A MORPHOMETRIC REEVALUATION OF THE PENINSULAR BIGHORN SUBSPECIES

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Abstract: Cowan's (1940) taxonomy of North American wild sheep (*Ovis canadensis*) has been used for a half century. However, Ramey's (1993) mitochondrial DNA analysis, and his reanalysis of Cowan's original morphometric data failed to find validity in Cowan's desert subspecies divisions. Cowan's desert subspecies were instead found to be a result of small sample sizes and different age distributions among samples. In this study, we reevaluated the Peninsular subspecies (*O. c. cremnobates*) by measuring 198 ram and 145 ewe skulls from the California region and the Sonoran and Chihuahuan Deserts, as well as 28 Rocky Mountain sheep (*O. c. canadensis*) and 13 Dall sheep (*O. dalli*) specimens. We found substantial age effects for adult rams, but not adult ewes. When age effects were removed, univariate, principal components, and discriminant function analyses: 1) failed to support a separate taxon in the Peninsular Ranges; 2) identified some differences in the Sierra Nevada; and, 3) revealed considerable difference between northern and southern regions of the Nelson subspecies (*O. c. nelsoni*). Therefore, we synonymize the Peninsular subspecies with the Nelson subspecies and suggest that the Nelson subspecies be viewed as a polytypic taxon.

Key words: morphometrics, mountain sheep, *Ovis canadensis*, Peninsular bighorn, taxonomy.
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INTRODUCTION

The currently accepted taxonomy of North American wild sheep (Shackleton 1985, Bowyer and Leslie 1992) was based on comparisons of skull measurements among populations made by Cowan (1940). Cowan described 4 desert subspecies in the southwestern United States: Nelson (*Ovis canadensis nelsoni*), Mexican (*O. c. mexicana*), Peninsular (*O. c. cremnobates*), and Weems (*O. c. weemsi*) bighorn sheep, as well as California bighorn sheep (*O. c. californiana*) in the Sierra Nevada. State and federal conservation programs have relied on Cowan's work as a guide to the differentiation of mountain sheep for 50 years. These taxonomic designations have influenced the choice of source populations for reintroductions and the allocation of monetary resources to conservation programs (Bureau of Land Management 1989).

A recent reanalysis of Cowan's (1940) original data using sophisticated modern analytical methods suggested that some of the subspecies he recognized may not be valid (Ramey 1993). This analysis showed that differences between putative subspecies in the southwestern deserts apparently resulted from small sample sizes and age-related size differences, as suggested by Cockrum (1961). Similar conclusions were reached by Gonzalez (1976) concerning the validity of *O. c. weemsi* in Baja California, and by Bradley and Baker (1967) regarding the status of *O. c. mexicana* relative to variation they found within *O. c. nelsoni*. Analysis of mitochondrial DNA (mtDNA) sequence variation by Ramey (1991, 1993) cast further doubt on the validity of the subspecies recognized by Cowan (1940) in the Southwest. Distribution of the small amount of mtDNA variation in the Southwest was not concordant with Cowan's subspecies boundaries, with the exception of sheep from the Sierra Nevada.

In addition to the lack of genetic support for desert subspecies, some of the boundaries between them have been inconsistent among authors, particularly for the Peninsular subspecies. The original distribution of *O. c. cremnobates* described by Elliot (1903) extended north through Baja California to near the U.S. border. With no evident additional data or analysis, Grinnell (1933) extended the boundary north through the Peninsular Ranges of California to San Gorgonio Pass. Cowan (1940: 565) shifted the boundary back south to include only "extreme southern California", including both sides of Imperial Valley. However, he noted that the region from the Santa Rosa Mountains to the San Bernardino Mountains appeared to be a zone of intergradation between *O. c. cremnobates* and *O. c. nelsoni*. Jones (1950:31) initially chose the boundaries of Grinnell (1933) rather than Cowan (1940), but subsequently switched, referring to the sheep in the Santa Rosa Mountains as *O. c. nelsoni* (Jones et al. 1957:179). Weaver (1957) followed Cowan (1940) in suggesting that the Santa Rosa Mountains might be a zone of intergradation, but Goodman (1962:43) questioned this, stating, "to my knowledge this fact has never been definitely established". Buechner (1960) and Barrett (1965) both extended *O. c. cremnobates* north into the Santa Rosa Mountains and miscited Cowan (1940) as support.

