AN INVESTIGATION OF SUBSPECIFIC RELATIONSHIPS OF THE GREY WOLF, CANIS LUPUS, IN BRITISH COLUMBIA

by

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ABSTRACT

Wolf populations in southern British Columbia have been increasing in recent years, especially on Vancouver Island. The objectives of this study were (a) to investigate the validity of subspecific designations for wolves in the Pacific Northwest, (b) to determine whether wolf-dog hybridization was occurring on Vancouver Island, (c) to determine whether wolves were immigrating to Vancouver Island from the mainland, and (d) to investigate the subspecific status of wolves reoccupying historic range in southern British Columbia and the adjacent United States.

Analysis of a series of skull measurements by multivariate methods suggested that there were two major groups of wolves present in British Columbia, a large, northern type and a smaller type occupying the coast and the northwestern United States. Those wolf types designated *Canis lupus fuscus* and *C.l. irremotus* appear to be extinct. *Canis lupus crassodon* was identified as a distinct type. No reason was found to designate the wolves of northeastern British Columbia as a separate type from those of the interior.

Multivariate analyses of dogs and wolves, and analysis of non-metric characters, suggested that hybridization had occurred on southern Vancouver Island, although to a very limited extent.

Recent Vancouver Island wolves were shown to resemble mainland wolves as much as the historic island population. It appears that immigrating wolves have diluted the original population so that it is no longer possible to distinguish Island from mainland coastal wolves.

Multivariate analysis of recent wolves from south-eastern B.C. and the northwestern United States strongly suggests that the wolves found there now have migrated south from Canada and are not remnant populations of the Northern Rocky Mountain wolf which formerly occupied this area.

It is recommended that, in the interests of maintaining genetic diversity, wildlife managers consider that the wolves of Vancouver Island and the mainland coast likely constitute the only surviving populations of the small southern wolf groups when designing their management plans for this species.

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For my parents ....

who wanted me to do this fifteen years ago

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GENERAL INTRODUCTION

The grey wolf, *Canis lupus*, had a range originally occupying much of North America, Europe, and Asia. In North America, its range extended from the Arctic islands southward into Mexico. Young and Goldman (1944) studied the two North American species of wolf, *C. lupus* and *C. rufus*, the red wolf, and included Goldman's (1944) descriptions of 23 subspecies of grey wolf. Hall and Kelson (1959) subsequently added another subspecies. In Europe and Asia only 8 subspecies have been described, and it has been suggested by several researchers (Jolicoeur 1959, Nowak 1979, Bogan and Mehlhop 1983) that there are probably far too many subspecific designations in use on this continent.

Since Goldman's work, a number of these subspecies have become extinct. By the 1920's, wolves had been nearly exterminated from the conterminous United States, with only a few remaining in Michigan and Minnesota, and possibly in northwestern Montana and northern Idaho. There may also be a remnant grey wolf population in the southwestern United States (Pisano 1977).

Wolf populations have since begun expanding again, following the cessation of bounty and control programs in the 1960's. Wolves are again being reported on the prairies throughout Canada and are occasionally reported in areas of the United States where they have not been seen in decades (Nowak 1983).

In British Columbia the decline was perhaps not so dramatic, but wolves had been considered almost eliminated from the southern portion of the province, and were extremely rare on Vancouver Island. Since 1970, wolves have been seen more and more frequently in southeastern B.C., and have become extremely common on Vancouver Island (Hebert *et al*. 1982). Suggested reasons for this increase have included wolf-dog hybridization, and immigration of mainland wolves to the island.

Whether the original subspecific designations are valid, and whether recent expanding populations can be referred to those subspecies, is of some management concern. Although some large mammals are managed on a subspecific basis in British Columbia (e.g. Roosevelt elk, Kermodi bear, mountain caribou), only the Vancouver Island wolf, *C.l. crassodon*, has really been considered separately in wolf management. One of the goals of wildlife management in British Columbia is "to maintain the diversity of species representative of the major biophysical zones of the Province." (B.C. Fish and Wildlife Branch 1979). Implicit within this is the goal of maintaining diversity within species. Schonewald-Cox (1983) states that "the survival of species in the long term depends upon their having enough genetic diversity contained both within and between their populations to accommodate new selection pressures brought about by environmental change." Although the use of minor, changeable character differences to define subspecies may be questionable, subspecies designations presently remain the best way of acknowledging the diversity existing within a species. Conserving subspecies is a way to preserve genetic diversity (Bunnell and Williams 1980, Chambers and Bayliss 1983). If the wolves in southeastern B.C. and the adjacent states, now re-occupying the historic range of *C.l. irremotus*, the Northern Rocky Mountain wolf, should prove to be allied to that subspecies, then the small population there could be considered a genetic reservoir of a virtually extirpated subspecies and deserving of considerable effort to maintain that population. Similarly, if the wolves currently found in coastal British Columbia should prove to be the last remnants of the Cascade wolf, *C.l. fuscus*, whose range occupied the west coast of the United States, then our management policies should reflect that. If the present-day wolves on Vancouver Island should prove not to be descended from the original Island population, then their management may be different from what it would be if they were shown to be an isolated island subspecies.

Wolves themselves are a confounding factor; they are highly variable animals with a tremendous capacity for long-range movements, and have been known to cross subspecific boundaries (Fritts 1983).

This study will attempt to answer the following questions:

a) Are the subspecies designations that Goldman (1944) proposed for the Pacific Northwest valid?

b) Has hybridization with dogs occurred among Vancouver Island wolves?

c) Did the Vancouver Island wolf population increase due to immigration from the mainland?

d) Are the wolves occasionally reported in the northwestern United States and southeastern British Columbia immigrants from the north or descendants of remnant local populations?

PART I

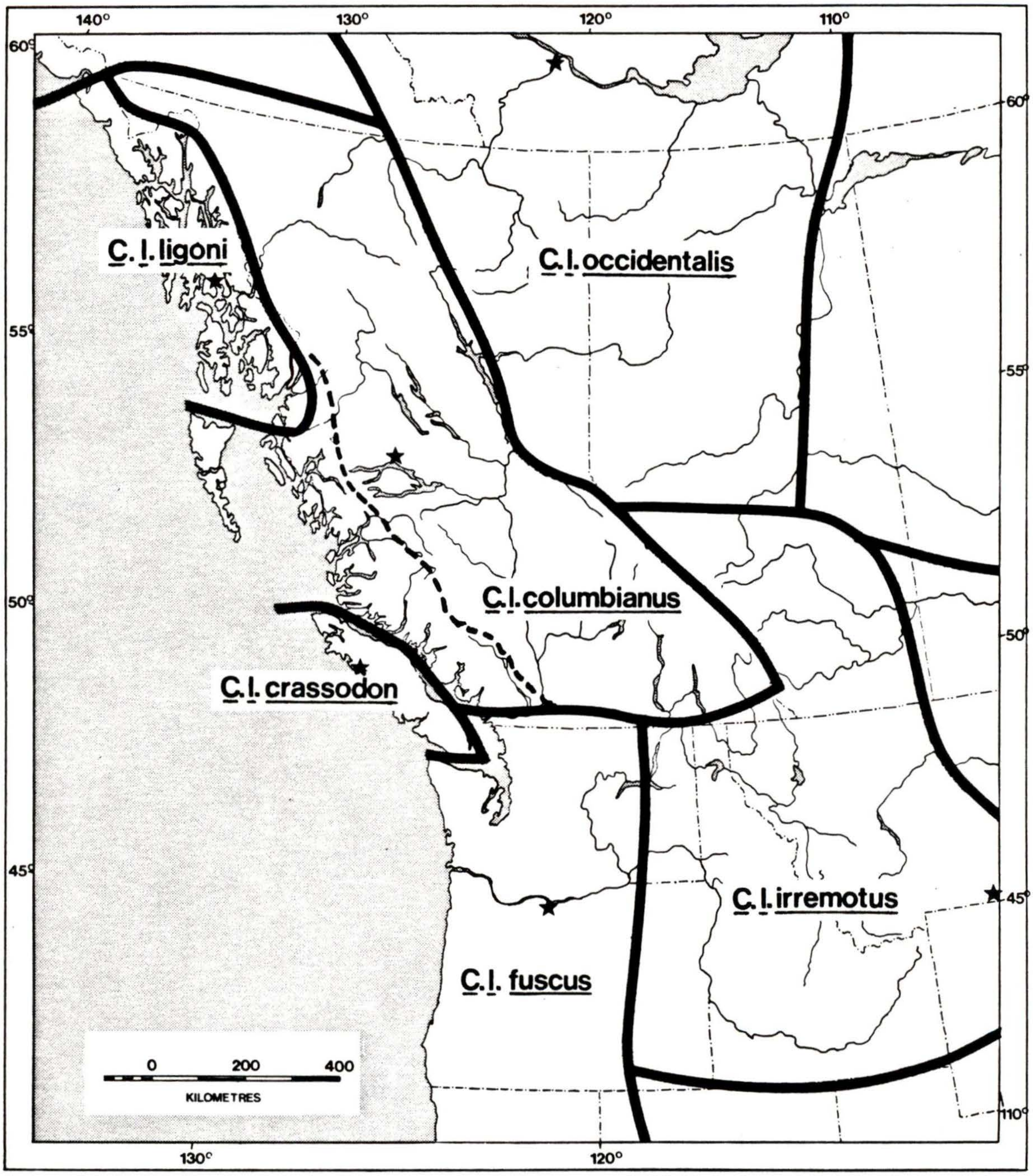
AN INVESTIGATION OF SUBSPECIFIC RELATIONSHIPS AND RANGES OF *CANIS LUPUS* IN BRITISH COLUMBIA

INTRODUCTION

Of the twenty-four currently accepted North American subspecies of the grey wolf, *Canis lupus*, six occurred in or adjacent to British Columbia at the time Goldman (1944) conducted his systematic work. Goldman used primarily the following characteristics: gross average size, general colour, general form and massiveness of the skull, profile, relative length of nasals, length of rostrum, relative size of molar teeth, and size of auditory bullae. He acknowledged that considerable overlap among subspecies occurred for any given character, but felt that the characters he noted were sufficiently distinctive to warrant subspecific designations. The six subspecies in the British Columbia area are described in Appendix 1.

The ranges of these subspecies as defined by Goldman are shown in Figure 1. Goldman showed the range of *C.l. fuscus* as extending to southern British Columbia, but did not have enough specimens to speculate on how far north the range should extend. Cowan and Guiguet (1964) felt, since the ecosystems were similar, that the range should be

Figure 1. Ranges of currently recognized subspecies of *Canis lupus* in the Pacific Northwest. Dotted line indicates range extension of *C. l. fuscus* as proposed by Cowan and Guiguet (1964). Stars indicate type locality for each subspecies.



140°
130°
120°
110°
60°
55°
50°
45°
C. l. ligoni
C. l. occidentalis
C. l. columbianus
C. l. crassodon
C. l. irremotus
C. l. fuscus
0 200 400
KILOMETRES
130°
120°
110°

extended to include the entire coast of B.C. west of the Cascades, although they felt there was some question of the validity of the characteristics used by Goldman (1944) to describe subspecies in British Columbia. Subsequent publications (Hall and Kelson 1959, Mech 1970, Nowak 1979) include range maps based on Goldman's range map, and showing this extension. Cowan and Guiguet (1964) did not feel there was sufficient justification for Goldman's extension of the ranges of _occidentalis_ or _irremotus_ into British Columbia, but Hall and Kelson did not incorporate those changes in their range maps.

Mayr _et al_. (1953) defined a species as "a group of actually (or potentially) interbreeding natural populations which is reproductively isolated from other such groups." (Although there are many problems with this definition, it does tend to hold with mammals.) Since grey wolves are interfertile with red wolves, coyotes, and dogs, behavioural and ecological separation play a role in maintaining the grey wolf as a distinct species.

Subspecies (Mayr _et al_. 1953) are "geographically defined aggregates of local populations which differ taxonomically from other such subdivisions of a species." Because subspecies are not reproductively isolated, no fixed range boundaries can be described. Subspecies may or may not be geographically isolated; Endler (1977) has shown that differentiation can occur in conjunct populations and indeed, may do so more frequently than in disjunct populations. A "cline" can occur between two conjunct but differentiated populations, or in the contact zone of secondary intergradation, when two isolated populations come into secondary contact. It may not be possible to distinguish between these two situations.

Goldman worked with a relatively small sample (n=38) of wolves from British Columbia. Since that time, a considerable number of specimens has become available from all parts of the province, making possible a review of these subspecific designations and ranges.

Since Goldman's time, a number of mathematical methods have been adapted to taxonomic work (Blackith and Reyment 1971, Neff and Marcus 1980). Whereas several characters considered individually may show overlap between two groups, these same characters considered simultaneously may provide good separation. These "multivariate" methods, with the advent of computers, have proven to be invaluable taxonomic tools.

Jolicoeur (1959) was the first to apply multivariate methods to canid taxonomy. He used discriminatory analysis to investigate geographic variation of wolves in western and northwestern Canada, and provided a clear explanation of the bases of multivariate analysis. He reported a gradual cline, southwest to northeast, with some minor general shape changes (possibly climate-related), and commented that there were probably far too many subspecific designations in use. Although he examined Vancouver Island wolves, his British Columbia sample was small (n=55) and he did not include wolves from the northwestern United States.

Numerous other authors have subsequently employed multivariate analysis in studies of canids, both at the specific (Lawrence and Bossert 1967, Elder and Hayden 1977, Nowak 1979) and at the subspecific (Kolenosky and Standfield 1975, Skeel and Carbyn 1976, Bogan and Mehlhop 1983) levels. The subspecific studies support Jolicoeur's (1959) comment that too many subspecific designations are in use. They suggest that the wolf is an extremely variable species, and that differences are due to gradual geographic variation, which form a continuum rather than distinct units. Nowak (1983) provides a good summary of these papers and suggests that North American wolves could be divided into five major groups, derived from populations isolated during Pleistocene glaciations. Two of these groups would occur in British Columbia, one occupying the northern interior of the province, and one occupying the northwestern United States, southern British Columbia, and possibly the British Columbia coast.

The objectives of Part 1 were:

a) <u>to investigate the validity of Goldman's subspecific designations</u>. For those characters that could be easily measured and were listed as diagnostic (Appendix 1), univariate tests were employed to determine if significant differences occurred. In addition, multiple discriminant analysis was employed on a larger set of characters than used by Goldman. If these methods revealed significant differences between groups, and if these differences could be used to identify reliably 75% of wolves tested (Mayr <u>et al</u>. 1953), then Goldman's designations were accepted.

b) <u>to determine whether the wolf groups of this study fell into two "supergroups" as postulated by Nowak (1983)</u>. If principal components analysis and cluster analysis revealed two major groupings, this was considered support for Nowak's hypothesis. In addition, if subset analysis and minimum spanning tree construction showed interior groups to be more closely related in an east-west direction than in a north-south direction, this was also considered support.

c) <u>to determine whether B.C. coastal wolves were more closely related to the wolves of Oregon, as suggested</u>

by Cowan and Guiguet (1964), or to other neighbouring wolf groups. If, in a multiple discriminant analysis of these groups, B.C. coastal wolves were entered as unknowns and assigned most often to the Oregon group, the range extension postulated by Cowan and Guiguet (1964) was accepted.

MATERIALS AND METHODS

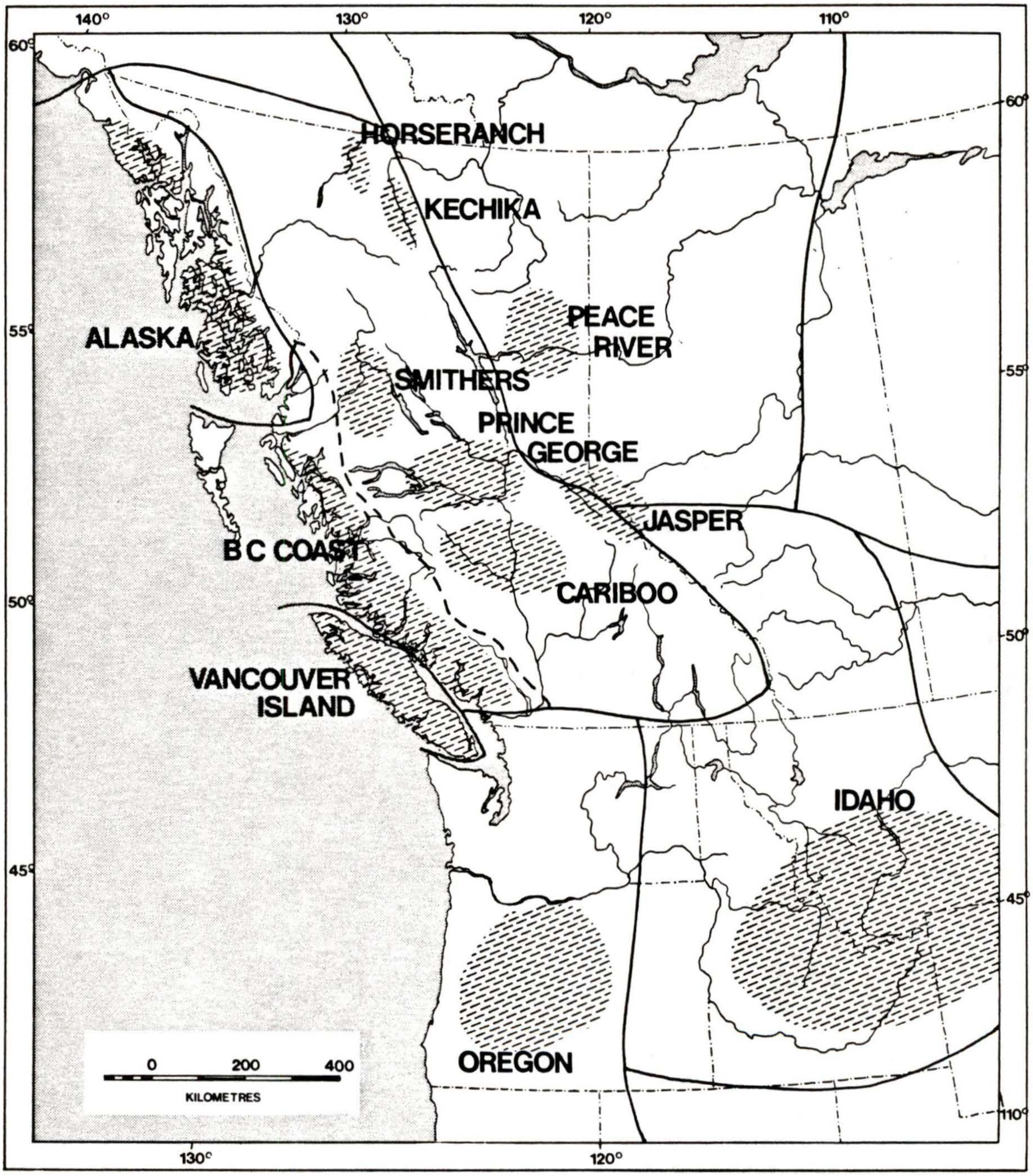
Location of Specimens and Study Area

Specimens used in this study were located in a number of museums across North America. The collection locations of these specimens, and the names of the museums holding them, are given in Appendix 2, and shown in Figure 2.

The specimens examined fell into 12 relatively discrete geographic areas (Figure 2). These are: Vancouver Island (collected prior to 1950), coastal British Columbia with immediately adjacent islands, Oregon, Idaho and western Montana, the Alaska Panhandle, the Cariboo-Chilcotin area, Prince George-Nechako area, the Bulkley Valley area near Smithers, the Horseranch Range region near Dease Lake, the Kechika River Valley, the Peace River lowlands, and the Rocky Mountains in the vicinity of Jasper National Park. These areas will be referred to by the names shown in Figure 2 for the remainder of this report.

Specimens from Smithers, Horseranch, Kechika, Peace, and many of those from Prince George, Cariboo and B.C. coast were collected by the Wildlife Branch after 1978. Specimens from other areas were collected in the first half of the century, prior to the virtual elimination of wolves from the southern part of their range.

Figure 2. Map showing geographic distribution of samples used in study.
Subspecific boundaries are shown as in Figure 1.


140°
130°
120°
110°
60°
55°
50°
45°
HORSERANCH
KECHIKA
PEACE
RIVER
ALASKA
SMITHERS
PRINCE
GEORGE
JASPER
B C COAST
CARIBOO
VANCOUVER
ISLAND
IDAHO
OREGON
0
200
400
KILOMETRES

Measurements

Mammalian taxonomy is traditionally based on skull characteristics; therefore, only skulls were used for the majority of the analyses. Ideally, systematic studies should include consideration of post-cranial material, biochemical and behavioural differences, and ecological characteristics. However, wolves have become extinct in much of North America, and museums have little post-cranial material of larger mammals in their collections.

Since wolves do not reach maximum growth until about 15 months of age (Nowak 1979), animals younger than this were not included in analyses on metric characters, but were sometimes examined for non-metric characters. Animals were aged by canine eruption, degree of tooth wear, and development of post-orbital processes. Juvenile animals had the enamel line of the canine generally within one millimetre of the alveolus, no discernible tooth wear, and rounded post-orbital processes. Premolars were sectioned and aged by cementum annulations for those animals necropsied at the Wildlife Laboratory. All available animals from the 12 study areas held at the museums I visited were examined including the type specimens for *C.l. crassodon*, *C.l. columbianus*, *C.l. irremotus*, and *C.l. ligoni*. No types were designated for *C.l. fuscus* or *C.l. occidentalis*; I was able to examine specimens from the type locality for fuscus but not for occidentalis. In addition to the specimens listed in Table 1, a number of wolf-dog hybrids, canids of uncertain specific identity, and wolves of uncertain subspecific identity were measured. These are referred to later in the report.

Measurements taken were selected from a variety of sources. First, I wished to evaluate the characteristics Goldman (1944) used to define his subspecies. Several multivariate studies have been carried out on canid taxonomy (Jolicoeur 1959, Lawrence and Bossert 1967, Skeel and Carbyn 1976, Elder and Hayden 1977, Nowak 1979, Bogan and Mehlhop 1983) and I selected from the characters tested by those authors, those characters that could be measured reliably and that I felt best described the dimensions and proportions of the skull. They were chosen to reflect basic differences in skull size, massiveness of teeth, breadth of rostrum, size and strength of jaws, and size of auditory bullae, since these were characters used by Goldman in his subspecific descriptions.

The following measurements were taken on all skulls (Figure 3):

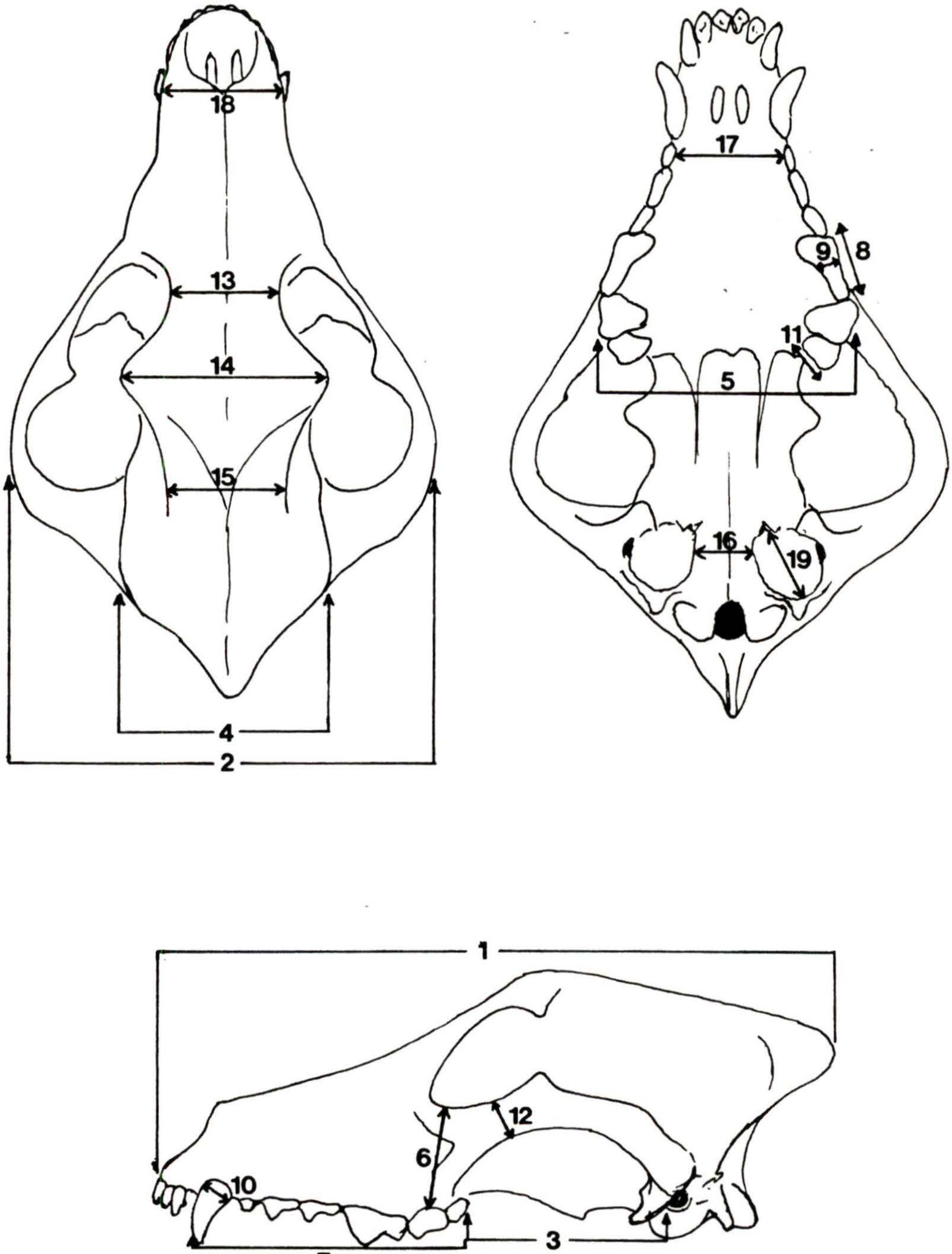
1. Total skull length, posthion to posterior point of inion.

Table 1. Geographic region and sample size of groups used in analyses. Only animals of known sex were included in multivariate comparisons of wolf populations.

Group	Male	Female	Sex Unknown	Total
Vancouver Island (pre-1950)	9	8	3	20
B.C. coast	5	3	8	16
Oregon	12	10	-	22
Alaska	11	11	11	33
Idaho	16	22	9	47
Smithers	6	4	19	29
Prince George	15	10	3	28
Cariboo	10	10	4	24
Horseranch	14	12	-	26
Kechika	19	18	-	37
Peace River	9	8	1	18
Jasper	12	12	1	25
Total	138	128	59	325
Recent Vancouver Island	46	25	0	71
Coastal islands	9	5	0	14
Dogs	0	0	39	39

Figure 3. Cranial measurements used in morphometric analysis.

