1988). It would be reasonable to hypothesize that with this change came a shrinking of larval habitat and, thus, populations, of the *Culicoides* gnats that transmit BT and EHD (Wehausen 1988). If so, a drop in exposure to BT/EHD might explain the dynamics of the population in the Old Woman Mountains. Data available are now adequate to test this hypothesis. The rise in recruitment rates in the Old Woman Mountains was already apparent in 1986 (Table 5), which resulted in the first statistically significant rise in population size in 1987. Of 21 blood samples collected from this range between October 1984 and September 1987, half (11) were from the 1984-85 pre-increase period, and half (10) were from the 1986-87 post-increase period. Respectively, disease prevalence in these two periods was 36% and 50% for BT, and 82% and 70% for EHD (Clark et al. 1985; R. Clark, unpubl. data). These data suggest no change in exposure to these viruses; thus they do not support the notion that the population increase has resulted from decreased exposure to BT/EHD.

Alternative Explanations

If BT/EHD exposure is not considered adequate to explain demographic differences, it is reasonable to look for alternative explanations. In particular, it would be desirable to be able to explain low densities by a mechanism other than BT/EHD exposure. However, in the absence of an overall correlation between FCP curves and population density, such explanations will necessarily be conjectures about individual populations, and as such, will be fairly tentative. As an *a priori* assumption, it is reasonable to postulate that population density potential for all ranges is somehow related to nutrient resources, and that other factors imposed on the populations decrease this density to some degree.

For the Cady Mountains, it is possible that a relatively low density is a natural consequence of poor forage resources. Much of the range inhabited by these sheep supports only very impoverished forage resources, due to hot, dry conditions. The ewe range for this population almost certainly has the lowest plant species diversity of the populations under study. It is possible that stands of *Hilaria rigida* and *Oryzopsis hymenoides* growing in substantial areas of sand are the staple that allows this population to exist. Additional years of FCP curves should better elucidate the nutritive status of this population compared with the others.

Despite the adverse impacts of cattle on habitat composition in parts of the Granite Mountains, current FCP data do not suggest that low density of the Granite Mountains population is explainable on the basis of poor forage resources. However, the Granite Mountains have a factor basically lacking in the other populations under study: regular use by mountain lions. The only other population receiving some predation by mountain lions is the Old Dad/Kelso Pks. population, where predation appears to be limited to parts of the Kelso Peaks. Fresh lion tracks have been observed on a number of occasions in the middle of mountain sheep habitat at the west end of the Granite Mountains, near the location where a radio collared ewe was killed by a lion. So far, that is the only such mortality documented; thus, any suggestions about the role of lion predation in demography are conjectural, and concern what is potential rather than documented.

One piece of information on the Granite Mountains that needs explanation is the high yearling:adult ewe ratio recorded. If this represents a general population composition, it is inconsistent with a population depressed in density due to poor recruitment, as would be predicted by the BT/EHD hypothesis. However, it would not be inconsistent with a population depressed by lion predation, if the predation included all age classes. It is also noteworthy that, for the small size estimated for the ewe population in the Granite Mountains, it would take only about 2-3 females killed per year to hold the population at a low density. It is conceivable that the lions in the Granite Mountains may play a key role in low sheep density recorded. Gasaway et al. (1983) pointed out that wolves could hold moose populations at low density once depressed.

The Granite Mountains also differ from the other ranges studied in having a resident deer population. However, this is apparently not a natural situation. A California Department of Fish and Game map of the area from 1945 listed no deer for the Granite, Providence, and New York Mountains, where they currently exist. This deer population stems from an introduction of mule deer from Modoc County in 1948. As such, they represent an exotic species in this part of the desert. Less can be said about the origin of the mountain lion population; however, it is noteworthy that neighboring mountain ranges that lack deer (e.g. Cady, Marble and Old Woman Mountains) also lack any evidence of mountain lions. North American deer are well documented to be the main staple of mountain lion diets (Dixon 1982). As such, it is reasonable to postulate that the mountain lion population in this part of the eastern Mojave Desert was able to colonize the area because of the presence of an exotic deer population. If so, the lions also can be considered an exotic species; and the predation that the native sheep incur from them can be considered "unnatural". What role feral cattle and donkeys play in the diet of the lion population in this area is a related question of interest, as they are also exotic species that may play an important role in allowing a lion population to exist.

While the dynamics of the population in the Old Woman Mountains give some reason to question the BT/EHD hypothesis, this population provides no obvious alternative explanation for its low density. If the recent population increase continues, it may soon rise out of the classification of "low density". However, that only begs the question of what caused the low density prior to the increase. I have no information basis from which to speculate on this. However, it seems interesting that the depressed status of this population correlates in time both with the wet period at the beginning of the decade, and with the expansion of cattle grazing to the west side of the range, where it did not occur in the previous grazing episode. It seems reasonable to postulate a disease process and cattle as a likely source.

Continuing Research

The results of this research to date remain tentative as to conclusions. The ultimate conclusions from this work have considerable potential implications relative to livestock grazing policies. As such, it is important not to arrive at an incorrect conclusion, one way or the other, relative to this question of disease implications. Currently, the conclusions are based on but a couple years of population increase in the Old Woman Mountains. Clearly, this population should be an important focus of further research. It would be desirable to document a continuing population increase there before arriving at a firm conclusion. Additionally, it is important to further measure exposure of that population to BT/EHD. Critical to the interpretation of results has been an apparent lack of change in exposure to these viruses. However, with the sample sizes involved, this could be a false conclusion based on sampling error. An additional sample of ten sheep would lend much strength to the conclusions. If, in fact, high exposure to BT/EHD does not consistently lead to high lamb mortality and depressed population density, it should be possible to find a population with high exposure and high population density. Continuing research should be oriented toward trying to document such a relationship.

Refutation of scientific hypotheses frequently leads to refinement, rather than total abandonment (Medawar 1969). The BT/EHD hypothesis investigated here was purposefully formulated as an unrefined general hypothesis. If the next phase of research contributes to its refutation, a logical further step would be to break it into more narrowly defined hypotheses based on the role of individual disease strains in sheep demography. Not only should BT and EHD be investigated as separate hypotheses, but also, individual serotypes should be considered.

ACKNOWLEDGMENTS

Over the five years since this study began, many people have contributed to it in various ways. Chronologically, field assistants have been Mike Hansen, Rob Ramey, Laura Brown, Dave Talley, Michael East, Jef Jaeger, and Tom Manning. Bill Clark, Rick Clark, Dave Hunter, Dave Jessup, Mike Kock, Nancy Kock, Vern Bleich, Jim Farrel, and Rocky Thompson have all helped in collaring sheep. Vern Bleich, Bob Vernoy, Andy Pauli, Jim Bicket, Les Coombes, Glenn Sudmeier, Dave Talley, Michael East, Jef Jaeger, Rocky Thompson, Christine Gronholt Leon Lesicka, Tom Jackson, John Fisher, Denyse Racine, Tom Manning, Gerry Mulcahy, Jim Landells, and Bill Parrack have served as observers in helicopter surveys. Pilots during helicopter surveys and collaring efforts have been Don Landells, Brian Novak, and Steve deJesus. This study has greatly benefitted from the regular fixed-wing telemetry flights carried out by Rich Anthes, Andy Pauli, Bob Vernoy, Gerry Mulcahy, and Jef Jaeger. Dick Weaver of the California Department of Fish and Game initiated this study and provided the funding for it through allocations from the California Environmental License Plate Fund. BLM has contributed some of the helicopter time for collaring and surveys. The Society for the Conservation of Bighorn Sheep funded one helicopter flight in the Marble Mountains and provided personnel for July water hole counts in the Old Woman Mountains in 1985 and 1986. Finally, Vern Bleich provided critical comments on the manuscript and has contributed in numerous ways to the success of this study.

APPENDIX

Test for Equal Observability of Marked Ewes

Tests for equal observability of marked ewes were carried out using the Kalmogorov-Smirnov goodness-of-fit test. Goodness-of-fit tests operate by comparing an observed distribution with one expected on the basis of some theoretical assumption. Whether the recorded data meet that assumption is what is tested. In this case, the assumption was that the marked ewes in each population were equally observable; thus the distribution of their resighting frequencies among the various counts should not differ significantly from what would be found from a series of random samplings of the population with the numbers of marked ewes in the samplings equal to the number of individually identified ewes in the series of counts in question. This was the null hypothesis being tested in each case.

To arrive at the expected distribution of resighting frequencies, it was necessary to enumerate every permutation by which a ewe could be observed any particular number of times, using the number of marked ewes identified for each count to calculate the probability of being observed, as well as the probability of not being seen. The number of permutations (thus equation terms) for the various resighting frequencies follows Pascal's triangle (Kemeny et al. 1974).

Marble Mountains

Because of the arithmetic intactability of testing this assumption for all ten counts listed in Table 2 without an appropriate computer program (one calculation would have 252 terms), it was done for only the seven counts in 1986 using the 13 collared adult ewes. These provided the following data:

Number of Times observed:	0	1	2	3	4	5	6	7
Expected Proportion of Ewes:	.020	.115	.264	.308	.202	.075	.014	.001
Observed Proportion of Ewes:	.000	.154	.154	.538	.000	.154	.000	.000

When these data were tested with the Kolmogorov-Smirnov test (Siegel 1956), the observed distribution was not significantly different from the expected distribution (D=.139; P>.20). Thus, this assumption was met.

Old Woman Mountains

For the Old Woman Mountains, this analysis was made for eight marked ewes present after April 1985 (Table 1), using six counts made between May 1985 and July 1986. The following data resulted:

Number of Times Observed:	0	1	2	3	4	5	6
Expected Proportion of Ewes:	.014	.090	.236	.318	.240	.090	.014
Observed Proportion of Ewes:	.125	.125	.125	.250	.125	.125	.125

As with the Marble Mountain data, when these were tested with the Kolmogorov-Smirnov test, the observed distribution was not significantly different from the expected distribution (D=.147; P>.20).

LITERATURE CITED

Aldous, M. C. 1957. Status of bighorn sheep on the Desert Game Range. *Trans. Desert Bighorn Counc.* 1:35-37.

Ayala, F. J. 1975. Scientific hypotheses, natural selection and the neutrality theory of protein evolution. Pages 19-42 *in* F. M. Salzano, ed., *The role of natural selection in human evolution.* North-Holland Publ. Co.

Bailey, N. T. J. 1951. On estimating the size of mobile populations from recapture data. *Biometrika* 38:293-306.

Beatley, J. C. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55:856-863.

Bradley, W. G., and D. P. Baker. 1967. Life tables for Nelson bighorn sheep on the Desert Game Range. *Trans. Desert Bighorn Counc.* 11:142-170.

Bruner, D. W., and J. H. Gillespie. 1966. Hagan's infectious diseases of domestic animals. Cornell Univ. Press, Ithaca, N. Y. 1105pp.

Buechner, H. K. 1960. The bighorn sheep in the United States: its past, present, and future. Wildl. Monogr. No. 4.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. *Adv. Appl. Biol.* 1:183-245.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York. 234pp.

Caughley, G. 1987. Ecological relationships. Pages 159-187 *in* G. Caughley, N. Shepherd, and J. Short, eds., *Kangaroos: their ecology and management in the sheep rangelands of Australia*. Cambridge Univ. Press, New York, N.Y.

Clark, R. K., D. A. Jessup, M. D. Koch, and R. A. Weaver. 1985. Survey of desert bighorn sheep in California for exposure to selected infectious diseases. *J. Amer. Vet. Med. Assoc.* 187:1175-1179.

Coggins, V. L. 1988. The Lostine Rocky Mountain bighorn die-off and domestic sheep. *Bienn. Symp. North. Wild Sheep and Goat Council* 6:57-64.

Conover, W. J. 1980. *Practical nonparametric statistics*. John Wiley & Sons, New York, 493pp.

DeForge, J. R. and J. E. Scott. 1982. Ecological investigations into high lamb mortality. *Trans. Desert Bighorn Council* 26:65-76.