The most consistent shift in the recognized northern boundary of *O. c. cremnobates* resulted from state listing of this subspecies under the California Endangered Species Act. The first listing in 1974 included bighorn sheep in the Santa Rosa Mountains, while those in the San Jacinto Mountains were added in 1980 (California Department of Fish and Game [CDFG] 1974, 1980, At the crossroads, a report on the status of California's endangered and rare fish and wildlife. 147pp.). Following these designations, sheep in these two northern Peninsular Ranges have been referred to consistently as *O. c. cremnobates* (Merritt 1974, Weaver 1975, Berger 1982, Turner and Payson 1982, DeForge 1984). In effect, these recent boundary changes have accepted Grinnell (1933) over Cowan (1940). All of these post-Cowan boundary changes share a common characteristic: they were made without any additional systematic research. A parallel unsupported shift in the boundary between *O. c. nelsoni* and *O. c. mexicana* was effected by Russo (1956) in Arizona.

The purpose of this investigation was to reevaluate taxonomic divisions between Nelson and Peninsular subspecies from a morphometric standpoint using a new data set.

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METHODS

We treated Cowan's (1940) taxonomic divisions as hypotheses to test. Our approach was to examine morphometric differences between Nelson and Peninsular bighorn specimens within the context of variation on 2 geographic scales: 1) the California region; and, 2) the Southwest. Both univariate and multivariate analyses were used.

We first broke the California region into 5 geographic units for univariate analyses: 1) the Peninsular subspecies distribution, including Baja California, as defined by Grinnell (1933), as well as by Cowan (1940); 2) the Mojave Desert from south of the Death Valley region to the Colorado River; 3) the Death Valley region, where Bradley and Baker (1967) indicated sheep to be morphologically different from neighboring Nevada, and which Wehausen (1991) suggested as a potential transition zone; 4) the White Mountains and neighboring west central Nevada; and, 5) the Sierra Nevada, which Cowan (1940) designated as the California subspecies. The San Gabriel Mountains were omitted due to inadequate sample sizes. Preliminary analyses found the Death Valley region to lack distinction from the White Mountains/Nevada region immediately to the north. Consequently, they were lumped for the analyses reported here and will be referred to as "Great Basin". This left 4 California geographic regions. Two represented reputed subspecies (*O. c. californiana* from the Sierra Nevada and *O. c. cremnobates* from the Peninsular Ranges), while the other 2 split the Nelson subspecies into northern and southern regions. This allowed comparisons of differences between reputed subspecies with variation within a subspecies.

Principal components analyses (PCA) were conducted on a larger geographic basis that included: 1) the San Gabriel Mountains of California; 2) southern Baja California; 3) Arizona and Sonora (Sonoran Desert); and, (4) New Mexico, Chihuahua, and Texas (Chihuahuan Desert). We also measured some skulls from the Rocky Mountain region and from Dall sheep to represent yet wider geographic variation.

Skulls from native populations were measured from collections at the Smithsonian National Museum in Washington, D.C., and several locations in California. Sample sizes by region were (ram/ewe): Chihuahuan Desert, 9/4; Sonoran Desert, 34/14; southern Baja California (*O. c. weemsi*), 5/5; Peninsular subspecies (including 11/8 from northern Baja California), 43/16 (Cowan's range), 57/21 (Grinnell's range); Mojave Desert, 35/46; San Gabriel Mountains, 4/4; Great Basin, 31/26; Sierra Nevada, 23/25; Rocky Mountain region, 10/18; and Dall Sheep, 5/8. While only a subset of these provided complete measurements, our sample size far exceeded what Cowan (1940) used as the basis of his taxonomy for all of North America (Ramey 1993).