1. Skull length
2. Zygomatic width
3. M^2 to auditory canal
4. Braincase width
5. Width across cheek teeth
6. M^1 to orbit
7. Tooth row length
8. Carnassial length
9. Carnassial width
10. Canine width
11. M^2 width
12. Jugal height
13. Width between orbits
14. Width across post-orbital processes
15. Width behind post-orbital processes
16. Distance between bullae
17. Distance between first premolars
18. Rostrum width at canines
19. Bulla length


18
13
14
15
4
2
17
9
8
11
5
16
19
1
12
6
10
7
3

2. Maximum width across zygomatic arches.
3. Distance from the posterior edge of the alveolus of the upper second molar to the opening of the auditory canal.
4. Width of the braincase at the parieto-temporal suture.
5. Maximum width across crowns of upper cheek teeth.
6. Minimum distance from the edge of the orbit to the alveolus of the upper first molar, between the roots (since skulls were often eroded up along tooth roots).
7. Length of tooth row from anterior edge of alveolus of canine to posterior edge of alveolus of second molar.
8. Maximum crown length along outside edge of upper carnassial.
9. Minimum crown width of upper carnassial, taken between roots.
10. Maximum width of canine, antero-posterior, at enamel line.
11. Maximum transverse width of upper second molar.
12. Minimum height of jugal bone.
13. Minimum distance across frontals between orbits.
14. Maximum distance across frontals at postorbital processes.
15. Minimum distance across frontals at postorbital constriction.
16. Minimum width of occipital bone between auditory bullae.

17. Distance between inner margins of alveoli of upper first premolars.
18. Width of rostrum across canines.
19. Length of bulla (suture with jugular process to tympanic notch).

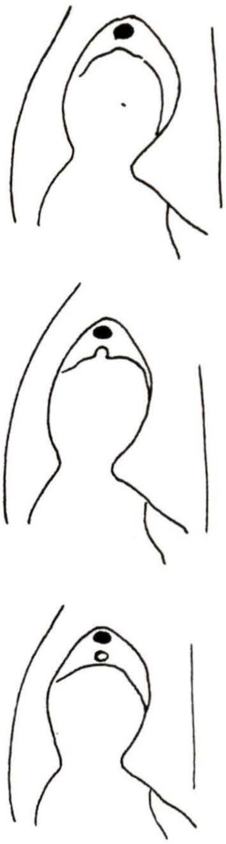
Measurements of the mandible were not taken because mandibles were often damaged or missing.

All measurements were taken to the nearest 0.1 mm using vernier calipers. Nearly all measurements were taken in a five-month period in 1983, to maximize consistency. Over 500 skulls were examined in total.

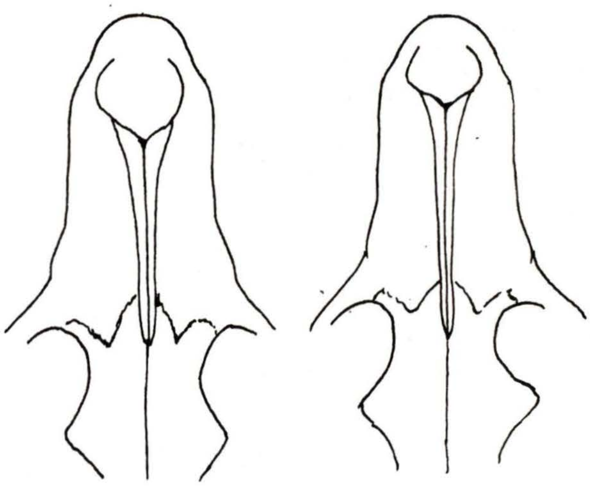
To avoid the possibility of environmental or dietary conditions influencing differences in measured characteristics, some workers have recommended using non-metric characters (tooth shape, number and size of foramina, suture shapes, etc.) as good indicators of genetic variation (Berry 1969, Andersen and Wiig 1982). A number of non-metric characters, illustrated in Figure 4, were evaluated. Shape of upper carnassial and length of nasals relative to maxillae were recorded for all specimens. Also noted were: whether a skull placed on a surface had its canines in contact with that surface, and the shape of the bone immediately dorsal to the lacrimal sac fossa. Each skull examined was photographed dorsally, ventrally, and laterally, so that non-metric characters could be confirmed or re-evaluated.

Figure 4. Non-metric characters used to evaluate differences among groups.

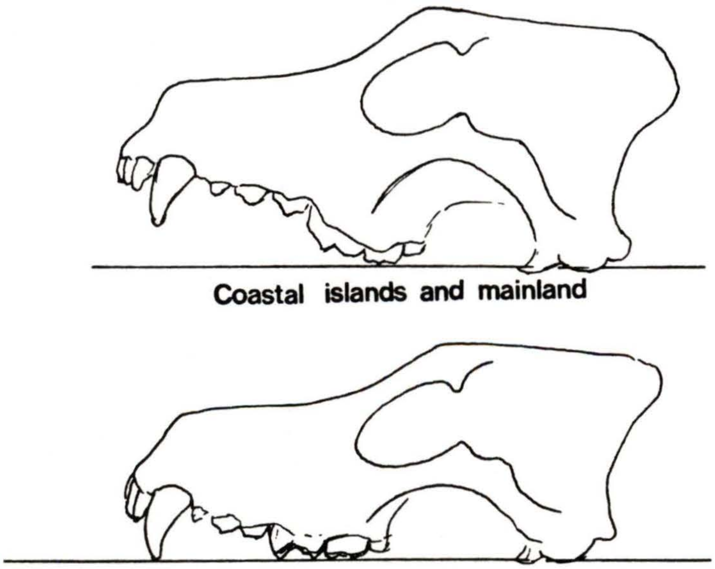
1. Shape of bone behind lacrimal fossa
2. Relative length of nasals
3. Position of canines of disarticulated skull
4. Shape of upper carnassial



1. Shape of bone behind lacrimal fossa



2. Relative length of nasals



3. Position of canines

4. Shape of upper carnassial

Statistical Methods

The data set was screened with the AM program of BMDP (Biomedical Computer Programs, Dixon and Brown 1979). I was able to obtain complete measurements on nearly all skulls; for those with one or two missing measurements, this program was used to estimate, by multiple regression, missing values. Of over 500 skulls measured, 22 had one missing measurement, 9 had no more than three.

Summary statistics were calculated with the condescriptive program of SPSS-X (Statistical Package for the Social Sciences). This allowed identification of data entry errors, and detection of possible outliers. Summary statistics are listed in Appendix 3. Univariate statistics were calculated with an Apple Stats Plus package (Madigan and Lawrence 1982).

Because males are significantly larger than females, (Nowak 1979), sexes (as designated on museum tags) were separated for most analyses. Animals of unknown sex could not be sexed accurately by discriminant function analysis (for example, the known-sex Smithers sample was too small to be used to sex the unknown specimens, and a discriminant function calculated on the Prince George population could not be used to sex the Smithers animals accurately). For this reason, unsexed animals were not included in multivariate analysis of wolf populations, except for those few which I felt I could confidently assign on the basis of size. Unsexed animals were included in evaluation of non-metric characteristics.

A series of multivariate methods was utilized to explore the data and various relationships within them. These methods and their applications are lucidly explained by such authors as Blackith and Reyment (1971), Sneath and Sokal (1973), Gnanadesikan (1977), and Neff and Marcus (1980).

I used the NT-SYS program (Numerical Taxonomy System of Multivariate Statistical Methods) of Rohlf, Kishpaugh, and Kirk (1982) for many of the analyses, primarily the following routines:

SIMINT: calculates matrices of similarity coefficients. Used to calculate taxonomic distance matrices (here, Euclidean distance in multidimensional space) and variance-covariance matrices.

TAXON: used here to perform cluster analyses on the taxonomic distance matrices, by the unweighted pair-group method using arithmetic averages. A phenogram and a matrix of cophenetic values are produced.

MSTSNGL: computes a single-linkage minimum spanning tree from the taxonomic distance matrix.

SUBSETS: finds within the taxonomic distance matrix all subsets that satisfy the condition that the minimum similarity between any two members is greater than the maximum similarity between any group member and any non-group member.

FACTOR: used to perform principal components analysis (PCA) on the variance-covariance matrix produced by SIMINT. The first principal component is calculated to account for the maximum amount of variance in the data set; the second, for the greatest possible amount of the remaining variance in a direction orthogonal to the first, and so on. Since, in similar studies, the first three factors usually accounted for over 90% of the variance, for these analyses only three factors were extracted.

MDSCALE: performs nonmetric multidimensional scaling on the taxonomic distance matrix. Rather than maximizing variation accounted for as in PCA, the reduced dimensions are calculated so that distances between points in the reduced space are as close as possible to the distances between points in the original distance matrix.

MXCOMP: a program for comparing the congruence of two matrices, useful for calculating the correlation between the original matrix and the result of one of the above analyses.

The multiple discriminant function analysis program in SPSS (Klecka 1975) was used to investigate differences among groups and to determine group membership of animals of unknown origin. Step-wise discriminant analysis selects the variable that provides the best separation among the groups, then the "next-best" discriminating variable given the variable already selected. The criterion of minimizing Wilks' lambda is used, and the process continues until a minimum F-value of 1.0 is reached. Discriminant functions are calculated to produce maximum separation between groups of known origin; these functions can then be used to infer the likely origin of other specimens.

As in univariate statistical methods, multivariate analyses have specific assumptions associated with them. Neff and Marcus (1980) give a good summary of these. All statistical tests assume random sampling, and in a study of this nature, with limited material available, this is not possible. Also, in order to make statistical inferences, multivariate normality and homogeneity of variance-covariance matrices must be assumed. Unfortunately, multivariate statistical package programs do not include a test for multivariate normality, and the test for homogeneity of variance-covariance matrices (Box's M) assumes multivariate normality.

When these methods are being used for exploratory purposes, violations of these assumptions may not be critical. Principal components analysis, for instance, when used to display interrelationships between individuals or variables, requires no assumptions (Neff and Marcus 1980). In multiple discriminant analysis, however, lack of homogeneity of variance-covariance matrices may result in inaccurate group assignments of unknown specimens. If group separation is clear and correct classification rates are high, identifications can be treated with some confidence.

Ideally, a multivariate analysis would be validated by analyzing two random samples from the same population, or, for example, calculating a discriminant function on one sample and using it to classify another. I did not have sufficient specimens to do this. Males and females were analyzed separately and results compared; although this approach does not comprise a split sample, I hoped to show similar patterns of variation for each sex.

Validity of Subspecific Designations

To represent *C.l. crassodon*, the Vancouver Island sample was used, Oregon for *C.l. fuscus*, Alaska for *C.l. ligoni*, Prince George for *C.l. columbianus*, Peace River for *C.l. occidentalis*, and Idaho for *C.l. irremotus*. Males and females were tested separately.

To evaluate the validity of Goldman's (1944) descriptions, two-sample t-tests were performed on the following characters, listed by Goldman as characteristics of those subspecies:

a) post-orbital process width: Prince George with Peace River.

b) width between orbits: Idaho with Oregon and with Prince George.

c) constriction behind post-orbital processes: Idaho with Oregon and with Prince George.

d) length of upper carnassial: Vancouver Island with Oregon and with Alaska; Prince George with Peace River.

e) width of upper carnassial: Vancouver Island with Oregon and with Alaska.

f) width of canine: Prince George with Peace River.

g) length of bullae and inter-bullar distance: Vancouver Island with Oregon and with Alaska, Alaska with Prince George.

To determine whether or not any groupings (corresponding to geographic location) were evident among individual wolves, I conducted principal components analyses on all male and all female wolves from the 12 areas. To determine whether significant differences existed between groups, and whether wolves belonging to these groups could be correctly identified, I conducted 12-group multiple discriminant function analyses on males and females separately.

Existence of Two Post-glacial Wolf Populations

To investigate phenetic relationships among groups, and to determine whether my wolf groups fell naturally into two "supergroups," I used the NT-SYS program to conduct cluster analyses, principal components analyses, and non metric multidimensional scaling on my 12 male and 12 female groups. The raw data matrix for these analyses was a matrix of the means of each variable for each group, and NT-SYS was used to calculate a taxonomic distance matrix and a variance-covariance matrix from this, on which the rest of the analyses were based.

To investigate further the degree of similarity among groups, subset and minimum spanning tree analyses were performed on the 12 male and 12 female groups, and results compared.

Systematic Status of Wolves on the British Columbia Coast

The systematic affinities of wolves on the coast of British Columbia were determined by conducting discriminant function analyses on wolves from Vancouver Island, Oregon, Alaska, and Cariboo. Coastal B.C. wolves were then entered as unknowns and assigned to the population they most resembled. Males and females were analyzed separately; coastal wolves of unknown sex were entered in both analyses and results compared. In addition, to test the validity of the discrimination, I ran a third analysis, combining males and females from the four areas and entering animals of unknown sex from these areas as unknowns to be classified.

Carnassial shape and length of nasals relative to frontomaxillary suture were also compared for these populations.

RESULTS

Validity of Subspecific Designations

The analyses of specific measurements suggested by Goldman as characteristic of certain subspecies failed to support most of his claims (Table 2). The only significant differences found, for both males and females, in the comparisons listed in the Methods section were: Idaho wolves were significantly narrower than Oregon and Prince George wolves for width between orbits and width behind post-orbital processes. Vancouver Island wolves had greater bulla length than Oregon wolves. Differences in dimensions of carnassial length, width across post-orbital processes, canine width, and distance between bullae were not significant for the groups compared.

Wolves are extremely variable animals and extensive overlap occurs in any one measurement among populations. For this reason, a multivariate approach is necessary to investigate differences among groups.

Principal components analysis of all male wolves from the reference groups showed no clear cut separation of groups. There was, however, a fairly distinct separation of animals from southern and coastal groups (Vancouver Island, B.C. coast, Alaska panhandle, Oregon, Idaho-Montana) from wolves from northern groups (Smithers, Horseranch,

Table 2. Results of two-sample t-tests on variables designated by Goldman (1944) as useful in distinguishing subspecies.

Variable	Groups compared	Males: Mean(mm)	Males: t-statistic	Males: Probability	Female: Mean	Female: t-statistic	Female: Probability
Carnassial length	Prince George	26.28	$t_{(22)}=-1.102$	0.2820	25.06	$t_{(16)}=-1.450$	0.1637
	& Peace River	26.89			25.81		
	Vancouver Island	25.43	$t_{(18)}=0.477$	0.6303	25.01	$t_{(17)}=2.768$	0.0127
	& Alaska	25.15			23.79		
	Vancouver Island	25.43	$t_{(19)}=0.184$	0.6563	25.01	$t_{(16)}=6.015$	<0.001
	& Idaho	24.99			24.08		
Carnassial width	Vancouver Island	10.01	$t_{(22)}=-1.629$	0.1143	9.45	$t_{(16)}=-1.833$	0.0826
	& Prince George	10.41			9.92		
	Vancouver Island	10.01	$t_{(18)}=-1.375$	0.1834	9.45	$t_{(17)}=-0.745$	0.4726
	& Alaska	10.36			9.62		
Width across post-orbital processes	Prince George	65.09	$t_{(22)}=-0.822$	0.4247	61.48	$t_{(16)}=0.043$	0.4598
	& Peace River	67.04			61.38		
Width between orbits	Oregon	48.71	$t_{(26)}=4.472$	<0.001	45.05	$t_{(30)}=3.353$	0.002
	& Idaho	43.51			41.19		
	Prince George	48.63	$t_{(29)}=3.761$	<0.001	44.26	$t_{(30)}=2.711$	0.0107
	& Idaho	43.51			41.19		
Width behind post-orbital processes	Oregon	42.94	$t_{(26)}=6.114$	<0.001	40.96	$t_{(30)}=3.211$	0.003
	& Idaho	37.44			37.62		
	Prince George	43.47	$t_{(29)}=6.223$	<0.001	41.78	$t_{(30)}=4.023$	<0.001
	& Idaho	37.44			37.62		
Canine width	Prince George	15.28	$t_{(22)}=-1.558$	0.1302	13.71	$t_{(16)}=-1.887$	0.0746
	& Peace River	15.99			14.44		
Distance between bullae	Vancouver Island	18.42	$t_{(19)}=-1.785$	0.0871	17.44	$t_{(16)}=-2.158$	0.0444
	& Oregon	19.68			18.91		
	Vancouver Island	18.42	$t_{(18)}=-1.657$	0.1118	17.44	$t_{(17)}=-0.952$	0.3570
	& Alaska	19.54			18.09		
	Alaska	19.54	$t_{(24)}=-0.595$	0.5617	18.09	$t_{(19)}=-1.546$	0.1354
	& Prince George	19.79			19.32		
Bulla length	Vancouver Island	33.77	$t_{(19)}=6.686$	<0.001	31.18	$t_{(16)}=3.379$	0.004
	& Oregon	28.92			27.43		
	Vancouver Island	33.77	$t_{(18)}=0.659$	0.5244	31.18	$t_{(17)}=-0.839$	0.4178
	& Alaska	33.16			32.12		
	Alaska	33.16	$t_{(24)}=0.840$	0.4139	32.12	$t_{(19)}=1.001$	0.3307
	& Prince George	32.55			31.48		

Kechika, Peace, and Jasper). Wolves from the interior of British Columbia (Cariboo and Prince George) overlapped these major groupings. A simplified version of this analysis is shown in Figure 5. Female wolves showed a similar organizational pattern (Figure 6).

The first principal component accounted for 73.7% of the total variance in males and 74.8% in females; the second for only 8.6% and 9.4%, respectively. All variables except width across post-orbital processes loaded most heavily on the first component for both males and females. All factor loadings on the first component were positive; this was primarily an expression of size. Shape differences may be reflected by the second component. Factor loadings and eigenvalues for males and for females are given in Table 3.

Multiple discriminant analysis of the 12 male groups is shown in Figure 7. The first discriminant function accounted for 37.0% of the variance and separated Oregon and Idaho wolves from the others. The second discriminant function accounted for an additional 19.4% of the variance and separated Oregon from Idaho. Vancouver Island, B.C. coast, and Alaska were also separated from the northern groups, with Prince George and Cariboo intermediate. The third function (not plotted in Figure 7) accounted for 16.0% of the variance and further separated Vancouver Island, B.C. coast, and Alaska. The northern and interior groups remained overlapping, with some separation occurring with

Figure 5. Positions of male wolves on a projection of first two principal components.

● Vancouver Island, B.C. Coast, Oregon, Alaska, Idaho

o Smithers, Horseranch, Kechika, Peace River, Jasper

* Cariboo, Prince George

First principal component accounts for 73.7% of variation, second for 8.6%.

Correlation with taxonomic distance matrix= 0.99

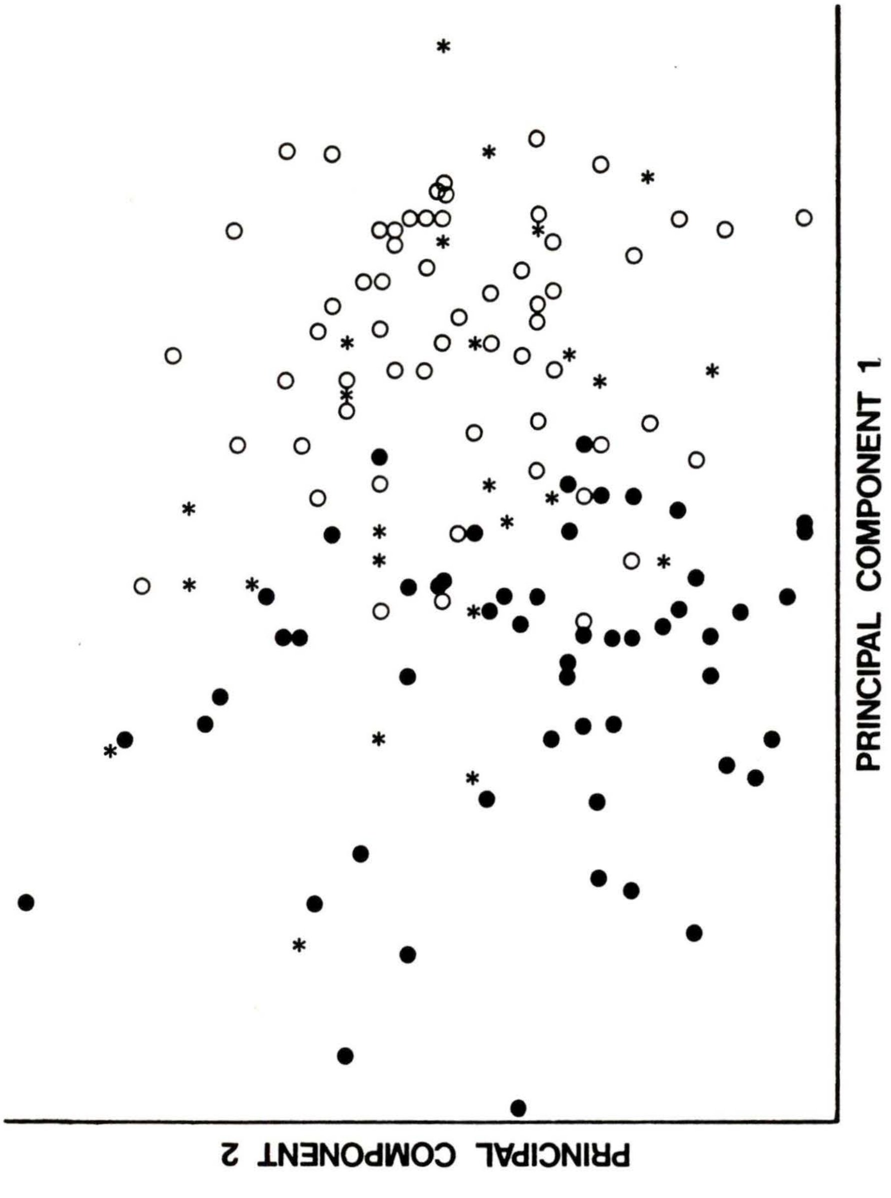

PRINCIPAL COMPONENT 1
PRINCIPAL COMPONENT 2

Figure 6. Positions of female wolves on a projection of first two principal components.

● Vancouver Island, B.C. Coast, Oregon, Alaska, Idaho

○ Smithers, Horseranch, Kechika, Peace River, Jasper

* Cariboo, Prince George

First principal component accounts for 74.8% of variation, second for 9.4%.

Correlation with taxonomic distance matrix= 0.99

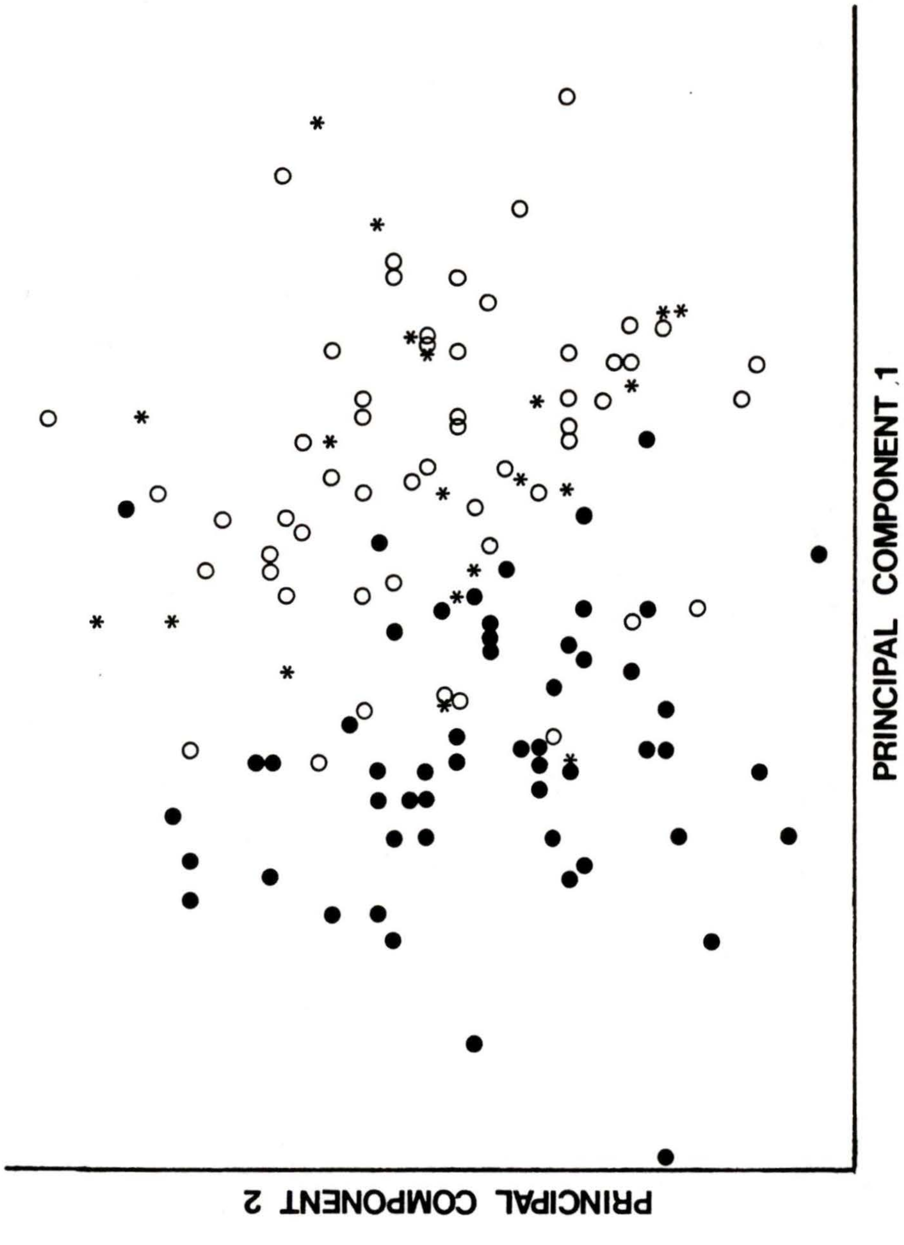

PRINCIPAL COMPONENT 1
PRINCIPAL COMPONENT 2

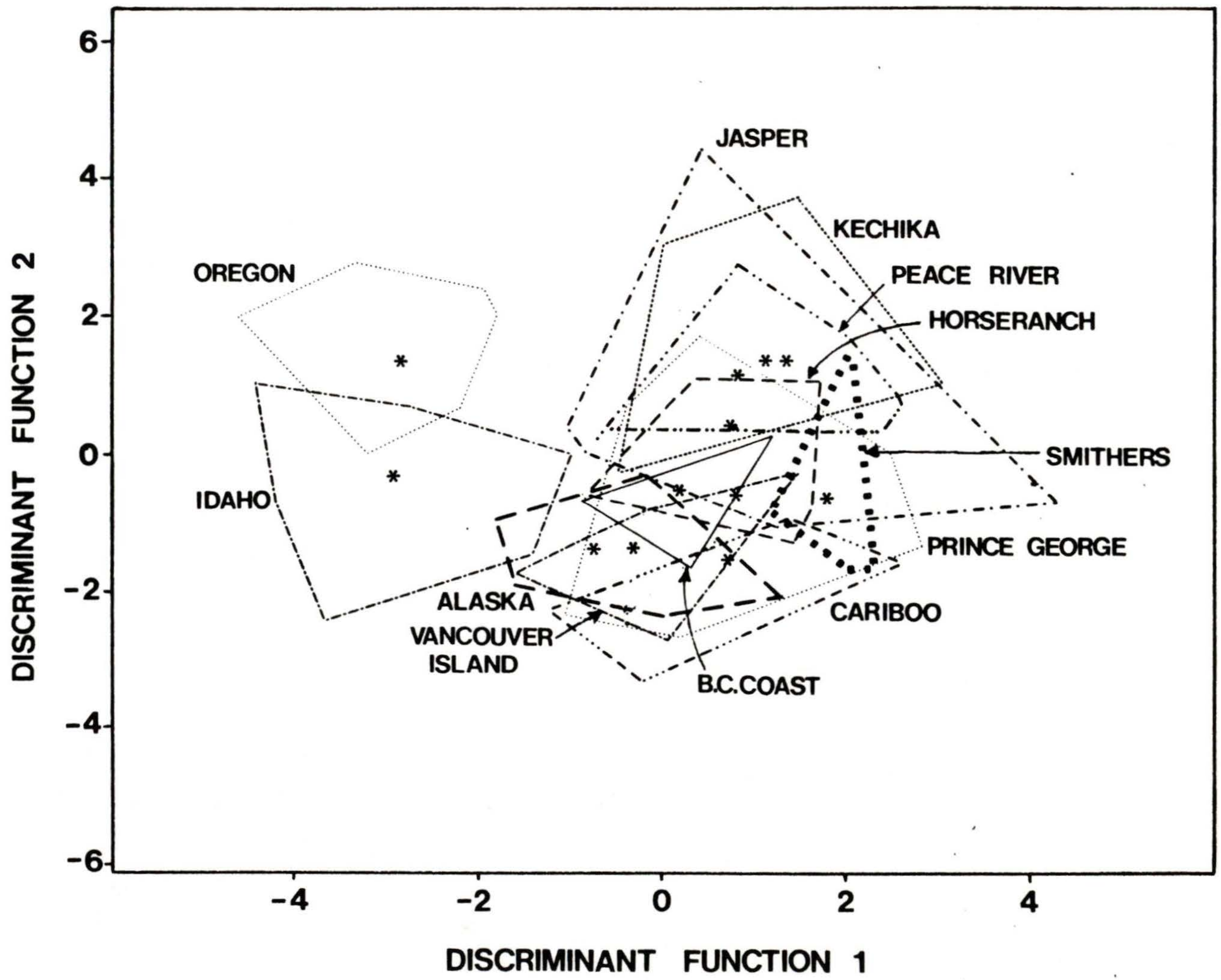
Table 3. Factor loadings and eigenvalues for first three components from principal components analysis on male and female wolves from 12 study areas.