DeForge, J. R., D. A. Jessup, C. W. Jenner, and J. E. Scott. 1982. Disease investigations into high lamb mortality of desert bighorn in the Santa Rosa Mountains, California. *Trans. Desert Bighorn Council* 26:76-81.

Dixon, K. R. 1982. Mountain lion. Pages 711-727 *in* J. A. Chapman, and G. A. Feldhamer, eds., *Wild mammals of North America*. The Johns Hopkins Univ. Press, Baltimore, MD.

Douglas, C. L. and D. M. Leslie, Jr. 1986. Influence of weather and density on lamb survival of desert mountain sheep. *J. Wildl. Manage.* 50:153-156.

Dunn, W. C. and C. L. Douglas. 1982. Interactions between desert bighorn sheep and feral burros at spring areas in Death Valley. *Trans. desert Bighorn Council* 26:87-96.

Festa-Bianchet, M. 1988. A pneumonia epizootic in bighorn sheep, with comments on preventive management. *Bienn. Symp. North. Wild Sheep and Goat Council* 6:66-76.

Foreyt, W. J. and D. A. Jessup. 1982. Fatal pneumonia of bighorn sheep following association with domestic sheep. *J. Wildl. Dis.* 18:163-168.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. *Wildl. Monogr.* 84. 50pp.

Geist, V. 1971. *Mountain sheep.* Univ. Chicago Press, Chicago., Ill. 383pp.

Hansen, C. G. 1967. Bighorn sheep populations of the Desert Game Range. *J. Wildl. Manage.* 31:693-706.

Hebert, D. M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Ph. D. diss., Univ. Brit. Columb., Vancouver. 357pp.

Hebert, D. M., J. Hebert, and M. Caskey. 1984. Fecal nitrogen as a determinant of animal condition in bighorn sheep. *Proc. North. Wild sheep and Goat Counc.* 4:317-340.

Hoff, G. L., and D. O. Trainer. 1981. Hemorrhagic diseases of wild ruminants. Pages 45-53 *in* J. W. Davis, L. H. Karstad, nd D. O. Trainer, eds., *Infectious diseases of wild mammals.* Iowa State Univ. Press, Ames.

Holechek, J. L., M. Vavra, and R. D. Pieper. 1982. Methods for determining the nutritive quality of range ruminant diets: a review. *J. Anim. Sci.* 54:363-376.

Jessup, D. A. 1985. Diseases of domestic livestock which threaten bighorn sheep populations. *Trans. Desert Bighorn Council* 29:29-33.

Kemeny, J. G., J. L. Snell, and G. L. Thompson. 1974. *Introduction to finite mathematics.* Prentice-Hall, Inc., Englewood Cliffs, NJ. 484pp.

Leslie, D. M. and C. L. Douglas. 1979. Desert bighorn sheep of the River Mountains, Nevada. *Wildl. Monogr.* 66. 56pp.

Leslie, D. M., and E. E. Starkey. 1985. Fecal indices to dietary quality of cervids in old-growth forests. *J. Wildl. Manage.* 49:142-146.

Marsh, H. 1965. Newsom's sheep diseases. The Williams & Wilkins Co., Baltimore, Md. 456pp.

McCullough, D. R. 1979. *The George Reserve deer herd.* Univ. Michigan Press, Ann Arbor. 271pp.

Medawar, P. B. 1969. *Induction and intuition in scientific thought.* Amer. Philos. Soc., Independence Square, Philadelphia, PA. 62pp.

Mullens, B. A., E. C. Loomis, and J. R. Anderson. 1986. Clues to control of bluetongue virus. *Calif. Agric.* 1986:23-25.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* 62:1-135.

Overton, W. S. 1971. Estimating the numbers of animals in wildlife populations. Pages 403-455 *in* R. H. Giles, Jr., ed., *Wildlife management techniques*, 3rd ed. The Wildl. Soc., Wash. D. C.

Parks, J., G. Post, T. Thorne, and P. Nash. 1972. Parainfluenza-3 virus infection in Rocky Mountain bighorn sheep. *J. Am. Vet. Med. Assoc.* 161:669-672.

Pielou, E. C. 1974. *Population and community ecology: principles and methods.* Gordon and Breach, New York. 424pp.

Popper, K. 1959. *The logic of scientific discovery.* Harper & Row, N.Y. 480pp

Post, G. 1971. The pneumonia complex in bighorn sheep. *Trans. North Amer. Wild Sheep Conf.* 1:98-102.

Post, G. 1976. Diagnostics and diseases of wild sheep. *Trans. North Amer. Wild Sheep Conf.* 2:61-65.

Robinson, R. M., T. L. Hailey, C. W. Livingston, and J. W. Thomas. 1967. Bluetongue in the desert bighorn sheep. *J. Wildl. Manage.* 31:165-168.

Rohlf, F. J., and R. R. Sokal. 1981. *Statistical tables.* W. H. Freeman and Co., New York. 219pp.

Sanchez, J. E. et al. 1988. Decline of the Carrizo Canyon peninsular desert bighorn population. *Trans. Desert Bighorn Council.* 32:31-33.

Seber, G. A. F. 1970. The effects of trap response on tag recapture estimates. *Biometrics* 26:13-22.

Seip, D. R., and F. L. Bunnell. 1985. Nutrition of Stone's sheep on burned and unburned ranges. *J. Wildl. Manage.* 49:397-405.

Siegel, S. 1956. *Nonparametric statistics for the behavioral sciences.* McGraw-Hill, New York. 312pp.

Thorne, E. T. 1982. Bluetongue. Pages 5-8 *in* E.T. Thorne, K. Kingston, W. R. Jolley, and R. C. Bergstrom, eds., *Diseases of wildlife in Wyoming.* Wyo. Game and Fish Dept., Cheyenne.

Thorne, E. T. 1982. Epizootic hemorrhagic disease. Pages 9-10 *in* E.T. Thorne, K. Kingston, W. R. Jolley, and R. C. Bergstrom, eds., *Diseases of wildlife in Wyoming.* Wyo. Game and Fish Dept., Cheyenne.

Wallace, G. W. 1988. Status of desert bighorn sheep in Utah, 1987. *Trans. Desert Bighorn Council* 32:25.

Wehausen, J. D. 1980. Sierra Nevada bighorn sheep: history and population ecology. Ph. D. diss., Univ. Michigan, Ann Arbor, MI. 240pp.

Wehausen, J. D. 1983. White Mountain bighorn sheep: an analysis of current knowledge and management alternatives. Admin. Rep., Inyo Natl. For., Bishop, Calif. 93pp.

Wehausen, J. D. 1988. Cattle impacts on mountain sheep in the Mojave Desert: report II. Final report completed under interagency agreement 85/86C-1492 between the University of California and the California Dept. of Fish and Game.

Wehausen, J. D. 1990. Some potentially adaptive characters of mountain sheep populations in the Owens Valley region. In C. A. Hall, Jr., and V. Doyle-Jones, eds. Natural history of the White-Inyo range Sympos. vol 3, Univ. Calif., White Mtn. Res. Sta., Bishop, Ca. (In Press).

Wehausen, J. D., and M. C. Hansen. 1986. Impacts of cattle grazing on bighorn sheep. Final report completed under interagency agreement C-913 between the University of California and the California Dept. of Fish and Game.

Wehausen, J. D., and M. C. Hansen. 1988. Plant communities as the nutrient base of mountain sheep populations. Pages 256-268 *in* C. A. Hall, Jr. and V. Doyle-Jones, eds., *Plant biology of eastern California.* Natural history of the White-Inyo range Sympos. vol 2, Univ. of Calif., White Mtn. Res. Sta., Bishop, CA.

Wehausen, J. D., V. C. Bleich, B. Blong, and T. L. Russi. 1987. Recruitment dynamics in a southern California mountain sheep population. *J. Wildl. Manage.* 51:86-98.

Wenstøp, F. 1988. *Statistikk og dataanalyse.* TANO A. S., Printing Data Center, Aurskog.

TABLE 1 - History of markings installed on sheep in the populations under study.

		E W E S			R A M S		
POPULATION	DATE	RADIO COLLARS	MARKING COLLARS	EAR TAG ONLY	RADIO COLLARS	MARKING COLLARS	EAR TAG ONLY
OLD WOMAN	10/84		2				
	3/85		4				1
	4/85	3			1		
	6/86		5				
	9/87	2			3		
MARBLE	6/86	5	9			1	
GRANITE	4/85		2			2	
	8/88	2					
	10/88	3					
OLD DAD	9/86				4		
	9/87	5		1	8		
	1/88	10	2		3		
	4/88				1		
	2/89				4	1	
	9/89				2		
CADY	5/86		3	1		4	
	9/88	5	1				

TABLE 2 - Data and estimates from four different estimators for the population of adult and yearling ewes in the Marble Mountains in 1986. The total number of collared ewes in the population (M) was 13.

DATE	EWES SAMPLED (n)	COLLARS IN SAMPLE (m)	PETERSEN Mn/m	BAILEY M(n+1)/(m+1)	SEBER [(M+1)(n+1)/(m+1)]-1	CUMULATIVE PROPORTION COLLARED M/(m/n)
7/15/86	26	3	112.7	87.8	93.5	
7/28/86	18	3	78.0	61.8	65.5	
9/7/86	33	5	85.8	73.7	78.3	
9/19/86	29	5	75.4	65.0	69.0	
9/28/86	34	7	63.1	56.9	60.2	
11/5/86	29	9	41.9	39.0	41.0	
12/9/86	32	7	59.4	53.6	56.8	
4/7/87	22	3	95.3	74.8	80.5	
5/13/87	43	9	62.1	57.2	60.6	
11/13/87	24	4	78.0	65.0	69.0	
		$\bar{X}$:	75.2	63.5	67.4	
	318	63				65.6

TABLE 3 - Lengths of winter-spring growing seasons in different years and populations of mountain sheep in the Mojave Desert of California and the results of integration of curves of the natural log of percent fecal crude protein (FCP) (Figure 13) for these growing seasons. Growing seasons were defined as the number of days between the fall-winter low point from which the initial rise began and the point in spring or summer at which another low point was obtained or the curve bent significantly toward horizontal.

	GROWING SEASON LENGTH (DAYS)					FCP ln%-DAYS ABOVE 5%				
POPULATION	1985	1986	1987	1988	1989	1985	1986	1987	1988	1989
CADY					132					102
GRANITE					166					113
OLD DAD				268	162				184	103
MARBLE		235	230	289	133		152	175	235	85
OLD WOMAN	218	212	261	292	166	190	163	204	255	122

TABLE 4 - Sampling results for mark-and-sample population estimations. Samplings and estimates are of the number of yearlings and adults present for the sex and year listed.

POPULATION	SEX	YEAR	COLLARS IN SAMPLE	SHEEP SAMPLED	PROPORTION COLLARED	95% CL	COLLARS IN POPULATION	POPULATION ESTIMATE	95% CL
OLD WOMAN	ewe	1984	20	77	.260	.166-.372	8	30.8	21.5-48.0
		1985	34	148	.230	.164-.306	8	34.8	26.1-48.6
		1986	23	81	.284	.189-.395	11	38.7	27.8-58.2
		1987	29	117	.248	.173-.336	11	44.4	32.7-63.7
		1988	31	127	.244	.172-.328	13	53.7	39.6-75.5
MARBLE	ewe	1986	63	318	.198	.156-.246	13	65.6	52.8-83.5
		1987	79	359	.220	.178-.266	14	63.6	52.5-78.6
		1988	65	288	.226	.179-.278	14	62.0	50.3-78.4
GRANITE	ewe	1989	7	13	.538	.252-.807	6	11.1	7.4-23.8
OLD DAD	ewe	1988	56	414	.135	.104-.171	17	125.6	99.4-163.9
		1989	27	274	.098	.069-.136	16	162.4	117.7-231.9
	ram	1988	29	359	.081	.055-.114	15	185.6	131.5-273.5
CADY	ewe	1989	14	44	.318	.186-.475	~~8~~ 7	~~25.2~~ 22.0	~~16.8-43.0~~ 14.7-37.6

TABLE 5 - Recruitment rates for the Old Woman, Marble, and Old Dad Pk. populations. Rates are expressed as lambs per 100 yearling and adult ewes for summer and fall, and as yearlings per 100 adults ewes the following winter-fall. Sample sizes are in all cases the number of adult and yearling ewes in the denominator.