We developed a set of measurements that described 4 attributes of skulls: length, width, height, and horns (Table 1). To the extent possible, we used homologous landmarks (Bookstein 1990) such as the intersections of sutures. We included among

Table 1. Skull and horn measurements made for this study. Abbreviations are in parentheses.

Cranial Length (CRANIAL): Distance from anterior lip of foramen magnum to posterior edge of palate at midline suture.
Palate Length (PALATE): Distance from posterior edge of palate at midline suture to posterior margin of the most intact anterior palatine foramen.
Premaxilla Length (PREMAX): Distance from posterior margin of anterior palatine foramen to tip of premaxillae along midline.
Average Upper Tooth Row (TOOTH)[a]: Average length of upper tooth rows measured as the greatest alveolar length of combined upper molars and premolars.
Palate Width (PM2)[a]: Least distance across palate between alveoli of second premolars.
Cheek Width (CHEEK): Greatest distance between malar eminences on the maxillary bones.
Interorbit Width (INTERORB)[a]: Least distance in a straight line taken with calipers resting in notch on inferior orbital rim at lower edge of lachrymal bones.
Intraorbit Width (INTRAORB): Width of largest orbit measured as greatest width of interior lip of orbit.
Zygomatic Width (ZYGO)[a]: Greatest distance between external margins of zygomatic arches taken on jugo-squamosal suture.
Post Orbit Width (POSTORB): Minimum width of frontal bone as measured posterior to orbits and anterior to horn cores.
Cranial Height (HEIGHT): Males: Greatest distance from anterior lip of foramen magnum to crest of cranium along midline suture; Females: Greatest distance from anterior lip of foramen magnum to crest of cranium along midline suture even with the anterior edge of horn cores.
Horn Core Length (CORL): Length of horn core measured along the superior edge from the burr to the tip using a steel tape.
Horn Core Basal Circumference (CORC)[a]: Circumference of largest horn core, measured around core near burr at right angle to the axis of the core at that point, using a steel tape.
Horn Core Volume (CORVOL): The estimated volume of ram horn cores when treated as a cone using the previous two measures as basal circumference and height.
Horn Basal Circumference (HORNC)[a]: Circumference of largest horn measured nearest its base using a steel tape.
Horn Length (HORNL)[a]: Measured along the superior horn keel from orbital corner to tip of horn with steel tape.
Horn Volume (HORNVOL): Volume of largest horn estimated from lengths and circumferences. The horn length was divided into four quarters and the circumference of the horn was measured with a steel tape at the base, each quarter, and at a measured length near the end just short of any brooming. The radius of the horn at its base and at each quarter was estimated by treating each circumference as a circle. Horn volume was estimated by calculating and summing the volumes between each circumference calculated as frustrums of conical sections (Hogman et al. 1961). A final conical section was then added from the last circumference to approximate brooming loss using a constant taper for all specimens. An analysis of the ends of unbroomed horns yielded a constant taper across all populations (distance between circumferences accounted for 96% of the variation in circumference differences; $n=19$).
Age (AGE): Growth years determined from annual horn growth rings. For specimens missing horn sheaths, a minimum age was determined from tooth replacement and wear. Specimens with minimum age estimated only from wear were not use in analyses where age was the independent variable.

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[a] Measurements from Cowan (1940)

our measurements several variables that Ramey (1993) found to be important in Cowan's (1940) data set. We also generated new variables potentially representing additional variation including some representing horns, horn cores, and the cranial region of the skull that could be measured on incomplete skulls. Horn measurements on rams included the lengths and circumferences necessary to calculate Boone and Crockett scores, but we used these in combination with additional measures to calculate an index of horn volume (Table 1).

