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CRANIAL MORPHOMETRIC AND EVOLUTIONARY RELATIONSHIPS IN THE NORTHERN RANGE OF *OVIS CANADENSIS*

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Univariate and multivariate statistical methods were used to examine geographic variation in skull and horn characters of 694 bighorn sheep (*Ovis canadensis*) specimens from the Great Basin north to British Columbia and Alberta to test previous taxonomic hypotheses. Substantially more morphometric variation in skull and horn size and shape was found west of the Rocky Mountains than within the Rocky Mountains. Our results did not support the recognition of Audubon's bighorn sheep (*O. c. auduboni*) as a subspecies separate from Rocky Mountain bighorn sheep (*O. c. canadensis*). California bighorn sheep (*O. c. californiana*) from Washington and British Columbia were not distinguishable from Rocky Mountain bighorn sheep but differed notably from populations in the Sierra Nevada considered part of that subspecies. Extirpated native populations from northeastern California, Oregon, and southwestern Idaho, also considered to be *O. c. californiana,* shared with Nelson bighorn sheep (*O. c. nelsoni*) from the Great Basin desert a horn-related character that distinguished them from Rocky Mountain bighorn sheep. Bighorn sheep from the Sierra Nevada were found to be distinguishable from those of the adjacent Great Basin region. Our morphometric results were concordant in geographic patterns with mtDNA data. We synonymize *O. c. auduboni* with *O. c. canadensis.* We also assign extant and extinct native populations of *O. c. californiana* from British Columbia and Washington to *O. c. canadensis.* Finally, we assign the extinct native populations of *O. c. californiana* from Oregon, southwestern Idaho, northern Nevada, and northeastern California to the Great Basin Desert form of *O. c. nelsoni,* recognizing that some transition to Rocky Mountain bighorn sheep probably occurred along that northern boundary. With these taxonomic revisions, the range of *O. c. californiana* includes only the central and southern Sierra Nevada.

Key words: bighorn sheep, *Ovis canadensis,* skull morphometry, taxonomy

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The long-accepted taxonomy of bighorn sheep (*Ovis canadensis*), based on comparisons of skull measurements by Cowan (1940), has separated bighorn sheep into 3 northern and 4 desert subspecies (Shackleton 1985). Although that taxonomy represented a pioneering attempt to introduce quantitative methods to describe variation and test taxonomic hypotheses, the resolution and results were influenced by small samples, age-related effects on size, and violation of statistical assumptions. As a result, statistical reanalysis of Cowan's (1940) original data has not found support for most of his subspecific designations, including the 4 desert subspecies (Ramey 1993). Consequently, there has been need for a revision of *O. canadensis* taxonomy based on new data.

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Patterns of mitochondrial DNA (mtDNA) variation were not concordant with Cowan's (1940) definitions of subspecies (Ramey 1993, 1995) but were consistent with Ramey's (1993) reanalysis of Cowan's (1940) limited data. Our development and analysis of a new and larger cranial morphometric data set has produced similar results, and on the basis of concordant results of morphometric and mtDNA analyses, we synonymized peninsular bighorn sheep (*O. c. cremnobates*) with *O. c. nelsoni* (Wehausen and Ramey 1993). However, considerable cranial morphometric variation was found within *O. c. nelsoni*, and bighorn sheep from the desert regions appeared to have general north–south differentiation into 2 basic forms, hot (Mohave, Sonoran, and Chihuahuan) desert sheep and cold (Great Basin) desert sheep (Wehausen and Ramey 1993, in litt.). Here, we expand the geographic scope of our cranial-morphometric analyses to investigate variation in the region of Cowan's (1940) 3 northern subspecies. Our previous analyses left the northern limit of *O. c. nelsoni* in the Great Basin undefined. Because the Great Basin connects the southern extremes of the ranges of *O. c. californiana* and *O. c. canadensis* as defined by Cowan (1940), it was necessary to include *O. c. nelsoni* in this investigation. Consequently, the southern boundary of this analysis includes the southern Sierra Nevada, adjacent desert to the east in California, all but very southern Nevada, and the Rocky Mountains of Colorado. Cowan (1940) considered the bighorn sheep of the river canyons of southern Utah to be the Rocky Mountain subspecies, but that was not supported by mtDNA data (Ramey 1995). Therefore, we have excluded specimens from that region for this analysis and will address morphometric affinities of that region elsewhere relative to the southwestern desert region.

Within this geographic region, Cowan (1940) identified 4 subspecies: the extinct *O. c. auduboni* that occupied river break and badlands habitats immediately east of the Rocky Mountains in eastern Montana and Wyoming, North Dakota, South Dakota, and western Nebraska; *O. c. canadensis* that ranged from the southern Rocky Mountains to Alberta; *O. c. californiana* that ranged west of the Rocky Mountains from British Columbia south through eastern Washington and Oregon, southwestern Idaho, northwestern Nevada, and northeastern California, to the southern Sierra Nevada; and *O. c. nelsoni*, occurring across the Great Basin desert of California and Nevada east of the southern and central Sierra Nevada.

Because morphological variation can reflect contributions of genetic and environmental components to individual development, it potentially describes genetic and ecophenotypic variation. Therefore, we consider our morphometric studies to be complementary to studies of variation in DNA sequences. However, our morphometric analyses also have allowed us to investigate regions for which no DNA data currently exist because of extinction of all native populations.

Ball and Avise (1992) suggested that subspecies should represent major subdivisions of the gene pool diversity within species where such subdivisions can be supported by concordant distribution of multiple independent genetically based traits. This criterion requires that subspecies be distinguishable and that they have an evolutionary basis. We used criteria of Ball and Avise (1992) to test the hypothesis that the current subspecies taxonomy based on Cowan (1940) reflects evolutionarily distinct units. We considered differences between reputed subspecies in the context of variation on a larger geographic scale. We also looked for variation not accounted for by current designations of subspecies. Our research attempts to identify evolutionarily significant units (ESUs—Moritz 1994a, 1994b; Ryder 1986) that can help conservation efforts focus attention to preserve the genetic diversity found within and among distinct population segments of this species.

Materials and Methods

We used univariate and multivariate statistical methods to examine geographic variation in skull and horn characters and to test previous taxonomic designations as hypotheses. Our specimens were limited to native populations, and we used measurements developed previously (Wehausen and Ramey 1993, in litt.) to describe 4 attributes of skulls: lengths, widths, height, and horns (Appendix I). To the extent possible, those were based on homologous landmarks such as intersections of suture lines (Bookstein 1990). Our horn measurements for males included 5 circumferences of the largest horn, which were used to calculate an index of horn volume. We previously found important discriminating variation among males in length of horn cores relative to volume of horns (Wehausen and Ramey 1993). Consequently, we measured circumferences of horn cores at 2 fixed distances back from the basal burr that allowed calculation of the rate at which cores taper (TAPER3–6). We revisited as many skulls previously measured as possible to add those new variables to our database. For the region of this analysis, our total sample size was 408 male and 249 female specimens (Appendix II).

All specimens were aged by tooth replacement and horn annuli or given a minimum age based on tooth wear if horns were lacking. Age was recorded as growth years. Based on previous analyses of curvilinear effects of age on many skull measurements (Wehausen and Ramey 1993), we eliminated that variation when possible by limiting ages to ≥8 growth years for males and ≥4 growth years for females, except where noted. That reduced our usable sample sizes for many analyses to the following by locations (male : female): Great Basin 55:61; Sierra Nevada 22:29; northeastern California 7:0; Oregon 4:1; southwestern Idaho 1:0; Salmon River, Idaho 11:10; Washington 17:7; British Columbia west of Rockies 24:54; Canadian Rockies 40:53; Montana and Waterton Lakes National Park 9:11; Wyoming 6:4; Colorado Rockies 14:15; and east of Rocky Mountains 1:4. When analyses yielded no justification for separation of adjacent geographic regions, we combined them to increase sample sizes and develop meaningful geographic boundaries. Many multivariate statistical analyses were limited to specimens having measurements for all variables used, resulting in varying sample sizes on some plots.