	BIRTH YEAR	RECRUITMENT RATES					
POPULATION	OF LAMBS	SUMMER	N	FALL	N	WINTER-FALL	N
OLD WOMAN	1981					16.7	36
	1982	23.1	39				
	1984					16.2	80
	1985	20.0	25	15.2	33	6.8	59
	1986	36.8	38			37.5	40
	1987	58.8	34	35.0	20	16.4	61
	1988	43.9	57	25.0	24	18.9	37
	1989	38.1	21				
MARBLE	1982			39.5**	38		
	1985					6.5	199
	1986			24.2	157	15.4	117
	1987			18.0	61	11.3	141
	1988			11.6	86	4.2	120
	1989			25.4	67		
OLD DAD	1982			44.0**	25		
	1986			42.3**	26		
	1987			25.8**	62	14.7	252
	1988	54.7	139	56.9	130	37.1	383
	1989	47.1	136	27.7	213		

** January surveys

TABLE 6 - Ewe densities by year for the Old Woman, Marble, Granite, Old Dad Pk., and Cady Mountains sheep populations. Area used is for ewes, measured in square miles, and density is in units of ewes per square mile.

POPULATION	YEAR	AREA USED	EWE POPULATION ESTIMATE	95% CL	EWE DENSITY	95% CL
OLD WOMAN	1984	58.25	30.8	21.5-48.0	0.53	0.37-0.82
	1985		34.8	26.1-48.6	0.60	0.45-0.83
	1986		38.7	27.8-58.2	0.66	0.48-1.00
	1987		44.4	32.7-63.7	0.76	0.56-1.09
	1988		53.7	39.6-75.5	0.92	0.68-1.30
MARBLE	1986	28.52	65.6	52.8-83.5	2.30	1.85-2.93
	1987		63.6	52.5-78.6	2.23	1.84-2.76
	1988		62.0	50.3-78.4	2.17	1.76-2.75
GRANITE	1989	22.09	11.1	7.4-23.8	0.50	0.33-1.08
OLD DAD	1988	66.36	125.6	99.4-163.9	1.89	1.50-2.47
	1989		162.4	117.7-231.9	2.45	1.77-3.49
CADY	1989	55.13	~~25.2~~ 22.0	~~16.8-43.0~~ 14.7-37.6	~~0.46~~ 0.40	~~0.30-0.78~~ 0.27-0.68

TABLE 7 - Mountain sheep removed from the Marble Mountains and Old Dad/Kelso Pks. populations during captures for reintroductions, 1983-89.

POPULATION	DATE	ADULT EWES	YRLG EWES	EWE LAMBS	RAM LAMBS	YRLG RAMS	ADULT RAMS	TOTAL
MARBLE	7/83	9	0	2	0	1	1	13
	12/83	7	1	0	0	0	2	10
	11/84	8	0	2	1	2	0	13
	7/85	11	1	2	1	2	2	19
	TOTAL	35	2	6	2	5	5	55
OLD DAD	7/83	2	3	0	2	1	1	9
	12/83	5	0	4	4	1	3	17
	11/84	16	3	2	1	2	7	31
	7/85	13	2	5	2	1	3	26
	9/86	18	3	2	2	0	5	30
	10/87	7	2	2	1	1	3	16
	12/89	28	9	0	0	4	2	43
	TOTAL	89	22	15	12	10	24	172

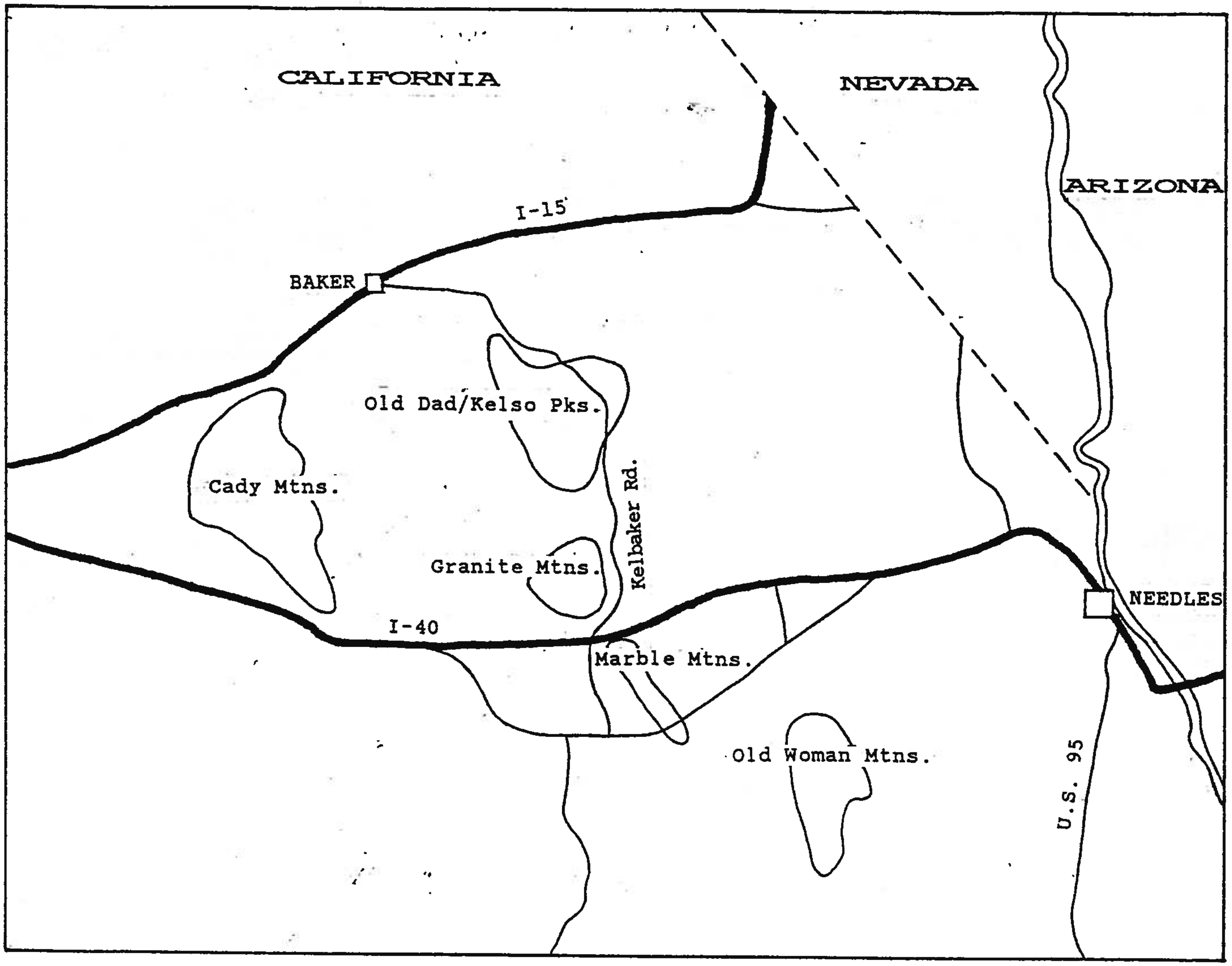


Figure 1 - Locations of study populations.