We further tested Ramey's (1993) suggestions on the influence of age. For many measurements, age effects were expected at least until 4 years, when tooth replacement is completed (Taber 1971). We investigated age effects for skulls ≥ 4 years by looking for a significant age covariate for each variable via analysis of covariance (ANCOVA). Because age effects are potentially curvilinear, in addition to AGE, we also tested lnAGE, and 1/AGE. The age covariate that accounted for the most variation in ANCOVA was used, while analysis of variance (ANOVA) was used instead if age effects were not significant, or did not have parallel slopes. The Bonferroni multiple comparisons test was used to compare differences between the Peninsular and Mojave Desert regions relative to other differences within the California region. We used $P=0.05$ as our cutoff for rejecting the null hypothesis in all statistical analyses.

Multivariate methods of analysis included PCA and discriminant function analysis (DFA). The former assumes nothing *a priori* about potential groupings within the data, instead generating principal components only on the basis of variance in the data. It was used as an exploratory tool (Reyment et al. 1984), both with and without horn variables included, to look at potential size and shape differences and patterns in the Southwest. We used PCA to see if any separation of geographic regions occurred, including Peninsular Ranges versus the Mojave Desert, and what variables were primarily responsible for any such separations. The variation most notable to the eye in series of ram and ewe skulls is horn size and shape. While we included horn variables in PCA, we also excluded them to investigate whether skull variables alone would generate geographic patterns of interest, and because of greater uncertainty regarding environmental (nutritional) influences on horn size. Since an age covariate cannot be used in PCA, we used the results on age effects to eliminate age effects by limiting ages to ≥4 years for ewes, and ≥8 years for rams. PCA was performed on a covariance matrix derived from pairwise analyses of $\log_e$ transformed variables. Pairwise analyses allowed the maximum amount of data to be used, including the use of specimens lacking some measurements. Only a limited subset of the specimens having all measurements could be used for plotting principal component scores. Log_e transformed variables were used for PCA so that the first principal component (PC1) might be interpreted as a size component (Reyment et al. 1984, James and McCulloch 1990).

DFA was used as a multivariate test of the distinction between Peninsular and neighboring Mojave Desert specimens. This was performed for all skull measurements and one horn measurement (HORNVOL) for rams only, since there were too few Peninsular ewe specimens containing complete measurements. Ages were again limited to ≥8 years. Classification success, posterior probabilities, as well as the results of a jackknife procedure (Afifi and Clark 1990), were used to evaluate the reputed distinction between these two geographic regions.

RESULTS AND DISCUSSION

Univariate Analyses

All but 2 variables (PREMAX and TOOTH) exhibited significant age effects for rams, and 1/AGE consistently explained more variation than the other age covariates. These age effects are contrary to the statement by Cowan (1940:561) that "age variation in the skull during this portion of the animals life [adulthood] is not great." When these age effects were removed, only 1 out of 13 variables showed a significant difference between the Mojave Desert and Peninsular subspecies for Grinnell's boundary, while 3 were significantly different for Cowan's boundary (Table 2). However, these 3 differences occurred only when specimens from the Santa Rosa and San Jacinto Mountains were deleted from the analysis. When specimens from these 2 ranges were added to the Mojave Desert instead, only 1 variable differed significantly. Other California regions differed considerably more from each other. For the 13 variables tested, 8 were significantly different between the northern and southern regions of the Nelson subspecies, and the Sierra Nevada was different from each of these 2 regions for 5-6 variables (Table 2). In contrast, Cowan (1940) found all but 3 of his variables to be significantly larger for *O. c. cremnobates* than *O. c. nelsoni*. Age effects apparently were responsible for most of these differences (Ramey 1993).

Only 2 variables (PM2, CHEEK) had significant age effects in the analyses of ewe skulls, and none of the variables were significantly different between the Mojave Desert and either geographic definition of the Peninsular subspecies. In contrast, the 2 regions within the Nelson subspecies differed significantly for 7 of 13 variables, and the Sierra Nevada differed from each of these for 3-4 variables (Table 2). Cowan (1940) noted that *O. c. nelsoni* females were smaller than *O. c. cremnobates* in every measure he took, but that not all were significantly different. Likewise, we found *O. c. cremnobates* larger for 9 of 13 variables summarized in Table 2 for Cowan's boundaries; however, none was significantly different.