We used principal components analysis (PCA) as a descriptive exploratory tool (Reyment 1990) to look for geographic patterns in distribution of variation across the study area and identify variables that contributed strongly to overall morphological variation. We ran PCA without horn size variables. PCA was performed on covariance matrices derived from pairwise analyses of natural-log-transformed variables (Reyment et al. 1984). Because we eliminated most age-related variation in size before analysis, we did not employ shearing (Humphries et al. 1981).

We tested univariate differences among subspecies and other regional groupings using analysis of variance (ANOVA) with the Bonferroni correction for multiple comparisons (Neter and Wasserman 1974). Fifteen variables were used for each sex. For *O. c. auduboni*, the sample of males contained only 2 from North Dakota (ages 3, 6); 2 from South Dakota (ages 4, 4); and 3 from eastern Montana (ages 7, 7, 8). For those, we used ANCOVA with an age covariate, or simple ANOVA when there was no significant age effect, to use every specimen.

On a multivariate level, we tested distinguishability between groups with linear discriminant analysis. We used an interactive stepwise procedure to develop the simplest models to maximize the ratio of sample size to variables included (Williams and Titus 1988) by eliminating statistically unimportant variables. We used jackknifed estimates of posterior probabilities and classification ability for discriminant models (Afifi and Clark 1990). Our criterion for distinguishability between groups was ≥90% of specimens of at least 1 sex correctly classified at jackknifed posterior probabilities ≥0.95. That criterion resulted in >95% correct jackknifed classifications but was more discriminating than using just percentage of specimens correctly classified.

We also further explored the relationship between length of horn cores and volume of horns of males as a discriminating shape variable to distinguish Rocky Mountain and desert bighorn sheep (Wehausen and Ramey 1993). That character was used for the region of northeastern California and Oregon, where small samples of largely fragmentary specimens precluded use of multivariate statistics.

Our previous work showed that horn volume exhibited the greatest overall variation. Although some of that variation may have represented useful genetic variation (Wehausen and Ramey 1993), much may have been derived from different nutritional levels and represented environmental noise. Consequently, to assess other variables that might be developmentally linked to horn growth, we investigated relationships for males between volume of horn and other skull variables via regressions, including log and reciprocal transformations to account for curvilinearity. We included samples from the entire desert region for this analysis.

RESULTS

Correlations between Horn Size and Skull Variables for Males

All variables except PREMAX were significantly correlated with horn volume. Relationships were largely curvilinear with natural log of horn volume accounting for more variation in almost all cases. Due to large sample sizes (397–610 for all ages and 219–329 for age ≥8), most regressions were highly significant, but many explained small proportions of the variation. Notable exceptions were variables that involved some aspect of frontal bone development (HEIGHT, POSTORB, CORC3), which explained greater percentages of horn volume variation (r^2 = 0.448–0.581 for all ages and 0.372–0.464 for age ≥8), indicating that skull and horn size do covary. However, rate of taper of the horn core (TAPER3–6) had a smaller correlation (r^2 = 0.041 for all ages; 0.043 for age ≥8) because that variable included important geographic variation not related to horn size (Wehausen and Ramey 1993). Variables that described the facial (anterior) region (PM2, CHEEK, TOOTH, PALATE, PREMAX) were least correlated with horn size (r^2 = 0.002–0.352 for all ages; 0.011–0.115 for age ≥8), indicating that the facial skull region may develop largely independently of the cranial region, as Shackleton (1973) noted.

Principal Components Analyses

For both sexes, principal component 1 (PC1) loaded strongest to horn core variables and premaxilla length (Table 1). Important horn core variables were rate of taper and, secondarily, circumference for males and circumference and, secondarily, length for females. For both sexes, premaxilla length had a stronger loading than the secondary core variable. Rocky Mountain males tended to score high on this axis compared with sheep from the Great Basin and Sierra Nevada because the former possessed horn cores with large basal circumference and a high rate of taper (Fig. 1A). Female Rocky Mountain sheep also scored high on this axis because of small horn cores and negative loadings for horn core variables (Fig. 1B, Table 1). For both sexes, that component suggested that Rocky Mountain sheep should have longer premaxillae. Core length joined the other core variables as dominant loadings of PC2 for males. A negative loading for core taper meant that long, large cores with low taper scored high on this axis, but many other variables contributed secondary positive loadings. That component may have been a general size component but effected no geographical separation for males. For females, palate width and premaxilla length loaded strongest on PC2, and horn core variables were among the weakest (Table 1). All positive loadings suggested that that axis reflected general skull size other than horn cores, for which Great Basin sheep tended to score lower than all other regions (Fig. 1B).

For males, premaxilla length loaded strongest on PC3, with strong negative loadings for horn core length and circumference. That axis substantially separated Sierra Nevada from adjacent Great Basin specimens (Fig. 1A). Premaxilla length was again one of the strongest loadings on PC3 for females, but that axis effected no geographic separation. Higher PCs produced no geographical separations for either sex.

For males, the plot of PC1 against PC3 produced the best geographical separation (Fig. 1A), with almost complete separation of Rocky Mountain, Great Basin, and Sierra

TABLE 1.—Loadings and percentage of variance explained for principal components from analyses based on the covariance matrix of log-transformed variables for skulls of bighorn sheep. Variables defined in Appendix 1.

	PC1	PC2	PC3	PC4	PC5
Males					
CRANIAL	0.012	0.024	0.029	0.004	−0.019
PALATE	0.018	0.023	−0.023	0.036	0.045
PREMAX	0.053	0.025	0.065	−0.052	0.013
TOOTH	0.012	0.008	0.003	−0.007	0.014
PM2	0.015	0.031	0.030	0.053	−0.025
CHEEK	0.017	0.025	0.022	0.018	−0.001
ZYGO	0.024	0.020	0.015	0.011	0.005
INTRAORB	0.012	0.004	−0.001	0.005	0.001
INTERORB	0.026	0.029	0.028	0.013	0.004
POSTORB	0.029	0.037	0.008	0.003	−0.002
HEIGHT	0.026	0.029	−0.002	0.001	0.002
CORL	−0.004	0.061	−0.051	−0.022	−0.032
CORC3	0.046	0.060	−0.046	−0.013	0.013
TAPER3–6	0.158	−0.055	−0.023	0.005	−0.013
% explained	38.026	19.357	15.042	9.047	5.338
Females					
CRANIAL	0.013	0.030	−0.013	0.001	0.017
PALATE	0.005	0.023	0.050	0.024	0.009
PREMAX	0.022	0.043	−0.043	0.004	0.018
TOOTH	0.002	0.015	0.007	0.017	0.015
PM2	0.005	0.062	0.010	−0.031	−0.034
CHEEK	0.003	0.035	0.009	−0.003	0.003
ZYGO	0.006	0.024	0.004	0.001	0.009
INTRAORB	0.001	0.015	−0.003	−0.001	0.001
INTERORB	0.009	0.031	0.007	0.002	0.005
POSTORB	−0.010	0.028	−0.002	0.012	0.002
HEIGHT	−0.003	0.024	0.000	0.009	0.004
CORL	−0.151	0.006	0.005	−0.021	0.020
CORC	−0.079	0.013	−0.018	0.040	−0.031
% explained	47.126	8.767	8.201	6.429	5.691