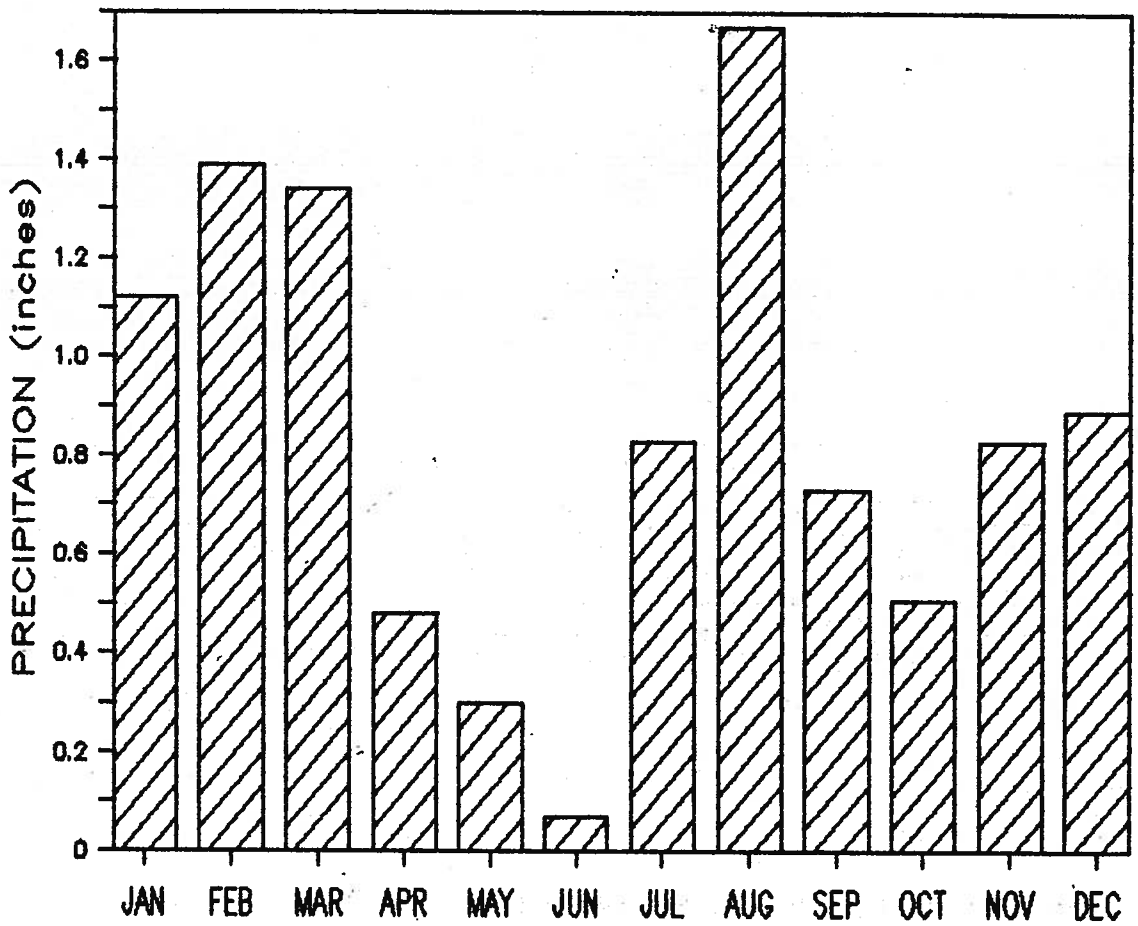
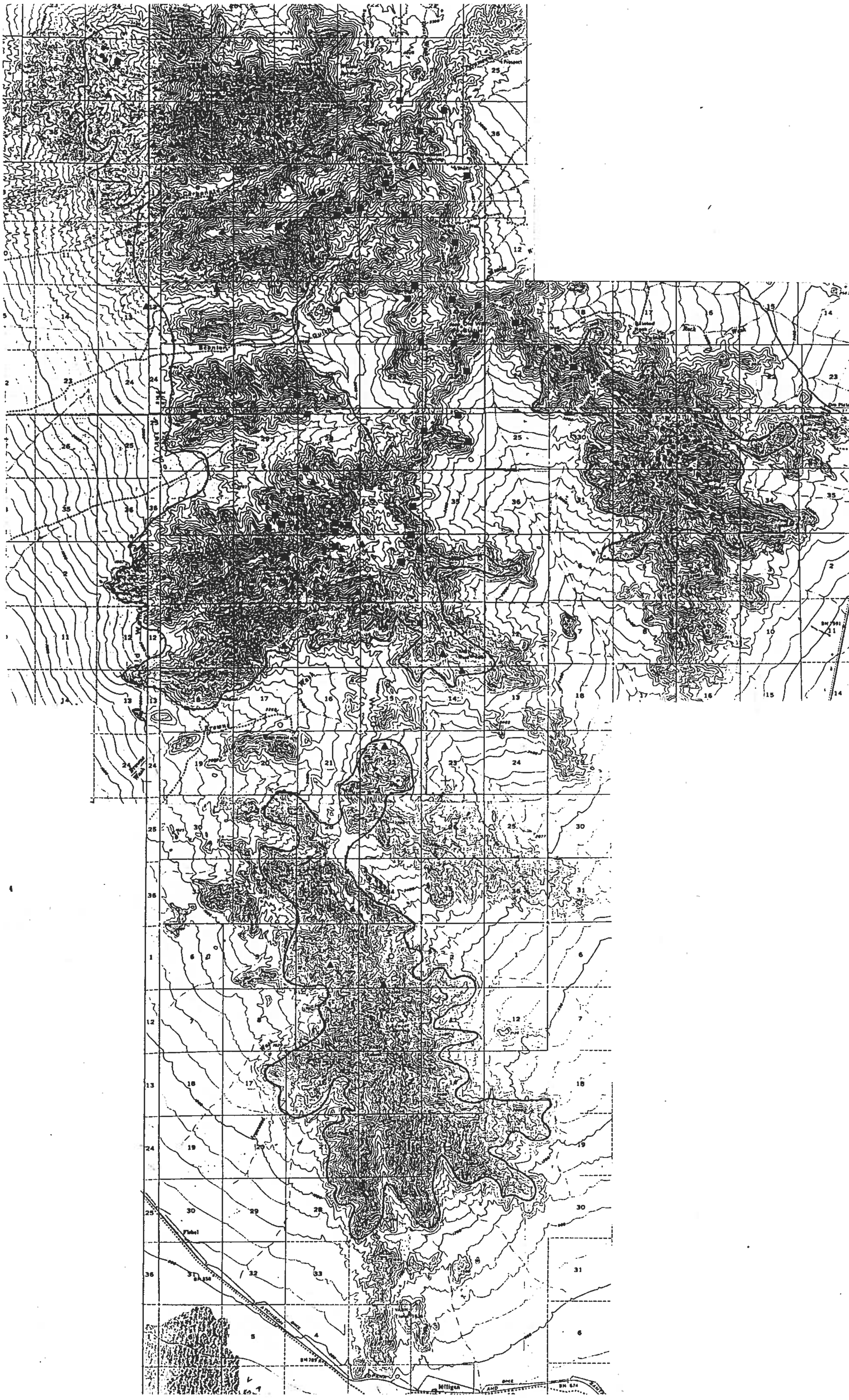
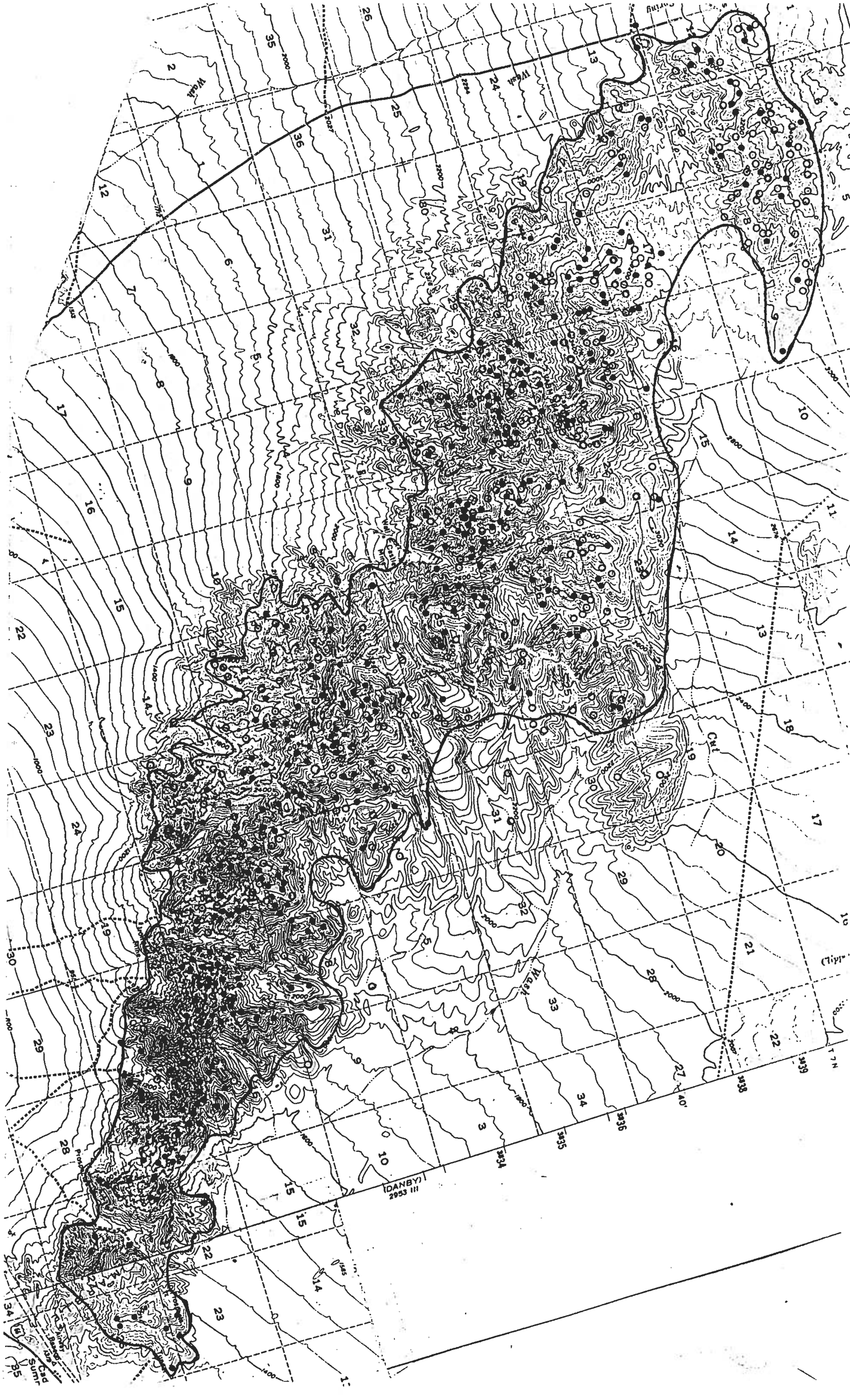
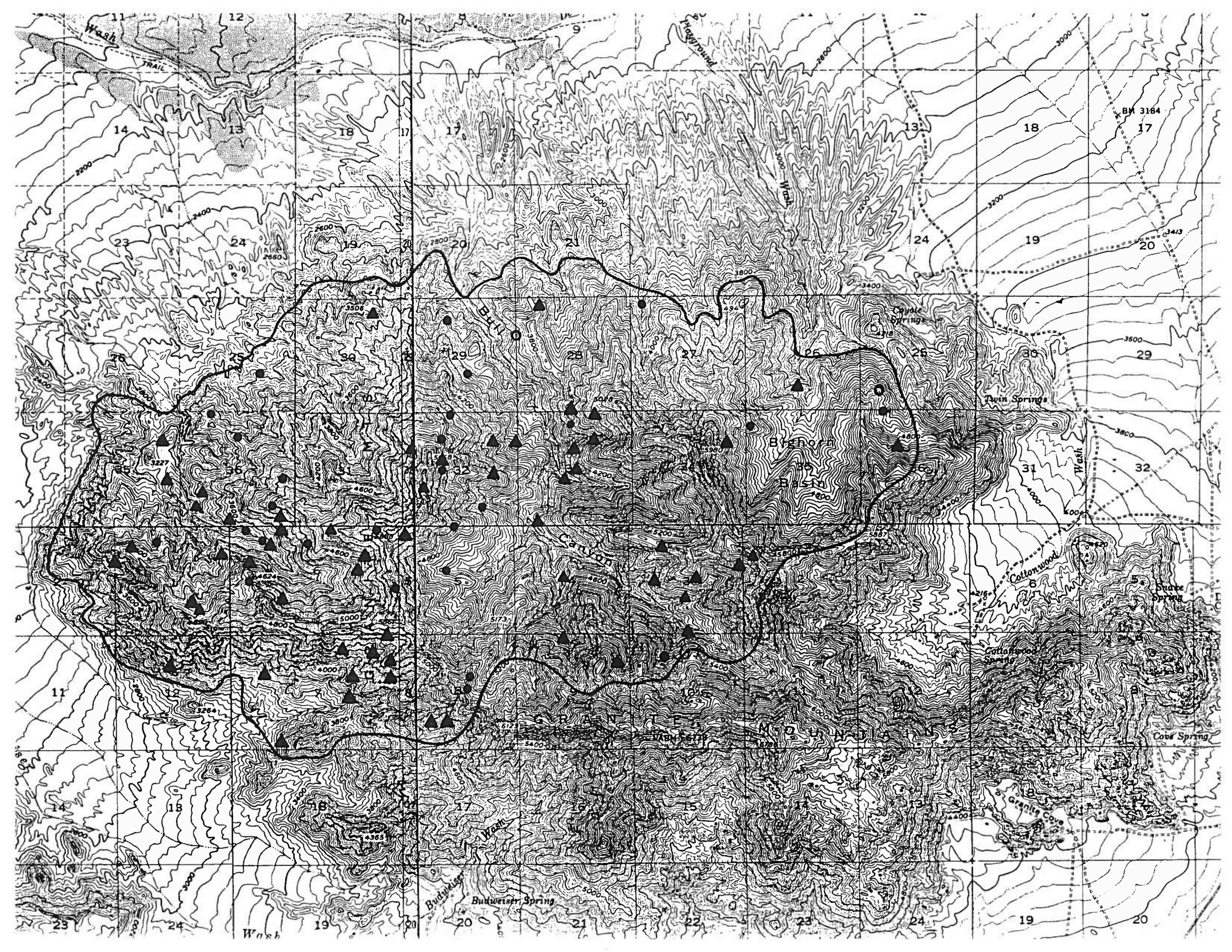


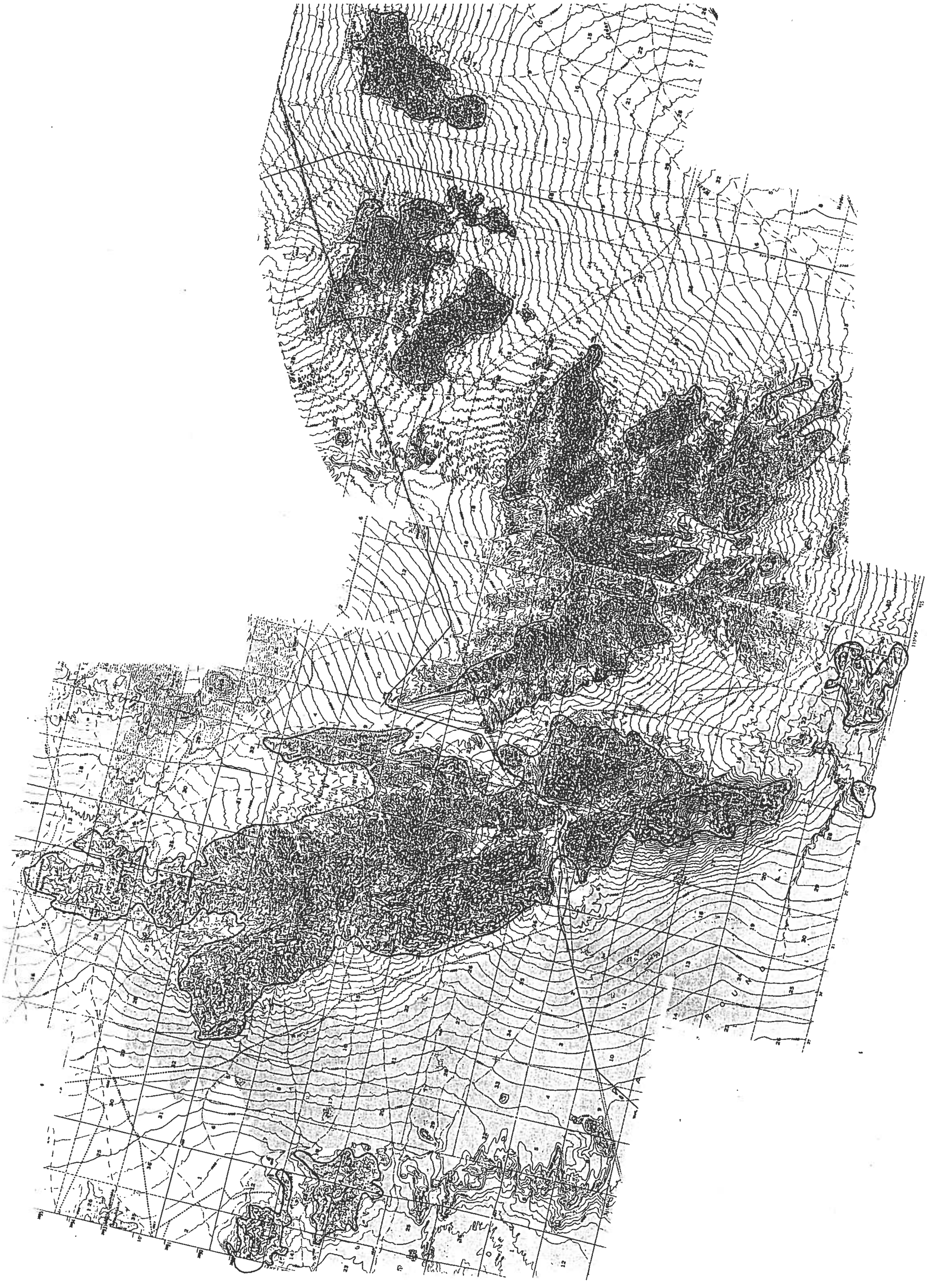
Figure 2 - Average monthly precipitation at Mitchell Caverns in the Providence Mountains.

