Microsatellite Diversity in Sierra Nevada Mountain Sheep Herds

Running title: Sierra Nevada mountain sheep genetic diversity

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Abstract: Mountain sheep in the southern and central Sierra Nevada of California are recognized as a separate subspecies. Following the influx of gold miners in the 1850s and the introduction of domestic sheep in the 1860s, these native sheep experienced a cascade of population losses that continued well into the twentieth century, with only 3 populations surviving. Two of those surviving populations were used to re-establish 3 populations during 1979-88, but all populations in that mountain range suffered substantial population declines in the 1990s. We investigated the effects of this overall population history on genetic diversity of 12 microsatellite loci, using DNA extracted from blood, dried tissue on skulls, and feces. We compared genetic diversity measures among Sierra Nevada herds and between the Sierra Nevada and other populations in southwestern U. S. Sierra Nevada populations all had strong evidence of past bottlenecks in allele frequencies, and exhibited the lowest levels of genetic diversity. Only a captive population derived from a small number of sheep had an equivalent level of genetic diversity. Within the Sierra Nevada, the 3 reintroduced herds exhibited the lowest genetic diversity, and their relative levels matched past demographic measures expected to influence genetic diversity. Recent population gains for all Sierra Nevada mountain sheep herds indicate that the current levels of genetic diversity will not limit potential recovery of the overall population.

Loss of genetic diversity due to genetic drift in small isolated populations is a concern of

conservation biology (Soulé 1980, Hedrick et al. 2001) and has resulted in suggested minimum population goals and population structures to minimize this loss (Franklin 1980, Templeton and Read 1983, 1998). The loss of genetic diversity in small, isolated populations may be exacerbated by "cryptic genetic bottlenecks" when few individuals contribute to subsequent generations yet census size of the population does not warrant immediate concern (Luikhart et al. 1998, Ramey et al 2000). In these and in very small isolated populations, inbreeding (mating between relatives) is a concern. Extreme inbreeding and loss of genetic diversity can lead to overt fitness effects with demographic consequences that may hasten extinction (Ralls and Ballou 1983). However, because of different time scales involved in demographic and gene pool dynamics, Lande (1988) suggested that demographic problems associated with small populations most likely will preempt genetic problems in importance. Nevertheless, an important consideration in endangered species management is the retention of as much genetic diversity as possible under the expectation of recovery of the population in question. In addition to reducing potential deleterious effects of inbreeding, this diversity is considered important for populations to be able to respond to selection from future environmental changes (Franklin 1980). There is growing evidence that genetic diversity manifested as heterozygosity levels of individuals is important to disease resistance (Carrington et al. 1999; Coltman et al. 1999). Indeed, novel disease pathogens are one form of environmental change.

Mountain sheep in the Sierra Nevada are recognized as a distinct subspecies (*Ovis canadensis sierrae*) found only in the central and southern portions of that mountain range (Wehausen and Ramey 2000, Wehausen et al. 2005). As has been typical of most mountain sheep habitat favorable for domestic sheep grazing, mountain sheep in the Sierra Nevada saw extensive losses of herds during the late 1800s and much of the 1900s (Wehausen et al. 1987) from at least 17 native herds to only 3 in the 1970s. When the first actual counts were made in the late 1970s, the 3 herds varied in size from 30 to 150 and totaled 250 sheep (Wehausen1980). From 1979-88 the two largest herds were used as stock to re-establish herds in three areas of historic range (Bleich et al. 1990). At least two of those new herds were sufficiently isolated geographically that genetic exchange with other herds was unlikely.

The 3 new herds were initiated with 27-38 sheep (Bleich et al. 1990). Genetic effective population sizes (N_e) were lower, in part because some sheep died before contributing genes to the next generation. Maximum numbers potentially contributing genes to the next generation for those herds were 21-26 (Table 1), and some of those sheep died after minimal opportunities to contribute genes. Given the further effects of a polygynous breeding system, N_e for each of the three reintroduced herds was probably less than 15 and possibly closer to 10.