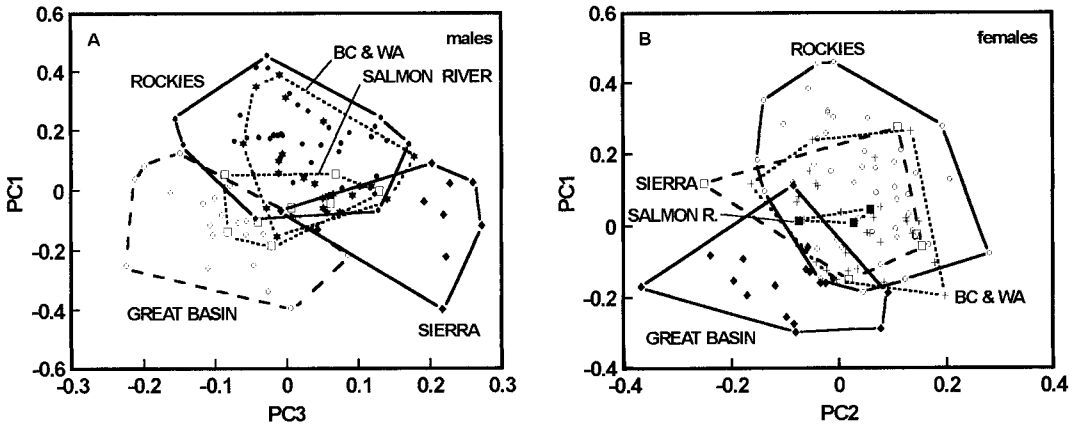

FIG. 1.—Plottings of principle components scores that yielded the greatest geographic separations for the northern region of A) male and B) female bighorn sheep.

TABLE 2.—Numbers of morphometric variables out of 15 that were significantly different ($P \leq 0.05$) in ANOVAs with Bonferroni multiple comparisons tests for male skulls of bighorn sheep from 4 western (left) and 4 Rocky Mountain (right) regions.

	Great Basin	Sierra Nevada	Northeastern California and Oregon		Alberta	Montana	Wyoming
Sierra Nevada	10			Montana	1		
Northeastern California and Oregon	11	7		Wyoming	0	0	
British Columbia and Washington	12	10	6	Colorado	4	0	0

Nevada specimens. *O. c. californiana* specimens from British Columbia and Washington almost entirely overlapped the Rocky Mountain polygon, whereas those from the Salmon River in west central Idaho were intermediate between the Rocky Mountain and Great Basin specimens, with a stronger affinity with the former (Fig. 1A). For females, the plot of PC1 against PC2 produced the most pronounced regional separation. The Great Basin and Rocky Mountains polygons only slightly overlapped. However, in contrast with males, the Sierra Nevada specimens largely fell within the Rocky Mountain polygon. Again, *O. c. californiana* specimens from British Columbia and Washington appeared to be a subset of Rocky Mountain bighorn sheep (Fig. 1B).

When a reduction in PCA variables to 9 (CRANIAL, TOOTH, PM2, CHEEK, POSTORB, HEIGHT, CORL, CORC3, TAPER3–6) was used for males to plot 1 specimen of *O. c. auduboni,* the same 3 groupings occurred but with more overlap. The *O. c. auduboni* specimen fell just outside the Rocky Mountain polygon. Specimens from Oregon and northeastern California fell entirely within the Great Basin polygon but also overlapped the Sierra Nevada, the Rocky Mountains, and Salmon River somewhat. When number of variables for females was decreased to 9 to allow inclusion of 3 *O. c. auduboni* specimens, those specimens fell within the Rocky Mountain bighorn polygon.

Analysis of Variance

Males.—A comparison between northeastern California and Oregon for males ≥6 years old (to enhance sample size) yielded significant differences for only 2 horn-related variables (POSTORB and CORC3), both of which were larger for northeastern California specimens. Consequently, we lumped those 2 adjacent and biogeographically continuous regions. Similarly, in the northern range of *O. c. californiana,* only CORC3 differed between specimens from Washington and British Columbia for age ≥8 years, so we also lumped those adjacent and biogeographically continuous regions.

We compared univariate differences in 4 regions west of the Rocky Mountains (Sierra Nevada, Great Basin, NE California and Oregon, and Washington and British Columbia) and 4 regions within the Rocky Mountains (Alberta, Montana, Wyoming, and Colorado) using ages ≥7 years to enhance sample sizes. Specimens from the region west of the Rocky Mountains showed much regional distinction, but Rocky Mountain samples showed little (Table 2). Colorado specimens dominated the few differences within the Rocky Mountains, having smaller means for CRANIAL, PALATE, CHEEK, and TOOTH. Because differences in sample sizes could influence that apparent difference in regional variation, average absolute differences between group means for the 4 western regions were compared with the 4 Rocky Mountain regions (excluding TAPER3–6, which had

TABLE 3.—Numbers of morphometric variables out of 15 that were significantly different ($P \leq 0.05$) in ANOVAs with Bonferroni multiple comparisons tests for female skulls of bighorn sheep from 3 western (left) and 3 Rocky Mountain (right) regions.

	Great Basin	Sierra Nevada		Alberta and Montana	Wyoming
Sierra Nevada	8		Wyoming	0	
British Columbia and Washington	12	5	Colorado	1	1

not been measured for many Colorado skulls), and the same pattern resulted. Differences among means within the region west of the Rocky Mountains were 4.2 times greater than those within the Rocky Mountains on average, and no variables in the western region showed smaller differences than within the Rocky Mountains.

Comparison of *O. c. californiana* specimens from Washington and British Columbia with Rocky Mountain samples from Alberta and Montana (age ≥8 years) yielded 6 significant differences (CRANIAL, PREMAX, POSTORB, HEIGHT, HORNVOL, and TAPER3–6) out of 15 variables, with Rocky Mountain bighorn sheep having larger values for all variables except TOOTH and horn volume greater by 1.72 liters on average.

Results of an ANCOVA comparing *O. c. auduboni* specimens with adjacent Montana and Wyoming samples combined found a significant difference only for PALATE ($P = 0.001$). All Audubon bighorn males had notably short palates but only barely exceeded the lower range for the Montana and Wyoming specimens. For comparisons of *O. c. auduboni* specimens with all Rocky Mountain samples, CRANIAL joined PALATE in significance ($P = 0.013$ for CRANIAL; $P < 0.001$ for PALATE). For CRANIAL, the mean was greater for *O. c. auduboni* specimens and the range slightly exceeded that of Rocky Mountain samples at the upper end. Because many of those skulls were quite weathered, loss of palate bone and separation along its midline suture probably caused an apparent increase in CRANIAL and related decrease in PALATE lengths. The combined length was not different ($P = 0.836$); consequently, we consider those differences as artifacts.

Females.—Comparison of *O. c. californiana* specimens between Washington and British Columbia revealed a difference only for INTRAORB ($P = 0.048$); therefore, those 2 regions were combined, leaving 3 geographic regions west of the Rocky Mountains. Comparison among the 4 Rocky Mountain states found only 3 significant differences, all involving Colorado specimens. Consequently, we combined Alberta and Montana to yield 3 geographic regions for comparison with the area to the west.

As with males, comparisons within the 3 western areas found considerable differentiation for females, but the Rocky Mountains showed little, all involving Colorado specimens (Table 3). On average, differences between group means for females from the western regions were 71.6% greater than for the Rocky Mountains, which was much less than for males. The Rocky Mountain specimens also had greater differences for 5 of 15 variables.

When *O. c. californiana* females from Washington and British Columbia were compared with Rocky Mountain samples from Alberta and Montana, only INTRAORB differed ($P = 0.048$).