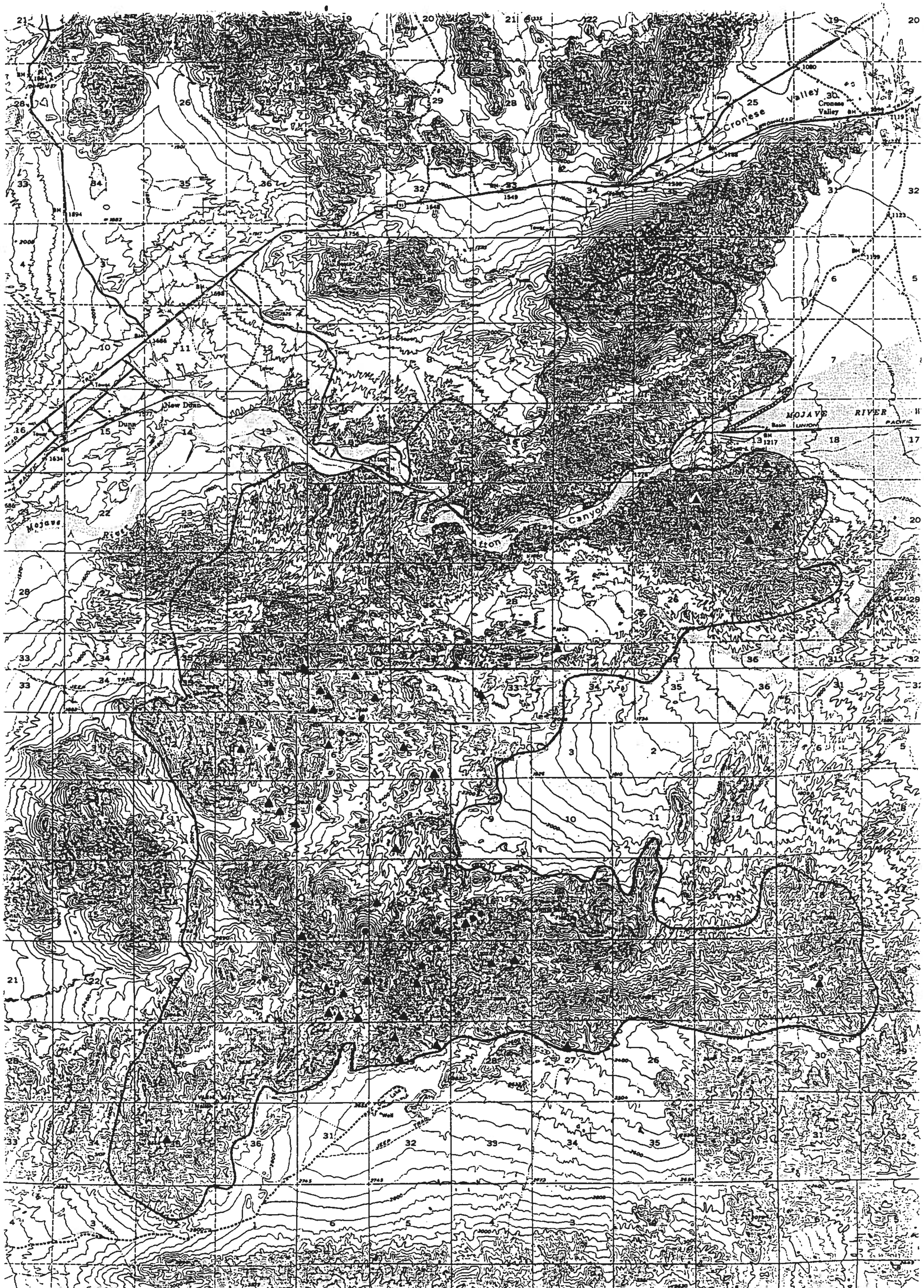
Figures 3-7. Range and sighting maps for the Old Woman, Marble, Granite, Old Dad/Kelso, and Cady Mountains populations, respectively. Closed circles are locations of groups observed containing ewes, and open circles are for groups observed containing only rams. Triangles are plottings of LORAN coordinates from fixed-wing aerial surveys of radio-collared ewes based on point of strongest signal. Squares are similar fixed-wing locations for radioed rams (Old Woman Mountains only). Range boundaries drawn are for ewes only.




DANBY
2953 III

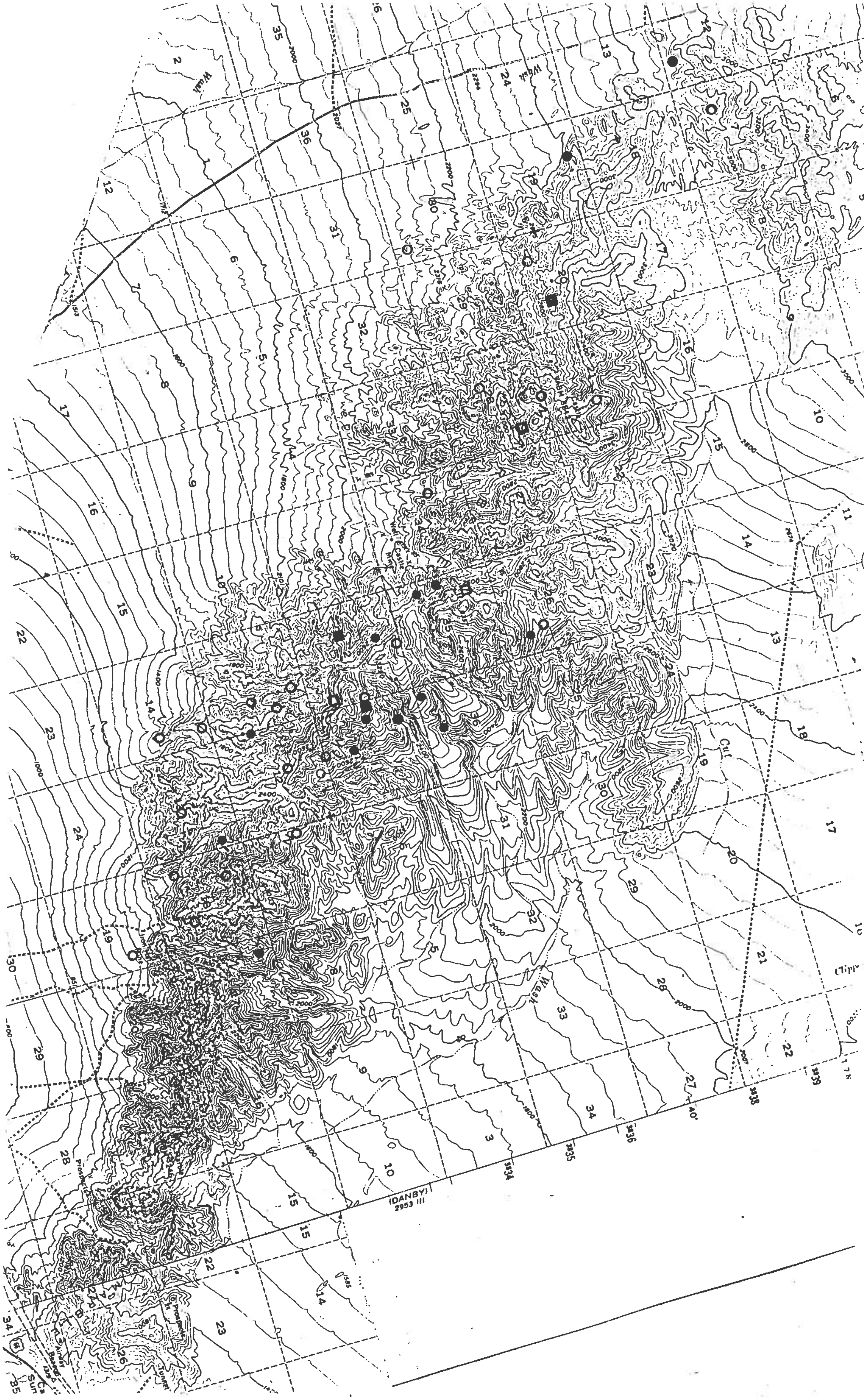

Bull
Bighorn
Basin
Canyon
GRANITE MOUNTAINS
Twin Springs
Coyote Springs
Cottonwood
Cottonwood Spring
Snake Spring
Cove Spring
Granite Cove
Budweiser Spring
Playground
Wash
TRAIL
BM 3184