Principal Component Analyses

Morphometric analyses often yield all positive loadings for PC1, and this axis is interpreted as representing overall size variation, whereas subse-

Table 2. Numbers of morphometric variables (13 total) that were significantly different ($P \leq 0.05$; Bonferroni multiple comparisons test) for bighorn sheep skulls from regions of California. Two definitions of the range of Peninsular sheep were investigated and are presented as Cowan/Grinnell. Variables included: CRANIAL, PALATE, PREMAX, TOOTH, PM2, CHEEK, ZYGO, INTERORB, INTRAORB, POSTORB, HEIGHT, CORVOL (rams), HORNVOL (rams), HORNC (ewes), and HORNL (ewes).

Region	Peninsular Ranges		Mojave Desert		Sierra Nevada	
	Rams	Ewes	Rams	Ewes	Rams	Ewes
Mojave Desert	3/1	0/0	-	-	-	-
Sierra Nevada	8/10	3/4	6/5	4/4	-	-
Great Basin	10/10	8/9	8/8	7/7	6/6	3/3

quent components with positive and negative loadings are interpreted as representing variation in shape (Reyment et al. 1984, Marcus 1990). PC1 is often disregarded as representing size variation due to age, sex, and environment, in favor of shape components. Since our analyses eliminated the first 2 of these sources of size variation prior to analysis, we began with less overall size variation. Consequently, our first 2 principal components did not account for most of the variation (our highest was 77.4%), which Reyment (1990) suggested as a criterion for interpretation of PC1 as strictly a size component. Also, not all of our PCA's had solely positive loadings for PC1. However, all positive loadings do not necessarily imply complete absence of shape variation (James and McCulloch 1990), and size variation is not necessarily extraneous relative to taxonomic questions. Our results provided an additional reason to treat PC1 as containing useful information.

When horn variables were excluded for rams, PC1 appeared to represent overall variation in skull size, primarily widths, and secondarily lengths and height. This axis largely separated the Sierra Nevada (large skulls) from the adjacent Great Basin region (small skulls; Fig. 1). When horn volume and core length were added to the analysis, horn volume strongly dominated the loadings of PC1, and the Sierra Nevada scored low on this axis along with the Great Basin (Fig. 2). In other words, Great Basin and Sierra Nevada rams both have small horns, but they differ substantially in skull size. If all this size variation were primarily environmentally driven, one would expect a correspondence between skull and horn size. Consequently, we did not disregard the size variation represented by PC1.

When horn variables were added to analyses, both sexes yielded a PC2 that largely represented the skull size variation accounted for by PC1 when horn variables were excluded (thus the separation of the Great Basin from the Sierra Nevada on the PC2 axis in Fig. 2). The subsequent 2 principal components (PC2 and PC3 without horn variables; PC3 and PC4 with horn variables) represented shape variation of the mouth region (feeding apparatus) for both sexes. These components failed to effect geographic separations for either sex, except possibly the San Gabriel Mountains (Fig. 1).

With horn variables included for ewes, PC1 separated the Great Basin and the Sierra Nevada (small horned) from the Mojave Desert and Peninsular Ranges, as it did for rams. Additionally, there was suggestion of a clinal pattern of decreasing horn size from the Mojave Desert and Peninsular Ranges to the Sonoran and Chihuahuan Deserts (Fig. 3).

In general, PCA plots suggested patterns found in univariate analyses -- major overlap between specimens from the Peninsular Ranges and the Mojave Desert, but much less or no overlap of Sierra Nevada and Great Basin specimens with the Mojave Desert and Peninsular Ranges, as well as with each other (Figs. 1-3).