The sample of *O. c. auduboni* females consisted of 3 skulls from eastern Montana (ages 4, 4, 5) and 1 from North Dakota (age 6). Comparisons of those specimens with samples from Montana and Wyoming combined yielded no significant differences, and comparisons with the entire Rocky Mountains yielded 1 difference: TOOTH was longer for *O. c. auduboni* ($P = 0.018$)

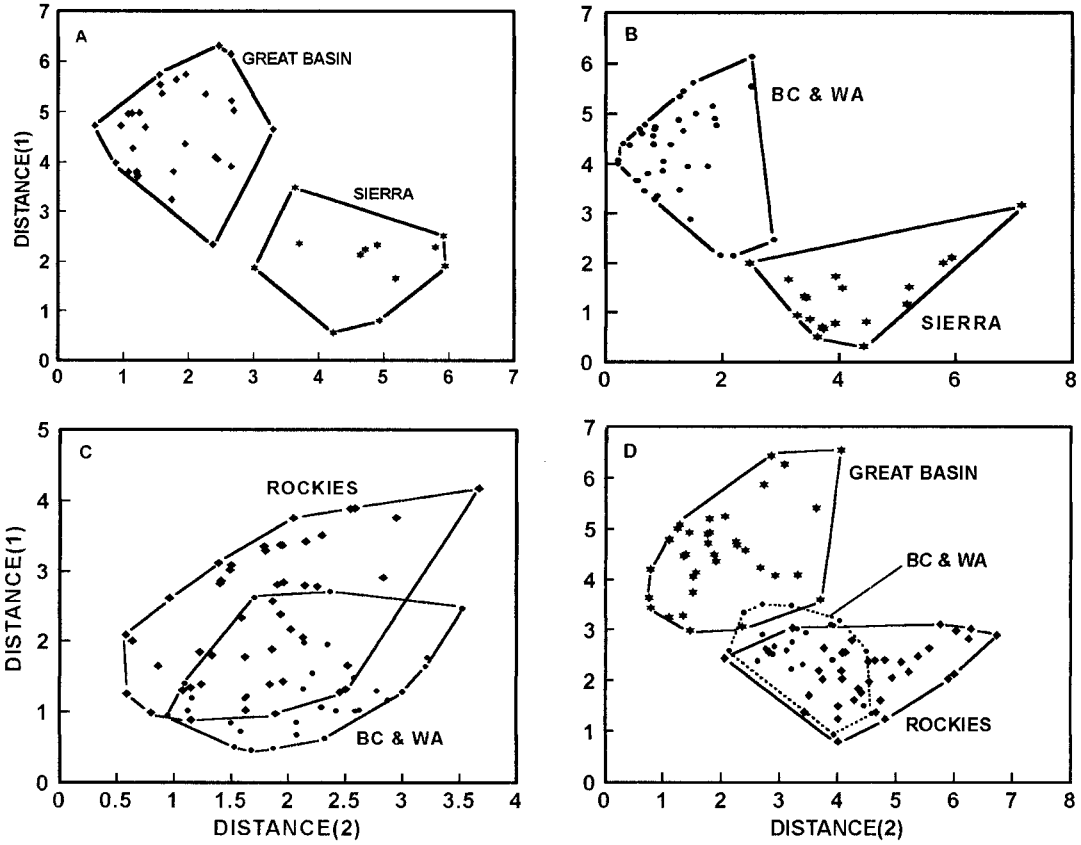

FIG. 2.—Plots of Mahalanobis distances from discriminant analyses of skull measurements of male bighorn sheep for A) the Great Basin Desert versus the Sierra Nevada, B) California bighorn from British Columbia and Washington versus the Sierra Nevada, C) California bighorn in British Columbia and Washington versus the Rocky Mountains north of Colorado, and D) northern Rocky Mountains versus Great Basin Desert, for which the discriminant function was used to plot specimens from British Columbia and Washington.

but fell entirely within the range for Rocky Mountain specimens. Neither CRANIAL nor PALATE showed differences as they did for males.

Discriminant Analyses

Males.—Comparison between the Sierra Nevada and Great Basin produced good discrimination using 4 variables (CRANIAL, PREMAX, CHEEK, and CORC; Fig. 2A). Correct classification occurred for 95.3% of the specimens, nd 90.7% of those were at $P \geq 0.95$. The Sierra Nevada also showed good discrimination from *O. c. californiana* from Washington and British Columbia using only 2 cranial variables (CRANIAL and HEIGHT), with 96.6% correctly classified and 93.2% at $P \geq 0.95$ (Fig. 2B). Addition of further variables strengthened that model.

In contrast, poor separation occurred between *O. c. californiana* from Washington and British Columbia and Rocky Mountain samples from Alberta, Montana, and Wyoming (Fig. 2C). The best model used CRANIAL, TAPER3–6, and HORNVOL but classified only 81.6% correctly and only 37.1% at $P \geq 0.95$.

Great Basin specimens were distinguishable from Rocky Mountain samples, with a

5-variable model (PREMAX, ZYGO, HEIGHT, CORL, and HORNVOL) correctly classifying 95.9% of specimens and 91.9% at $P \geq 0.95$. When *O. c. californiana* specimens from British Columbia and Washington were classified by that model, they showed a strong Rocky Mountain affinity (78.3% classified as Rocky Mountain) but some tendency toward the Great Basin (Fig. 2D). Specimens from the Salmon River in western Idaho showed a similar tendency with 7 of 8 specimens classified as Rocky Mountains.

We attempted to develop a discriminant function separating the Great Basin from the Rocky Mountains to classify intermediate regions containing only fragmentary skulls (skull caps with horn cores). Many of those specimens were aged conservatively as ≥5 years; consequently that minimum age was used in the analysis. However, using just horn core variables (CORL, CORC3, and TAPER3–6), only 40% of specimens were classified correctly at $P \geq 0.95$, and 10% were misclassified. Thus, although core shape has important geographic differences between these regions, alone it was insufficient to discriminate between them reliably.

Females.—The best model to separate the Sierra Nevada from the adjacent Great Basin included 3 variables (CRANIAL, INTERORB, and CORL) but did not meet our criterion for distinguishability. Classifications were correct for 92.5% of the specimens, but only 87.5% were at $P \geq 0.95$ (Fig. 3A). Four variables (CRANIAL, PREMAX, POSTORB, and CORL) adequately separated the Great Basin from the Rocky Mountains, with 95.1% correctly classified and 93.4% at $P \geq 0.95$. Classification of *O. c. californiana* specimens from British Columbia and Washington again showed a stronger Rocky Mountain affinity (61.3% classified as Rocky Mountains), but more of an intermediate tendency than for males (Fig. 3B).

As with males, *O. c. californiana* from Washington and British Columbia showed poor separation from the Rocky Mountains north of Colorado. The best model included 4 variables (CRANIAL, INTRAORB, POSTORB, and HORNC) and correctly classified only 87.5% and 35.5% at $P \geq 0.95$ (Fig. 3C). *O. c. californiana* specimens from Washington and British Columbia versus those from Sierra Nevada also failed to meet our criterion for distinguishability. Although 3 variables (CRANIAL, INTRAORB, and TOOTH) correctly classified 96.1% of the specimens, only 76.5% were at $P \geq 0.95$ (Fig. 3D).

Relationship between Horn Core Length and Horn Volume for Males

The relationship between horn volume and horn core length for the Great Basin desert was linear, but curvilinear for the Rocky Mountains (Fig. 4). Results of ANCOVA could not distinguish specimens from northeastern Nevada from the rest of the Great Basin in that relationship ($P = 0.973$). A combined sample from northeastern California and Oregon similarly was not distinguishable from the Great Basin ($P = 0.931$), despite some particularly large horn volumes where the Great Basin and Rocky Mountains are most divergent in this relationship (Fig. 4).

DISCUSSION

Our results suggest that male *O. canadensis* show more geographic distinction than females. In part, this may be due to some convergent evolution among females in the Rocky Mountains and Sierra Nevada. Because our criterion for morphometric distinction required differences in only 1 sex, we were able to identify 3 groups that warranted consideration for subspecific status. Geographically, these did not coincide with the subspecies taxonomy derived from Cowan (1940). We discuss these differences by traditional subspecies designations.