All 3 reintroduced herds persist today. However, beginning in the 1980s all bighorn sheep herds in the Sierra Nevada began avoiding low elevation winter ranges coincident with rising levels of mountain lion predation on those ranges (Wehausen 1996). The results were

significant declines in all herds, with the total population of this taxon reaching a low of just over 100 sheep in 1995 that encompassed 9 different female groups. All female groups dropped to reproductive bases of <10, and many to <5, with the smallest reaching a low of just a single female. All herds have shown increasing numbers since that bottleneck.

The combination of population losses beginning in the 1860s, probable past bottlenecks in surviving native herds, founder effects for re-established herds, geographic isolation of some herds, and the recent bottleneck that all herds experienced would be expected to have resulted in losses of genetic diversity. The current level of diversity for these herds is unknown. Consequently, what actions might be needed to manage for genetic diversity is not clear. The purpose of this study was to develop a sample of genetic diversity for all existing herds that can be used as a basis of conservation decisions.

METHODS

Study Populations, Sources of DNA, and Sample Sizes.

We sampled all existing mountain sheep populations in the Sierra Nevada. The frequency of male-mediated gene migration between demographically separate female groups can be expected to vary with distance between them. In defining populations for sampling and analysis we combined areas in which female groups were essentially contiguous or overlapping in distribution into a single population definition; other situations were treated as separate populations. This produced five populations in the Sierra Nevada of which two were native and three reintroduced. The native populations were the Mount Williamson and Mount Baxter (including all sheep from Kearsarge Pass to Taboose Pass) populations. The reintroduced populations were Mount Langley, Wheeler Ridge, and Mono Basin (including sheep both south and north of Lee Vining Creek). We developed additional data sets to use comparatively for interpretation of data: (1) the Mount Baxter herd during the late 1970s and 1980s before it declined in size; (2) the native sheep in the northern White Mountains on the east side of Owens Valley about 120 km N of the Mount Baxter herd; (3) the Willow Creek herd in the Inyo Mountains about 30 km directly east across the southern Owens Valley from the two native Sierra Nevada herds and about 90 km S of sheep sampled in the White Mountains; and (4) Hunter Mountain, about 55 km SE of the Willow Creek herd and about 75 km from the Mount Williamson herd in the Sierra Nevada.

Sources of DNA included recent and past blood samples, tissue removed from skulls, and fecal samples. DNA for current herds in the Sierra Nevada was derived primarily from fecal samples except the Wheeler Ridge herd, which consisted mostly of DNA from blood. Samples from the White Mountains were a mixture of blood and tissue samples from the 1980s and recent blood and tissue samples. The Inyo Mountains samples were all derived from fecal samples

collected in 2003, and Hunter Mountain samples were a combination of recent blood and fecal samples from the south side of Hunter Mountain and recent fecal samples from the Dodd Spring area on the north side of that mountain. Final sample sizes varied from 20 different sheep at Hunter Mountain to 63 for the current population in the Mount Baxter region.

For DNA derived from fecal samples we eliminated duplicate genotypes as redundant samples from the same individual using 12 loci. For each population we used the probabilities of obtaining identical microsatellite genotypes from different unrelated individuals ($P_{(ID)}$; Taberlet and Luikart 1999, Waits et al 2001) to gauge our resolution in distinguishing individuals. This probability was calculated for each locus and those probabilities were multiplied to arrive at the final $P_{(ID)}$ value. We bounded this probability by also calculating that measure for siblings ($P_{(ID)sib}$) using equations in Taberlet and Luikart (1999); both measures vary in parallel with genetic variation. $P_{(ID)}$ varied from 0.000018 (Mount Langley) to 0.0000022 (Mount Baxter) and $P_{(ID)sib}$ varied from 0.0056 (Mount Langely) to 0.0022 (Mount Baxter). Thus, our worst probability of falsely eliminating a duplicate sample was about 6 in 1000 for full siblings from the Mount Langley herd, which we considered acceptable.