Variable	Males (n = 138)			Females (n = 128)		
	PCI	PC2	PC3	PCI	PC2	PC3
1. Skull length	0.976	0.198	0.063	0.974	0.204	0.035
2. Zygomatic width	0.879	-0.337	-0.292	0.883	-0.356	0.128
3. M^2 to auditory canal	0.842	0.135	0.132	0.818	0.196	-0.487
4. Braincase width	0.421	0.037	0.125	0.609	0.253	0.186
5. Width across cheek teeth	0.777	-0.063	-0.325	0.766	-0.110	0.222
6. M^1 to orbit	0.834	-0.056	-0.091	0.892	-0.076	0.117
7. Tooth row length	0.868	0.191	-0.001	0.888	0.161	0.157
8. Carnassial length	0.651	0.125	-0.165	0.447	0.270	0.241
9. Carnassial width	0.555	0.209	-0.153	0.452	0.192	0.166
10. Canine width	0.412	0.031	-0.139	0.416	-0.080	0.082
11. M^2 width	0.530	0.039	-0.107	0.529	-0.078	0.238
12. Jugal height	0.703	-0.117	-0.064	0.703	-0.207	0.040
13. Width between orbits	0.719	-0.412	0.232	0.723	-0.467	-0.156
14. Width across post-orbital processes	0.543	-0.727	0.346	0.574	-0.709	-0.250
15. Width behind post-orbital processes	0.524	-0.259	0.465	0.559	-0.416	0.023
16. Distance between bullae	0.573	0.087	0.092	0.536	0.097	-0.013
17. Distance between first premolars	0.576	-0.189	-0.364	0.551	-0.300	0.317
18. Rostrum width at canines	0.773	-0.184	-0.199	0.791	-0.249	0.070
19. Bulla length	0.448	-0.021	0.101	0.547	0.088	-0.027
Eigenvalue	273.102	31.996	14.885	256.098	32.324	12.428
% of variance	73.7%	8.6%	4.0%	74.8%	9.4%	3.6%

Figure 7. Plot of relative positions of 12 male wolf groups on first two discriminant functions.

Asterisks indicate group centroids.

First function accounts for 37.0% of variation, second for 19.4%.



JASPER
KECHIKA
OREGON
PEACE RIVER
HORSERANCH
SMITHERS
IDAHO
PRINCE GEORGE
ALASKA
CARIBOO
VANCOUVER ISLAND
B.C.COAST
DISCRIMINANT FUNCTION 2
DISCRIMINANT FUNCTION 1
6
4
2
0
-2
-4
-6
-4
-2
0
2
4

the fourth and fifth functions. The analysis failed to find significant differences between Vancouver Island and either the B.C. coast or Alaska; between Prince George and Smithers, Cariboo, or Horseranch; between Horseranch and Peace River; or between Jasper and Horseranch, Kechika and Peace River. Oregon and Idaho were significantly different from all other groups and from each other.

All variables except carnassial length and distance from M^2 to auditory canal were included in the analysis. The discriminant function coefficients (Table 4) indicated the relative importance of each variable to each function. Thus, for the first function skull length and distance from M^1 to orbit contributed most significantly; for the second function, zygomatic width, distance across cheek teeth, length of tooth row, and width between orbits were most important.

The classification table (Table 5) shows the success of the discriminant analysis. Coastal and southern groups tended to have the highest correct classification rates, northern groups the lowest. Misclassification occurred most often with other members of the same "supergroup".

The results of the multiple discriminant analysis on female groups is shown in Figure 8. The first function accounted for 46.0% of the variance and again separated Oregon and Idaho. The second function (19.7%) separated Oregon from Idaho, and Vancouver Island from the remainder.

Table 4. Variables selected during multiple discriminant analysis of 12 male wolf groups, with standardized discriminant coefficients for five significant functions.

Variable	Standarized Discriminant Coefficients				
	DF1	DF2	DF3	DF4	DF5
1. Skull length	0.676	0.563	-0.690	-0.272	0.196
2. Zygomatic width	0.320	-0.825	-0.544	0.222	-0.242
4. Braincase width	-0.096	0.247	-0.058	-0.045	0.243
5. Width across cheek teeth	-0.328	0.616	-0.267	0.770	-0.421
6. M^1 to orbit	0.715	-0.158	0.146	-0.131	0.172
7. Tooth row length	-0.083	-0.524	0.737	-0.675	-0.291
9. Carnassial width	-0.100	0.276	-0.262	0.573	-0.152
10. Canine width	0.016	-0.326	0.118	0.185	0.826
11. M^2 width	0.103	0.228	0.057	0.090	0.075
12. Jugal height	-0.316	0.488	0.318	0.098	-0.451
13. Width between orbits	-0.037	0.529	-0.422	-0.370	0.385
14. Width across post-orbital processes	-0.409	0.173	0.911	0.539	0.119
15. Width behind post-orbital processes	0.397	-0.029	0.611	-0.053	-0.447
16. Distance between bullae	0.020	0.137	-0.061	0.459	0.124
17. Distance between first premolars	0.094	-0.498	-0.465	0.081	-0.426
18. Rostrum width at canines	-0.361	0.074	0.444	-1.115	0.486
19. Bulla length	0.381	-0.338	-0.127	0.676	0.215
Eigenvalue	2.496	1.307	1.071	0.695	0.370
% of variance	37.0%	19.4%	15.9%	10.3%	5.5%

Table 5. Classification table produced by multiple discriminant analysis of 12 male wolf groups.

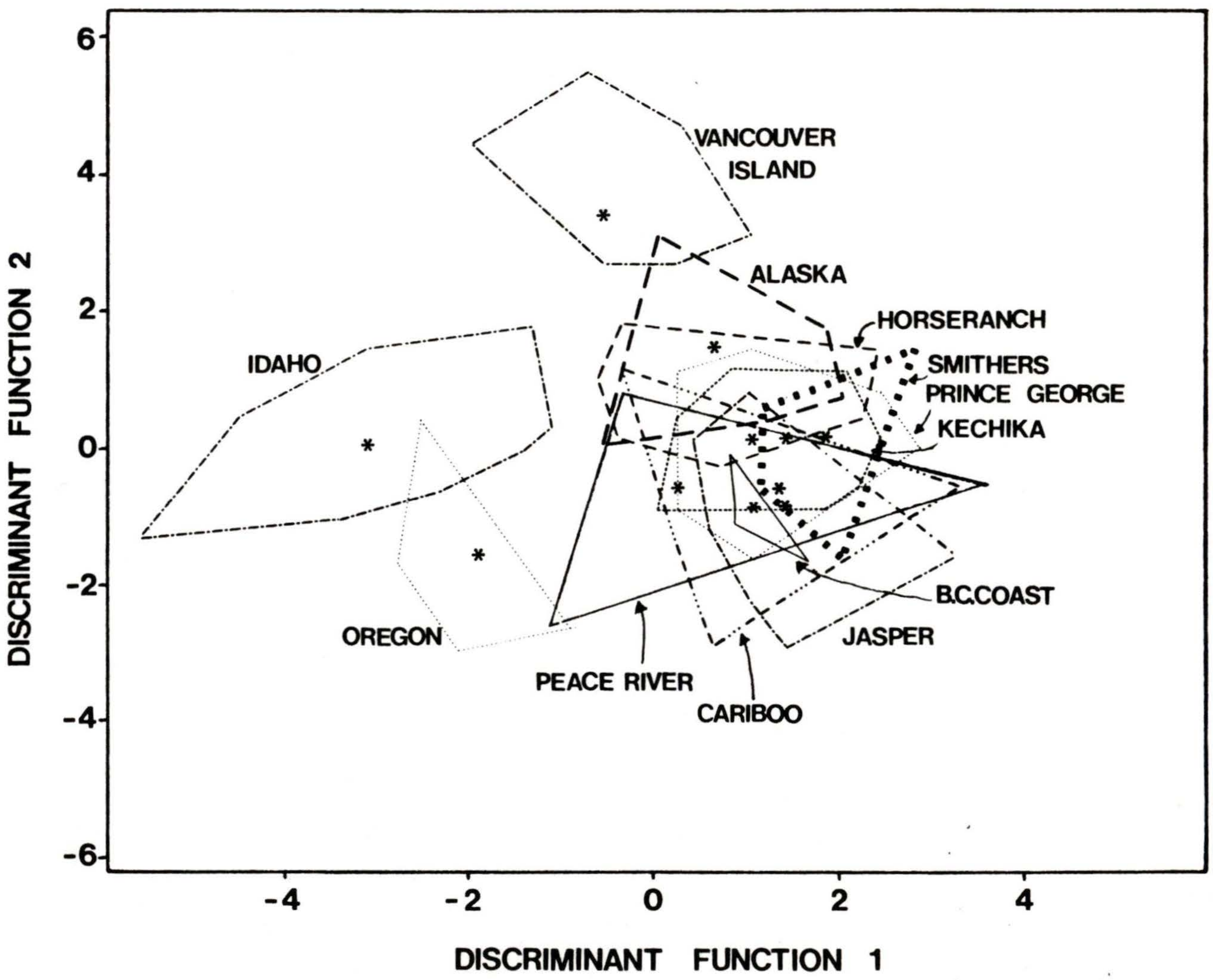
		PREDICTED GROUP MEMBERSHIP											
ACTUAL GROUP	No. of Cases	Vancouver Island	B.C. Coast	Oregon	Alaska	Idaho	Smithers	Prince George	Cariboo	Horse-ranch	Kechika	Peace River	Jasper
Vancouver Is.	9	8 88.9%	0	0	1 11.1%	0	0	0	0	0	0	0	0
B.C. Coast	5	0	5 100.0%	0	0	0	0	0	0	0	0	0	0
Oregon	12	0	0	12 100.0%	0	0	0	0	0	0	0	0	0
Alaska	11	0	1 9.1%	0	8 72.7%	0	0	0	1 9.1%	0	1 9.1%	0	0
Idaho	16	1 6.3%	0	0	0	14 87.5%	0	0	1 6.3%	0	0	0	0
Smithers	6	0	0	0	0	0	5 83.3%	0	0	0	1 16.7%	0	0
Prince George	15	0	1 6.7%	0	1 6.7%	0	0	9 60.0%	2 13.3%	0	1 6.7%	0	1 6.7%
Cariboo	10	0	0	0	0	0	1 10.0%	1 10.0%	8 80.0%	0	0	0	0
Horseranch	14	0	0	0	0	0	2 14.3%	0	0	7 50.0%	2 14.3%	1 7.1%	2 14.3%
Kechika	19	0	2 10.5%	0	0	0	0	0	0	1 5.3%	12 63.2%	1 5.3%	3 15.8%
Peace River	9	0	0	0	0	0	0	0	0	1 11.1%	0	7 77.8%	1 11.1%
Jasper	12	1 8.3%	0	0	0	0	1 8.3%	2 16.7%	0	1 8.3%	1 8.3%	3 25.0%	3 25.0%

Overall classification rate: 71.0%

Figure 8. Plot of relative positions of 12 female wolf groups on first two discriminant functions.

Asterisks indicate group centroids.

First function accounts for 46.0% of variance, second for 19.7%


VANCOUVER
ISLAND
ALASKA
HORSERANCH
SMITHERS
PRINCE GEORGE
KECHIKA
IDAHO
B.C.COAST
JASPER
OREGON
PEACE RIVER
CARIBOO
DISCRIMINANT FUNCTION 2
DISCRIMINANT FUNCTION 1
6
4
2
0
-2
-4
-6
-4
-2
0
2
4

The third function (not shown) separated northern groups slightly. No significant difference was found between Prince George and Horseranch or Peace River, Cariboo and Horseranch, or Peace River and Jasper. Vancouver Island, Oregon and Idaho were significantly different from all other groups.

The stepwise analysis selected all variables but zygomatic width, distance from M^2 to auditory canal, width across upper cheek teeth, transverse diameter of M^2, and height of jugal (Table 6). The discriminant function coefficients suggested that variables important in separating females were different from those in the male analysis: Distance M^1 to orbit, width between orbits, width of constriction behind post-orbital processes, distance between bullae, and length of bullae were of near equal importance on the first discriminant function. Skull length, length of tooth row, and width across post-orbital processes contributed most to the second function.

The first five functions together contributed significantly (Table 6) to the discrimination and accounted for 90.9% of the variance. The classification table (Table 7) shows that, as with males, misclassification most often occurred within "supergroups" and that southern groups had higher correct classification rates than northern groups.

Although most groups maintained the same relative position in the male and female analyses, the Oregon and

Table 6: Variables selected during multiple discriminant analysis of 12 female wolf groups, with standardized canonical discriminant function coefficients for five significant functions.

	Standarized Discriminant Coefficients				
Variable	DF1	DF2	DF3	DF4	DF5
1. Skull length	0.448	-1.921	-0.362	0.019	1.182
4. Braincase width	-0.024	0.569	0.380	-0.152	0.131
6. M^2 to orbit	0.547	0.204	0.038	0.229	-0.269
7. Tooth row length	-0.039	0.985	0.483	-0.200	-0.629
8. Carnassial length	-0.063	0.279	0.625	-0.478	0.524
9. Carnassial width	-0.402	0.183	0.405	0.679	-0.133
10. Canine width	0.002	0.002	-0.575	-0.139	0.300
13. Width between orbits	-0.536	-0.555	0.067	0.558	0.179
14. Width across post-orbital processes	0.060	0.711	-0.554	-0.193	0.413
15. Width behind post-orbital processes	0.583	-0.240	-0.338	-0.279	-0.344
16. Distance between bullae	0.560	0.119	-0.001	-0.132	-0.514
17. Distance between first premolars	0.248	0.084	-0.311	0.383	0.928
18. Rostrum width at canines	-0.449	-0.069	0.399	-0.513	-1.160
19. Bulla length	0.540	0.595	-0.137	0.461	-0.367
Eigenvalue	3.258	1.392	0.841	0.483	0.460
% of variance	46.0%	19.7%	11.9%	6.8%	6.5%

Table 7. Classification table produced by multiple discriminant analysis of 12 female wolf groups.

		PREDICTED GROUP MEMBERSHIP											
ACTUAL GROUP	No. of Cases	Vancouver Island	B.C. Coast	Oregon	Alaska	Idaho	Smithers	Prince George	Cariboo	Horse-ranch	Kechika	Peace River	Jasper
Vancouver Is.	8	7 85.7%	0	0	0	1 12.5%	0	0	0	0	0	0	0
B.C. Coast	3	0	3 100.0%	0	0	0	0	0	0	0	0	0	0
Oregon	10	0	1 10.0%	8 80.0%	0	1 10.0%	0	0	0	0	0	0	0
Alaska	11	0	0	0	9 81.8%	0	0	0	0	1 9.1%	1 9.1%	0	0
Idaho	22	0	0	1 4.5%	0	20 90.9%	0	0	0	0	0	1 4.5%	0
Smithers	4	0	0	0	0	0	4 100.0%	0	0	0	0	0	0
Prince George	10	0	0	0	1 10.0%	0	1 10.0%	5 50.0%	0	1 10.0%	0	2 20.0%	0
Cariboo	10	0	1 10.0%	0	1 10.0%	0	1 10.0%	0	7 70.0%	0	0	0	0
Horseranch	12	0	0	0	0	0	0	1 8.3%	2 16.7%	8 66.7%	1 8.3%	0	0
Kechika	18	0	1 5.6%	0	1 5.6%	0	0	0	0	0	14 77.8%	0	2 11.1%
Peace River	8	0	0 12.5%	1	0	0	0	1 12.5%	0	0	0	4 50.0%	2 25.0%
Jasper	12	0	0	0	0	0	1 8.3%	1 8.3%	1 8.3%	0	1 8.3%	1 8.3%	7 58.3%

Overall classification rate: 75.0%

Vancouver Island populations had their direction of separation reversed. This reversal was true of all groups but Smithers, Cariboo, Horseranch, and Kechika.

Analysis of Non-metric Characters

The shape of the bone behind the lacrimal fossa showed some variation among groups. The southern animals tended to have a smooth edge to the bone or only a slight indentation; in northern groups an increasing proportion of the animals had a deep indentation or an actual foramen formed (Table 8).

The length of the nasal bones relative to the maxillofrontal suture (Figure 4) is mentioned by Goldman (1944) as characteristic of C.l. fuscus. Of 22 Oregon wolves examined, 20 had nasals even with or only slightly above the sutures. This was true of only 1 of 16 wolves from coastal B.C., which has been considered within the range of this subspecies. All other groups except Horseranch had some animals with short nasals, but proportions were low (Table 9).

An unpublished provincial museum report suggests, as a method of distinguishing Vancouver Island from adjacent mainland wolves, placing a disarticulated skull on a flat surface. Seventeen of 19 Vancouver Island skulls checked had canines either in contact with or very close to touching

Table 8: Differences in shape of bone behind lacrimal fossa.

Wolf group	Proportion of wolves Shape of bone		
			
Vancouver Island	18 (94.7%)	1 (5.3%)	0
B.C. coast	7 (43.8%)	7 (43.8%)	2 (12.3%)
Oregon	15 (68.2%)	6 (40.0%)	1 (6.7%)
Alaska	18 (54.5%)	14 (42.4%)	1 (3.0%)
Idaho	38 (80.9%)	7 (14.9%)	2 (4.3%)
Smithers	15 (51.7%)	12 (41.4%)	2 (6.9%)
Prince George	12 (44.4%)	10 (37.0%)	5 (18.5%)
Cariboo	13 (54.2%)	8 (33.3%)	3 (12.5%)
Horseranch	9 (34.6%)	11 (42.3%)	6 (23.1%)
Kechika	10 (27.0%)	20 (54.1%)	7 (18.9%)
Peace River	6 (33.3%)	10 (55.6%)	2 (11.1%)
Jasper	12 (50.0%)	11 (45.8%)	1 (4.2%)
Recent Vancouver Island	43 (66.2%)	19 (29.2%)	3 (4.6%)
Coastal islands	11 (84.6%)	1 (7.7%)	1 (7.7%)

Table 9. Length of nasals relative to fronto-maxillary suture for 12 wolf groups. (See Figure 4)

	Proportion of wolves with nasals		
Group	even	slightly above	above
Vancouver Island	1(5.0%)	2(10.0%)	17(85.0%)
B.C. Coast	0	1(6.3%)	15(93.8%)
Oregon	14(63.6%)	6(27.3%)	2(9.1%)
Alaska	1(3.0%)	9(27.3%)	23(69.7%)
Idaho	6(12.8%)	11(23.4%)	30(63.8%)
Smithers	4(13.8%)	1(3.4%)	24(82.8%)
Prince George	4(14.8%)	4(14.8%)	19(70.4%)
Cariboo	2(8.3%)	5(20.8%)	17(70.8%)
Horseranch	0	0	26(100.0%)
Kechika	2(5.4%)	4(10.8%)	31(83.8%)
Peace River	2(11.1%)	1(5.6%)	15(83.3%)
Jasper	3(12.5%)	2(8.3%)	19(79.2%)

the surface, but only 9 of 16 coastal skulls displayed this characteristic (Table 10).

Goldman's claim that Vancouver Island wolves had thicker carnassials than other groups is apparently a function of shape rather than actual size. As can be seen in Figure 4, Island wolves typically had the anterior border of the crown directed backwards. This shape was rare in other groups (Table 11).

Existence of Two Post-glacial Wolf Populations

A cluster analysis of the twelve reference groups (Figure 9) showed southern and coastal groups forming one major cluster and northern groups forming a second, for both males and females. Prince George clustered with the northern group for both sexes, despite the intermediate position shown on the principal components analysis (Figures 5 and 6). Cariboo clustered with the southern group for males and with the northern group for females. The northern groups clustered at a much lower level than the southern groups, suggesting a much greater variability in the southern populations.

A principal components analysis of the twelve reference groups showed the same grouping (Figure 10). Since the first component accounted for 87.6% of the total male variance and 85.0% of the female variance with the second accounting for

Table 10. Position of canines of disarticulated cranium for 12 wolf groups. (See Figure 4)

	Proportion of wolves with canines		
Group	On surface	Just above surface	Well above surface
Vancouver Island	13(68.4%)	4(21.1%)	2(10.5%)
B.C. Coast	4(25.0%)	5(31.3%)	7(43.8%)
Oregon	6(31.6%)	4(21.1%)	9(47.4%)
Alaska	10(34.5%)	7(24.1%)	12(41.4%)
Idaho	23(53.5%)	12(27.9%)	8(18.6%)
Smithers	12(42.9%)	10(35.7%)	6(21.4%)
Prince George	15(55.6%)	6(22.2%)	6(22.2%)
Cariboo	12(52.2%)	10(43.5%)	1(4.3%)
Horseranch	15(57.7%)	7(26.9%)	4(15.4%)
Kechika	6(16.2%)	26(70.3%)	5(13.5%)
Peace River	7(38.9%)	3(16.7%)	8(44.4%)
Jasper	8(36.4%)	8(36.4%)	6(27.3%)

Table 11: Occurrence of carnassial shapes in wolf populations.

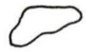
Wolf group	Proportion of wolves Carnassial shape		
			
Historic Vancouver Island	14 (73.7%)	5 (26.3%)	0
B.C. coast	3 (18.8%)	12 (75.0%)	1 (6.3%)
Oregon	2 (10.0%)	12 (60.0%)	6 (30.0%)
Alaska	1 (3.2%)	26 (83.9%)	4 (12.9%)
Idaho	2 (4.3%)	31 (66.0%)	14 (29.8%)
Smithers	0	20 (79.2%)	7 (20.8%)
Prince George	2 (7.4%)	21 (77.8%)	4 (14.8%)
Cariboo	0	17 (69.6%)	7 (30.4%)
Horseranch	0	20 (78.6%)	6 (21.4%)
Kechika	4 (11.4%)	23 (65.7%)	8 (22.9%)
Peace River	0	10 (71.4%)	4 (28.6%)
Jasper	0	17 (70.8%)	7 (29.2%)
Recent Vancouver Island	27 (39.7%)	36 (52.9%)	5 (7.4%)
Coastal islands	3 (21.4%)	8 (57.1%)	3 (21.4%)

Figure 9. Phenograms of 12 male (top) and 12 female (bottom) wolf groups, based on taxonomic distance.

The taxonomic distance matrix is calculated from a matrix of the means of each variable for each group.