Discriminant Function Analyses

The DFA of ram specimens for the Peninsular and Mojave Desert groups correctly classified 86% and 88% of the specimens for the Grinnell and Cowan definitions, respectively. However, only 46% and 42% of these respective samples were classified with ≥95% probability, suggesting poor classification ability. A jackknife analysis for the Cowan definition verified this yielding a 29% prob-

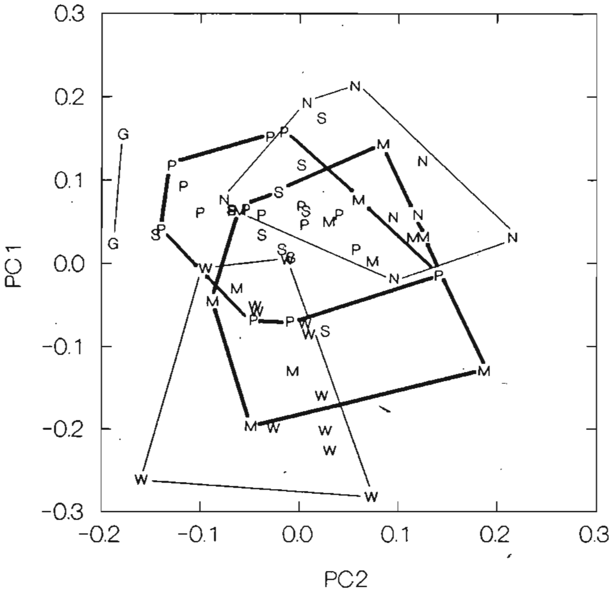

Figure 1. Principal component score plotting for analysis of mountain sheep ram skulls from southwestern United States and Mexico excluding horn variables. G=San Gabriel Mountains; M=Mojave Desert of California south of I-15; N=Sierra Nevada; P=Peninsular subspecies populations as defined by Grinnell (1933); S=Sonoran Desert; W=White Mountains, Death Valley region, and neighboring west central Nevada (Great Basin).

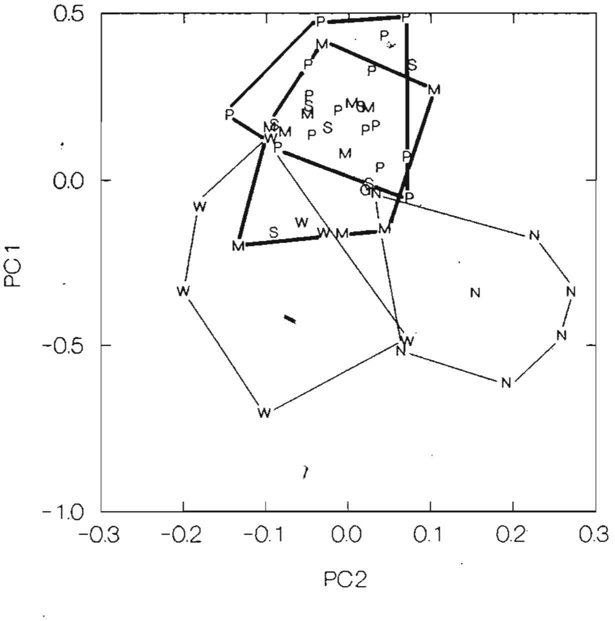

Figure 2. Principal component score plotting for analysis of mountain sheep ram skulls from southwestern United States and Mexico including horn variables. G=San Gabriel Mountains; M=Mojave Desert of California south of I-15; N=Sierra Nevada; P=Peninsular subspecies populations as defined by Grinnell (1933); S=Sonoran Desert; W=White Mountains, Death Valley region, and neighboring west central Nevada (Great Basin).