Loci Investigated and Methods of Data Development

We surveyed variation at the following 12 microsatellite loci (with annealing temperatures): MAF209 (Buchanan and Crawford 1992a; 51C); MAF33 (Buchanan and Crawford 1992b; 55C); MAF48 (Buchanan et al. 1991; 55C); OarFCB11 (Buchanan and Crawford 1993; 56C); MAF36 (Swarbrick et al 1991; 56C); OarFCB304 (Buchanan and Crawford 1993; 56C); MAF65 (Buchanan et al. 1992; 60C); FCB266 (Buchanan and Crawford 1993; 55C); FCB 128 (Buchanan and Crawford 1993;55C); OarAE16 (Pentry et al. 1993; 60C); OarHH47 (Henry et al. 1993; 51 C); and OarHH62 (Ede et al. 1994; 56C), of which the first 9 were utilized by Gutierrez-Espeleta et al . (1998, 2000) for bighorn sheep in the southwestern United States. Loci with the same annealing temperatures and similar signal strength were multiplexed in PCRs. Forward primers were dye labeled for use on ABI sequencers and 2-7bp tails were added to some reverse primers to aid in separation of allele sizes among loci. PCR reactions varied depending on the DNA source material. Reactions (25ul) contained 2 units AmpliTaq Gold polymerase, 1x AmpliTaq buffer with MgCl2 added to final concentrations of 1.75- 2.25mM, 200mM dNTP, 5-10mg/ml BSA, and varying concentrations of DNA. PCRs were performed on Eppendorf Matercycler gradient thermocyclers in 96 well polycarbonate plates with silicone sealing mats (Costar) or in 0.2ml strip tubes (Eppendorf). The following temperature profile was optimized and used for amplifications: heated lid temperature of 96 C, a 7.5 minute initial denature and Taq activation step of 94 C, followed by 40 cycles of 94 C for 30 sec, 51-61 C for 30 sec, and 72 C for 30 sec. A final extension step of 60 C for 30 seconds was added and PCR products were held at 4 C until stored in the dark at <-20 C until use.

Dye labeled PCR products were combined with deionized formamide, loading dye, and GeneScan 350 size standard (ABI), denatured at 90 C for 2 minutes then chilled immediately to <0 C. Reactions were run on an ABI 373XL or 377 automated DNA sequencer using Singel Long Ranger burst packs (FMC) for the gel matrix. Chromatograms were analyzed using the program GeneScan 3.0 (Applied Biosystems Inc.).

For fecal samples DNA was extracted from the outer mucilaginous coat. Initially the removal of this coat included a small amount of inner pellet material and results required at least 4 replicate PCRs for reliable genotyping. Part way through this study it was found that careful scraping of just the outer mucilaginous coat yielded notably better results (Wehausen et al. 2004), allowing just 2 replicate PCRs to be run for each locus for most samples (Wehausen et al. 2004). The actual number of replicates varied with levels of failed reactions and rates of allelic dropout so as to attain at least 99% confidence for homozygotes (Taberlet et al. 1996).

Methods of Analysis

We used the bottleneck test of heterozygosity excess (program BOTTLENECK; Cornuet and Luikart 1996; Luikart and Cornuet 1997; http://www.ensam.inra.fr/URLB/bottleneck/bottleneck.html) to determine if mountain sheep populations showed the genetic signature of one or more substantial genetic bottlenecks. When a population undergoes a genetic bottleneck, both the number of alleles (allelic diversity) and heterozygosity are reduced, but allelic diversity is reduced faster than heterozygosity. This leaves a transient deficiency in the observed number of alleles relative to the number of alleles expected under drift-mutation equilibrium for the expected heterozygosity (H_e) calculated from allele frequencies (Cornuet and Luikart 1996). BOTTLENECK detects this loss of rare alleles in bottlenecked populations using allele frequency data for multiple microsatellite and/or allozyme loci (Cornuet and Luikart 1996).