Ovis canadensis auduboni.—Cowan (1940) reported that females of the Audubon subspecies had wider nasal and maxillary widths, and possibly also mastoid

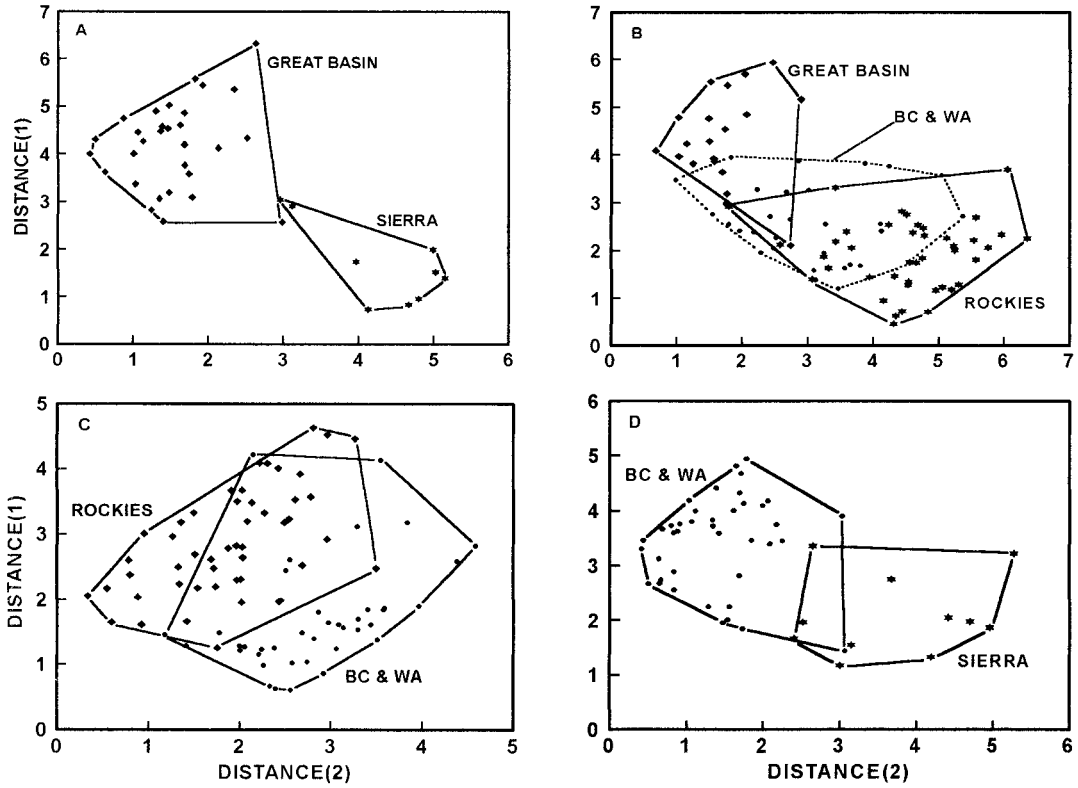

FIG. 3.—Plots of Mahalanobis distances from discriminant analyses of skull measurements of female bighorn sheep for A) the Great Basin Desert versus the Sierra Nevada, B) the Great Basin Desert versus the Rocky Mountains north of Colorado, for which the discriminant function was used to plot California bighorn specimens from British Columbia and Washington, C) California bighorn in British Columbia and Washington versus the Rocky Mountains north of Colorado, and D) California bighorn from British Columbia and Washington versus the Sierra Nevada.

breadth, whereas males had larger basioccipital width and possibly longer upper tooth row. Cowan's (1940) sample of *O. c. auduboni* included only 2 males (both immature at 4 years) and 2 females (one immature and one 6 years old). Because his sample sizes were small, he used the variance from his Rocky Mountain sample to derive a standard deviation for *O. c. auduboni* and calculate probabilities of significance. This is not a valid statistical technique. Cowan (1940:543) cautiously stated that "*O. c. auduboni* based as it is on slight cranial characters presented by a small number of specimens is to be regarded as a weak race." We consider this evidence to be insufficient support for taxonomic distinction.

With our larger sample, we found only a single difference between females of *O. c. auduboni* and *O. c. canadensis*, and 2 differences for males that were probably weathering artifacts. These few differences must be interpreted in the context of larger geographic variation. If Audubon bighorn sheep were to be considered a valid subspecies on the basis of the few differences found, then the Colorado Rockies should similarly be considered a separate subspecies in that region. However, this is not supported by molecular genetic data (Luikart and Allendorf 1996). It is difficult to imag-

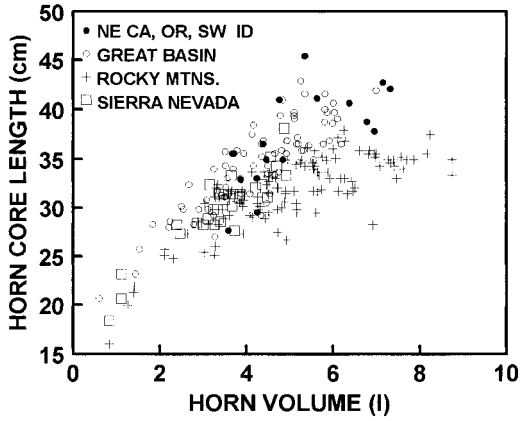

FIG. 4.—The relationship between horn core length and horn volume for skulls of male bighorn sheep from 4 regions: northeastern California, Oregon, and southwestern Idaho; the Great Basin Desert of California and Nevada; the Sierra Nevada Mountains of California; and the Rocky Mountains.

ine any biogeographic barriers that would have separated Audubon and Rocky Mountain bighorn sheep, especially given that during periods of Pleistocene glacial advance, most of the foothills of the Rocky Mountains and plains to the east were open steppe habitat (Barnosky et al. 1987) conducive to bighorn sheep dispersal. Based on our findings and the lack of support in Cowan's (1940) analysis, we synonymize *O. c. auduboni* with *O. c. canadensis.*

Ovis canadensis californiana.—Mitochondrial DNA analysis found *O. c. californiana* to be polyphyletic because specimens from the Sierra Nevada were assigned to the desert bighorn sheep clade while British Columbia samples had the same haplotype as Rocky Mountain bighorn sheep to the east and thus were part of the Rocky Mountain clade (Ramey 1993). Our morphometric results showed the same pattern. California bighorn sheep from Washington and British Columbia were not distinguishable from Rocky Mountain bighorn sheep but were notably different from those in the Sierra Nevada.

Males of *O. c. californiana* have been considered to have smaller horns than the Rocky Mountain subspecies (Cowan 1940). While horn volume was one of the variables selected for the best discriminant analysis model, the model nevertheless could not distinguish *O. c. californiana* specimens from Washington and British Columbia reliably from *O. c. canadensis* samples. Indeed, many *O. c. canadensis* specimens had similarly small horns. Variation in horn growth within the Rocky Mountains has been well documented (Shackleton 1973; Wishart and Brochu 1982), and this variation has been attributed to differences in annual diet quality as affected by soil, climate, and migratory patterns (Blood et al. 1970; Shackleton 1973; Wishart 1969; Wishart and Brochu 1982). We suggest that the perceived tendency to smaller horn size among male bighorn sheep west of the Rocky Mountains in British Columbia may reflect environmental, rather than genetic variation. Bighorn sheep in this region live mostly along low-elevation river breaks, are largely nonmigratory, and therefore, do not have nutritional benefits of seasonal elevational migration and alpine forage (Hebert 1973). Nevertheless, our morphometric findings suggest that British Columbia and Washington populations considered *O. c. californiana* have a partial affinity with Great Basin populations.