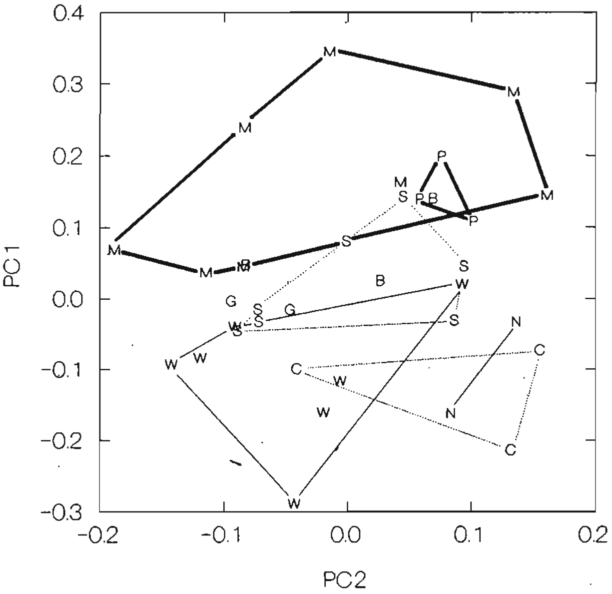

Figure 3. ***Principal component score plotting for analysis of mountain sheep ewe skulls from southwestern United States and Mexico including horn variables. B=southern Baja California; C=Chihuahuan Desert; G=San Gabriel Mountains; M=Mojave Desert of California south of I-15; N=Sierra Nevada; P=Peninsular subspecies populations as defined by Grinnell (1933); S=Sonoran Desert; W=White Mountains, Death Valley region, and neighboring west central Nevada (Great Basin).***

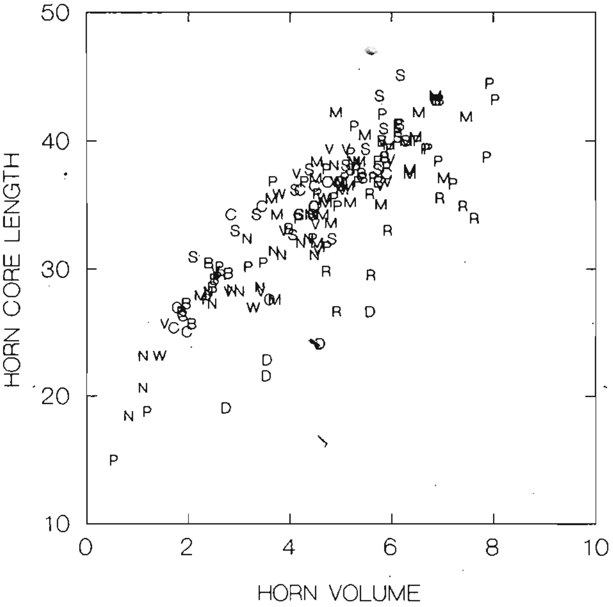

Figure 4. ***The relationship between horn core length (cm) and an index of horn volume (l) for mountain sheep ram skulls from southwestern United States, Mexico, the Rocky Mountains, and Dall Sheep from Canada and Alaska. B=southern Baja California; C=Chihuahuan Desert; G=San Gabriel Mountains; M=Mojave Desert of California south of I-15; N=Sierra Nevada; P=Peninsular subspecies populations as defined by Grinnell (1933); S=Sonoran Desert; W=White Mountains, Death Valley region, and neighboring west central Nevada (Great Basin); R=Rocky Mountains; and D=Dall Sheep.***

ability of misclassifying Peninsular specimens as Mojave Desert, and a 60% probability of misclassifying Mojave Desert specimens as Peninsular. Overall, this was a 46% probability of misclassification, about equivalent to flipping a coin weighted by the proportions of each group in the sample, which would yield a misclassification rate of 49%. In other words, DFA was unable to differentiate Peninsular and Mojave Desert ram skulls.

The Role of Horns Relative to Evolution and Taxonomy

Cowan (1940) noted that the largest horned ewes in North America were the Peninsular and Weems subspecies, and that *O. c. cremnobates* rams had larger horns than *O. c. nelsoni* rams. Our results refuted both of these statements about horns. It was not possible to distinguish sheep on the basis of horn size between Peninsular Ranges and the Mojave Desert when age effects were removed; this was true of both sexes.