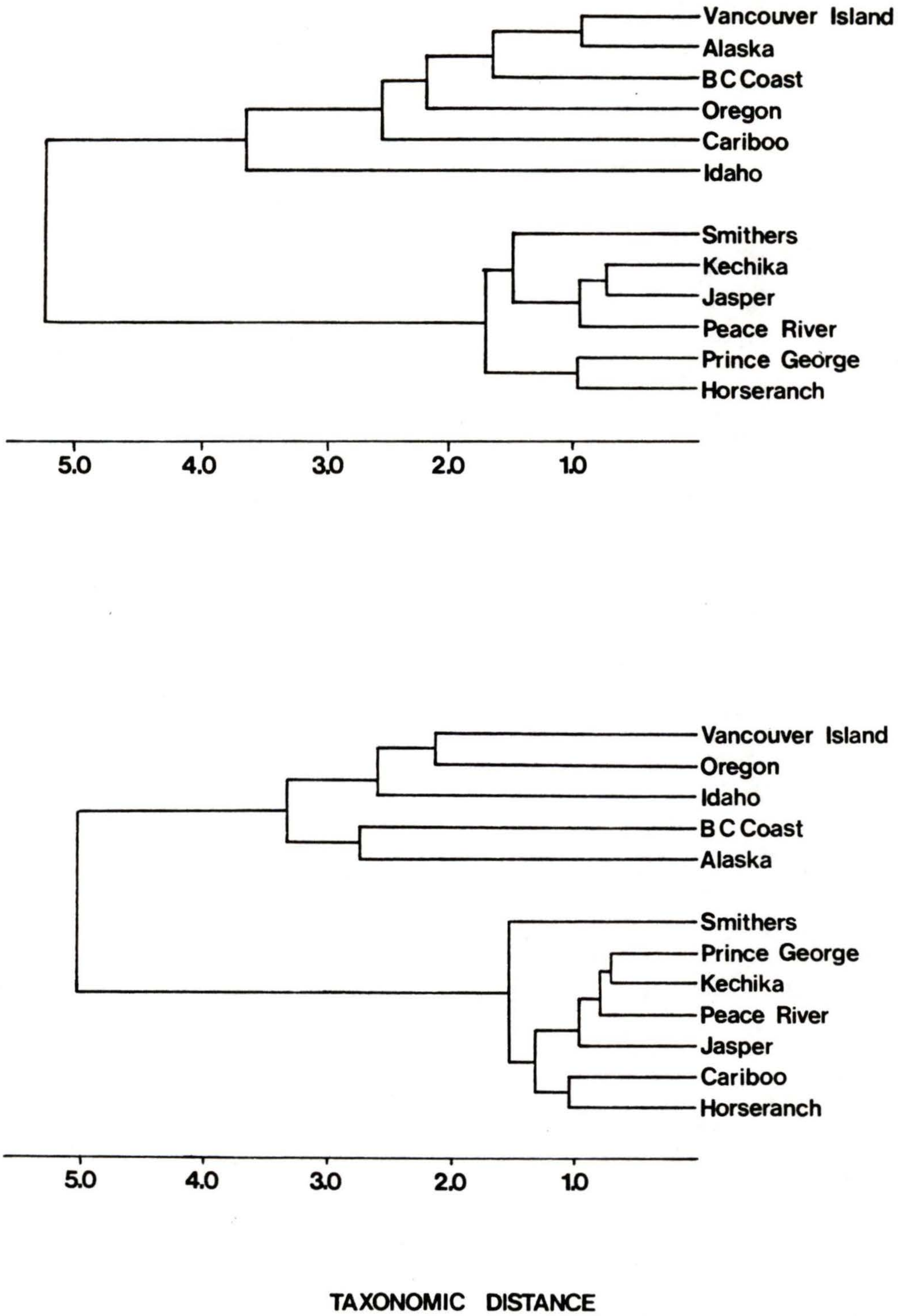
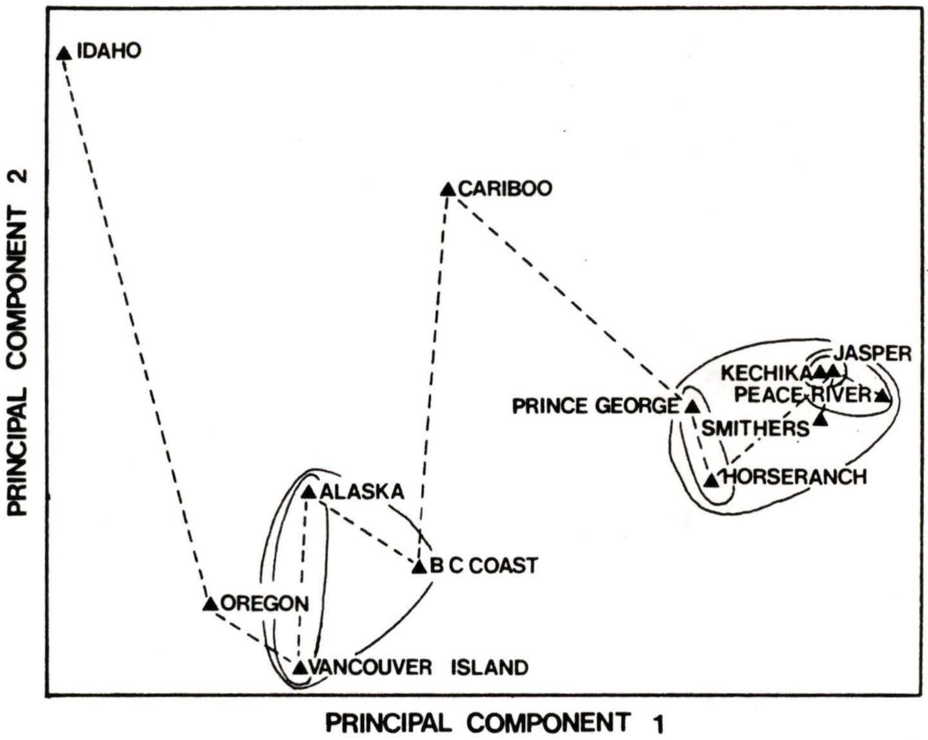

Vancouver Island
Alaska
BC Coast
Oregon
Cariboo
Idaho
Smithers
Kechika
Jasper
Peace River
Prince George
Horseranch
5.0
4.0
3.0
2.0
1.0
Vancouver Island
Oregon
Idaho
BC Coast
Alaska
Smithers
Prince George
Kechika
Peace River
Jasper
Cariboo
Horseranch
5.0
4.0
3.0
2.0
1.0
TAXONOMIC DISTANCE

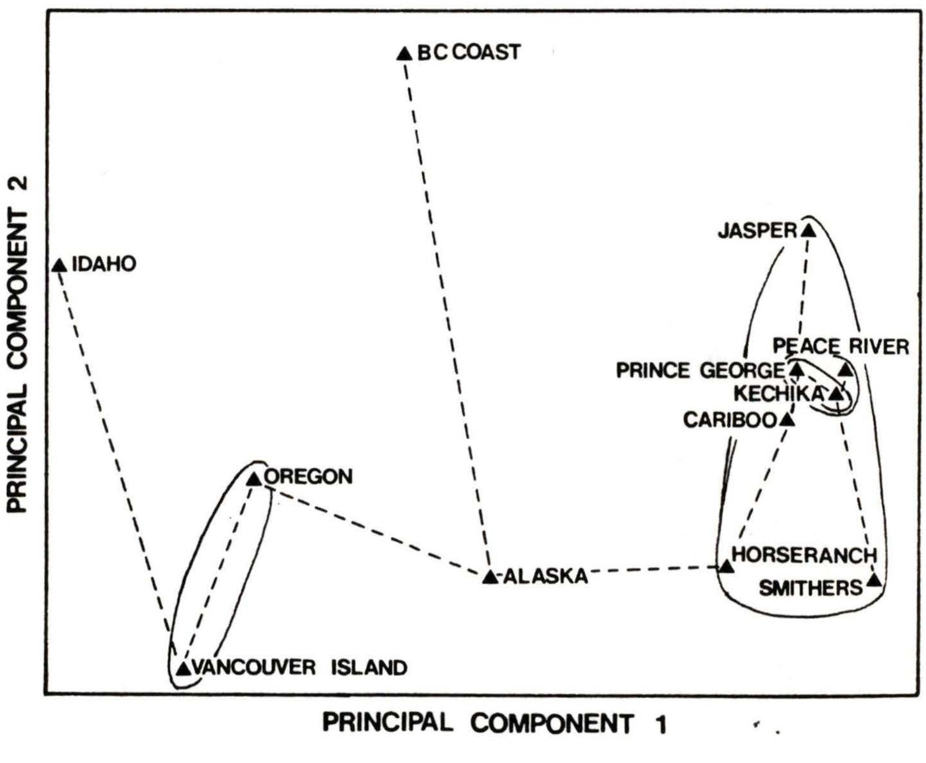
Figure 10. Plot of relative positions of 12 male (top) and 12 female (bottom) wolf groups on first two principal components.

First component accounts for 87.6% of variance in males, 85.0% in females; second, for 5.2% and 8.7%.

Correlations with taxonomic distance matrices are 0.999 and 0.987.

Dotted lines indicate minimum spanning tree linkages, solid lines enclose groups defined by subset analysis.


IDAHO
CARIBOO
JASPER
KECHIKA
PEACE RIVER
PRINCE GEORGE
SMITHERS
HORSERANCH
ALASKA
B C COAST
OREGON
VANCOUVER ISLAND
PRINCIPAL COMPONENT 2
PRINCIPAL COMPONENT 1


B C COAST
JASPER
IDAHO
PEACE RIVER
PRINCE GEORGE
KECHIKA
CARIBOO
OREGON
HORSERANCH
ALASKA
SMITHERS
VANCOUVER ISLAND
PRINCIPAL COMPONENT 2
PRINCIPAL COMPONENT 1

only 5.2% and 8.7%, respectively, dispersion along the second axis is not particularly meaningful. Projection of the points onto the first axis produced results similar to the cluster analysis. In the male group analysis, all variables loaded most heavily on the first component except width across post-orbital processes, width of constriction behind post-orbital processes (second component), and length of bulla (third component) (Table 12). For females, all variables loaded most heavily on the first component except width across post-orbital processes (second component) and upper carnassial length (third component). The mixed signs of the second and third components are indicative of shape variation (Pimentel 1979). However, the fact that these components together only account for 5.2% of the variation in males and 8.7% in females suggested that size is the major factor separating populations, with shape a rather minor consideration.

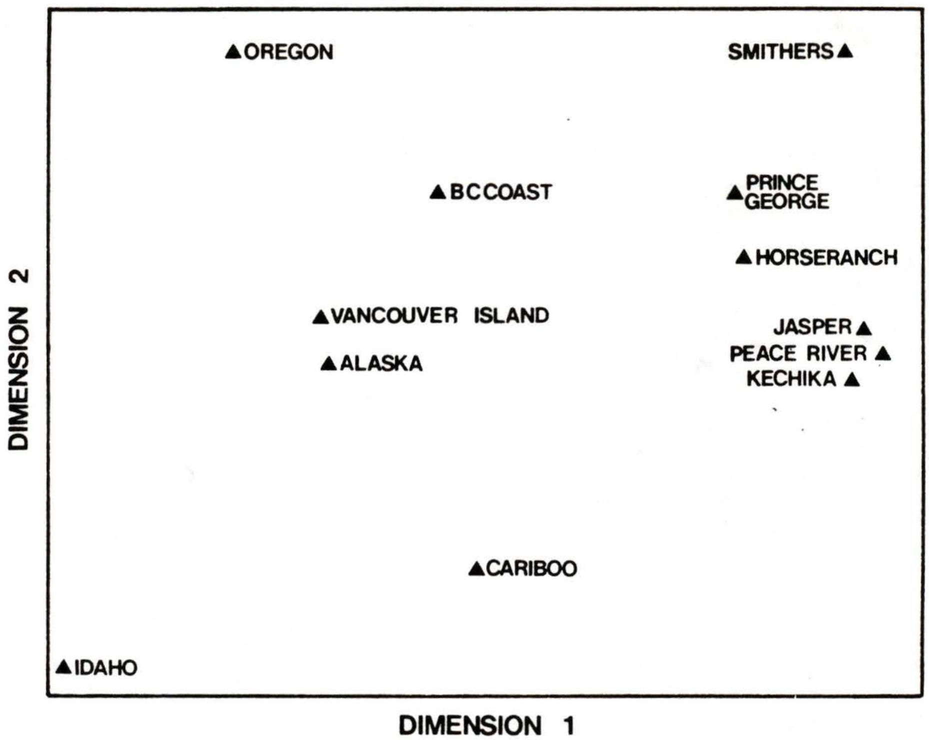
In both male and female groups, Idaho, Oregon, and Vancouver Island wolves were the smallest, and the northeastern groups the largest. The varying positions of other groups may indicate differing degrees of sexual dimorphism. Nonmetric multidimensional scaling (Figure 11) did not produce significantly different results. Although dispersion along the second axis varied between males and females, projection of points onto the first axis showed virtually identical groupings. The northern groups were

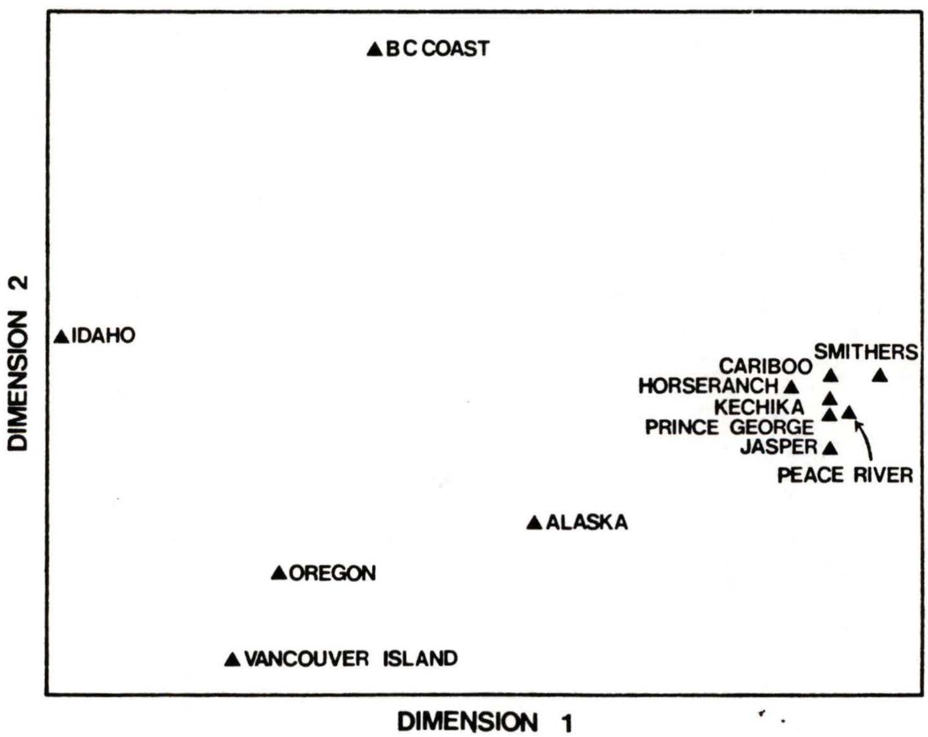
Table 12: Factor loadings and eigenvalues for first three components from principal components analysis on male and female wolf groups (mean value of each variable used for each group).

Variable	Males (n = 12)			Females (n = 12)		
	PCI	PC2	PC3	PCI	PC2	PC3
1. Skull length	0.995	0.074	-0.031	0.984	0.173	-0.004
2. Zygomatic width	0.943	-0.106	0.248	0.913	-0.394	0.068
3. M^2 to auditory canal	0.943	0.147	-0.246	0.945	0.163	-0.234
4. Braincase width	0.893	-0.068	-0.081	0.725	-0.330	0.302
5. Width across cheek teeth	0.845	0.076	-0.144	0.836	-0.197	0.376
6. M^1 to orbit	0.965	-0.041	0.123	0.970	-0.050	0.054
7. Tooth row length	0.954	-0.009	0.165	0.948	-0.036	0.204
8. Carnassial length	0.890	0.075	-0.185	0.519	0.117	0.593
9. Carnassial width	0.722	0.176	-0.193	0.601	0.111	0.528
10. Canine width	0.517	-0.138	-0.177	0.491	-0.344	0.041
11. M^2 width	0.758	-0.143	0.042	0.601	-0.518	0.333
12. Jugal height	0.832	-0.197	-0.324	0.858	-0.059	-0.226
13. Width between orbits	0.791	-0.244	-0.484	0.767	-0.399	-0.349
14. Width across post-orbital processes	0.428	-0.874	-0.195	0.455	-0.817	-0.305
15. Width behind post-orbital processes	0.638	-0.678	0.044	0.717	-0.376	-0.212
16. Distance between bullae	0.805	0.124	-0.398	0.596	0.586	-0.317
17. Distance between first premolars	0.753	0.215	0.382	0.747	-0.411	0.105
18. Rostrum width at canines	0.909	0.088	-0.266	0.894	-0.159	-0.107
19. Bulla length	0.542	-0.202	0.624	0.651	-0.369	0.426
Eigenvalue	154.213	9.165	5.681	133.533	13.726	4.007
% of variance	87.6%	5.2%	3.2%	85.0%	8.7%	2.6%

Figure 11. Plot of relative positions of 12 male (top) and 12 female (bottom) wolf groups on first two dimensions produced by non-metric multi-dimensional scaling.

Minimum stress achieved was 0.024 for males, 0.034 for females.


OREGON
SMITHERS
BC COAST
PRINCE GEORGE
HORSERANCH
VANCOUVER ISLAND
JASPER
PEACE RIVER
ALASKA
KECHIKA
CARIBOO
IDAHO
DIMENSION 2
DIMENSION 1


BC COAST
IDAHO
SMITHERS
CARIBOO
HORSERANCH
KECHIKA
PRINCE GEORGE
JASPER
PEACE RIVER
ALASKA
OREGON
VANCOUVER ISLAND
DIMENSION 2
DIMENSION 1

much more closely related to one another than were the southern and coastal groups.

Subset and minimum spanning tree groupings (Figure 10) showed that the results of these two analyses were not distorted from the original data, as confirmed by the high matrix correlations. Subset analysis, while confirming the similarity of northern groups, failed to provide evidence of close groupings among the southern and coastal forms. Minimum spanning trees showed direction of group similarity to be from northeastern British Columbia westward across the coast mountains, southward along the coast, then eastward across the northwestern United States. Jasper and Idaho, though relatively close geographically, were most dissimilar.

Systematic Status of Wolves on the British Columbia Coast

The results of multiple discriminant analysis on groups adjacent to the British Columbia coast is shown in Figure 12. The male analysis provided better group separation than the female plot. Zygomatic width, width across cheek teeth, width across post-orbital processes, and width between first premolars contributed most heavily to the first function (Table 13), and separated Oregon wolves from the other groups. Distance from M^2 to auditory opening, skull width across canines, as well as cheek tooth width and post-

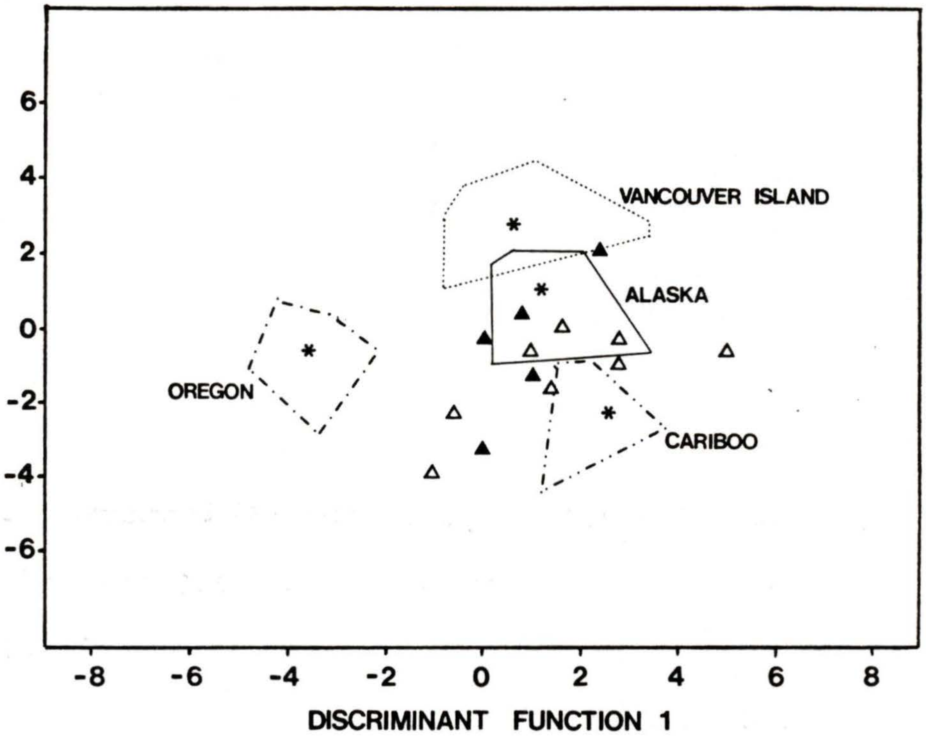
Figure 12. Plot of relative positions of Vancouver Island, Oregon, Alaska and Cariboo male (top) and female (bottom) wolf groups on first two discriminant functions.

First function accounts for 60.1% of variance in males, 56.7% in females; second for 35.3% and 37.4%.

▲ B.C. Coast wolves of known sex.

△ B.C. Coast wolves of unknown sex

* group centroids.


VANCOUVER ISLAND
ALASKA
OREGON
CARIBOO
6
4
2
0
-2
-4
-6
-8 -6 -4 -2 0 2 4 6 8
DISCRIMINANT FUNCTION 1

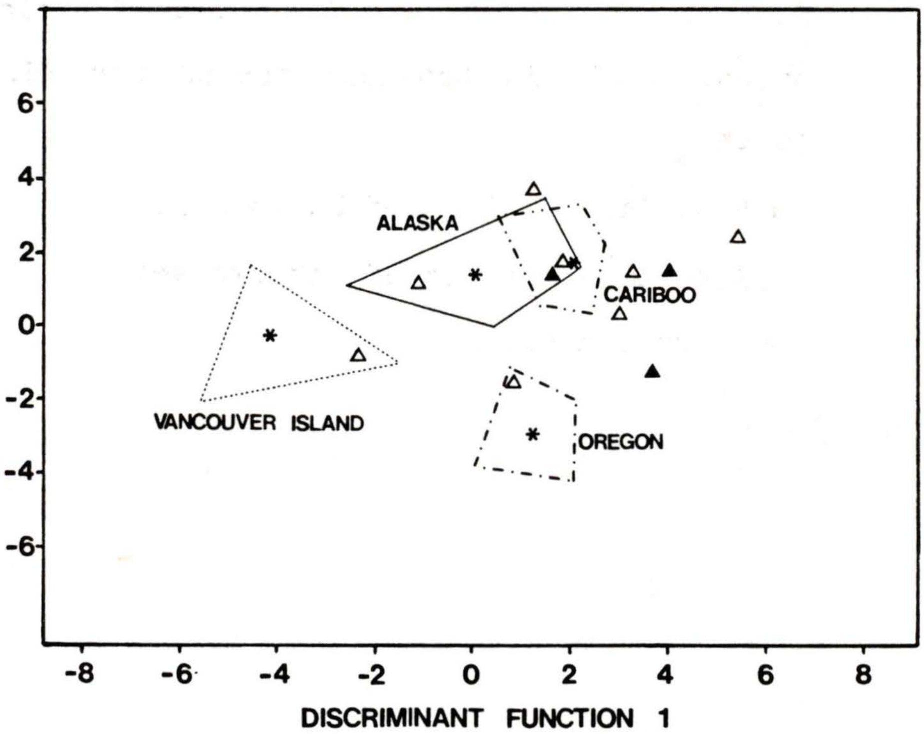

ALASKA
CARIBOO
VANCOUVER ISLAND
OREGON
6
4
2
0
-2
-4
-6
-8 -6 -4 -2 0 2 4 6 8
DISCRIMINANT FUNCTION 1

Table 13. Variables selected during multiple discriminant analysis of four male coastal groups, with standardized discriminant coefficients.

Variable	Standardized Discriminant Coefficients		
	DF1	DF2	DF3
2. Zygomatic width	1.302	0.316	0.086
3. M^2 to auditory canal	0.105	-1.027	0.049
4. Braincase width	-0.162	-0.310	0.446
5. Width across cheek teeth	-1.075	1.097	0.073
9. Carnassial width	-0.295	-0.291	0.885
10. Canine width	0.223	0.576	-0.723
13. Width between orbits	-0.719	-0.208	-1.012
14. Width across post-orbital processes	-1.034	1.015	0.454
17. Distance between first premolars	1.178	-0.470	0.717
18. Rostrum width at canines	-0.002	-1.052	-0.234
19. Bulla length	0.825	0.464	-0.474
Eigenvalue	6.416	3.764	0.491
% of variance	60.1%	35.3%	4.6%

orbital process width again, were the variables contributing most to the second discriminant, which separated the remaining three groups. The third discriminant was non-significant.

By contrast, the first discriminant function in the female analysis separated Vancouver Island and, to a lesser extent, Alaska, from Oregon and Cariboo (Figure 12). Distance from M^2 to auditory opening, width of braincase, and distance between bullae contributed most to this function (Table 14). Distance from M^1 to orbit and skull width across canines contributed most to the second function, which separated Oregon from Alaska and Cariboo. The third function was non-significant.

In both analyses, the Oregon and Vancouver Island populations were well separated from the other groups. When wolves from the British Columbia coast were entered in this analysis as unknowns, all but two were assigned to either the Alaska or Cariboo populations (Tables 15 and 16 and Figure 12). The exceptions were a female wolf, taken from Princess Royal Island in 1937 (assigned to Oregon) and a wolf of unknown sex taken from the Bella Coola Valley around 1980 (assigned to Vancouver Island in the female analysis but not the male analysis). Although Box's test of equality of group covariance matrices could not be calculated because of small group sizes, the matrices were almost certainly heterogeneous. Nevertheless, the good separation of the

Table 14. Variables selected during multiple discriminant analysis of four female coastal groups, with standardized discriminant coefficients.

Variable	Standardized Discriminant Coefficients		
	DF1	DF2	DF3
3. M^2 to auditory canal	1.293	-0.153	0.212
4. Braincase width	-1.181	0.020	0.163
6. M^1 to orbit	-0.150	0.808	0.067
7. Tooth row length	-0.895	-0.030	-0.208
8. Carnassial length	-0.428	0.065	0.816
11. M^2 width	-0.304	-0.551	-0.138
14. Width across post-orbital processes	-0.466	0.100	-0.474
15. Width behind post-orbital processes	0.711	0.275	0.256
16. Distance between bullae	1.205	0.340	-0.071
17. Distance between first premolars	0.753	0.595	-1.000
18. Rostrum width at canines	0.026	-0.906	0.701
19. Bulla length	0.511	1.336	-0.223
Eigenvalue	5.524	3.647	0.570
% of variance	56.7%	37.4%	5.9%

Table 15: Classification table produced by multiple discriminant analysis of four male coastal groups, showing allocation of wolves from the coast of British Columbia.

ACTUAL GROUP	No. of Cases	PREDICTED GROUP MEMBERSHIP Vancouver Island	Oregon	Alaska	Cariboo
Vancouver Is.	9	9 100.0%	0	0	0
Oregon	12	0	12 100.0%	0	0
Alaska	11	0	0	10 90.9%	1 9.1%
Cariboo	10	0	0	0	10 100.0%
B.C. coast (males)	5	0	0	3 60.0%	2 40.0%
B.C. coast (unknown sex)	8	0	0	5 62.5%	3 37.5%

Table 16: Classification table produced by multiple discriminant analysis of four female coastal groups, showing allocation of wolves from the coast of British Columbia.

ACTUAL GROUP	No. of Cases	PREDICTED GROUP MEMBERSHIP Vancouver Island	Oregon	Alaska	Cariboo
Vancouver Is.	8	8 100.0%	0	0	0
Oregon	10	0	10 100.0%	0	0
Alaska	11	1 9.1%	0	10 90.9%	0
Cariboo	10	0	0	1 10.0%	9 90.9%
B.C. coast (females)	3	0	1 33.3%	0	2 66.7%
B.C. coast (unknown sex)	8	1 12.5%	1 12.5%	1 12.5%	5 62.5%

four groups led to confidence in the group assignments of the unknowns.

The analysis of these groups, with sexes combined, emphasized the distinctness of the Vancouver Island and Oregon populations (Figure 13, Tables 17 and 18). The unsexed Vancouver Island wolves were accurately assigned, but the correct classification rate for Alaska and Cariboo was not particularly high.

As mentioned previously, B.C. coast wolves did not show the short nasals characteristic of Oregon wolves (Table 9).

Figure 13. Plot of relative positions of Vancouver Island, Oregon, Alaska and Cariboo wolf groups, sexes combined, on first two discriminant functions.