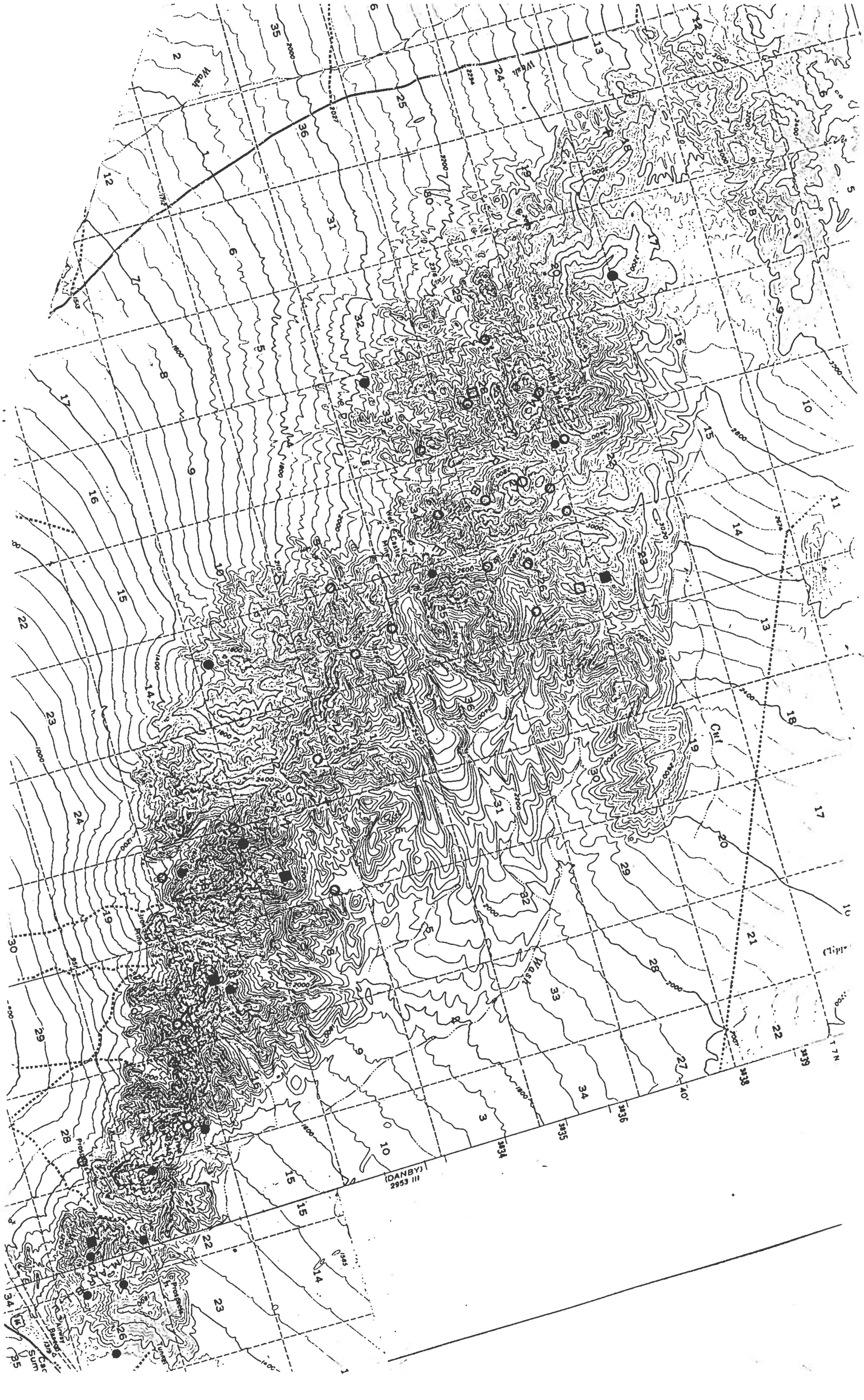


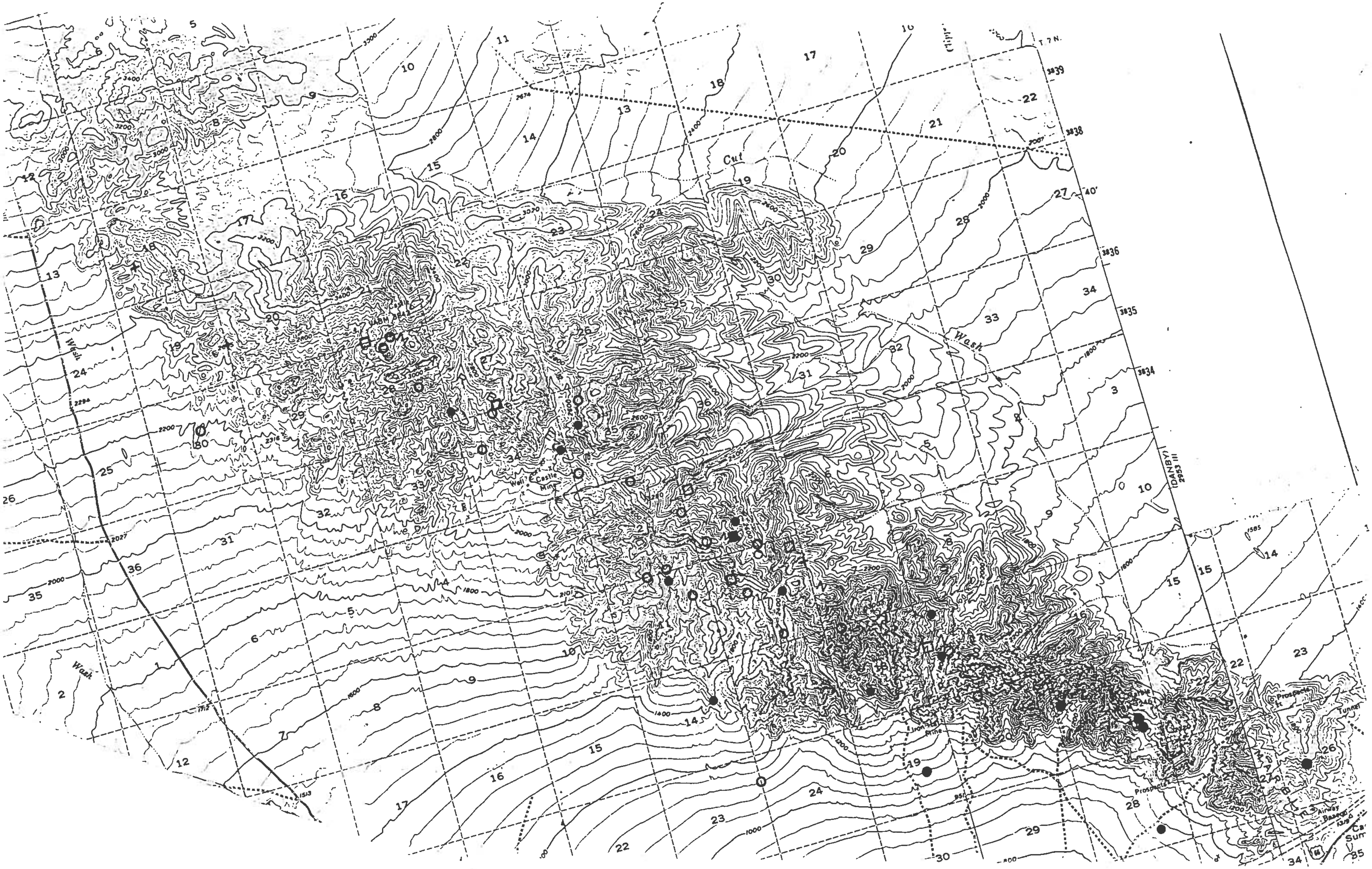


Cronese Valley
Cronese Valley
MOJAVE RIVER
UNION PACIFIC
New Dunn
Dunn
Mojave River
Afton Canyon
JEEP TRAIL

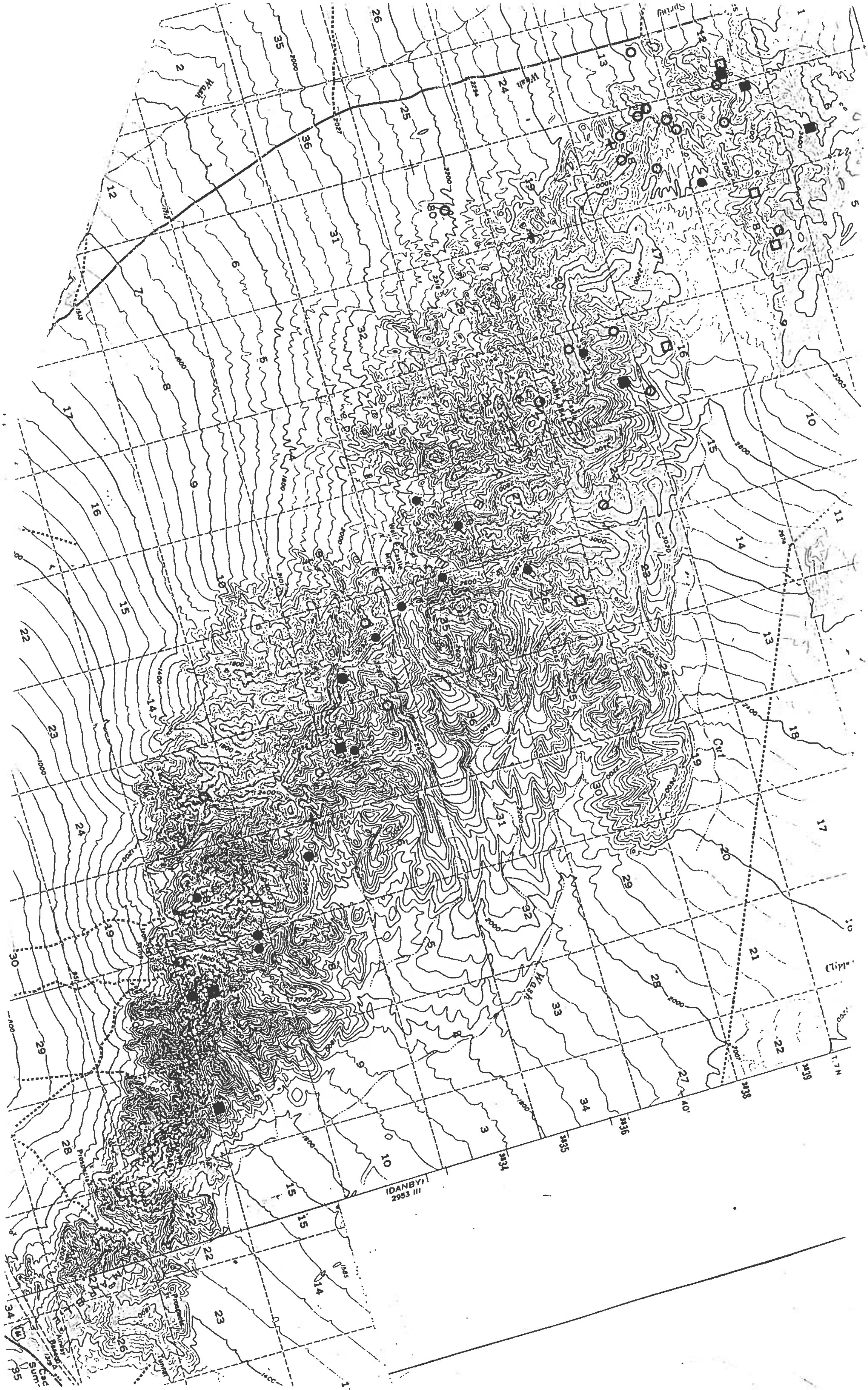
Figures 8-12. Location maps for five radio-collared ewes in the Marble Mountains (frequencies .315, .295, .305, .265, and .275, respectively). Open symbols are for the hot season (May-October), and closed symbols are for the cool season (November-April). Circular symbols are plottings of LORAN coordinates from fixed-wing aerial surveys based on point of strongest signal. Square symbols are direct observations from the ground or a helicopter. Locations of water sources are marked with x's.