Bottleneck tests were run for all variable loci for the infinite allele model (IAM) and stepwise mutation model (SMM). These represent two extremes among possible mutation models, thus effectively set bounds (Cornuet and Luikart 1996). Microsatellite loci likely fall at the SMM end of this spectrum (Cornuet and Luikart 1996); consequently, we ran two additional hybrid models (two phased models; TPM) incorporating 70% SMM with a variance of 30 and 90% SMM with a variance 4, which likely set reasonable bounds appropriate to microsatellite loci (Luikart, pers. comm; Ramey et al. 2000). In all bottleneck tests we utilized 2000 iterations to develop heterozygosities expected under drift-mutation equilibrium and the Wilcoxen one-tailed test of heterozygosity excess, in addition to the modeshift test of the overall distribution of allele frequencies (Cornuet and Luikart 1996).

We used two measures of genetic diversity, of which $P_{(ID)}$ was one. To produce a

positive relationship between $P_{(ID)}$ and genetic diversity we used the reciprocal of the final $P_{(ID)}$ (Petkau et al. 1998), and this was divided by one million or one thousand depending on the number of loci used to produce final indices. $P_{(ID)}$ is informative as a diversity measure in that its value varies with the number of alleles per locus and the frequency distribution of those alleles, while correcting for sample size. In addition to comparisons within the Sierra Nevada and across the Owens Valley, this index was used to place Sierra Nevada populations in a larger geographic context by calculating this index for data provided by Gutierrez-Espeleta et al. (2000) using the 9 of our loci that they also ran. We limited this comparison to populations for which they sampled at least 20 individuals.

Our second measure of genetic diversity was H_e, the level of heterozygosity expected from measured allele frequencies and corrected for sampling bias (Nei 1987). This measure also was compared among populations within and outside the Sierra Nevada. H_e is calculated separately for each locus and averaged for all loci.

RESULTS

All Sierra Nevada populations showed signatures of recent bottlenecks. Allele frequencies all showed a significant shift away from the L-shaped distribution expected under drift-mutation equilibrium. For the number of alleles present, expected heterozygosities exceeded what was expected under drift-mutation equilibrium for the different models run, with probabilities mostly <0.005 (Table 2). In contrast, the Hunter Mountain, Inyo Mountains, and White Mountains populations showed considerably less evidence of genetic bottlenecks. Only the Hunter Mountain population exhibited a shifted patterns of allele frequencies, which was not supported by most of the probabilities (Table 2).

There was considerable overall variation in genetic diversity among the populations examined, with Sierra Nevada herds at the low end of the range of values. Only the captive population at Red Rock, New Mexico exhibited similar low genetic diversity, although the H_e value for the Old Dad Peak population in the Mojave Desert of California also overlapped the Sierra Nevada (Table 3). The only evident break in the genetic diversity continuum separated the 4 populations with the highest diversity, including Hunter Mountain and the Inyo Mountains from the rest (Table 3). Within the Sierra Nevada, there was some variation among populations, with the 3 reintroduced herds showing slightly lower genetic diversity than the two native herds (Table 3).

DISCUSSION

It is possible that the 4 populations exhibiting the highest genetic diversity (Table 3) are representative of original levels of genetic diversity, while all other populations sampled have

seen varying degrees of erosion of genetic diversity due to past population dynamics and loss of connectivity within metapopulations.