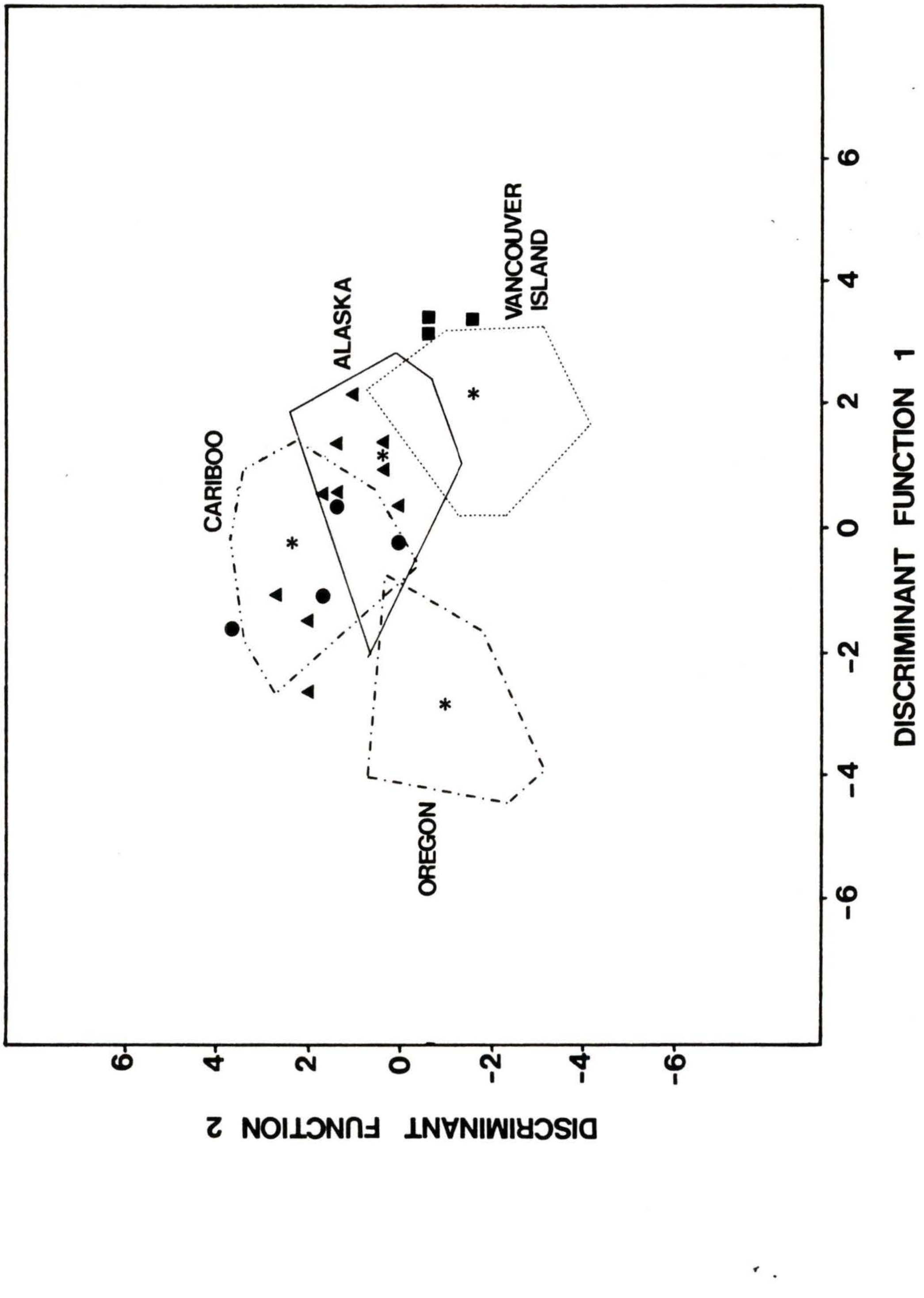
First function accounts for 56.7% of variance, second for 34.8%

* group centroids

● Cariboo wolves of unknown sex

▲ Alaska wolves of unknown sex

■ Vancouver Island wolves of unknown sex



CARIBOO
ALASKA
VANCOUVER
ISLAND
OREGON
DISCRIMINANT FUNCTION 1
DISCRIMINANT FUNCTION 2
-6
-4
-2
0
2
4
6

Table 17. Variables selected during multiple discriminant analysis of four coastal groups, male and female wolves combined, with standardized discriminant coefficients.

Variable	Standardized Discriminant Coefficients		
	DF1	DF2	DF3
2. Zygomatic width	0.788	-0.227	0.166
3. M^2 to auditory canal	-0.942	1.060	-0.088
4. Braincase width	-0.100	0.191	0.539
5. Width across cheek teeth	0.121	-0.795	0.717
6. M^1 to orbit	0.555	0.345	0.496
8. Carnassial length	0.168	-0.215	-0.958
9. Carnassial width	0.273	0.144	0.515
10. Canine width	-0.260	-0.315	-0.494
12. Jugal height	-0.541	-0.328	0.438
13. Width between orbits	-0.781	0.206	-0.065
14. Width across post-orbital processes	0.325	-0.938	0.288
15. Width behind post-orbital processes	0.223	-0.034	-0.615
16. Distance between bullae	-0.161	0.326	0.412
17. Distance between first premolars	0.247	0.693	0.713
18. Rostrum width at canines	-0.358	0.292	-0.899
19. Bulla length	0.761	0.368	0.096
Eigenvalue	3.566	2.187	0.534
% of variance	56.7%	34.8%	8.5%

Table 18: Classification table produced by multiple discriminant analysis of four coastal groups, sexes combined, showing allocation of wolves of unknown sex from these groups.

ACTUAL GROUP	No. of Cases	PREDICTED GROUP MEMBERSHIP Vancouver Island	Oregon	Alaska	Cariboo
Vancouver Is.	17	16 94.1%	0	1 5.9%	0
Oregon	22	0	21 95.5%	1 4.5%	0
Alaska	22	1 4.5%	1 4.5%	19 86.4%	1 4.5%
Cariboo	20	0	0	2 10.0%	18 90.0%
Vancouver Is. (sex unknown)	3	3 100.0%	0	0	0
Alaska (sex unknown)	10	0	0	6 60.0%	4 40.0%
Cariboo (sex unknown)	4	0	0	2 50.0%	2 50.0%

DISCUSSION

Validity of Subspecific Designations

The analysis of the characteristics of subspecies as described by Goldman (1944) shows that few of his taxa are separable when tested with samples that are larger than he used. The shape of the upper carnassial is quite distinctive for Vancouver Island wolves, the length of the nasals is distinctive for Oregon wolves, and a narrow post-orbital construction is typical of Idaho wolves. Thus, although these populations are probably derived from the same Pleistocene population, minor differences do occur which separate certain groups. Considering the quite different habitats that they occupy compared to the relatively uniform habitats of the northern groups studied, this is perhaps not surprising.

No evidence was found to justify separation of *C.l. ligoni* as a distinct subspecies confined to the Alaska panhandle. Considering the fact that B.C. coast wolves were most frequently assigned to either this or the Cariboo groups, perhaps the range of this group should be extended southward rather than the range of *C.l. fuscus* northward. The eastern extent of the range in southern British Columbia is not sharply defined.

There is also no justification for a separate subspecific designation for the wolves of northeastern British Columbia. The Peace River wolves, from Goldman's suggested occidentalis range, are indistinguishable from the groups occupying the range of columbianus. Further comparisons with wolves north and east of British Columbia would be required to clarify the status of these populations.

The "75 percent rule" (Mayr et al. 1953) is a rough criterion for evaluating subspecific status. Briefly, it states that group A can be considered subspecifically distinct from group B if 75% of the individuals of A are different from "all" the individuals of B. Using this as a rough guide, and looking at Tables 5 and 7 showing the correct classification rates for multiple discriminant analysis of wolf groups, we can see that only the southern and coastal groups are sufficiently distinct, by this criterion, to warrant their subspecific designations.

Generally, wolves of the study area increase in size from south to north and from west to east. The largest wolves were found in the Peace River, adjacent to northwestern Alberta where the largest (recorded) grey wolf skulls have been collected (Gunson and Nowak 1979).

Whether or not the minor differences between southern and coastal populations are sufficient to justify their separation into subspecies is not within the scope of this study. Certainly, the Vancouver Island, Oregon and Idaho groups meet Mayr's "75% rule." The differences that can be identified are of value for determining relationships between populations, and will be explored more fully in the following sections. Those workers who have investigated wolf populations in other areas (Jolicoeur 1959, Nowak 1979, Bogan and Mehlhop 1983) concur that far too many subspecific designations exist. However, as Pisano (1977) points out, these categorizations are useful as a spatial status index for populations, and there is some value in retaining them for that purpose.

Existence of Two Post-glacial Wolf Populations

Analysis of wolf populations in British Columbia utilizing principal components analysis, multidimensional scaling, and multiple discriminant analysis all support Nowak's (1981) suggestion that in the Pacific Northwest there are basically two types of wolves: a large, northern (boreal) group, and a smaller, southern group that has expanded north along the B.C. coast and intergraded with the northern wolf in the B.C. Interior. It may be that these two types are representative of separate wolf populations isolated in Alaska and in the southwestern United States by the Wisconsin Glaciation (Nowak 1983). The Wisconsin ice advance resulted in a number of large mammal species, including wolves, being isolated in Alaska and the Yukon

Territory (Guthrie 1968), and these wolf populations undoubtedly expanded southward as the ice receded, eventually meeting other populations expanding north. This relatively sharp north-south distinction was also found by Kolenosky and Standfield (1975) in their study of Ontario wolves, and by Skeel and Carbyn (1976) in their study of wolves in central Canada.

Colour is a highly variable characteristic in wolves. Nonetheless, Goldman's subspecies descriptions, and my own personal observations, do allow some generalizations: black and white phase animals appear to be restricted to the northern subspecies. *Canis l. fuscus*, *C.l. irremotus*, and *C.l. crassodon* have not had black phase recorded and are described as suffused with varying degrees of tan, cinnamon, or brown (Appendix 1). If wolf populations have indeed expanded as suggested, this is consistent with Gloger's rule: Reddish or yellowish-brown phaeomelanins prevail in arid climates where blackish eumelanins are reduced, and phaeomelanins are subject to reduction in cold climates. Bergmann's rule (smaller-sized races of a species are found in the warmer parts of its range) is also demonstrated here.

The southern groups show considerable variability and the wolves of Oregon and Idaho are quite distinct from one another and from other members of the supergroup. However, these differences are not as great as those separating the two supergroups.

Systematic Status of Wolves on the British Columbia Coast

Multiple discriminant analysis to clarify the status of the wolves on the British Columbia coast clearly shows that these wolves bear far less resemblance to the wolves of Vancouver Island or Oregon, than they do to Alaskan and B.C. Interior wolves. This is supported by non-metric characteristics: These wolves lack the distinctive carnassial shape of the Vancouver Island wolves and the shorter nasals of the Oregon wolf. In addition, the unusual cinnamon-brown colour of _C.l._ _fuscus_, for which it was named, has not been reported here, whereas black phase, reported as common on the B.C. Coast by Cowan and Guiguet (1964) was not reported to occur in Oregon wolves (Goldman 1944). The number of specimens available remains small; however, there is no evidence here for the presence of _C.l._ _fuscus_ in coastal British Columbia. If this is the case, then unless remnant populations exist in Washington or Oregon (which is extremely unlikely), this subspecies must be considered extinct.

The Vancouver Island wolf (_C.l._ _crassodon_), like Oregon's _C.l._ _fuscus_, is relatively distinct from other groups. Similarities are greater with other coastal groups than with wolf groups east of the coastal mountains. Residents of the mainland coast suspect wolves may occasionally move down the river valleys from the interior (A. Karup, pers. comm.). This could account for sightings of black wolves on the coast, would explain the resemblance of some B.C. coast wolves to Cariboo wolves, and would explain the intermediate and rather variable status of Cariboo wolves in the principal components and cluster analysis as "hybrids" between the northern and southern supergroups.

PART 2

INVESTIGATION OF DOG-WOLF HYBRIDIZATION ON VANCOUVER ISLAND

INTRODUCTION

Hybridization of wolves and dogs has been suggested as a possible reason for the increase of wild canids on Vancouver Island. The suggestion was originally made because of the general appearance of the Vancouver Island wolf, which at first glance, vaguely resembles the German Shepherd breed (Canis familiaris). This is primarily due to the similar colouration; differences between dog and wolf in head shape, neck ruff, coat length, leg length, and size of feet are quite pronounced (Mech 1970). The high incidence of contacts with people, apparent fearlessness, and an occasional alleged attack on humans have all contributed to the theory that these are not "real" wolves but hybrids.

All members of the genus Canis in North America are inter-fertile and produce fertile hybrids. Wolves and coyotes (C. latrans) have been bred with dogs in captivity (Iljin 1941, Silver and Silver 1969, Mengel 1971, Zimen 1981). There are numerous mostly unsubstantiated reports of such hybrids occurring in the wild (Young and Goldman 1944), but there is little evidence that these occur with any frequency. Wolf packs generally react aggressively to strange canids and it is unlikely that under normal circumstances a dog, especially a male, could become integrated into a wolf pack. It is possible, however, that in areas where feral dogs occur and where wolf populations are very low, hybridization may take place. These circumstances were present on southern Vancouver Island in the late 1970's. Hunters have reported dogs, or dog tracks, in areas remote from human habitation, and several skulls have been turned into the Wildlife Laboratory. A female dog was shot running wild in the vicinity of a wolf pack near Coombs, and a second female was shot after killing sheep near Sooke. Neither showed any evidence of a domestic existence.

Detection of hybridization is a difficult task. Members of the genus Canis are virtually identical biochemically (Seal 1975) and karyotypically (Chiarelli 1975). Since no reliable differences have yet been found between dog, coyote, red wolf (C. rufus), or grey wolf, biochemical methods are of little help in identifying hybrids.

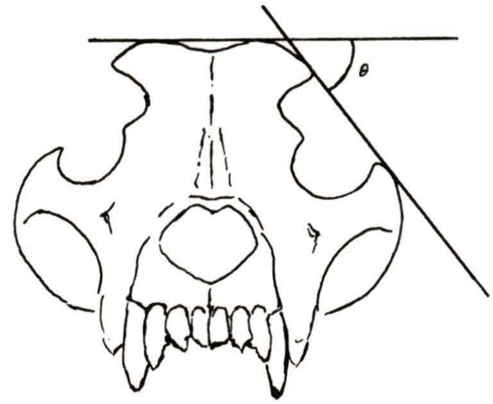
Several authors have suggested ways of distinguishing dogs, wolves, and their hybrids, and Iljin (1941) provides a good summary. Generally, dogs tend to be smaller, with more defined markings, have broader chests, and frequently have "lop" ears and curled tails. The dog skull usually has broader frontals and a higher forehead, relatively narrower zygomata and broader rostrum, smaller, more flattened auditory bullae, smaller canines and carnassials, and a smaller cranial capacity. It should be noted that some dogs may exhibit inflated auditory bullae as do wolves, and indeed no single one of these characters is adequate to identify a wolf positively. Some, however, will give almost certain identification of a dog. Iljin (1941) also describes the difference in orbital angle and in the shape of the zygomaticomaxillary suture (Fig. 14). The F_1 hybrids which Iljin studied exhibited wolf-type bullae, intermediate orbital angles, and intermediate angles of the zygomaticomaxillary suture.

Although F_2 hybrids were produced in captive breeding trials (Iljin 1941, Mengel 1971, Zimen 1981), the reported shift in breeding season of wolf-dog (Iljin 1941) and coyote-dog (Mengel 1971) hybrids make it seem unlikely that hybrids could perpetuate in a wild situation. Thus, introgression of dog genes into a wild population is likely to be minimal. However, since the legal status of wolf-dog hybrids as wildlife is unclear, it is necessary to know if hybridization is occurring.

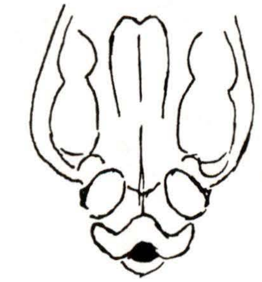
Several methods have been proposed for identifying hybrids. Lawrence and Bossert (1967), Nowak (1979), and Moore _et al_. (1983) have all used discriminant function analysis, interpreting a position intermediate between known populations as evidence of hybridization. Neff and Smith

Figure 14. Characters used to separate dogs from wolves.

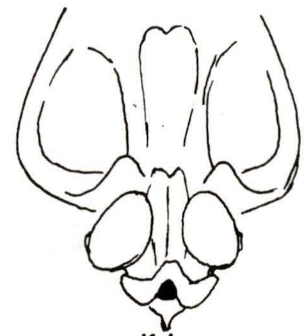
1. Orbital angle
2. Size of auditory bullae
3. Shape of zygomaticomaxillary suture
4. Whether or not skull rocks on articulated lower jaw



1. Orbital angle: dog $>50^{\circ}$
wolf $<45^{\circ}$

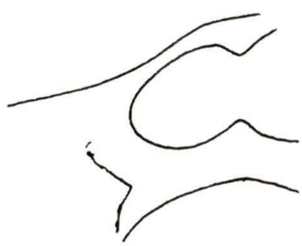


dog small

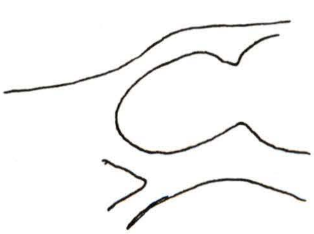


wolf large

2. Auditory bullae

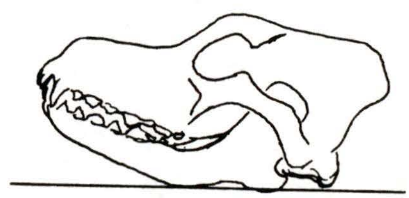


dog obtuse

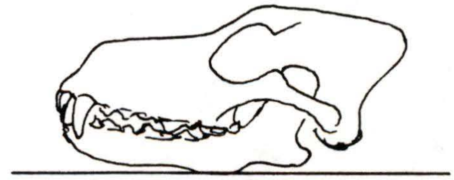


wolf acute

3 Shape of zygomatico-maxillary suture



dog doesn't rock?



wolf rocks?

4. Whether or not articulated skull rocks

(1979) warn against casual acceptance of this sort of analysis, pointing out that discriminant function analysis assumes that all unknowns belong to one of the "known" groups, and that a supposedly intermediate organism may in fact be very different in an unidentified direction. They recommend conducting a principal components analysis, which makes no assumptions about groupings within the data, to see whether purported hybrids do in fact occupy an intermediate position; if they do, discriminant function results can be interpreted with more confidence. The work of Nowak (1979) and Moore _et al_. (1983) with known hybrids suggests that discriminant function analysis can in fact be used in this fashion with wolves.

The objective of this part of the study is to determine, by the use of multivariate methods, if evidence exists of hybridization between dogs and wolves on Vancouver Island. A position intermediate to parent populations on both principal component and discriminant function plots, supported by non-metric characters, will be considered evidence necessary for accepting that hybridization has occurred.

METHODS

The wolf groups studied in the preceding section served as my reference samples for these analyses. Dog specimens were studied at the Western College of Veterinary Medicine at the University of Saskatchewan, and at the University of British Columbia. The museums I visited (Appendix 2) also had small collections. Skulls were selected to be as wolf-like as possible in shape and size. Since sex information was lacking for many specimens, and since variation among breeds was greater than sex variation, sexes were not treated separately. In analyses including wolves and dogs, wolf groups were analyzed with sexes combined.

The same measurements were taken as described in Part 1. In addition, orbital angle was measured, but since this is a difficult measurement to take accurately, and since it is primarily a function of zygomatic width, it was not included in multivariate analyses. Non-metric characters recorded included shape of zygomaticomaxillary suture, size of auditory bullae, and whether or not the skull rocked on its articulated lower jaw (Figure 14).

All animals collected on Vancouver Island and adjacent coastal islands since 1950 were considered as "unknown canids" for the purposes of this study. Some animals had been noted at necropsy as being atypical in some way: exceptionally dark, unusually small feet or short legs, white chest spots, etc.; and some, on the basis of small size, colour, small teeth, "lop" ears, or curled tails, were clearly dogs. Several animals from museum collections, which were labelled as known or suspect hybrids, were included for comparative purposes. I had also noted some skulls, both dog and wolf, which, for reasons of size or shape, I suspected might have been classified incorrectly.

To investigate possible hybridization on Vancouver Island, I conducted a discriminant function analysis using dogs, historic Vancouver Island wolves, and B.C. coast wolves as my known groups. I repeated the analysis with Oregon and Idaho wolves, since most of the "suspect" hybrids in other museums were from the western United States.

Following Neff and Smith's (1979) suggestion, I also conducted a principal component analysis on the Vancouver Island, B.C. coast, and dog groups, including the "questionable" animals, to determine if this would produce results similar to the discriminant analysis.

Orbital angle and the non-metric characters of zygomaticomaxillary suture shape and relative size of auditory bullae suggested by Iljin (1941) were checked for confirmation of the multivariate procedures.

RESULTS

The orbital angles of wolves ranged from 35° to 48°, with a mean of 42.3°. Orbital angles of dogs ranged from 37° to 63°, with a mean of 51.5°.

The criterion of whether or not an articulated skull rocks is supposed to be diagnostic of dog or wolf (wolves rock; dogs do not) (B.C. Provincial Museum unpublished report). However, since 37% of the wolf skulls did not rock (and 12% of dogs did), this was not pursued.

The results of the discriminant function analysis on British Columbia coastal wolves and dogs are shown in Figure 15. The first discriminant function was comprised primarily of skull length, distance from M^2 to auditory opening, and width between first premolars (Table 19). This function accounted for 92.6% of the variance and separated dogs from wolves. The second function expressed skull length and width between orbits, and separated the two wolf populations. The bipolar coefficients indicated discrimination was expressing shape as well as size differences.

Group covariance matrices, not unexpectedly, were heterogeneous; however, species separation was very well-defined. Assignment to wolf or dog was likely reliable; assignment to one or other of the wolf groups may not have been so in this case.

Figure 15. Plot of relative positions of dogs and wolf groups (Vancouver Island and B.C. Coast) on two discriminant functions. Suspect hybrids and canids of uncertain identity plotted as unknowns.

First function accounts for 92.6% of variance.
Asterisk: group centroid
Letters indicate location of specimens listed in Table 20.

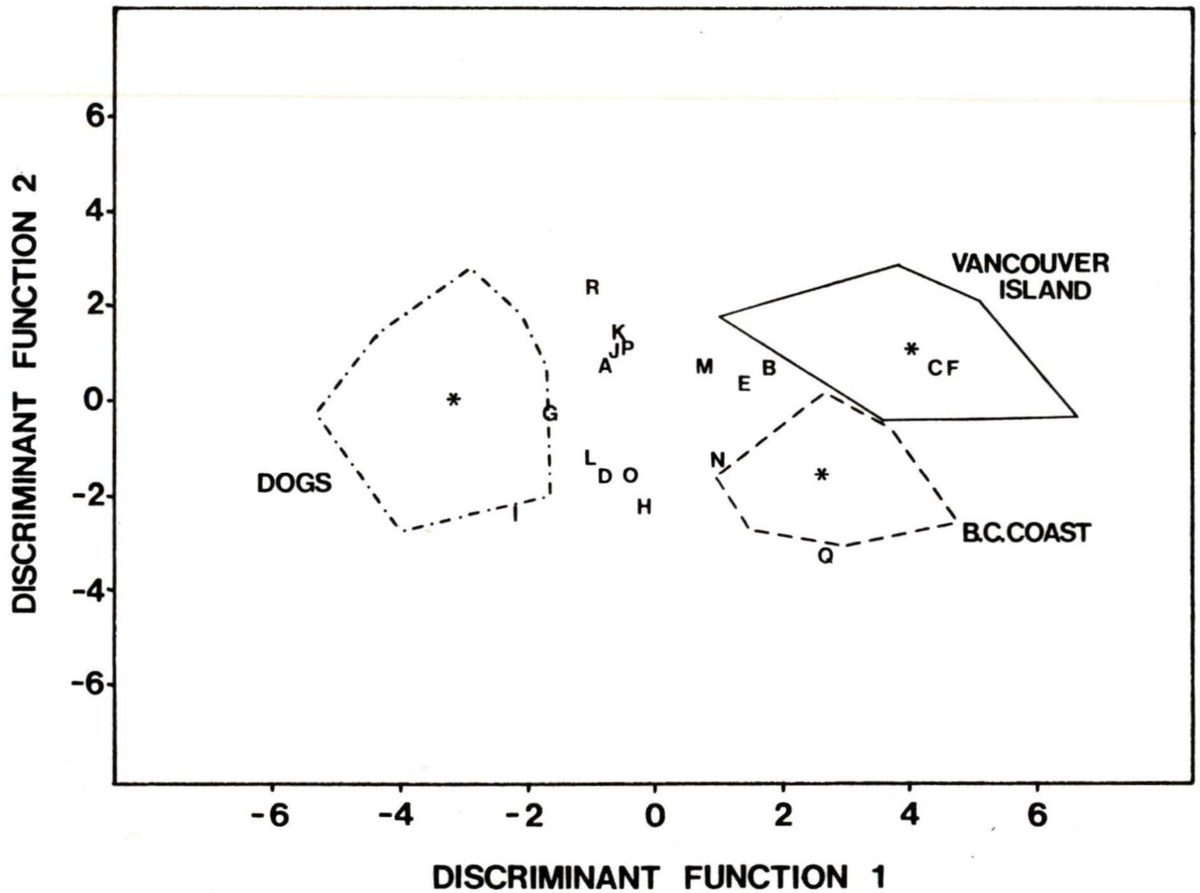

DISCRIMINANT FUNCTION 2
DISCRIMINANT FUNCTION 1
6
4
2
0
-2
-4
-6
-6
-4
-2
0
2
4
6
VANCOUVER ISLAND
DOGS
B.C.COAST
R
K
JP
A
M
B
E
C F
G
L
D
O
H
I
N
Q

Table 19. Variables selected during multiple discriminant analysis on Vancouver Island wolves, B.C. coast wolves, and dogs, with standardized discriminant coefficients.

Variable	Standardized Discriminant Coefficients	
	DF1	DF2
1. Skull length	1.628	-0.925
2. Zygomatic width	0.743	-0.633
3. M^2 to auditory canal	-1.448	-0.673
4. Braincase width	0.528	-0.167
5. Width across cheek teeth	0.263	0.949
6. M^1 to orbit	-0.432	-0.669
8. Carnassial length	0.308	-0.090
9. Carnassial width	0.380	-0.233
11. M^2 width	-0.059	0.748
13. Width between orbits	-0.213	1.439
17. Distance between first premolars	-1.128	-0.028
19. Bulla length	0.042	0.561
Eigenvalue	11.685	0.934
% of variance	92.6%	7.4%

Origin of the unknown specimens is given in Table 20. Two known hybrids (D and H) entered in this analysis occupied positions intermediate to the dog and wolf populations. The suspect hybrid from Coombs (P) was shot within three weeks of, and in the same area as, a feral female dog (R).

Five specimens in museum collections labelled as wolf (G, I, J, K, L) were identified as dogs in my analysis. For four of these (G, I, J, L), shape of the zygomatico-maxillary suture supported the identification, along with size of auditory bullae for three (G, I, L), and orbital angle for two (I, L). The fifth animal (K) was immature, and since non-metric characters would indicate wolf, this may be an incorrect identification due to lack of full adult proportions. In addition, two specimens in collections labelled dog (E, F) were identified as wolf. This diagnosis was supported by non-metric characters, as shown in Table 20.

The principal components analysis showed known and suspect hybrids lying generally intermediate to the dog and wolf populations (Figure 16). The Vancouver Island and mainland wolves formed an intermingled but relatively discrete group, interspersed with the presumably misclassified animals. The scatter of the dog points emphasized the tremendous variability within this species. Positions of animals identified as dog, wolf, or suspect

Table 20. Canids to be tested for hybrid status against dogs and Vancouver Island and coastal wolves.