However, other regions showed marked differences in horn size. Until variation in horn growth of mountain sheep can be partitioned between genetic and environmental components, some caution should be exercised in the interpretation of differences in horn measurements relative to taxonomy. Wehausen (1991) suggested a possible adaptive reason for larger horns on ewes from the warm deserts. Our results also provided reasons to believe that more than environmental variation underlies horn size variation in rams. First was the lack of correspondence between skull and horn size for rams from the Southwest. Second was the finding that horn core length in rams may be an important shape variable on a larger geographic scale. For the Southwest alone, there was a strong ($r^2=0.843$) curvilinear relationship between horn core length and horn volume (lnHORNVOL), suggesting a coupled growth pattern for horns and cores. However, Rocky Mountain and Dall sheep had shorter cores for equivalent horn volume (Fig. 4), implying different developmental patterns. Therefore, we conclude that horns and their supporting cores should not be ignored in morphometric studies.

Some of the variation in horn size and core length of rams may be adaptive. Taylor (1966) and Geist (1971) discussed the high potential for heat loss through horns. Our finding that horn size of both sexes decreased from the hot deserts of California north to the cold desert regions suggests possible hypotheses regarding selection relative to heat loss through these appendages. The apparent decreasing size of ewe horns from the Mojave Desert to the hot Sonoran Desert does not support the idea of selection for larger horns in the desert for heat dissipation. However, these findings do not preclude the possibility that heat loss has selected against large horns in the cold deserts, especially alpine habitats, where winter temperatures and wind chills can be severe (Picard et al. 1994). Heat loss from horns should be related to the amount of vascularized core. The correlation of horn volume and core length for southwestern rams means that smaller horns will be associated with reduced potential for heat loss, and might explain the smaller horns in the colder climates of the Sierra Nevada and Great Basin ranges.

The short horn cores of Rocky Mountain and Dall sheep may represent a different evolutionary solution to this problem that does not necessarily compromise horn size. Winter heat loss should be most extreme for Dall sheep. They have particularly short cores relative to horn volume (Fig. 4), and may combine this adaptation with limited horn growth to minimize winter heat loss. Thus, while sexual selection (Trivers 1972) should select for large horns in rams, an opposing selection related to heat loss and winter survival may vary with habitat and be responsible for some of the horn-related variation in North American wild sheep.

CONCLUSIONS

Darwin (1859) noted that there are no clear criteria for designating taxonomic divisions below the species level, and there remains no convention in this regard. However, Avise and Ball (1990:60) suggested that subspecies should be, "actually or potentially interbreeding populations phylogenetically distinguishable from, but reproductively compatible with, other such groups". This study found no evidence that the Peninsular subspecies could be reliably distinguished from the adjacent Mojave Desert, a finding corroborated by genetic results (Ramey 1993). Given Ramey's (1993) reanalysis of Cowan's (1940) original data, there really never has been any support for a Peninsular subspecies. Consequently, we synonymize it with the Nelson subspecies.

In contrast, we found notable differentiation between regions within the Nelson subspecies, as suggested by Bradley and Baker (1967). Similarly, the Sierra Nevada showed substantial differences from other regions investigated, including the adjacent Great Basin. These patterns also are corroborated by Ramey's (1993) findings of a unique mtDNA haplotype for all samples from the Sierra Nevada and a haplotype unique to and well represented in the Great Basin region. While these findings lend support for taxonomic distinction in the Sierra Nevada relative to nearby regions, they do not necessarily provide support for Cowan's (1940) definition of the California subspecies as a whole.

Current subspecies classification of mountain sheep reflects an antiquated typological thinking that lacks an adequate evolutionary basis (Mayr 1982). Cowan (1940) at least acknowledged a shortcoming in this approach by designating intergradation zones. To use our findings of apparent uniqueness in the Great Basin to propose the separation of *O. c. nelsoni* into 2 subspecies would be to further perpetuate a typological approach. Instead, we consider *O. c. nelsoni* to be a polytypic taxon possessing some regional genetic and morphological differentiation. If a taxonomic label is a prerequisite for adequate conservation attention, we believe that the more appropriate choice would be the designation of geographic races that reflect some of this variation. As a taxonomic term, geographic race lacks any connotation of incipient speciation or possession of characters that clearly distinguish it from other races (Mayr 1969).

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