During the last glacial advance of the Pleistocene, which ended approximately 12,000 years ago, glaciers covered the Rocky Mountains of Canada and areas west to the Coastal Mountains and south to ca. 47.5°N (Dyke and Prest 1987). Therefore, mountain sheep now inhabiting these regions are derived from populations that persisted south of the glacial advance (e.g., Montana and Idaho) and colonized this area <12,000 years ago with the opening of habitat in the Holocene. A reasonable explanation for the existence of 2 subspecies in this region would require 2 Pleistocene refugia, one in the Columbia River Valley for *O. c. californiana* and one farther east in northern Idaho–Montana for *O. c. canaden-*

sis. Although the Columbia River may have been a major north–south biogeographic barrier at times during the Pleistocene, there is no support for an east–west biogeographic barrier to separate bighorn sheep into 2 refugia.

Recognition of *O. c. californiana* as a separate subspecies from *O. c. canadensis* requires that there be a degree of genetic difference between these regions that is detectable by several independent measures, is greater than the variation found within subspecies (e.g., *O. c. canadensis*), and has resulted in distinguishability from *O. c. canadensis* to the east. Lacking such support, we assign extant and extinct native populations of *O. c. californiana* from Washington and British Columbia to *O. c. canadensis.*

South of Washington, we found 2 distinguishable bighorn sheep groups in the Great Basin and Sierra Nevada. These also are consistent with mtDNA patterns, which include a unique haplotype found in all Sierra Nevada samples. This haplotype was basal to all other desert sheep sampled. These haplotypes of the Great Basin, including the Sierra Nevada, were on a separate clade from those in the Rocky Mountains and British Columbia, and there were no shared haplotypes between these 2 regions (Ramey 1993, 1995). This mtDNA reciprocal monophyly suggests that these morphometric differences reflect a genetic signal rather than ecophenotypic noise. Hafner and Sullivan (1995) found a similar biogeographic pattern for genetic distances of allozymes of pikas (*Ochotona princeps*), suggesting a zoogeographic separation of the Rocky Mountains and Cascade Range from the Great Basin and Sierra Nevada.

Our results are not consistent with an interpretation of nutritional variation underlying regional morphometric differences. Sierra Nevada males have particularly wide skulls but small horns, whereas males from the adjacent Great Basin to the east have larger horns but narrower skulls. If nutritional constraints underlay such differences, we would expect horn and skull characteristics to covary (Wehausen and Ramey 1993). In the absence of such covariance, we interpret this as meaningful shape variation with a genetic basis.

We also consider the relationship between horn core length and horn volume to be an important shape variable that can help distinguish Rocky Mountain bighorn sheep from those in the entire desert region. On the basis of this shape variable, the northern boundaries for Great Basin bighorn sheep apparently included all of northern Nevada, Oregon, and the southwestern corner of Idaho. Therefore, we expand the original distribution of *O. c. nelsoni* to include this region, where no native populations survive. However, this is based on only a single shape variable, and this northern cold desert region was probably transitional with Rocky Mountain bighorn sheep, as suggested by specimens from British Columbia and Washington and the Salmon River of Idaho.

Of the California subspecies range defined by Cowan (1940), only the Sierra Nevada portion remains. Based on horn core morphology (Fig. 4), bighorn sheep from the Sierra Nevada have a clear affinity with the southwestern desert region, which corroborates findings from analysis of mtDNA variation (Ramey 1993, 1995). Sierra Nevada populations also exhibit general morphometric distinction (Figs. 1–3; Wehausen and Ramey 1993), which is consistent with mtDNA results (Ramey 1995). Therefore, Sierra Nevada bighorn sheep fit the subspecies criteria of Ball and Avise (1992).

The range of bighorn sheep in the central and southern Sierra Nevada is the westernmost suitable habitat for this species in this region. The genetic uniqueness of Sierra Nevada bighorn sheep relative to Great Basin populations to the immediate east may result from the lake and river system, including riparian vegetation, along the floor of the Owens Valley. Those biogeographic barriers were geographically mostly continuous during Pleistocene pluvial periods

(Gill and Cahill 1992). Although there have been southern and northern gaps in this barrier during drier periods, including the Holocene, there is no comparable temporally continuous barrier between mountain ranges of the Great Basin to the east.

Ovis canadensis canadensis.—We found little morphometric variation within the Rocky Mountains, most of which involved differences between Colorado and the northern Rocky Mountains. Similarly, Luikart and Allendorf (1996) found no evidence of long-term population isolation or differentiation within the Rocky Mountains from mtDNA markers and suggested that the Rocky Mountains have lacked subdivision by long-term biogeographic barriers. Even during periods of glacial advance, much of the Rocky Mountains supported open steppe habitat (Barnosky et al. 1987) that would have favored gene flow among populations.

The native bighorn sheep from the Salmon River in western Idaho have not been included in DNA studies. Our morphometric results largely indicated a Rocky Mountain affinity, but also some intergradation with the Great Basin. The Snake River Plain in southern Idaho would have presented a partial biogeographic barrier separating the Salmon River region from the cold desert region to the south. Gene flow between these regions would have most likely occurred from the west near the border with Oregon and to the east via mountains near the Wyoming–Utah border.

Conservation.—Conservation is dependent upon accurate information on patterns of genetic variation in the natural world and evolutionary processes that brought about those patterns of variation. However, much of past taxonomy at or below the species level is antiquated because it lacks an adequate quantitative basis and reflects an archaic typological view of species and subspecies not consistent with an evolutionary perspective (Mayr 1982). This has been particularly true below the species level where inconsistent criteria for distinguishing subspecies have prevailed (Cronin 1997).

Our revisions to the taxonomy of *O. canadensis* are made with the goal of identifying units of conservation using the concordant distributions of independent measures of variation (morphological and molecular) to the maximum extent possible and of placing these conservation units within an evolutionary context. Those units can be used to allocate conservation effort to preserve unique genetic resources, reintroduce sheep genetically most similar to what was originally present, and better understand the evolutionary history of these groups. Because we examined variation among adjoining regions within a larger geographic context and used the criterion that subspecies be distinguishable based on concordant distributions of several genetically based traits (Ball and Avise 1992), our results have not supported many of the geographic subspecies divisions currently in use. One result is that some regions (e.g., Oregon, northwestern Nevada, and southwestern Idaho) have been restocked during reintroductions with sheep apparently different from the original populations.

Within our range of consideration, we found 3 groups of sheep that would qualify as ESUs using the criteria of Moritz (1994a, 1994b): Rocky Mountain, Great Basin, and Sierra Nevada bighorn. The first 2 of these encompass large geographical ranges. In contrast, Sierra Nevada bighorn sheep occupy a single mountain range. Given its small overall population size and recent population declines (Wehausen 1996), this subspecies is currently more deserving of conservation attention than any other group of bighorn sheep. With only ca. 100 sheep remaining (J. D.Wehausen, in litt.), Sierra Nevada bighorn are currently one of the rarest mammalian taxa in North America.

Our results found important concordance between mtDNA and morphometric relationships in identifying divisions that would qualify for subspecies designations, which in this circumstance we consider equivalent

to ESUs. This involved use of reciprocal monophyly (Moritz 1994a) and our stringent criteria for morphometric distinguishability based on discriminant analysis for subspecies designations. Although these criteria provide an opportunity for each data set to serve as a test for the other, in our study, they also have led to providing the concordant patterns necessary under the subspecies criteria of Ball and Avise (1992). This suggests that the combination of morphometric and molecular data can be a particularly useful approach for addressing evolutionary questions of conservation importance.

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Literature Cited

Afifi, A. A., and V. Clark. 1990. Computer-aided multivariate analysis. Van Nostrand Reinhold, New York.

Ball, M. R., and J. C. Avise. 1992. Mitochondrial DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. The Auk 109:626–636.

Barnosky, C. W., P. M. Anderson, and P. J. Bartlein. 1987. The northwestern U.S. during deglaciation; vegetational history and paleoclimatic implications. Pp. 289–321 in North America and adjacent oceans during the last deglaciation: the geology of North America (W. F. Ruddiman and H. E. Wright, Jr., eds.). Geological Society of America, Boulder, Colorado.