Specimen	Origin	Shape of zygomatic suture	Orbital Angle(°)	Size of bullae	Identification
A. 169529 AMNH	Wolf, Yakutat		44	Medium	Possible hybrid
B. 15306 ROM	Suspect hybrid, Ontario		47	Medium-full	Wolf
C. 19980 ROM	Suspect hybrid, Ontario		44	Medium-full	Wolf
D. 12933 ROM	Wolf-Alsatian hybrid		34	Medium-full	Hybrid
E. 20150 ROM	"German shepherd"		43	Large	Wolf
F. 5724 NMC	"Sled-dog", NWT		48	Medium	Wolf?
G. 6147 UBC	Wolf, Daisy Lake, B.C.		46	Small	Dog
H. 268 UBC	Dog-wolf hybrid		43	Small	Hybrid
I. 6956 BCPM	"Wolf", Nitinat Lake		55	Small	Dog
J. 8580 BCPM	"Wolf", Coombs		48	Medium	Dog
K. 8873 BCPM	"Wolf", Qualicum		46	Medium	Dog
L. 9709 BCPM	"Wolf", Port Alberni		57	Small	Dog
M. 13961 BCPM	Wolf, White River		46	Large	Wolf
N. 13957 BCPM	Wolf, Campbell River		43	Large	Wolf
O. 14030 BCPM	Wolf, Nanaimo River		45	Medium, inflated	Hybrid
P. 14031 BCPM	"Wolf", Coombs		45	Medium, inflated	Hybrid
Q. 14032 BCPM	Wolf, Sidney Island		41	Medium	Wolf
R. 81009 BCFW	"Wolf", Coombs		50	Large, inflated	Dog

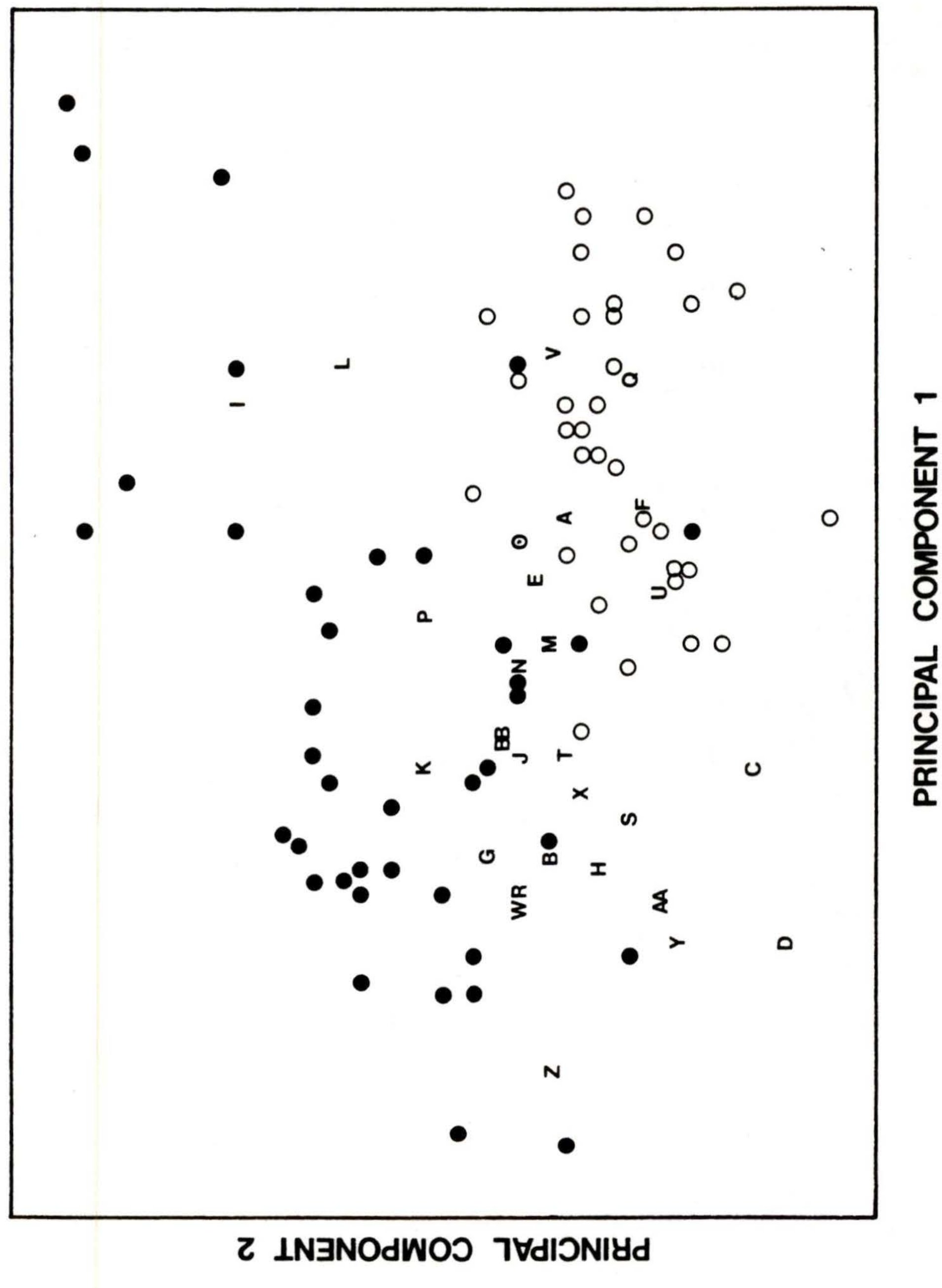
Figure 16. Plot of relative positions of dogs and wolves (Vancouver Island and B.C. Coast) on first two principal components. Suspect hybrids and canids of uncertain identity included.

First component accounts for 75.8% of variance, second for 8.6%.

● dogs

o wolves

Letters indicate location of specimens in Table 20.


PRINCIPAL COMPONENT 1
PRINCIPAL COMPONENT 2
A
AA
B
BB
C
D
E
F
G
H
I
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K
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M
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U
V
W
X
Y
Z

hybrid by discriminant function analysis were supported by the principal components analysis. Juvenile wolves entered in either analysis tended to occupy positions intermediate to dog and wolf, emphasizing the danger of using specimens other than adult animals in the analyses.

The first component, accounting for 75.8% of the variance, was a size factor; the second, accounting for 8.6%, expressed shape. Variables loading most heavily on each factor are given in Table 21.

Suspect hybrids in the USNM collection were from the western United States (Table 22) so were entered in an analysis with Oregon and Idaho wolves and dogs. Also included were three animals in the _fuscus_ and _irremotus_ collection of the USNM which I suspected might be hybrids.

As in the prior discriminant analysis, the first discriminant separated dogs from wolves and the second, the two wolf populations. Zygomatic width and width between premolars (Table 23) contributed most to the first, skull length and jugal height to the second.

All but one of the suspect hybrids fell intermediate between dog and wolf (Figure 17). Of the three animals I had suspected were hybrids, all were identified as wolves (and as from the correct group).

One specimen entered in the USNM collections as a wolf, but tagged "Indian dog," was identified as wolf. However, a study by Walker and Frison (1982) on Amerindian dogs

Table 21. Factor loadings and eigenvalues for first three components from principal components analysis on coastal wolves, dogs, and canids of uncertain identification. Sample size = 103.

Variable	PCI	PC2	PC3
1. Skull length	0.980	0.064	0.182
2. Zygomatic width	0.839	-0.421	-0.313
3. M^2 to auditory canal	0.837	0.388	0.006
4. Braincase width	0.525	-0.456	0.018
5. Width across cheek teeth	0.800	-0.235	-0.335
6. M^1 to orbit	0.871	0.017	-0.191
7. Tooth row length	0.913	-0.142	0.208
8. Carnassial length	0.585	-0.603	0.170
9. Carnassial width	0.667	-0.497	-0.002
10. Canine width	0.710	-0.319	-0.023
11. M^2 width	0.663	-0.442	0.150
12. Jugal height	0.766	-0.140	-0.230
13. Width between orbits	0.649	0.567	-0.313
14. Width across post-orbital processes	0.653	0.500	-0.475
15. Width behind post-orbital processes	0.572	0.105	-0.310
16. Distance between bullae	0.211	0.656	-0.122
17. Distance between first premolars	0.473	0.297	-0.537
18. Rostrum width at canines	0.779	0.160	-0.408
19. Bulla length	0.702	-0.440	0.044
Eigenvalue	547.902	62.463	46.802
% of variance	75.8%	8.6%	6.5%

Table 22. Canids to be tested for hybrid status against dogs and Oregon and Idaho wolves. (all in U.S. National Museum. Skulls W through BB were labelled as suspect hybrids.)

Specimen	Origin	Shape of zygomatic suture	Orbital angle(°)	Size of bullae	Identification
S. 159366	Wolf, C. l. irremotus		45	Medium	Wolf, C. l. irremotus
T. 231160	Wolf, C. l. irremotus		44	Medium	Wolf, C. l. irremotus
U. 4763	"Indian dog"		42	Medium	Wolf, C. l. irremotus
V. 235530	Wolf, C. l. fuscus		45	Large	Wolf, C. l. fuscus
W. 245538	Hybrid, Montana		45	Large	Hybrid
X. 245840	Hybrid, New Mexico		46	Medium	Wolf?
Y. 241960	Hybrid, Montana		43	Medium	Hybrid
Z. 241961	Hybrid, Montana		46	Large	Hybrid
AA.245842	Hybrid, New Mexico		42	Medium	Wolf
BB.242516	Hybrid, Arizona		46	Medium	Hybrid

Table 23. Variables selected for multiple discriminant analysis on Idaho and Oregon wolves, and dogs.

Variable	Standardized Discriminant Coefficients	
	DF1	DF2
1. Skull length	0.662	-0.860
2. Zygomatic width	0.898	0.316
3. M^2 to auditory canal	-0.573	0.332
4. Braincase width	0.586	0.166
5. Width across cheek teeth	-0.191	-0.562
6. M^1 to orbit	-0.558	-0.557
7. Tooth row length	0.071	0.567
9. Carnassial width	0.674	-0.522
10. Canine width	-0.094	0.504
12. Jugal height	0.222	1.224
13. Width between orbits	0.363	-0.497
14. Width across post-orbital processes	-0.362	0.591
15. Width behind post-orbital processes	-0.406	0.394
16. Distance between bullae	-0.174	0.313
17. Distance between first premolars	-0.935	-0.624
Eigenvalue	8.788	1.233
% of variance	87.7%	12.3%

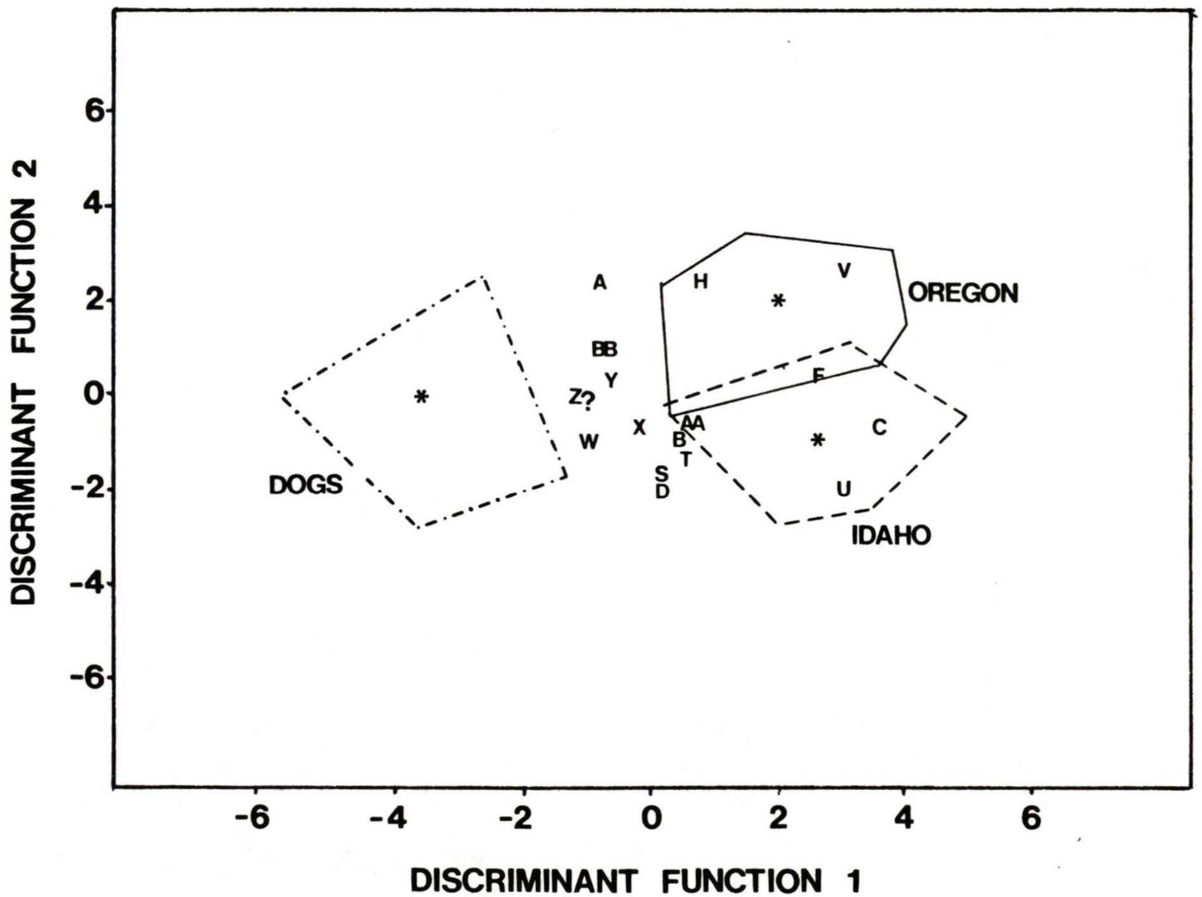
Figure 17. Plot of relative positions of dogs and wolves (Oregon and Idaho) on two discriminant functions. Suspect hybrids and canids of uncertain identity plotted as unknowns.

First function accounts for 87.7% of variance.

* group centroids

Letters indicate specimens referred to in Tables 20 and 22.

? wolf in Idaho sample which may be hybrid.


DISCRIMINANT FUNCTION 2
DISCRIMINANT FUNCTION 1
6
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2
0
-2
-4
-6
-6
-4
-2
0
2
4
6
DOGS
OREGON
IDAHO
A
H
V
BB
Y
Z?
F
X
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U

describes a large, wolf-like breed of the American plains, which, unlike dogs of European ancestry, could be confused with wolves. This may be the case with this specimen.

One wolf specimen in the *irremotus* sample appeared to show marked dog characteristics and may be either a dog or a hybrid.

DISCUSSION

The discriminant function analysis demonstrated the occurrence of hybridization of wolves with dogs, although only to a very limited extent. The shape of zygomaticomaxillary suture, size of carnassials, size of auditory bullae, and orbital angle appear to be useful indicators for identifying dogs, but a multivariate approach may be necessary for confirmation. As Iljin (1941) reported, hybrids tend to have wolf-type bullae, and intermediate zygomaticomaxillary sutures.

Principal components analysis is of no particular value in identifying hybrids. Its use here was intended to demonstrate that hybrids do indeed occupy an intermediate position relative to parent populations and hence that increased confidence can be placed in the results of the discriminant function analysis. Three known dogs (two sled-dogs and a Great Dane) fell within the wolf region. Although they fell within the size range of wolves, on the basis of carnassial and canine size they would not have been confused with wolves.

No wolves from Vancouver Island north of Campbell River showed any evidence of hybrid features. It is likely that the natural antagonism of a wolf pack towards a strange canid is generally a barrier to cross-breeding, even though the species are interfertile. The hybrids that were identified were from areas where wolf populations were extremely low and where feral dogs did occur. No evidence has been found elsewhere of wild hybrids perpetuating past the first generation, probably due to such factors as shift of breeding season so pups are born in winter or lack of male hybrid parental care (Nowak 1979). It is extremely unlikely that there has been any significant introgression of dog genes into the wolf population.

PART 3

SYSTEMATIC AFFINITIES OF PRESENT-DAY WOLVES ON VANCOUVER ISLAND

INTRODUCTION

Due to intensive predator control activity, wolves had been almost eliminated from the southern third of British Columbia and from the northern United States by the mid-twentieth century (Nowak 1983). By 1970, wolves were seen so rarely on Vancouver Island that the subspecies, *Canis lupus crassodon*, was considered for rare and endangered status (Hebert *et al*. 1982). Such status was granted to the Northern Rocky Mountain wolf, *C.l. irremotus*, and concern has been expressed for the status of the Cascade wolf, *C.l. fuscus* (Pisano 1979).

On Vancouver Island, however, dramatic population increases have occurred since the 1970's. From a very low level, numbers increased to densities among the highest reported on the continent (Hebert *et al*. 1982). Numerous suggestions were made to explain this increase: that high deer populations triggered a corresponding increase in wolf numbers; that there had been an invasion of wolves from the mainland; or that wolves had been hybridizing with dogs, and pure wolves no longer existed on the Island.

This research showed that hybridization can be ruled out as a significant factor, but immigration is certainly feasible. Wolves regularly appear on potential bridge islands such as Read and Cortes, and the distances to Vancouver Island are no greater than from the mainland to these islands (less than 2 km in places). Deer are frequently seen swimming between islands and fishermen occasionally report seeing wolves doing the same (G. Jones, pers. comm.).

The objective of this part of the study is to determine the origin of present-day Vancouver Island wolves. If, in a discriminant analysis, recently collected wolves are indistinguishable from mainland wolves, immigration will be assumed to have occurred. If present-day Vancouver Island wolves most closely resemble the historic Vancouver Island wolves, it will be assumed that resident wolf numbers have increased, due to increased availability of prey species or other unknown factors.

METHODS

Wolves collected on Vancouver Island since 1950 and wolves from coastal islands were all considered as being of unknown origin. Cowan and Guiguet (1964) considered wolves on coastal islands as belonging to *C.l. fuscus*, but, as demonstrated in Part 1, this designation for B.C. coastal wolves is not appropriate.

I conducted a multiple discriminant analysis using historical Vancouver Island, B.C. coast, Alaska, Cariboo, and Oregon wolves as my known populations, and recently collected wolves as unknowns. Canids identified as possible hybrids by the preceding analysis were excluded. Males and females were analyzed separately.

The non-metric characters of carnassial shape, distance of canines from surface, and length of nasals (Figure 4) were also compared.

RESULTS

The results of the discriminant function analysis of male wolves from Vancouver Island, B.C. coast, Oregon, Alaska, and Cariboo showed that Oregon wolves were very distinct along the first function (Figure 18, Table 24). The second function separated Vancouver Island and Alaska from B.C. coast and Cariboo; the third function separated these pairs. The fourth function was not significant. The unknown recent wolves from Vancouver Island were assigned, 19.6% to the historical Vancouver Island group, and 80.4% to mainland populations (Table 25). All but one of the unknown wolves from the coastal islands were also assigned to mainland populations.

The analysis of female wolves (Figure 19, Table 26) also showed Oregon wolves to be distinct. Although the relative group locations differed, assignment of recent Vancouver Island wolves was similar: 24% to historic Vancouver Island, 76% to the mainland (Table 27).

Of the five female wolves collected on the islands between Vancouver Island and the mainland during the 1970s, two were assigned to the historic Vancouver Island population (Table 27, Figure 19) and the rest to the B.C. coast or Alaska populations. Origin of recent wolves included in these analyses is shown in Figure 20.

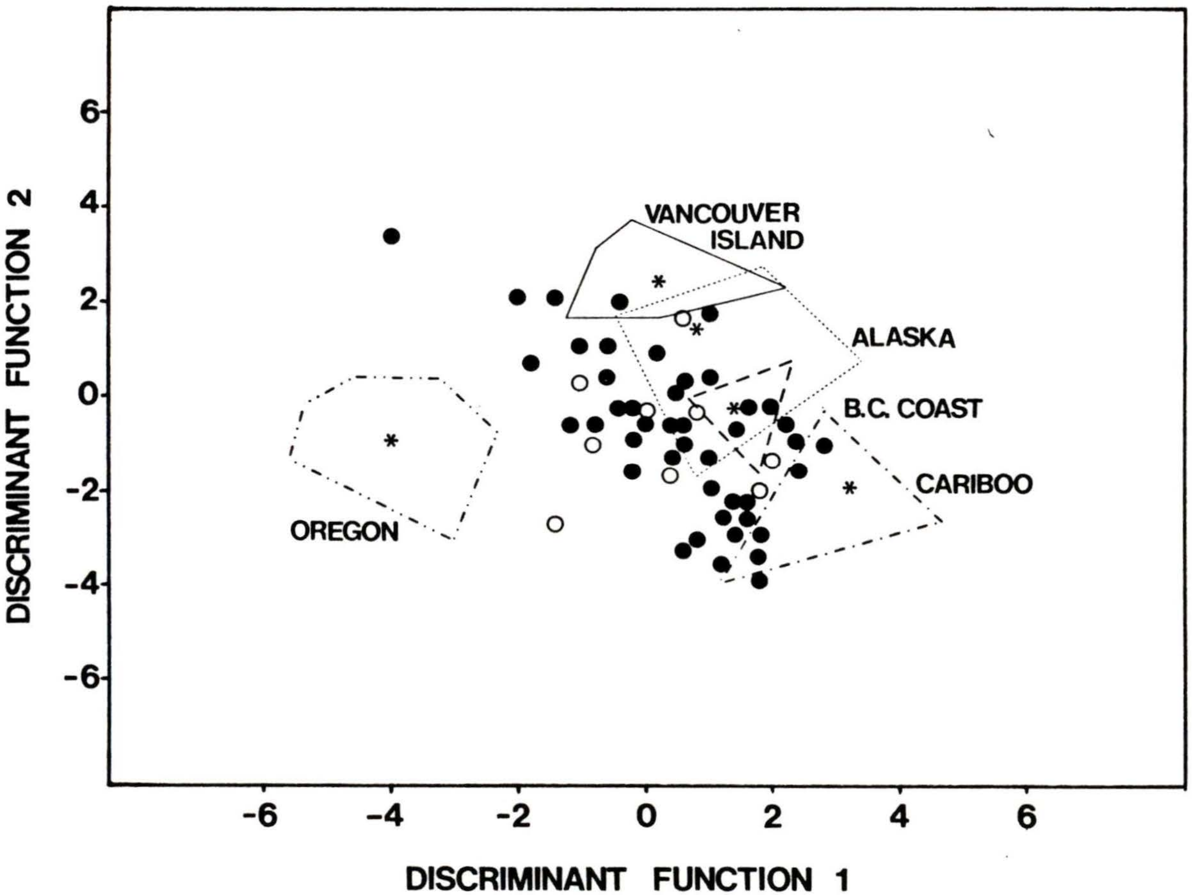
Figure 18. Plot of positions of Vancouver Island, B.C. Coast, Oregon, Alaska and Cariboo male wolves on first two discriminant functions, with recent Vancouver Island coastal island male wolves plotted as unknowns.

First function accounts for 62.1% of variance, second for 26.4%.

* group centroids

● Vancouver Island wolves

o coastal island wolves



VANCOUVER ISLAND
ALASKA
B.C. COAST
CARIBOO
OREGON
DISCRIMINANT FUNCTION 2
DISCRIMINANT FUNCTION 1
6
4
2
0
-2
-4
-6

Table 24. Variables selected for multiple discriminant analysis of five male coastal groups, with standardized discriminant coefficients for three significant functions.

Variable	Standardized Discriminant Coefficients		
	DF1	DF2	DF3
2. Zygomatic width	1.202	1.224	0.125
3. M^2 to auditory canal	0.296	-1.167	-0.241
5. Width across cheek teeth	-1.392	0.354	0.199
6. M^1 to orbit	0.562	-0.505	-0.692
9. Carnassial width	-0.139	0.019	-0.281
10. Canine width	-0.013	0.567	0.259
12. Jugal height	-0.631	0.096	0.020
13. Width between orbits	-0.905	-0.176	0.967
14. Width across post-orbital processes	-0.999	0.499	-0.655
15. Width behind post-orbital processes	0.256	0.369	-0.769
16. Distance between bullae	-0.207	0.071	0.987
17. Distance between first premolars	1.233	-0.099	0.203
18. Rostrum width at canines	0.449	-1.081	-0.399
19. Bulla length	0.461	0.459	0.684
Eigenvalue	7.456	3.167	0.870
% of variance	62.1%	26.4%	7.3%

Table 25: Classification table produced by multiple discriminant analysis of five male coastal wolf groups.

ACTUAL GROUP	No. of Cases	PREDICTED GROUP MEMBERSHIP Vancouver Island	B.C. Coast	Oregon	Alaska	Cariboo
Vancouver Is.	9	8 88.9%	0	0	1 11.1%	0
B.C. Coast	5	0	5 100.0%	0	0	0
Oregon	12	0	0	12 100.0%	0	0
Alaska	11	0	1 9.1%	0	10 90.9%	0
Cariboo	10	0	0	0	0	10 100.0%
Recent Vancouver Island	46	9 19.6%	18 39.1%	0	8 17.4%	11 23.9%
Coastal Islands	9	1 11.1%	4 44.4%	0	3 33.3%	1 11.1%

Figure 19. Plot of positions of Vancouver Island, B.C. Coast, Oregon, Alaska and Cariboo female wolves on first two discriminant functions, with recent Vancouver Island and coastal island female wolves plotted as unknowns.

First function accounts for 56.9% of variance, second for 27.5%.

* group centroids

● Vancouver Island wolves

o coastal island wolves

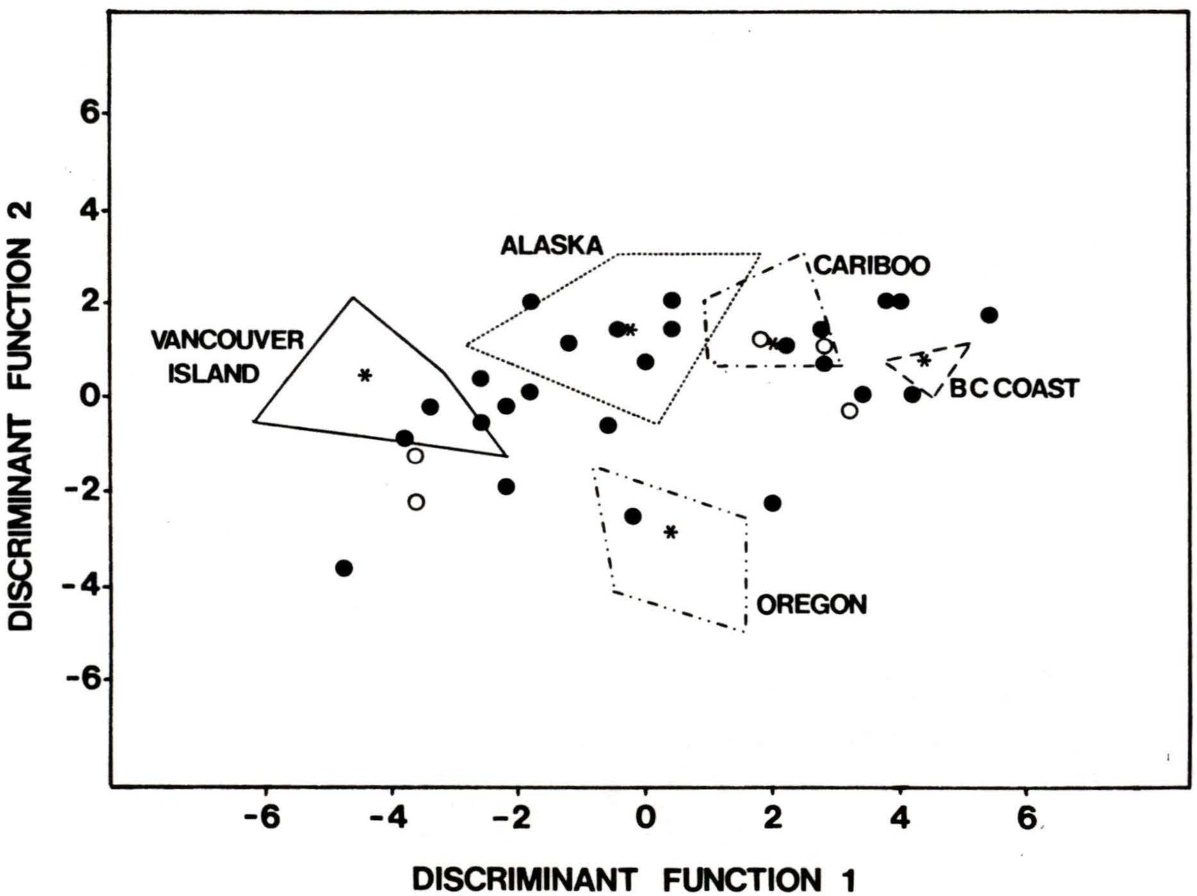

DISCRIMINANT FUNCTION 2
DISCRIMINANT FUNCTION 1
6
4
2
0
-2
-4
-6
ALASKA
CARIBOO
VANCOUVER ISLAND
B C COAST
OREGON

Table 26. Variables selected for multiple discriminant analysis of five female coastal groups, with standardized discriminant coefficients for three significant functions.