There was a clear contrast between Sierra Nevada populations and those east across the Owens Valley in evidence of recent bottlenecks and genetic diversity. Hunter Mountain and the Inyo Mountains were among the genetically most diverse populations of bighorn sheep sampled to date. In contrast, the White Mountains exhibited levels of genetic diversity only slightly greater than the Sierra Nevada (Table 3). Among the local populations, the White Mountains and Sierra Nevada share a history of considerable domestic sheep grazing beginning in the 19th century (Wehausen 1983). This has undoubtedly led to numerous die-offs in both ranges from contact between these sheep species, given that domestic sheep commonly carry pneumophyllic bacterial strains that are fatal to bighorn sheep (Martin et al. 1996). The overall population in the White Mountains was known to have dropped to about 40 sheep in the late 1970s (Wehausen 1983) and might have been even lower earlier that decade. Apparently that and probable earlier die-offs were not sufficient bottlenecks to leave a clear signature detectable by the bottleneck test. Greater gene flow within that metapopulation compared with the Sierra Nevada may have affected the detectability of a bottleneck in the White Mountains.

The consistent signature of recent bottlenecks among the Sierra Nevada populations is not surprising given recent demographic histories, potential founder effects for the 3 reintroduced populations, and results suggesting that the source for those 3 populations (Mount Baxter) also was bottlenecked when used as the source of that stock. It is likely that the 2 native herds in the Sierra Nevada have seen repeated bottlenecks since domestic sheep grazing began in the 1860s.

The 3 reintroduced populations showed the lowest genetic diversity in the Sierra Nevada, with Mount Langley the lowest, followed by the Wheeler Ridge and Mono Basin populations (Table 3). This order in current genetic diversity matches the order among these populations in both the number of translocated sheep available to contribute genes and the bottleneck population size (Table 1). Both factors would be expected to influence subsequent genetic diversity.

The 2 native populations have quite different population histories. Prior to the mid 1970s, casual observations suggested that sheep on Mount Williamson were reasonably abundant (Jones 1950; Vic Taylor, pers. comm. 1977). During 1978-85, however, optimal census opportunities on low elevation winter ranges consistently yielded only 29-31, of which 14 were females (Wehausen 1980, unpubl.). Sheep began avoiding those winter ranges in 1986 and have not used them since then. Subsequent population dynamics are unknown for more than a decade. In 1996, population monitoring efforts resumed at high elevations in summer, at which time fecal DNA genotypes indicate only 6 females existed as the reproductive base. Our genotype data

indicate that this population increased thereafter.

In contrast, the population in the Mount Baxter region numbered as many as 220 in the late 1970s when its use as translocation stock began (Wehausen 1980). Following the development of winter range avoidance by those sheep in the 1980s, that population underwent a dramatic decline in numbers (Wehausen 1996). However, at its lowest point in 1997-98, surveys could account for a reproductive base of at least 16 females. Recent discovery of sheep wintering west of the Sierra Nevada crest in Bubbs Creek suggest that the number of females may have approached or exceeded 20; and the total population may have been twice that. This minimum population size may account for the apparent lack of decline in genetic diversity from the 1980s to present (Table 3).

The history of the Mount Baxter population contrasts with the herd on Mount Williamson. A prediction from the difference in histories of the Mount Baxter and Mount Williamson populations would be lower genetic diversity at Mount Williamson. While the genetic diversity measures support that prediction (Table 3), the difference between those two populations is small. One possible reason for that is gene flow between populations. Mount Williamson lies between the Mount Baxter and Mount Langley populations with distances small relative to what males may cover. Further, it is known that at least two male sheep translocated to Mount Langley ended up at Mount Williamson instead, and at least 2 others traversed Mount Williamson on their way back to their native ranges near Mount Baxter.

One an ordinal scale, the $P_{(ID)}$ index and H_e values produce similar, but not quite identical results, but the former spreads populations over a much larger scale (Table 2). As measures of genetic diversity, average H_e and the $P_{(ID)}$ differ in a fundamental way relative to fixed loci. The former measure is additive while the latter a multiplicative. H_e for a fixed locus is zero, which is computed into the average H_e and thereby lowers that index. In contrast, the $P_{(ID)}$ value of a fixed locus is 1. Because the final $P_{(ID)}$ is the product of $P_{(ID)}$ values for all loci, the effect of a fixed locus is to not change the index value, rather than moving it in the direction of less diversity. This is one difference that accounts for somewhat different patterns for those two genetic diversity indices (Table 3).