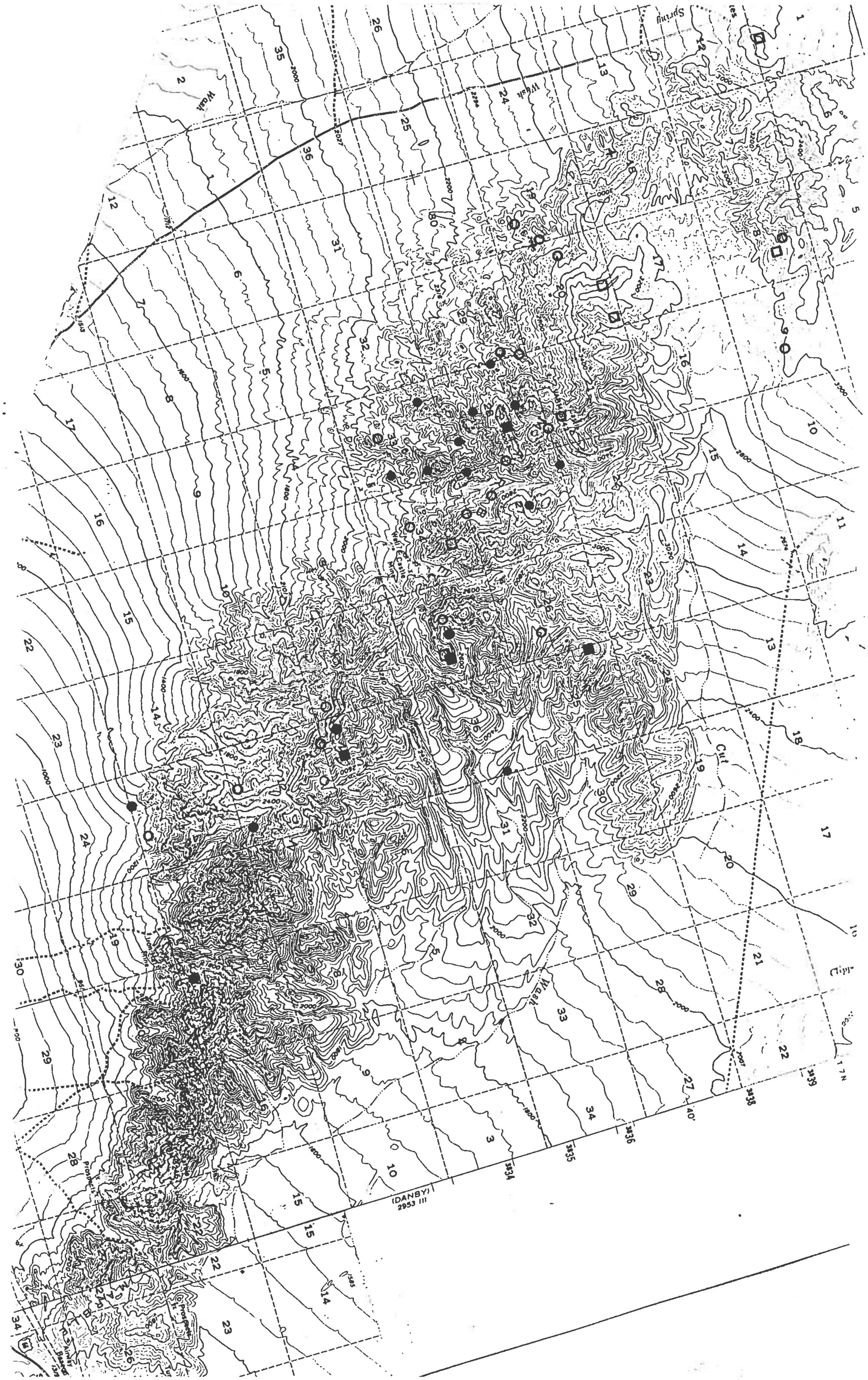

(DANBY)
2953 III





Cut
Wash
Castle Mts
Iron Mine
Prospects
(DANBY)
2953 III
T 7 N.


(DANBY)
2953 III


(DANBY)
2953 III

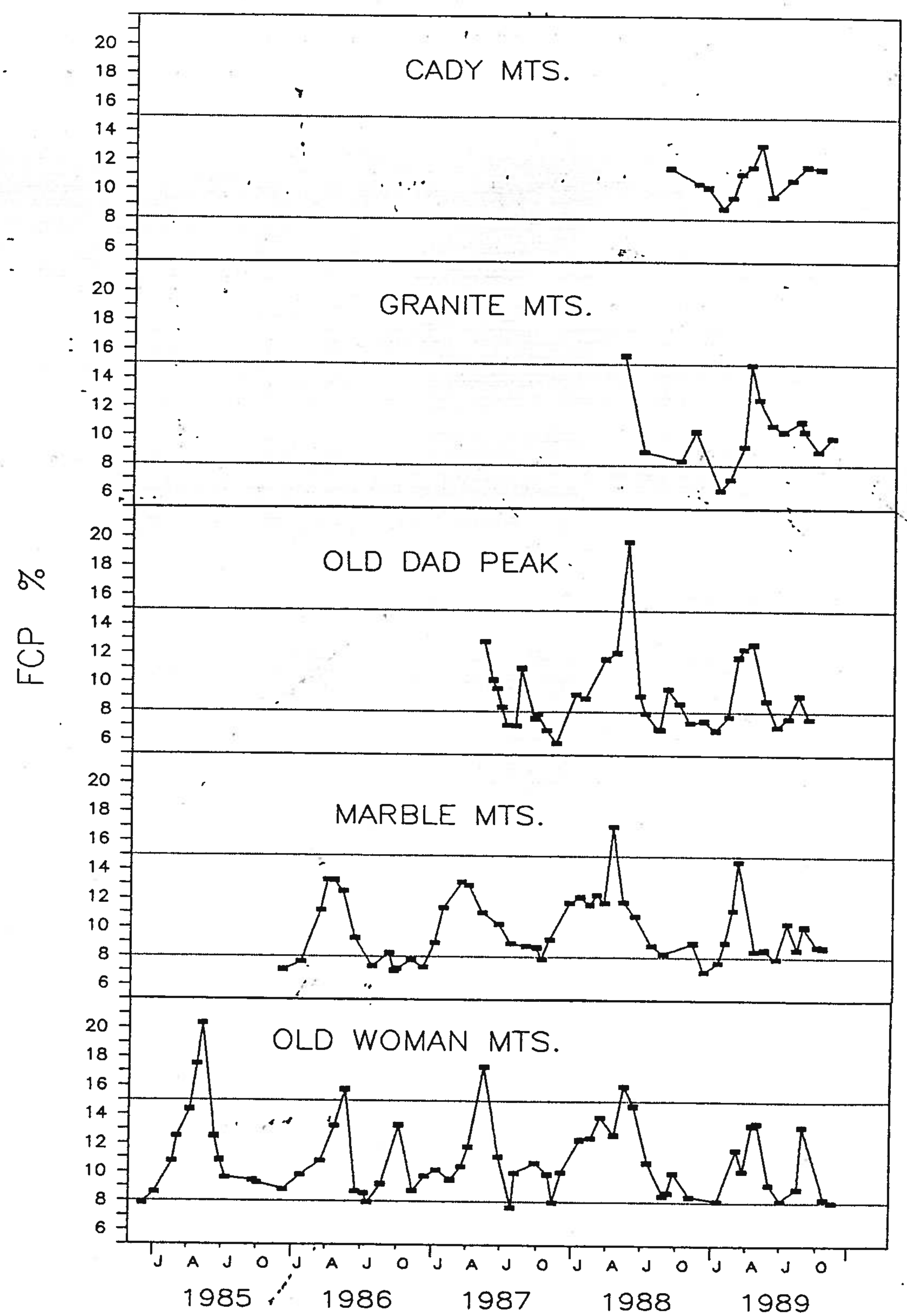


Figure 13 - Curves of % fecal crude protein (FCP) for the study populations.

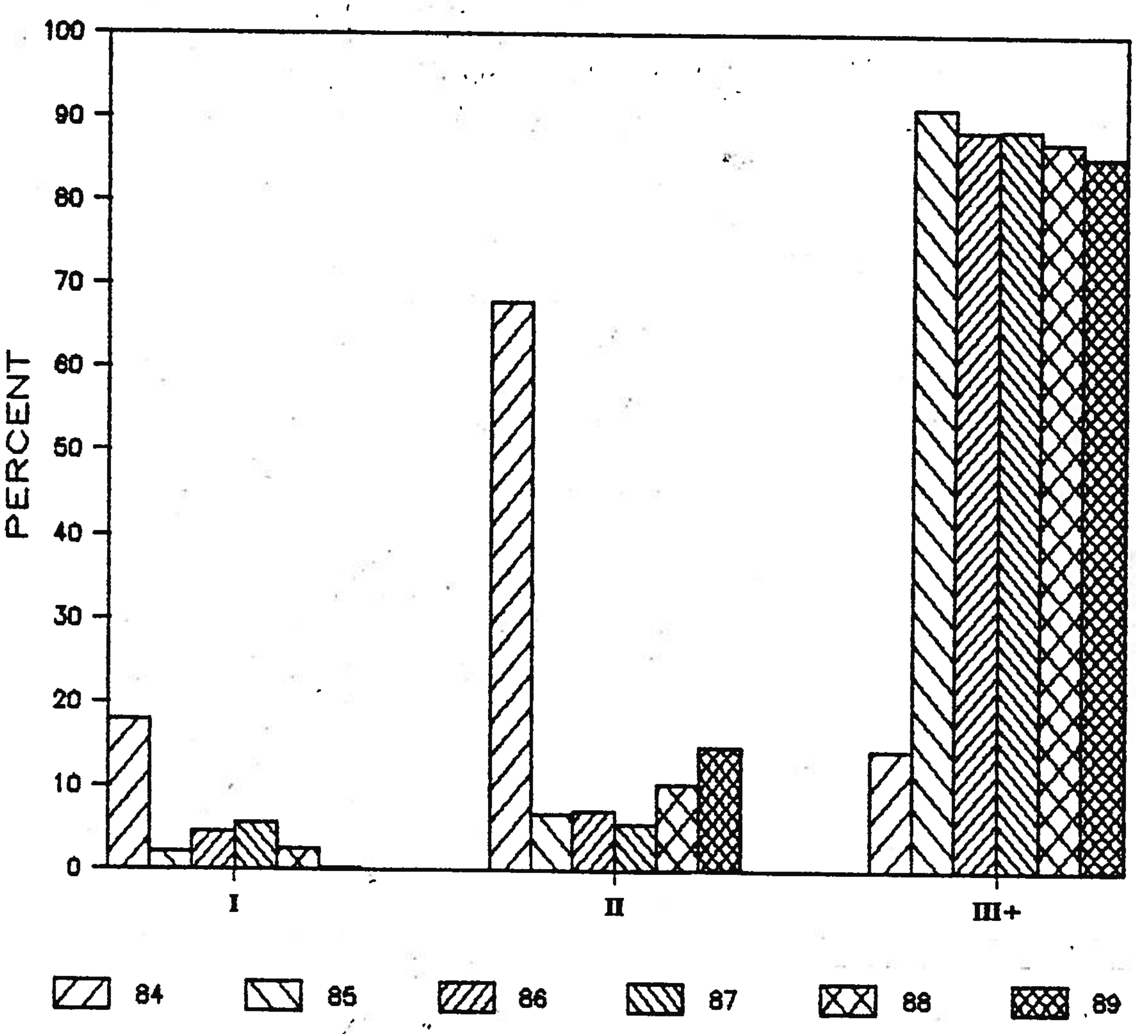


Figure 14 - Size class structure of the ram population in the Marble Mountains, 1984-89.