Blood, D. A., D. R. Flook, and W. D. Wishart. 1970. Weights and growth of Rocky mountain bighorn sheep in western Alberta. The Journal of Wildlife Management 34:451–455.

Bookstein, F. L. 1990. Introduction and overview: geometry and biology. Pp. 61–74 in Proceedings of the Michigan morphometrics workshop (F. J. Rohlf and F. L. Bookstein, eds.). The University of Michigan Museum of Zoology Special Publication 2:1–380.

Cowan, I. M. 1940. Distribution and variation in the native sheep of North America. The American Midland Naturalist 24:505–580.

Cronin, M. A. 1997. Systematics, taxonomy, and the Endangered Species Act: the example of the California gnatcatcher. Wildlife Society Bulletin 25:661–666.

Dyke, A. S., and V. K. Prest. 1987. Paleogeography of northern North America, 18,000–5,000 years ago. Geological Survey of Canada Map 1703A, Ottawa, Ontario, Canada.

Gill, T. E., and T. A. Cahill. 1992. Playa-generated dust storms from Owens Lake. Pp. 63–73 in The history of water: eastern Sierra Nevada, Owens Valley, White-Inyo Mountains (C. A. Hall, Jr., V. Doyle-Jones, and B. Widawski, eds.). White Mountain Research Station Symposium, White Mountain Research Station, Bishop, California 4:1–453.

Hafner, D. J., and R. M. Sullivan. 1995. Historical and ecological biogeography of nearctic pikas (Lagomorpha: Ochotonidae). Journal of Mammalogy 76:302–321.

Hebert, D. M. 1973. Altitudinal migration as a factor

in the nutrition of bighorn sheep. Ph.D. dissertation, University of British Columbia, Vancouver, Canada.
HUMPHRIES, J. M., F. L. BOOKSTEIN, B. CHERNOFF, G. R. SMITH, R. L. ELDER, AND S. G. POSS. 1981. Multivariate discrimination by shape in relation to size. Systematic Zoology 30:291–308.
LUIKART, G., AND F. W. ALLENDORF. 1996. Mitochondrial DNA variation and genetic–population structure in Rocky Mountain sheep (*Ovis canadensis canadensis*). Journal of Mammalogy 77:109–123.
MAYR, E. 1982. The growth of biological thought. Harvard University Press, Cambridge, Massachusetts.
MORITZ, C. 1994a. Defining 'Evolutionary significant units' for conservation. Trends in Ecology and Evolution 9:373–375.
MORITZ, C. 1994b. Applications of mitochondrial DNA analysis in conservation: a critical review. Molecular Ecology 3:401–411.
NETER, J., AND W. WASSERMAN. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, Illinois.
RAMEY, R. R. 1993. Evolutionary genetics and systematics of North American Mountain sheep. Ph.D. dissertation, Cornell University, Ithaca, New York.
RAMEY, R. R. 1995. Mitochondrial DNA variation, population structure and evolution of mountain sheep in the southwestern United States and Mexico. Molecular Ecology 4:429–439.
REYMENT, R. A. 1990. Reification of classical multivariate statistical analysis in morphometry. Pp. 123–144 in Proceedings of the Michigan morphometrics workshop (F. J. Rohlf and F. L. Bookstein, eds.). The University of Michigan Museum of Zoology Special Publication 2:1–380.
REYMENT, R. A., R. E. BLACKITH, AND N. A. CAMPBELL. 1984. Multivariate morphometrics. Academic Press, Orlando, Florida.
RYDER, O. 1986. Species conservation and systematics: the dilemma of subspecies. Trends in Ecology and Evolution 1:9–10.
SHACKLETON, D. M. 1973. Population quality and bighorn sheep (*Ovis canadensis canadensis* Shaw). Ph.D. dissertation, University of Calgary, Alberta, Canada.
SHACKLETON, D. M. 1985. *Ovis canadensis.* Mammalian Species 230:1–9.
WEHAUSEN, J. D. 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. Wildlife Society Bulletin 24:471–479.
WEHAUSEN, J. D., AND R. R. RAMEY. 1993. A morphometric reevaluation of the Peninsular bighorn subspecies. Desert Bighorn Council Transactions 37:1–10.
WILLIAMS, B. K., AND K. TITUS. 1988. Assessment of sampling stability in ecological applications of discriminant analysis. Ecology 69:1275–1285.
WISHART, W. D. 1969. Bighorns and little horns. Alberta Department of Lands and Forests. Lands-Forests-Parks-Wildlife 12(3):4–10.
WISHART, W. D., AND D. BROCHU. 1982. An evaluation of horn and skull characters as a measure of population quality in Alberta bighorns. Biennial Symposium of the Northern Wild Sheep and Goat Council 3:127–142.

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APPENDIX I

Descriptions of skull and horn measurements used in this study (abbreviations are in parentheses).—1) Cranial length (CRANIAL): distance from anterior lip of foramen magnum to posterior edge of palate at midline suture. 2) Palate length (PALATE): distance from posterior edge of palate at midline suture to posterior margin of the most intact anterior palatine foramen. 3) Premaxilla length (PREMAX): distance from posterior margin of anterior palatine foramen to tip of premaxilla along midline. 4) Upper tooth row length (TOOTH, following Cowan 1940): length of longest tooth row measured as the greatest alveolar length of combined upper molars and premolars. 5) Palate width (PM2, following Cowan 1940): least distance across palate between alveoli of second premolars. 6) Cheek width (CHEEK): greatest distance between malar eminences on the maxillary bones. 7) Interorbit width (INTERORB, following Cowan 1940): least distance in a straight line taken with calipers resting in notch on inferior orbital rim at lower edge of lachrymal bones. 8) Intraorbit width (INTRAORB): width of largest orbit measured as greatest width of interior lip of orbit. 9) Zygomatic width (ZYGO, following Cowan 1940): greatest distance between external margins of zygomatic arches taken on the jugo–squamosal suture. 10) Post orbital width (POSTORB): greatest width of frontal bone as measured posterior to orbits and anterior to horn cores. 11) 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. 12) Horn core length (CORL): length of horn core measured along the superior edge from the burr to the tip using a steel tape. 13) Horn core circumference (CORC, following Cowan 1940; CORC3): circumference of largest horn core, measured around core near burr (CORC) and at 7.6 cm (3 inches) from the burr (CORC3), at right angle to the axis of the core, using a steel tape. 14) Horn core taper (TAPER3–6): rate of change of core circumference between 7.6 and 15.2 cm (3 and 6 inches) along the superior edge from the burr. 15) Horn basal

circumference (HORNC, following Cowan 1940): circumference of largest horn base measured nearest its base using a steel tape. 16) Horn length (HORNL, following Cowan 1940): measured along the superior horn keel from orbital corner to tip of horn. 17) Horn volume (HORNVOL; males only): volume of largest horn estimated from lengths and circumferences. Horn length was divided into 4 quarters and 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 horn loss from wear. 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. A final conical section was added from the last circumference to approximate horn loss from wear using a constant taper for all specimens. An analysis of the ends of horns lacking wear yielded a constant taper across all populations (distance between circumferences accounted for 96% of the variation in circumference differences; $n = 19$).

Appendix II

Catalog of specimens from the northern range of *Ovis canadensis* used in this study by region and sex. Acronyms defined in the Acknowledgments.