Management Implications

Are the levels of genetic diversity low enough in some Sierra Nevada populations to warrant genetic intervention? This is the conservation geneticist's dilemma. On the one hand, there is a theoretical benefit to augmenting some populations to raise levels of genetic diversity. On the other hand, augmenting is expensive, can dilute locally adapted genetic variation if divergent populations or subspecies are used as source stock, and has the potential to adversely affect the recipient population through introduction of new pathogens. Without direct evidence

of inbreeding or observations of reduced population fitness that are independent of other causes, augmentation to increase genetic diversity may not be justified.

We suggest a comparative and stepwise approach to deciding when to intervene. First, is there evidence indicating fitness differences among populations that are correlated with genetic diversity and not explainable by more parsimonious factors, such as habitat (e.g.nutritional) differences? Second, how do the genetic diversity measures compare with other populations (of the same species) for which demographic information exists; e.g. are they similar to populations that have been shown or suggested to have fitness compromised by genetic diversity? Third is the question of trend in genetic variation (comparing a population with itself over time). If there is evidence that genetic variation is continually eroding, it is likely that eventually it will reach a point where fitness is negatively affected. Halting such a trend is an important first step; reversing it may be considerably more difficult and may not be important. The former will be accomplished by a change in population parameters (e.g. through habitat manipulations), while the latter will require also augmentation with animals from other populations. Any efforts toward genetic management also should be allocated relative to need, focusing first on the populations most at risk of genetic problems.

These principles can be applied to the mountain sheep in the Sierra Nevada. Is there any evidence that lower genetic diversity in the Sierra Nevada affects fitness? All populations in the Sierra Nevada have shown strong population increases in the past 5 or more years. This finding does not support the hypothesis of a fitness effect. Of the other populations compared, the captive population at Red Rock, New Mexico, and the Old Dad Peak population in California have similar low genetic diversity. Neither of those populations exhibits fitness effects. The population at Old Dad Peak has been particularly productive and served as the source of many sheep used for translocations (Bleich et al. 1990). In a survey of North American brown bears, Petkau et al. (1998) found genetic variation in the Kodiak Island population that was considerably lower than has been recorded for bighorn sheep; yet, demographically that brown bear population is robust.

It is highly likely that bighorn sheep in the Sierra Nevada once had greater genetic diversity, with the current levels a reflection of numerous decades of erosion of that diversity. With recent substantial population gains in all bighorn sheep herds in the Sierra Nevada, genetic diversity is probably mostly stable. As a federal endangered species, there is a mandate to increase numbers through greater geographic distribution. This will be the most reliable way to preserve genetic diversity. It is inevitable that populations will undergo dynamics that may sometimes threaten the maintenance of genetic diversity. The sheep in the Mount Baxter region are a prime example of the positive effect of good geographic distribution. The Mount Baxter population sampled for this study actually consists of at least 3 different contiguous female demes that function as a metapopulation. The lack of detectable decline in genetic diversity in

this larger population, despite the severe population declines that occurred beginning in the 1980s, attests to the genetic benefits of functional metapopulations. Increasing total sheep numbers in other populations by establishing additional demes of females nearby should help maintain the existing genetic diversity. For the reintroduced herds, this also may function to increase genetic diversity if the sources of those new demes come from Sierra Nevada populations that have appropriate complementary allele frequencies. The microsatellite loci used in this study are a tiny fraction of the genome. To the extent that they represent the larger genome, they can be used as the basis for choosing sources of translocation stock where multiple sources are available.

Actual trends in genetic diversity will be known only through comparative re-samplings at appropriate intervals. A further question concerns how much genetic variation might have been lost between 1860 and the 1970s associated with the loss of most populations in the Sierra Nevada. Using DNA extracted from bone, it may be possible to develop data from historic skull specimens to examine this question to some extent. This would place the current situation in a broader context that relates to the question of whether some induced migration from the east side of Owens Valley might be appropriate.