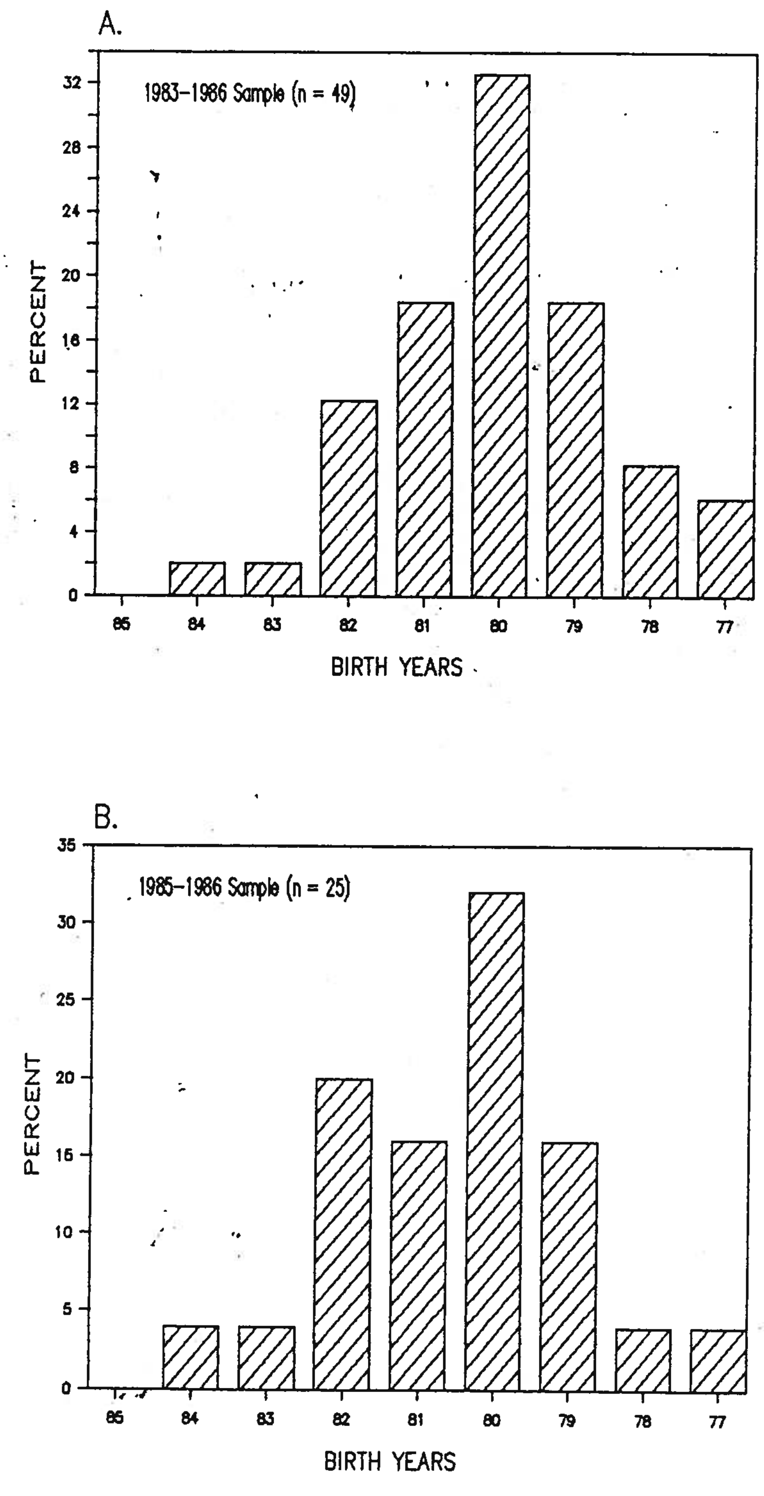
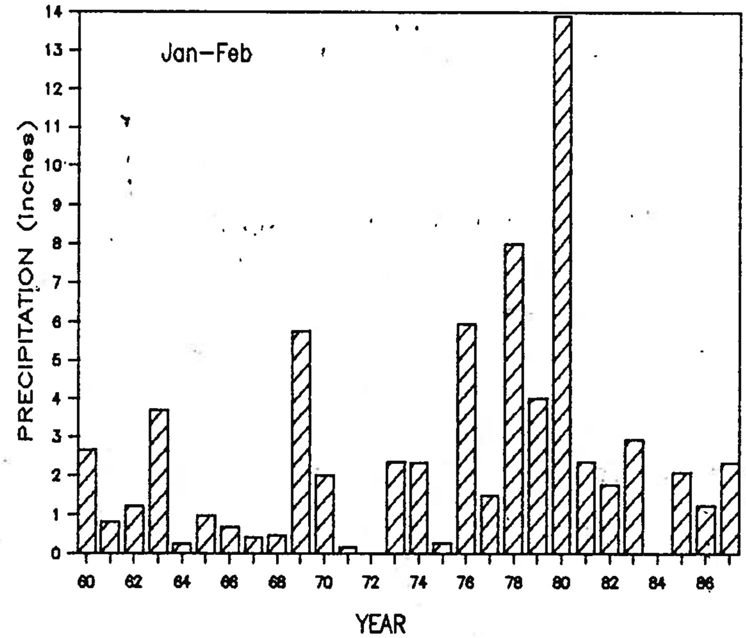


Figure 15 - Distributions of birth years for yearling and older ewes aged during captures in the Marble Mountains, 1983-86.



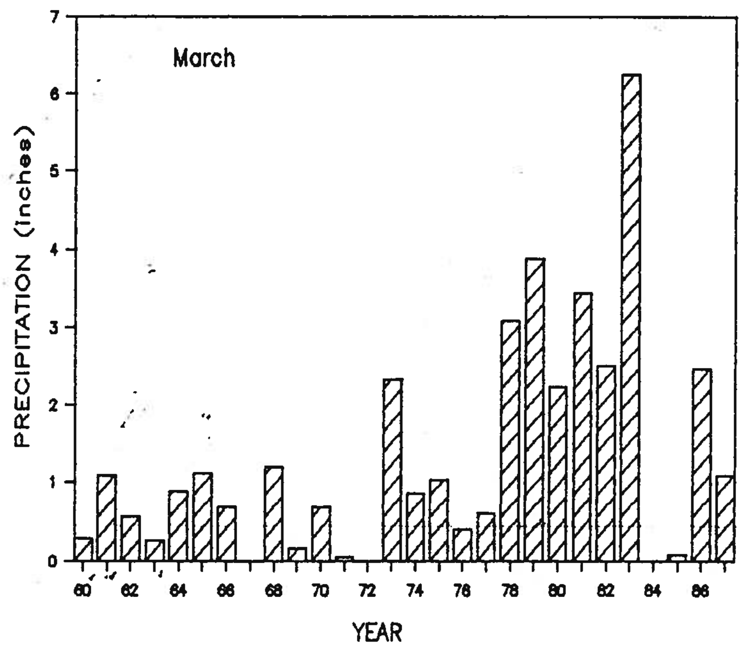


Figure 16 - January-February and March precipitation at Mitchell Caverns in the Providence Mountains for the years 1960-89.

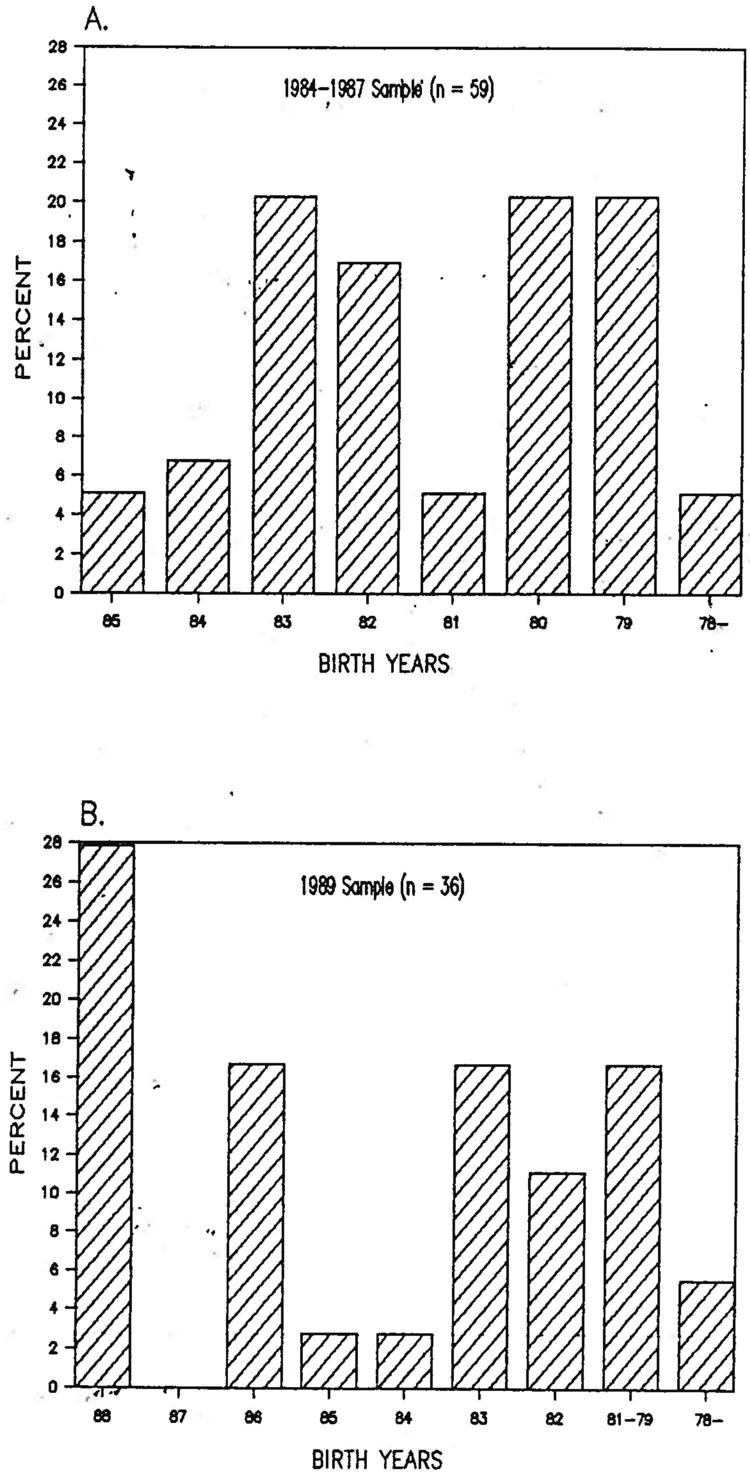


Figure 17 - Distributions of birth years for yearling and older ewes aged during captures at Old Dad Peak, 1984-87 and 1989.

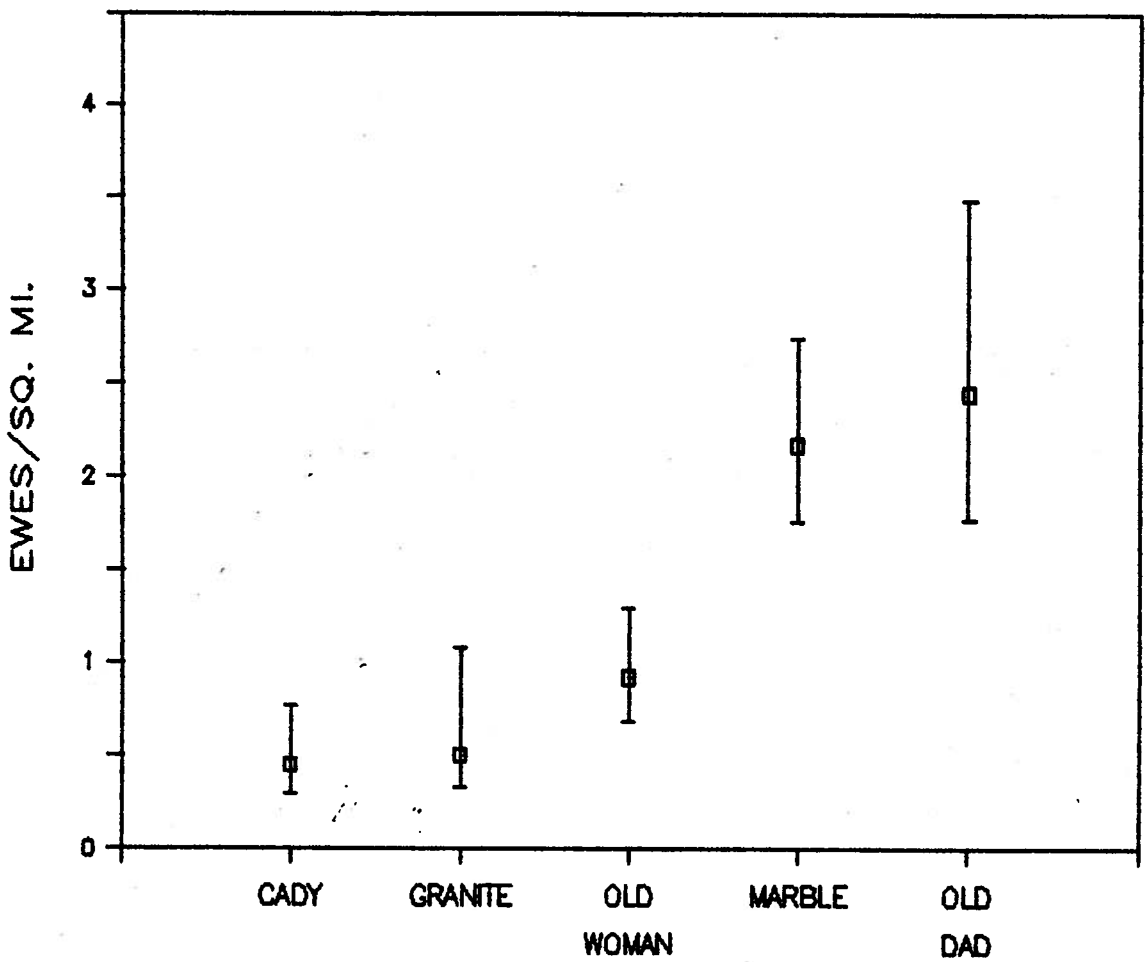


Figure 18 - Densities and 95% confidence limits for ewes in the five study populations.