Great Basin.—Males. BYU: 1 uncataloged; CAS: CA4391, CA4392, CA4393; CAR: 7280; DEVA: 14982, 15092, 15095, 15099, 15100, 15102, 20830, 20831, 20833, 3629, 3836, 4054; CDFG: 15, 16, 161, 164, 165, 166, 167, 174, 158, 107, 171, J-8, J-9; ELY: 4 uncataloged; MVZ: 40887, 40888, 64556, 71146, 79610, 88137, 88138, 93097, 119384; USNM: 205915, 205919, 205922, 208988, 209420, 210245, 210246, 210247, 211041, 211042, 211043, 226877, 226878, 274694, 274704, 206342; UAZ: 10-64, 10-68, 11-61, 139, 15-67, 1-61, 17-63, 24-67, 25-66, 28-68, 31, 34-61, 37-65, 41-63, 46-61, 62-61, 7-62, 7-64, 76-60, 846, T-10, T-15, T-222; UKAN: 48116, 84887, 84888; UNLV: 2 uncataloged. Females. DEVA: 1, 15233, 1877, 1878, 27872, 3357, BS-36, BS-49, BS-80, 3 uncataloged; CDFG: 135, 61, 62, 63, 64, 65, 66, J-1, J-2, J-3, J-4, J-5, J-6, J-7; ELY: 1 uncataloged; MVZ: 132219, 134117, 88136; USNM: 205926, 208993, 209704, 209706, 209755, 28384, 28390, 40487; UAZ: 14-61, 1-62, 18-64, 22-62, 24-65, 27-67, 28-61, 29-68, 2?-??, 30-61, 34-62, 35-62, 35-63, 36-66, 41-56, 42-56, 44-61, 4-85, 53-60, 53-66, 5-63, 7-68, 85-60.

Sierra Nevada.—Males. CDFG: 108, 109, 125, 126, 127, 128, 129, 14, 162, 163, 172, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 31, 4, 7, 8, 195, 196, 2 uncataloged; MVZ: 35368, 169998, 170000, 170001; USNM: 250072. Females. CAS: CA332, CA333, CA8262; CDFG: 117, 118, 119, 120, 177, 178, 179, 180, 197, 74, 77, 78, 80, 81, 82, 83, 84, 86, 87, 89; MVZ: 170005, 170006, 170009, 78270; USNM: 206464, 206465.

Oregon, Northeastern California, and Southwestern Idaho.—Males. KCM: 2797, 785; LABE: LABE2797, LABE2852, LABE2884, LABE5541, LABE5833, LABE5834, LABE5835, LABE5836; MVZ: 20966, 31349, 34172, 84217; USNM: 209834, 210548, 210549, 214790, 221883, 235241, 235242, 235243, 235244, 235245, 235246, 241611, 243340, 214789, 224607, 224613, 224616, 225040, 225209, 228311, 242345, 245605, 247237; JK: 1 uncataloged; VG: 1 uncataloged.

Salmon River, Idaho.—Males. SPEN: ID87-19, ID76, ID77, ID87-30, ID87-31, ID87-32, ID87-33, ID87-35, ID87-38, ID87-39, ID87-40, ID87-41, ID87-42, ID87-43, ID87-44, ID87-45, ID87-46, ID87-47, ID91-122, ID91-124, ID92-232, IDA118, IDA83-64, 2 uncataloged. Females. SPEN: 11 uncataloged.

Washington, British Columbia west of Rocky Mountains.—Males. BCM: 15668, 1861, 5222, 6806, 6812, 7718, 7963, 8018, 8020, 8021, 8026, 8027, 8030, 8031, 8032, 8034, 8061, 8083; ALFW: 84AB0510; USNM: 227651, 242346, 174922, 202967, 202968, 203148, 203149, 208989, 208990, 208991, 208995; WAL: 20, 25, 32, 4, 5, 3 uncataloged; UKAN: 1771, 1796, 1797, 1769, 1770, 1772, 1773, 1774, 1775, 1776, 1777, 1778, 1779, 1780, 1781, 1782, 1788, 1789, 1790, 1793, 1794, 1795, 1798, 1799, 1801, 1803; UBC: 2887, 3112, 3403, 6886, 8007, 8572; WIL: 16, BC5936, BC5937, BC5938, BC5942, BC5944, BC7733, BC7756, BC7757, BC7795, BC7798, BC7799. Females. BCM: 6835, 6839, 8036, 8037, 8038, 8039, 8040, 8041, 8042, 8045, 8051, 8054, 8055, 8059, 8060, 8064, 8065, 8067, 8068, 8069, 8071, 8072, 8073, 8074, 8075, 8076, 8078, 8079, 8080, 8081, 8112,

8557, 9536; USNM: 202969, 202970, 203150, 203151, 268005; WAL: 24, 31, 43, 3 uncataloged; UKAN: 1802, 1805, 1806, 1807, 1820; UBC: 16280, 2888, 3448, 3525, 6635, 8558, 8697, 8698, 8700, 8701; WIL: 41, 6/17, 1 uncataloged.

Canadian Rockies.—Males. ALM: 80.42.10, 80.42.11, 80.42.8, 81.117.4, 90.33.1, 90.33.12, 90.33.7; BCM: 11769, 11770, 11771, 11773, 11775, 11780, 11833, 11834, 11835, 12492, 12560, 12562, 12563, 13708, 13710, 15664, 6851; CAR: 21798, 22917, 22918; CRAN: 7853, 3 uncataloged; ALFW: 482111, 84AB0168, 84AB0169, 84AB0509, 84AB0534, 84AB0538, 84AB0575, 84AB0595, 87ABO394, ET44, 4 uncataloged; MVZ: 4375; USNM: 174512, 205155, 210209, 217433, 268004, 81801, 202963, 202966, 205158, 209397, 241002, 244190, 246294, 247059; UBC: 1522, 815, 817, 818, 819, 821, 822, 822.1, 825, 826, 931, 932, 935, 9359, 936, 938. Females. ALM: 78.127.4, 78.9.17; BCM: 11772, 11776, 12494, 12495, 12497, 12498, 12499, 12500, 12501, 12503, 12504, 12506, 12845; CAR: 7555; CRAN: 4 uncataloged; ALFW: 312, 394, 396, 45C, B85-1088, ET38, 282, 44, 49, 59, 63, 84, 7 uncataloged; USNM: 202965, 205157, 240319, 18104, 81803, 205156, 240320; UBC: 812, 813, 9042, 9050, 9054, 9194, 9196.

Montana and Waterton Lakes National Park, Alberta.—Males. CAS: CA467; ALFW: 1 uncataloged; MVZ: 78262, 77357, 47327, 78261, 78260, 78269, 96104, 78258; USNM: 105263; UMT: 3365, 8456; WLNP: W-B-1, W-VR-6, 4 uncataloged. Females. MVZ: 78259, 78265, 78266, 78267, 78268; USNM: 242973, 242974; WLNP: W-G-4, W-G-8, W-G-9, W-VR-4.

Wyoming.—Males. DEN: 2446; MVZ: 181222; USNM: 223562, 223560, 238729, 171884, 239122, 239124, 239123; Private collection: 1 uncataloged. Females. USNM: 169335, 223564, 2593, 86421.

Colorado.—Males. CAR: 8716; FCOL: 051, 1 uncataloged; GJCT: 1663, 201, 203, 3 uncataloged; JM: 243, 244; GUN: 1 uncataloged; DM: 1 uncataloged; KW: 1 uncataloged; LS: 1 uncataloged; USNM: 113380, 202174, 202175, 242630, 243749, 247110; RMNP: 6929, 92036, 9204; UCM: OS-335, OS-339, UCM-5883. Females. CAR: 8705, 8718; GJCT: 2 uncataloged; CUR: 1 uncataloged; DEN: 6914, 7870; GNM: 148-610; USNM: 179327; UCM: UCM-7170; BD: 1 uncataloged; DR: 1 uncataloged; JM: 2 uncataloged.

East of Rocky Mountains.—Males. USNM: 22610, 828, 13962, 14002, 210285; UMT: 17503, 1 uncataloged. Females. USNM: 12032, 12033, 13242, 202535.