ACKNOWLEDGMENTS

This research began as a cooperative project between the Sierra Nevada Bighorn Sheep Foundation and the University of California's White Mountain Research Station with funding from the Genetic Resources Conservation Program at U.C. Davis, Patagonia, the national and San Diego chapters of Safari Club International, and the Biological Resources Division of the U.S. Geological Survey. This first phase was possible due to the availability of the genetics lab at the San Diego Zoo thanks to O. Ryder. Funding from the California Department of Fish and Game as part of the Sierra Nevada Bighorn Sheep Recovery Program and the donation of automated DNA sequencers by the R. W. Johnson Pharmaceutical Research Institute allowed the completion of this study.

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Table 1. Demographic parameters for the three reintroduced Sierra Nevada populations. Losses include sheep that died or emigrated prior to contributing genes to the next generation.

	Mono Basin	Langley	Wheeler
Years of translocations	'86, '88	'80, '82, '87	'79, '80, '82, '86
Total sheep translocated	38	28	27
Initial losses	12	7	4
Highest count prior to 1995	80	42	31
Population low since 1995 winter	23	16	18
2003 population (females $\geq$ 1 yr.)	14	24	34

Table 2. Bottleneck test results (one tailed probabilities that the data came from an unbottlenecked population at drift-mutation equilibrium) for the infinite allele model (IAM), stepwise mutation model (SMM), two-phased models (TPM; #1: 70% SMM, variance 30; #2: 90% SMM, variance 4). MODE is an assessment of the overall allele frequency distribution pattern.

POPULATION	LOCI	I A M	S M M	T P M #1	T P M #2	MODE
Hunter Mountain	12	0.032	0.66	0.19	0.54	shifted
Inyo Mountains	12	0.00012	0.60	0.0012	0.10	normal
White Mountains	11	0.034	0.42	0.12	0.52	normal
Mount Baxter (1980s)	10	0.00049	0.00049	0.00049	0.00049	shifted
Mount Baxter (current)	10	0.00049	0.00049	0.00049	0.00049	shifted
Mount Williamson	10	0.00049	0.00049	0.00049	0.00049	shifted
Mount Langley	10	0.0015	0.053	0.0034	0.053	shifted
Wheeler Ridge	10	0.00049	0.0024	0.00098	0.0015	shifted
Mono Basin	10	0.00098	0.0015	0.00098	0.00098	shifted

Table 3. Values of two genetic diversity indices calculated for 12 loci and 9 of those also run by Gutierrez-Espeleta et al. (1998, 2000). Sample size (N) is number of sheep.

POPULATION	N	$1/P_{(ID)}/10^6$ (12 loci)	$1/P_{(ID)}/10^3$ (9 loci)	H_e (12 loci)	H_e (9 loci)
Eagle Mountains, CA	22		6250		0.612
Hunter Mountain, CA	20	2940	4350	0.600	0.586
Castle Dome, AZ	20		1890		0.564
Inyo Mountains, CA	31	667	1060	0.606	0.571
San Gorgonio, CA	22		87		0.452
San Ysidro Mountains, CA	22		83		0.466
White Mountains, CA	30	1.6	48	0.472	0.477
Mount Nutt, AZ	28		24		0.444
Old Dad Peak., CA	23		18		0.427
Mount Baxter, CA (current)	62	0.45	8.1	0.468	0.434
Mount Baxter, CA (1980s)	46	0.36	5.6	0.454	0.412
Mount Williamson, CA	37	0.37	4.4	0.446	0.390
Mono Basin, CA	42	0.18	3.8	0.430	0.384
Wheeler Ridge, CA	35	0.13	4.0	0.420	0.489
Red Rock, NM (captive)	25		1.0		0.324
Mount Langley, CA	40	0.06	0.7	0.396	0.324