Variable	Standardized Discriminant Coefficients		
	DF1	DF2	DF3
3. M^2 to auditory canal	1.537	-0.154	-0.529
4. Braincase width	-1.125	0.016	-0.302
7. Tooth row length	-0.827	-0.089	-0.422
8. Carnassial length	0.089	0.136	-1.325
9. Carnassial width	-0.648	0.145	1.224
10. Canine width	0.133	-0.502	-0.723
11. M^2 width	-0.778	-0.239	0.827
13. Width between orbits	-0.380	-0.770	0.736
14. Width across post-orbital processes	-0.552	0.360	0.379
15. Width behind post-orbital processes	0.923	0.557	-0.279
16. Distance between bullae	1.370	0.678	0.005
17. Distance between first premolars	0.855	0.613	0.278
19. Bulla length	0.664	1.480	0.476
Eigenvalue	6.756	3.265	1.358
% of variance	56.9%	27.5%	11.4%

Table 27: Classification table produced by multiple discriminant analysis of five female coastal wolf groups.

ACTUAL GROUP	No. of Cases	PREDICTED GROUP MEMBERSHIP Vancouver Island	B.C. Coast	Oregon	Alaska	Cariboo
Vancouver Is.	8	8 100.0%	0	0	0	0
B.C. Coast	3	0	3 100.0%	0	0	0
Oregon	10	0	0	10 100.0%	0	0
Alaska	11	0	1 9.1%	0	10 90.9%	0
Cariboo	10	0	0	0	1 10.0%	9 90.0%
Recent Vancouver Island	25	6 24.0%	4 16.0%	3 12.0%	7 28.0%	5 20.0%
Coastal Islands	5	2 40.0%	2 40.0%	0	1 20.0%	0

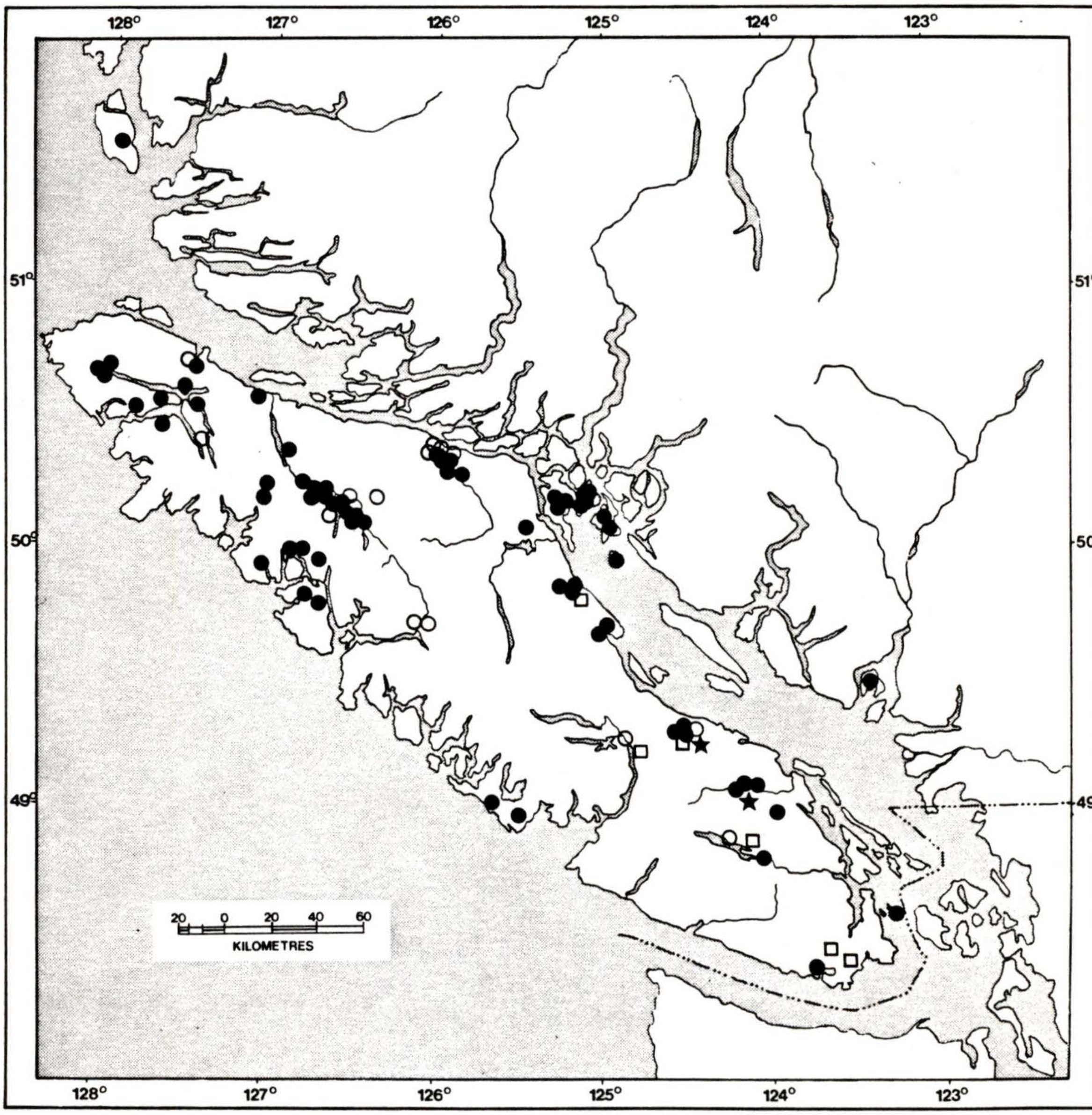
Figure 20. Geographic location of recent Vancouver Island and coastal island wolves included in study.

● wolves assigned to mainland populations by discriminant analysis

○ wolves assigned to Vancouver Island historic population by discriminant analysis

□ areas in which feral dogs have been reported or collected.

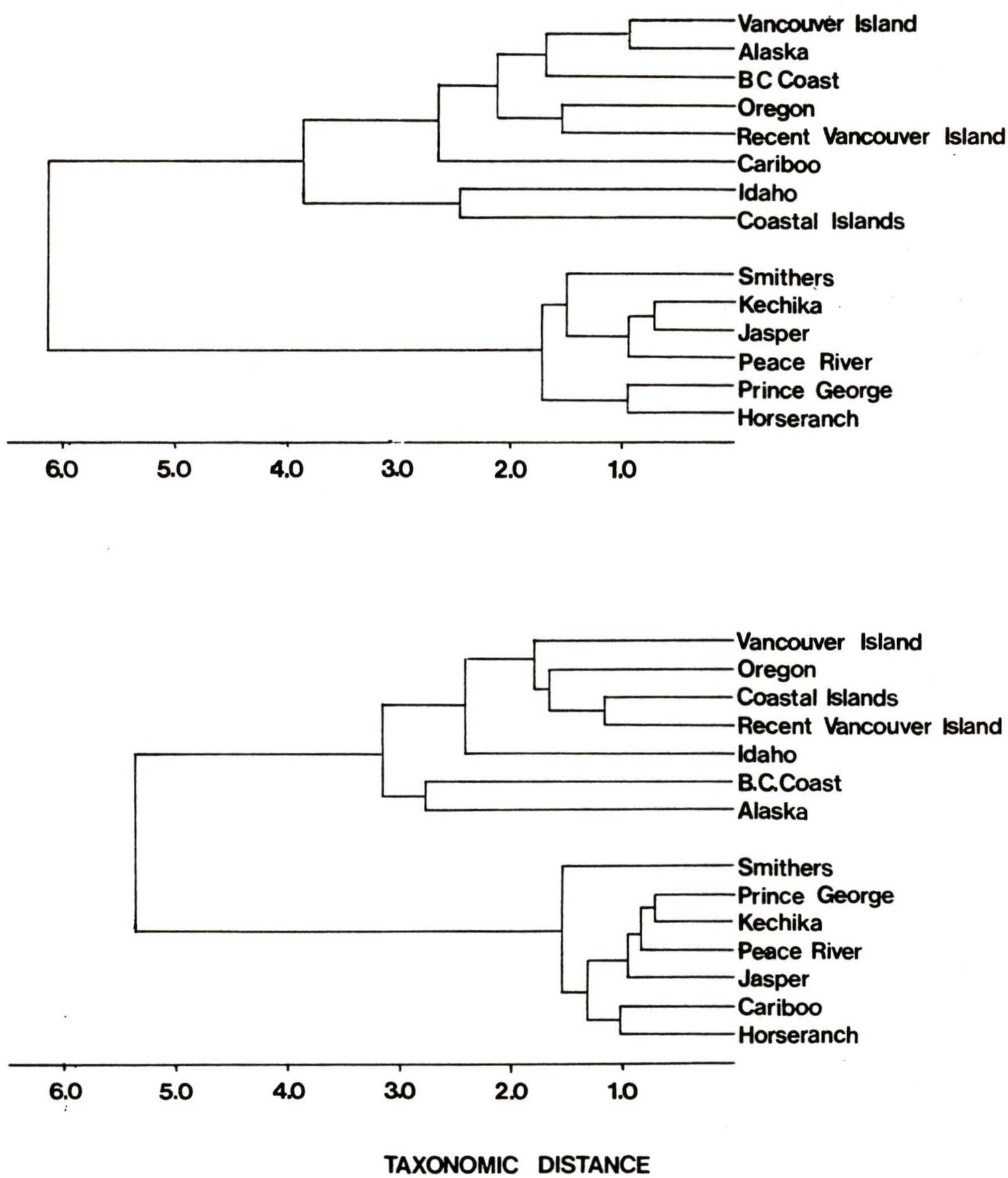
★ areas where suspect hybrids were collected.


128°
127°
126°
125°
124°
123°
51°
50°
49°
20 0 20 40 60
KILOMETRES

A cluster analysis of the recent Vancouver Island and coastal island populations with the reference groups showed these populations clustering with the southern group but more closely with mainland groups than with the historic Vancouver Island group (Figure 21).

Of 68 wolves examined from Vancouver Island since 1970, only 25 (39.7%) had the distinctive carnassial shape of *C.l. crassodon* as described by Goldman (1944) and reported in Part 1 of this study. In addition, only 34 of 62 wolves (54.8%) had, when skulls were placed on a flat surface, canines in contact with the surface. This is in contrast to 14 of 19 (73.7%) and 17 of 19 (89.5%) for these two characters, respectively, for historic Vancouver Island wolves.

Figure 21. Phenogram of 12 male and 12 female reference wolf groups, including recent Vancouver Island wolves.


Vancouver Island
Alaska
B C Coast
Oregon
Recent Vancouver Island
Cariboo
Idaho
Coastal Islands
Smithers
Kechika
Jasper
Peace River
Prince George
Horseranch
6.0
5.0
4.0
3.0
2.0
1.0
Vancouver Island
Oregon
Coastal Islands
Recent Vancouver Island
Idaho
B.C.Coast
Alaska
Smithers
Prince George
Kechika
Peace River
Jasper
Cariboo
Horseranch
6.0
5.0
4.0
3.0
2.0
1.0
TAXONOMIC DISTANCE

DISCUSSION

The original Vancouver Island wolf population, as described by Goldman (1944), was quite distinct, as demonstrated in Part 1, but these distinctions are no longer obvious. Discriminant analysis, while clearly separating the population of original wolves, showed recent wolves to resemble mainland wolves more than the original population. Also, the frequency of occurrence of the non-metric character states of carnassial shape and canine position have shifted to levels intermediate between historic Vancouver Island and mainland groups. This suggests that the original population, while not extirpated, has been so invaded by wolves immigrating from the mainland as to be no longer distinguishable as a separate population. Provincial Wildlife Branch problem wildlife reports and wolf sighting records show wolves were first reported on coastal islands between Vancouver Island and the mainland in the late 1960's and early 1970's. Subsequently they were seen in the Sayward area, and then, within a very few years, spread north and south over the entire island. This, together with the analyses reported here, offers strong support for the immigration hypothesis.

PART 4

SYSTEMATIC AFFINITIES OF PRESENT-DAY WOLVES IN SOUTHEASTERN BRITISH COLUMBIA AND THE NORTHWESTERN UNITED STATES

INTRODUCTION

The Northern Rocky Mountain wolf, *Canis lupus irremotus*, occurred historically throughout Idaho, most of Montana and Wyoming, parts of Washington and Oregon, and possibly southern B.C. and Alberta (Figure 1). Today only scattered sightings occur. *Canis l. irremotus* was listed as endangered by the U.S. Secretary of the Interior in 1973, and in 1978 the entire species was listed as endangered in Mexico and all the lower 48 states except Minnesota (U.S. Fish and Wildlife Service 1980).

Since the termination of control programs in British Columbia and Alberta in the 1960's (Tompa 1981, Gunson 1981), wolf populations have been increasing throughout British Columbia. Wolves are becoming more common in southeastern British Columbia and are occasionally reported in Washington, Idaho, Oregon, and Montana (Mattson and Ream 1980).

The objective of this part of the study is to determine the affinities of wolves in southeastern British Columbia and adjacent areas. If, in a discriminant analysis, wolves collected prior to 1940 were assigned to southern wolf populations (as would be expected if the range of *C.l.* *irremotus* extended into Canada) and wolves collected since 1940 are assigned to northern populations, the Northern Rocky Mountain wolf will be considered to have been extirpated and replaced by wolves immigrating from the north.

METHODS

To determine systematic affinities of wolves in southeastern British Columbia and southwestern Alberta, and that of wolves shot in the northwestern United States in recent years, I conducted a multiple discriminant analysis with wolves from Cariboo, Jasper, and Idaho as my known groups. All specimens, historic and recent, from the area in question were entered in this analysis as unknowns, to determine to which populations they bore the greatest resemblance. By doing this, I hoped to determine the northern extent of the historic range of C.l. irremotus, and the origin of the occasional wolves appearing in the northwestern United States. Measurements on the recent U.S. wolves were taken by Dr. Ron Nowak (Office of Endangered Species, U.S. Fish and Wildlife Service), who kindly allowed me to use his data for this analysis.

RESULTS

The analysis of male wolves from Cariboo, Jasper, and Idaho is shown in Figure 22. The first discriminant function separated the southern from the northern groups. Width across cheek teeth and carnassial length were the most important variables in this function (Table 28). The second discriminant function separated Cariboo from Jasper wolves, and was comprised primarily of width across cheek teeth again, as well as canine width and width of skull across canines. Both functions were significant.

Of the wolves collected prior to 1945 (Table 29), wolves from Hope, Vernon, and Lethbridge were assigned to the small southern group. Wolves from Kamloops, Calgary, Banff, Edmonton, and Smith Landing were assigned to the northern groups. Origin of these specimens is shown in Figure 23. This supports Goldman's depiction of the range of irremotus as including a small part of southern B.C. and southwestern Alberta. However, all wolves taken in this area since 1945 were assigned to the northern groups, except for one wolf collected in Montana in 1964.

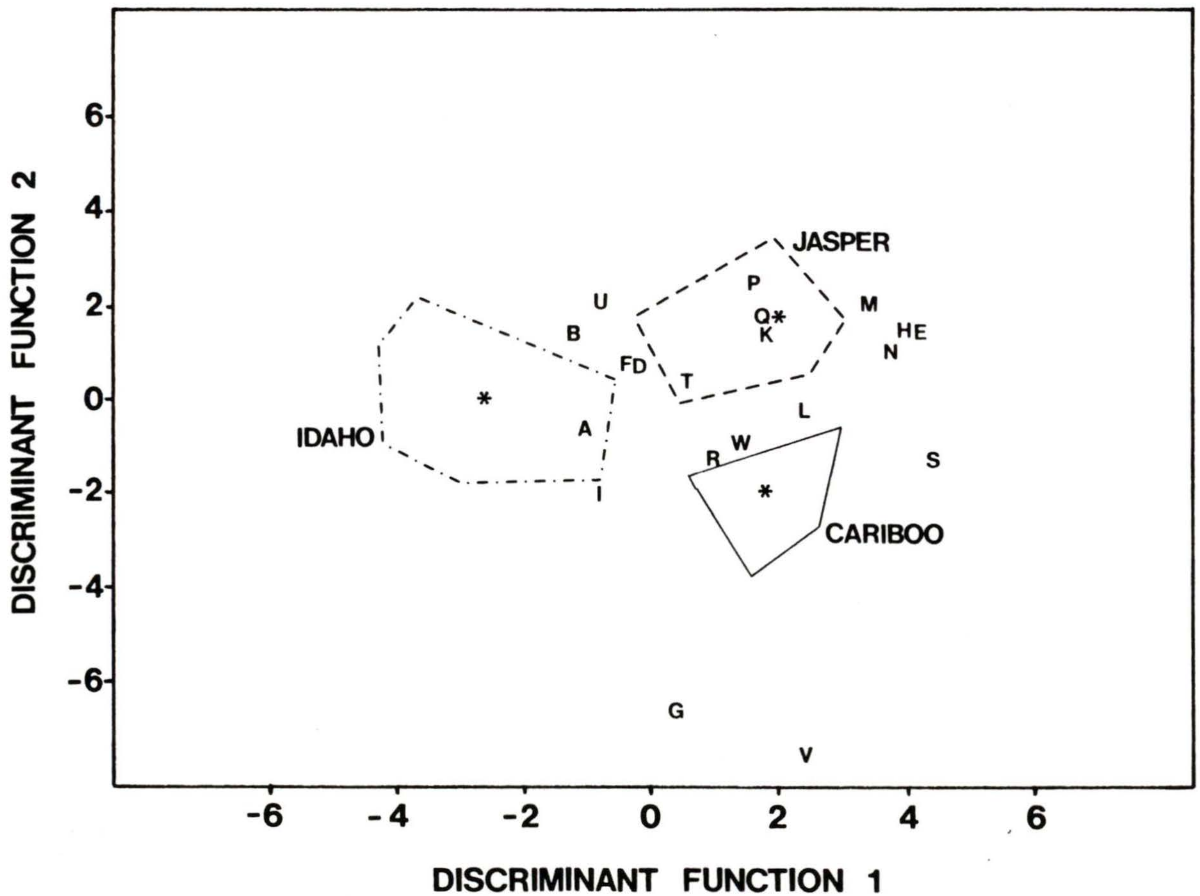
The analysis of female wolves showed a very similar pattern to the male analysis (Table 30, Figure 24). I examined very few female wolves from the area being considered; however, a wolf from Lethbridge in 1901 was assigned to the southern group, whereas wolves from Nelson

Figure 22. Plot of relative positions of Cariboo, Jasper and Idaho male wolf groups on two discriminant functions, with wolves from southern British Columbia and adjacent areas plotted as unknowns.

First function accounts for 72.6% of variance.

Asterisk: group centroids

Letters indicate specimens referred to in Table 29.


DISCRIMINANT FUNCTION 2
DISCRIMINANT FUNCTION 1
6
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2
0
-2
-4
-6
-6
-4
-2
0
2
4
6
JASPER
IDAHO
CARIBOO
U
B
P
Q
K
M
HE
N
FD
T
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L
W
R
S
I
G
V

Table 28: Variables selected for multiple discriminant analysis on Cariboo, Jasper and Idaho male wolves, with standardized discriminant coefficients.

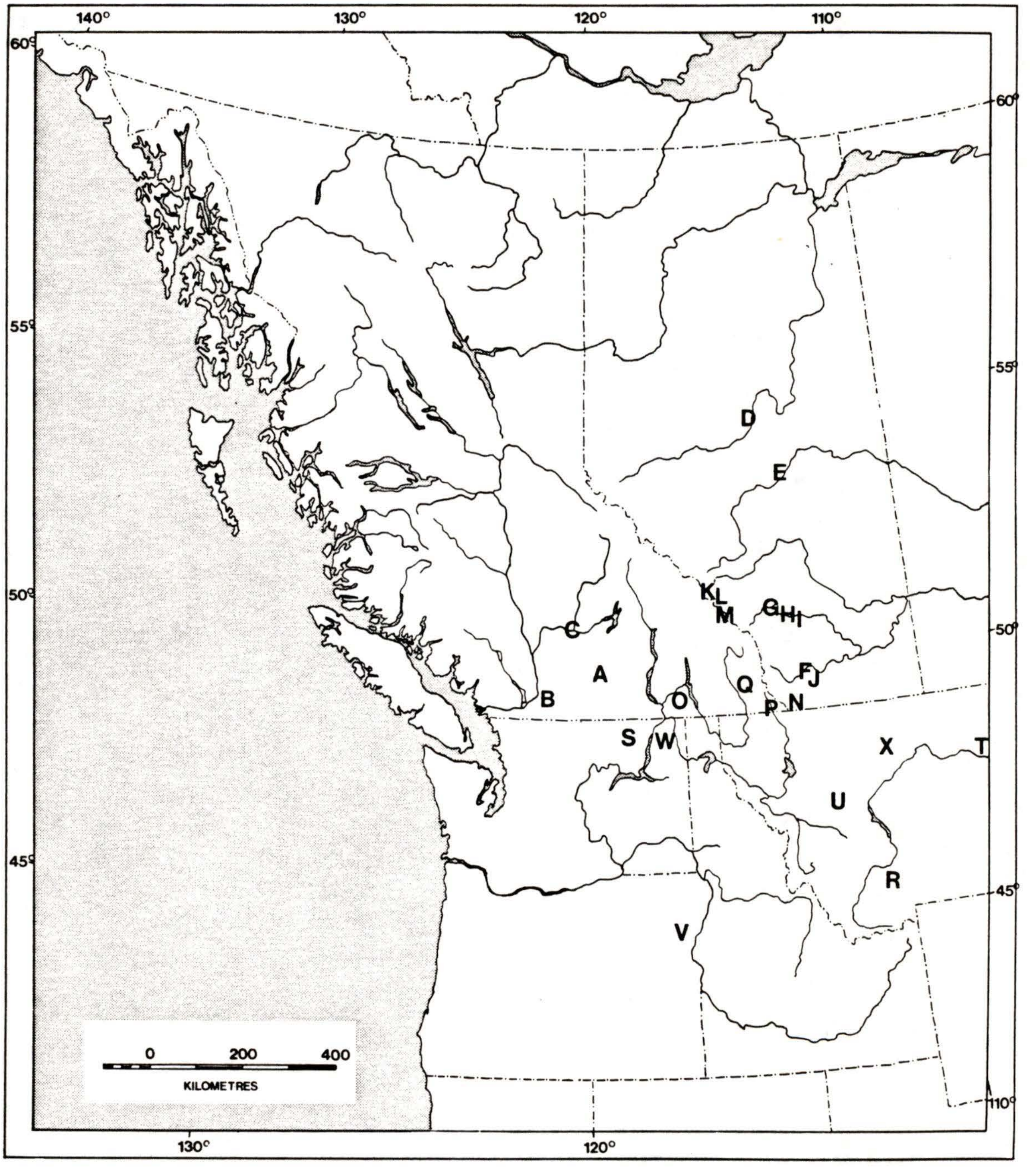
Variable	Standardized Discriminant Coefficients DF1	DF2
4. Braincase width	0.316	0.709
5. Width across cheek teeth	-1.328	1.397
7. Tooth row length	0.541	-0.275
8. Carnassial length	0.857	-0.273
10. Canine width	-0.147	0.833
11. M^2 width	-0.526	0.549
14. Width across post-orbital processes	0.291	1.097
15. Width behind post-orbital processes	0.697	-0.677
16. Distance between bullae	0.385	-0.081
17. Distance between first premolars	-0.303	-0.675
18. Rostrum width at canines	0.629	-0.979
Eigenvalue	5.453	2.057
% of variance	72.6%	27.4%

Table 29. Wolves from southeastern B.C. and adjacent areas, to be tested for subspecific affinity. (Locations shown in Figure 22.)

Specimen		Origin	Identification (northern or southern)
A	1350 BCPM	Male, Vernon, 1892	Southern
B	249 UBC	Male, near Hope, 1941	Southern
C	273 UBC	Female, Kamloops, 1942	Northern
D	77370 USNM	Male, Smith Landing, Alta., 1911	Northern
E	42907 USNM	Male, Edmonton, 1907	Northern
F	78120 USNM	Male, Lethbridge, 1896	Southern
G	31626 AMNH	? , Calgary, 1910	Northern
H	31624 AMNH	? , Calgary, 1910	Northern
I	31629 AMNH	? , Calgary, 1910	Southern
J	16851 AMNH	Female, Lethbridge, 1901	Southern
K	23405 ROM	Male, Banff, 1952	Northern
L	23406 ROM	Male, Banff, 1952	Northern
M	4198 UBC	Male, Banff, 1952	Northern
N	1494 UBC	Male, Waterton, 1945	Northern
O	11437 BCPM	Female, Nelson, 1982	Northern
P	14034 BCPM	Male, Flathead, 1981	Northern
Q	14033 BCPM	Male, Cranbrook, 1984	Northern
R	71651 USNM	Male, Gallatin County, Montana, 1941	Northern
S	51-143 CRCM	Male, Ferry Co., Washington, 1950	Northern
T	Montana FW&P	Male, Valley Co., Montana, 1956	Northern
U	9264 MSU	Male, Lewis & Clark Co., Montana, 1964	Southern (?)
V	OSU	Male, Baker Co., Oregon, 1974	Northern
W	PSNHM	Male, Douglas Co., Washington, 1975	Northern
X	Montana FW&P	Female, Valley Co., Montana, 1978	Northern

Figure 23. Geographic location of wolves from southern British Columbia, southwestern Alberta and northwestern United States included in study.

Letters indicate specimens referred to in Table 29.


140°
130°
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110°
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S
T
U
V
W
X
0
200
400
KILOMETRES

Table 30. Variables selected for multiple discriminant analysis on Cariboo, Jasper and Idaho female wolves, with standardized discriminant coefficients.

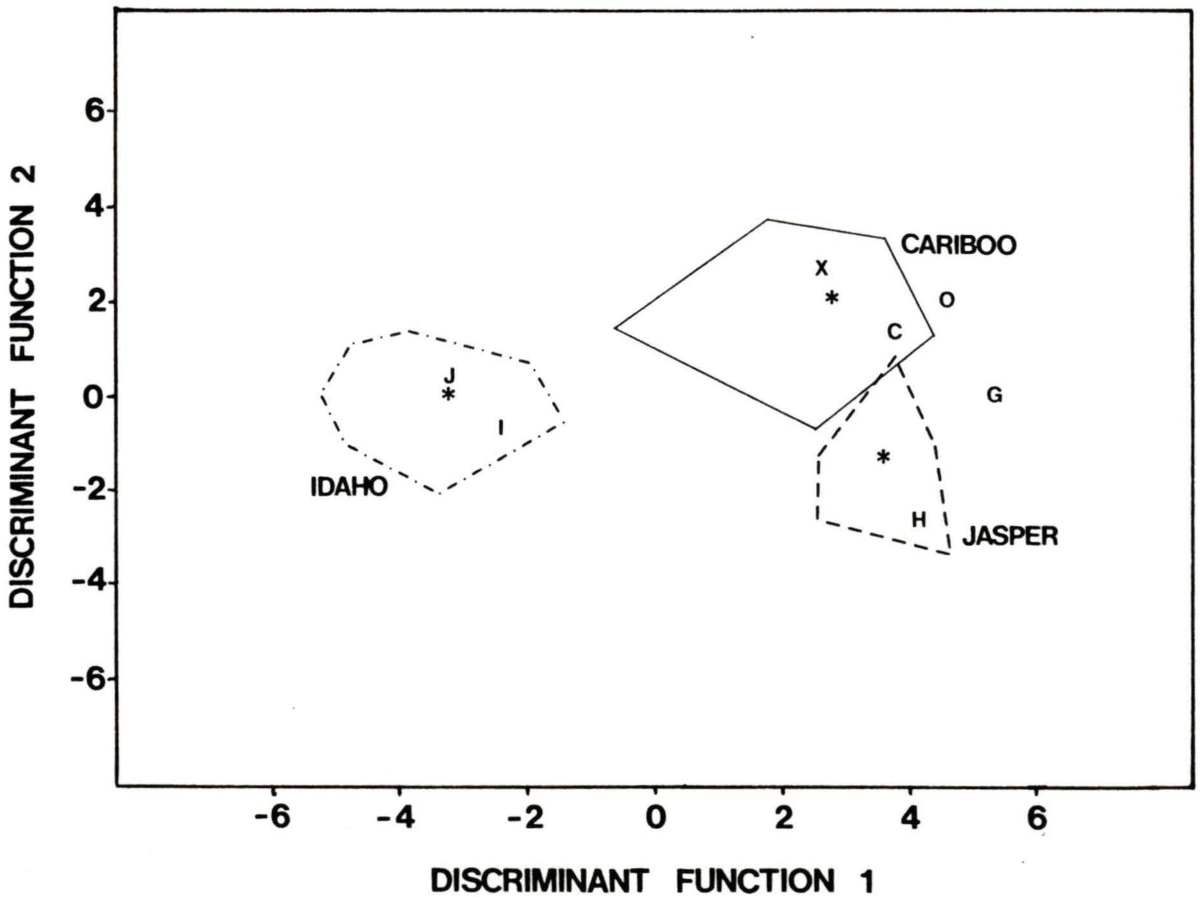
Variable	Standardized Discriminant Coefficients DF1	DF2
2. Zygomatic width	1.390	0.351
5. Width across cheek teeth	-0.644	-0.312
6. M^1 to orbit	0.829	0.366
7. Tooth row length	-0.564	-0.790
8. Carnassial length	0.355	-0.703
9. Carnassial width	-0.695	0.305
10. Canine width	-0.315	0.965
12. Jugal height	-0.060	-0.963
15. Width behind post-orbital processes	-0.942	0.314
16. Distance between bullae	1.393	-0.296
17. Distance between first premolars	0.196	0.503
19. Bulla length	0.739	0.518
Eigenvalue	11.260	1.465
% of variance	88.5%	11.5%

Figure 24. Plot of relative positions of Cariboo, Jasper and Idaho female wolf groups on two discriminant functions, with wolves from southern British Columbia and adjacent areas plotted as unknowns.

First function accounts for 88.5% of variance.

* group centroids

Letters indicate specimens referred to in Table 29.


CARIBOO
IDAHO
JASPER
X
O
C
G
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I
H
6
4
2
0
-2
-4
-6
DISCRIMINANT FUNCTION 2
DISCRIMINANT FUNCTION 1

in 1982 and Montana in 1978 were both assigned to the northern groups (Table 29).

Caution must be used in interpreting results, since dispersion matrices are not homogeneous and sample sizes are fairly small. Nevertheless, group separation and classification rates were good and it can be stated with some confidence that the wolves occasionally reported within the historic range of *irremotus* today are far more closely related to the large northern wolves than to *irremotus*.

DISCUSSION

The discriminant analysis of central British Columbia and Idaho wolves showed a very sharp differentiation between the two groups, as reported in Part 1. Unfortunately, I had no access to any historic wolf specimens from the northwestern corner of Montana; however, the identification of specimens collected around the turn of the century suggests that the range of _C.l._ _irremotus_ at that time extended north to the Lethbridge area in Alberta, and possibly into southern B.C. Wolves reported in this area, and in the northwestern United States today, are unmistakably related to the northern wolves. As further support, wolves being reported in the U.S. Northwest today are most often described as grey or black (U.S. Fish and Wildlife Service 1980), whereas Goldman (1944) describes _C. l._ _irremotus_ as light buff or varying shades of grey, with black phase extremely rare.

Wolves have been known to travel straight-line distances as great as 886 km (Fritts 1983), and to cross several subspecific "boundaries" along the way. It is apparent that Canadian wolves have been gradually expanding their range southward into the area formerly occupied by _C. l._ _irremotus_. I found no evidence for the continued existence of the Northern Rocky Mountain wolf as a distinct subspecies, using the limited material available to me.

GENERAL CONCLUSIONS

The wolves of the Pacific Northwest can be separated into two major groups - a large, northern wolf, and a smaller wolf occupying the western United States and west coast of British Columbia. It has been suggested that wolf size may be related to prey size (Rosenzweig 1968), but this seems unlikely to have any bearing on this north-south size differential. The wolves of the Alaska panhandle are reasonably large, yet feed on Sitka black-tailed deer; the smaller C.l. nubilus (eastern neighbour of irremotus) preyed on plains bison (Nowak 1983). Also, the prey base in the Canadian Rockies is of much the same composition as that through the American Rockies, yet the Canadian wolves are much larger.

Endler (1977) states that it is not necessary to postulate expansion from glacial refugia to explain clines between conjunct populations. Nevertheless, the sharp cline in wolf size from British Columbia (this study) through the prairies (Skeel and Carbyn 1976) and into Ontario (Kolenosky and Standfield 1975) is not easily explained by chance differentiation or adaptive differentiation due to environmental gradients. It is known that wolves were isolated in Alaska (Guthrie 1968) and the southern United States (Nowak 1979) during the Wisconsin Glaciation, and secondary contact of expanding populations seems the most likely explanation.

Although wolves are capable of migrating long distances, they tend not to do so unless wolf populations are low in surrounding areas (Theberge 1983). When populations are high and habitats saturated, there is little effective dispersal, and the wolf pack will tend to breed within itself (Shields 1983). This philopatry and inbreeding maintains species-wide diversity, and results in the localized differences defined as subspecies.

The specimens that Goldman (1944) examined for his taxonomic study were mostly collected before the wide-scale recent extirpation of the wolf in the southern portion of its range. Hence, his subspecific designations are not necessarily appropriate for wolves today reoccupying the southern portions of their range.

The wolves of the northern part of the province could not be reliably distinguished. Thus, the Prince George, Smithers, Horseranch, Kechika, Jasper, and Peace River wolves all belong to one group. Although C.l. occidentalis is assumed to occur in the Peace River area, these results suggest all northern B.C. wolves can be referred to C.l. columbianus. Further work with wolves from the Yukon, Northwest Territories, and Alberta would be required to determine if, in fact, differences among the northern wolf group justify subspecific divisions.

Fears that wolves had been virtually extirpated in southern British Columbia and the northwestern United States appear to have been well-founded. I have found no evidence for the continued existence of either the Cascade wolf, C. l. fuscus, or the Northern Rocky Mountain wolf, C. l. irremotus. These populations have either been eliminated or so invaded by immigrating wolves as to be no longer identifiable.

In addition, the Vancouver Island wolf, C.l. crassodon, is no longer a distinct population. Whether immigration is still occurring is unknown, but at the present time island wolves cannot be reliably distinguished from coastal mainland wolves.

These analyses would suggest, however, that the wolves of Vancouver Island, the B.C. coast, and possibly the Alaska panhandle, may be the only populations remaining descended from the southern wolves isolated by the Wisconsin Glaciation. In the interests of maintaining genetic diversity - the stated aim of wildlife management in British Columbia - this possibility should be considered by wildlife biologists in designing their management strategies for this species.

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APPENDIX 1

DESCRIPTIONS OF SUBSPECIES OF CANIS LUPUS IN THE PACIFIC NORTHWEST

The currently accepted subspecific status of wolves in the Pacific northwest is defined by Young and Goldman (1944). Excerpts of Goldman's (1944) descriptions follow, concentrating on skull characteristics, especially those that can be easily compared between populations:

a) *Canis lupus occidentalis* Richardson, type specimen not designated. Type locality Fort Simpson, Northwest Territories. "Among the largest of North American wolves .... skull ... very similar to that of *columbianus*, but usually larger; postorbital processes stouter, less tapering ... dentition as a whole heavier, but second lower molars smaller .... Normal color ... usually lacking any buffy suffusion." Black phase common. Specimens examined: 42 skulls, 3 skins.

b) *Canis lupus irremotus* Goldman, type specimen from Red Lodge, Montana, USNM 214869. "A light-colored subspecies of medium to large size .... size similar [to *fuscus*]; frontal region flatter, less convex in profile, and distinctly narrower, less inflated behind postorbital processes; rostrum and nasals longer, the nasals usually ending well behind posterior plane of maxillae. Compared with *columbianus*: size smaller; frontal region narrower, more constricted behind postorbital processes; supraoccipital shield narrower, more tapering toward apex .... Color ... "light buff" or varying shades of grey, sparingly overlaid with black." [Black phase extremely rare]. Specimens examined: 139 skulls, 98 skins.

c) *Canis lupus columbianus* Goldman, type specimen from Wistaria, B.C., BCPM 3559. Size large .... Skull ... very similar to that of *occidentalis*, but usually smaller; postorbital processes slenderer, more tapering; dentition as a whole lighter, but second lower molars larger, canines slenderer; carnassials relatively narrower. Compared with irremotus: Size larger; frontal region broader, less constricted behind postorbital processes; supraoccipital shield usually broader, more rounded near apex; dentition similar. Compared with fuscus: Size larger; nasals relatively longer, extending farther posteriorly beyond ends of maxillae; second lower molar relatively larger. Differs from that of crassodon in lighter dentition, especially the narrower carnassials. Differs from that of ligoni most obviously in greater average size. Color - Variable ... mixed white and black with a pale buffy, or yellowish suffusion ... or ... suffused with "cinnamon-buff or "pinkish-buff." Black phase occurs. Specimens examined: 17 skulls, 11 skins.

d) Canis lupus ligoni Goldman, type specimen from Kupreanof Island, Alaska, USNM 243323. A dark-colored subspecies of medium size .... Skull ... closely resembling that of columbianus, but smaller; auditory bullae usually larger, more fully inflated. Similar in size and general form to crassodon, but auditory bullae smaller, less inflated; upper carnassials distinctly smaller and narrower, the anterior borders more transverse to longitudinal axis of skull, instead of oblique and directed inward and backward as in crassodon. Color ... pale buff heavily overlaid with black." Black phase fairly common. Specimens examined: 34 skulls, 21 skins.

e) Canis lupus fuscus Richardson, type specimen not designated, type locality banks of the Columbia River, below the Dalles. "Size medium; skull rather short .... Compared with irremotus: Size similar; frontals broader between orbits and broader, more inflated behind postorbital processes; rostrum and nasals shorter, the nasals usually ending nearer the posterior plane of maxillae. Compared with crassodon: Size and general form similar; nasals usually shorter, more nearly conterminus with maxillae posteriorly; auditory bullae smaller, less inflated; dentition, especially the larger molariform teeth, lighter; upper carnassial narrower anteriorly, with border of crown more nearly transverse to longitudinal axis of skull (anterior border of crown directed more obliquely inward and backward in crassodon).

Compared with columbianus: size smaller, nasals relatively shorter, less extended posteriorly; second lower molars relatively smaller .... Distinguished by peculiar dark coloration .... Owing ... to the dark "cinnamon" or "cinnamon-buff" general ground color." Black phase not recorded. Specimens examined: 27 skulls, 20 skins. Three skulls only from British Columbia.

f) Canis lupus crassodon Hall; type specimen from Tahsis Canal, Vancouver Island, MVZ 12456. Size medium .... Skull - Similar in size and general proportions to that of fuscus; nasals usually longer ... auditory bullae larger, more inflated; dentition, especially the larger molariform teeth, heavier; upper carnassial distinctly broader anteriorly, with border of crown directed more obliquely inward and backward .... Differs from that of columbianus in about the same details .... Color ... drab grayish ... heavily overlaid with black ... lackng the "cinnamon" or "cinnamon-buff" suffusion [of fuscus]." Black phase not recorded. Specimens examined: 11 skulls, 1 skin.

APPENDIX 2

SPECIMENS EXAMINED

Information on specimen localities was taken from specimen labels. This information was often imprecise, but sufficient to locate specimens within study areas given. Place names are often of the nearest recognizable geographic feature; wolves may have been collected several kilometres distant. Sex is indicated by M (male), F (female) or U (sex unknown).

Acronyms for institutions in which this material is held are:

AMNH	American Museum of Natural History, New York
BCFW	British Columbia Fish and Wildlife Branch, Victoria
BCPM	British Columbia Provincial Museum, Victoria
CRCM	Charles R. Conner Museum, State College, Washington
MSU	Montana State University, Bozeman
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
NMC	National Museum of Natural Sciences, Ottawa
OSU	Oregon State University, Corvallis
PSNHM	Puget Sound Natural History Museum, Tacoma

ROM Royal Ontario Museum, Toronto

SDNH San Diego Natural History Museum, San Diego

UBC Vertebrate Museum, University of British Columbia, Vancouver

Vancouver Island (historic)

Sooke, 2M, 1F (BCPM); Alberni, 1M (BCPM); Cowichan, 2M 1F (BCPM); Alberni, 1F (BCPM); Beaver Creek, 1M (UBC); Tahsis Canal, 1M 1V (MVZ): Englishman's River, 1U (MVZ); "West coast,: 1U (BCPM); Quatsino Sound, 1F, 6U (USNM).

B.C. coast

Burrard Inlet, 1M (BCPM); Pemberton, 1M (BCPM), 2M, 2F, 1U (UBC); Kingcome Inlet, 1M (NMC): Powell River, 2U (BCFW); Bella Coola Valley, 2U (private collection), 3U (BCFW): Prince Rupert, 1F (UBC).

Oregon

Tiller, 1M (USNM): Glide, 1M, 2F (USNM); Silver Lake, 1M (USNM); Foster, 1M (USNM); Peavine Mountain, 1M (MVZ), 2M 1F (SDNH); Cascadia, 1M, 2F (USNM); Rogue River, 1M, 1F (USNM); Estacada, 1M, 1F (USNM); Clackamas Lake, 1M (SDNH); Crane Prairie, 1F (USNM); Lane Co., 1F (SDNH); Linn Co., 1F (SDNH); Elwha Mountains, Olympic Peninsula, Washington, 1M (USNM).

Alaska

Craig, 2F (USNM); Wrangell, 7M, 2F (USNM); Ketchikan, 2F (USNM); Revillagigedo Island, 1M (USNM); Kupreanof Island, 1M, 1F (USNM); Kuiu Island 1M, 2F (USNM); Eleanor Cove, 1M (ROM); Dry Bay, south of Yakutat, 1F (ROM), 5U (AMNH); Conclusion Island, 1U (USNM); Prince of Wales Island, 6U (USNM).

Idaho

Boise National Forest, 1M (USNM); Belt, 1F (USNM); Alridge, 2F (USNM); Angora, 1M (USNM); Dillon, 2F (USNM); Chief Mountain, 1U (USNM); Castleford, 1M (USNM); Ingomar, 1F (USNM); Kruger, 1U (USNM); Leadore, 1M 3F, 2U (USNM); Little Belt, 1M 2F (USNM); Lodge Grass, 1M (USNM); Lame Deer, 1U (USNM); Otto, 2U (AMNH); Powderville, 3M 1F (USNM); Pocatello, 1F (USNM); Red Lodge, 2M (USNM); Riceville, 1F (USNM); Redrock, 1F (USNM); Soda Springs, 4M 6F, 1U (USNM); Ridge, 1U (USNM); Tygee Basin, 1M, 1F (USNM).

Smithers

Quick, 1M, 1F, 2U (UBC); Kispiox, 1M (BCPM); Telegraph Creek, 1U (BCPM); 1U (MVZ); Smithers-Telkwa-Bulkley Valley area, 3M, 3F, 15U (BCPM and BCFW).

Prince George

Fort St. James, 1M, 1F (NMC); Hixon, 3M, 2F (BCPM); Nechako River, 1M (BCPM); Ootsa Lake, 2M, 2F (BCPM), 3U (UBC); Prince George 1M (BCPM); Salmon River, 1M 1F (BCPM); Saxton Lake, 1F (BCPM); Vanderhoof, 4M, 2F (BCPM); 1M (NMC); Woodpecker, 1M (BCPM).

Cariboo

Alexandria, 1M, 1F (UBC); Anahim Lake, 1M, 1U (UBC); Atnarko, 1M, 1F (BCPM); Batnuni, 1U (BCPM); Buffalo Lake, 2U (UBC); Chezacut, 1M, 1U (BCPM), 1U (UBC), 1U (BCFW); Clearwater, 1U (UBC); Horsefly, 1F (BCPM); Lac la Hache, 1M, (ROM), 1F (NMC); Quesnel, 1M, 4F (UBC); Tatla Lake, 1M (NMC); Williams Lake, 1F (NMC).

Horseranch

Dease River, Mustela Creek, Rapid River, Goat Mountain: 14M, 12F (BCPM).

Kechika

Kechika River drainage, from Split Top Mountain to Scoop Lake: 19M, 18F (BCPM).

Peace River

Cache Creek, 5M, 2F (BCPM); Carbon River, 1F (USNM); Groundbirch, 3M 1F (BCPM); Fellers Heights, 1M (BCPM);

Fort Nelson, 1F (NMC); Halfway River at Kobes Creek, 1F (BCPM); Hudson Hope, 1F (BCPM); Peace River, 1U (UBC); Wonowan, 1F (BCPM).

Jasper

Crescent Spur, 1F (BCPM); Bowron River, 2F (BCPM); Jasper National Park, 1M, 1F (UBC), 4M 5F, 1U (NMC); Mcbride, 1M (BCPM); Robson Park, 1M (BCPM); Raush Valley, 2F (BCPM); Valemount, 2M (BCPM); Yellowhead Pass, 3M, 1F (UBC).

Recent Vancouver Island wolves (all in BCPM unless otherwise specified).

Artlish River, 1F; Atluck Lake, 1M; Bacon Lake, 1M (private); Black Creek, 2F; Campbell River, 1F; Coal Harbour, 1F; Coombs, 2M, 1F; Courtenay, 1M, 1F; Cowichan, 2F; Gold River, 1U; Heart Lake, 1U; Heber River, 1F; Holberg, 1M, 1F; Hoomak Lake, 1M, 1F; Iron River, 1U; Kelsey Bay, 4M; Kewquodie River, 1M; Klaklakama Lakes, 4M, 3F; Koprino River, 1M; Marble River, 1M; Mt. Ozzard, 1M; Nanaimo River, 3M; Nimpkish Valley, 2M (BCFW), 5M, 1F, 1U; Nootka Island, 1M (BCFW), 1F; Pacific Rim National Park, 1F (UBC); Port Alberni, 1M; Port Alice, 1M; Port Eliza, 1F; Port Hardy, 2F; Port McNeill, 1M; Qualicum, 1M; Quatsino, 1M (private); Salmon River, 1F; San Josef, 1M, 1F;

Sayward, 2M, 1F; Schoen Lake, 1M; Sooke, 1F; White River, 1M, 1F; Woss Lake, 1F, 1U; Zeballos, 1M, 1U.

Coastal island wolves (all in BCPM)

Calvert Island, 1M; Cortes Island, 2M; Gambier Island, 1M; Hernando Island, 1F; Quadra Island, 1M, 2F; Reid Island, 4M, 1F; Sidney Island, 1M.

Appendix 3

SAMPLE STATISTICS

This appendix lists the mean, minimum, maximum and standard deviation for each of the 19 cranial measurements taken on males and females of the twelve reference groups, and for dogs. All measurements are in millimetres. Sample size is given for each group; number in parentheses indicates number for which sex was uncertain. These measurements are:

1. Total skull length, incisors to end of sagittal crest.
2. Greatest width across zygomatic arches.
3. Distance from alveolus of M^2 to external opening of auditory bulla.
4. Width of braincase at parieto-temporal suture.
5. Maximum width across upper cheek teeth.
6. Minimum distance from M^1 alveolus to orbit.
7. Length of tooth row, alveolus of canine to alveolus of M^2.
8. Crown length of upper carnassial.
9. Crown width of upper carnassial, taken between roots.
10. Maximum anteroposterior diameter of canine at enamel line.
11. Maximum transverse diameter of M^2.
12. Minimum height of jugal anterior to postorbital process.
13. Minimum width between orbits.
14. Maximum breadth across post-orbital processes (width of frontal shield).
15. Minimum width of constriction behind postorbital processes.
16. Distance between auditory bullae.
17. Minimum distance between inner alveoli of first upper premolars.
18. Width of rostrum across canines.
19. Length of auditory bulla.

MEASUREMENTS

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Vancouver Island, pre-1950, males; n=9 (2)																			
Mean	254.76	140.50	73.41	65.98	81.04	40.84	106.31	25.43	10.01	15.13	14.22	18.94	45.66	67.89	43.70	18.42	30.86	47.02	33.77
Min.	245.7	133.3	69.8	51.3	77.9	37.8	101.5	20.8	9.2	14.6	13.2	18.0	42.7	63.1	37.2	15.2	27.7	43.1	31.2
Max.	262.2	143.9	77.6	72.1	83.7	43.7	110.7	26.7	10.5	15.5	15.4	21.1	49.9	71.9	48.1	20.6	33.0	51.0	36.6
S.D.	6.18	3.44	2.55	5.93	2.05	2.06	3.08	1.84	0.43	0.38	0.80	0.91	2.49	3.51	3.07	1.79	1.74	2.22	1.94
Vancouver Island, pre-1950, females; n=8 (3)																			
Mean	235.25	129.85	66.39	67.58	76.61	36.73	100.94	25.01	9.45	13.89	14.00	17.20	41.96	62.63	42.15	17.44	29.69	44.20	31.18
Min.	225.4	121.6	60.4	64.3	74.3	34.5	98.5	23.7	8.4	12.8	13.3	14.6	39.8	56.2	38.2	15.1	27.5	42.0	27.5
Max.	243.1	135.1	71.9	70.7	80.3	40.0	103.1	25.7	10.3	14.7	15.1	18.8	46.6	65.8	45.0	19.8	32.8	48.5	36.0
S.D.	6.43	4.20	4.67	2.18	2.18	1.73	1.59	0.67	0.59	0.60	0.56	1.46	2.21	3.40	2.14	1.50	1.80	2.08	3.20
British Columbia coast, males; n=5																			
Mean	259.30	140.98	76.98	66.84	81.44	42.56	105.88	25.26	10.04	14.78	14.08	20.44	45.78	66.64	45.38	18.06	32.58	48.52	31.90
Min.	247.0	136.9	73.6	64.3	77.5	40.2	100.5	24.3	9.8	13.5	13.5	19.5	43.8	62.7	42.8	17.3	30.1	46.3	30.4
Max.	266.1	144.3	82.4	71.9	85.4	46.3	109.9	27.4	10.4	16.5	15.3	21.9	48.1	70.1	51.6	19.1	34.7	51.6	33.3
S.D.	7.54	3.32	3.44	3.08	3.55	2.32	4.12	1.38	0.22	1.27	0.70	0.94	1.79	3.61	3.60	0.70	1.83	2.02	1.13
British Columbia coast, females; n=3																			
Mean	246.90	126.33	72.90	65.83	74.87	38.30	101.70	24.10	9.43	13.30	12.53	18.03	40.80	56.40	41.47	20.93	29.60	44.17	29.40
Min.	238.7	124.7	70.4	65.6	70.5	36.3	97.7	23.9	9.0	13.0	11.4	17.0	39.1	55.1	40.9	20.2	28.7	43.3	28.2
Max.	259.1	127.6	76.3	66.2	78.1	40.6	106.4	24.4	10.3	13.8	13.5	19.0	42.4	57.6	42.6	21.8	30.5	45.6	30.1
S.D.	10.77	1.48	3.05	0.32	3.93	2.17	4.39	0.27	0.75	0.44	1.06	1.00	1.66	1.25	0.98	0.81	0.90	1.25	1.04
Alaska, males; n=11																			
Mean	255.54	139.76	73.64	67.20	81.62	40.56	107.34	25.15	10.36	14.77	14.32	19.10	44.64	65.47	42.32	19.54	32.14	47.53	33.16
Min.	244.0	125.2	65.7	64.9	78.7	37.8	101.0	24.4	9.4	14.2	13.3	17.4	39.8	57.2	40.8	17.6	30.0	44.8	28.3
Max.	268.4	147.5	78.3	69.9	85.6	42.3	112.4	26.5	11.8	15.5	15.6	20.4	49.2	74.1	44.2	21.7	37.1	50.2	36.5
S.D.	7.24	6.80	3.49	1.91	2.20	1.40	3.26	0.74	0.66	0.46	0.79	0.89	2.87	5.20	1.09	1.21	1.89	1.81	2.11
Alaska, females; n=11																			
Mean	244.65	134.43	71.43	66.49	78.08	39.28	102.78	23.79	9.62	13.46	13.55	18.26	43.42	61.95	41.48	18.09	31.26	45.72	32.12
Min.	234.8	130.1	69.3	63.4	75.6	35.0	100.3	22.0	9.1	12.6	12.4	16.1	40.8	58.2	36.5	15.9	28.8	43.4	29.4
Max.	253.5	141.9	74.2	70.6	79.8	43.1	105.7	25.9	10.4	14.5	14.6	19.8	47.6	67.4	46.1	20.2	33.4	47.8	34.0
S.D.	4.72	4.13	1.54	1.87	1.44	2.71	1.74	1.11	.40	0.60	0.65	1.06	2.33	3.19	2.37	1.46	1.48	1.50	1.67
Oregon, males; n=12																			
Mean	252.37	136.10	75.33	67.15	81.29	38.82	104.26	25.32	10.13	14.64	13.54	20.03	48.71	67.61	42.94	19.68	30.76	48.40	28.92
Min.	236.7	118.3	66.1	62.6	72.4	32.4	98.8	23.3	9.4	13.5	11.4	18.2	41.9	57.5	38.5	17.0	27.6	43.0	27.0
Max.	261.7	143.3	80.4	69.6	84.5	42.8	108.6	26.7	11.3	15.7	14.8	22.1	54.8	75.0	45.2	21.7	34.1	51.2	31.6
S.D.	6.93	7.35	3.88	1.66	3.35	2.90	2.87	1.06	0.47	0.75	0.92	1.21	3.18	4.96	1.78	1.43	1.98	2.26	1.39
Oregon, females; n=10																			
Mean	239.14	128.06	70.54	64.09	74.90	36.13	99.05	23.06	9.11	13.52	12.96	18.25	45.05	62.54	40.96	18.91	29.58	45.62	27.43
Min.	228.0	121.3	68.1	60.7	71.6	34.5	95.8	21.9	8.7	12.4	12.1	16.5	39.7	55.5	35.3	16.7	28.2	42.8	25.0
Max.	252.0	137.0	77.2	67.8	77.3	38.7	103.7	24.1	9.5	15.6	13.9	19.4	50.7	68.5	44.3	21.7	31.3	48.8	29.9
S.D.	6.79	4.57	2.81	2.67	2.02	1.27	2.38	0.70	0.28	0.93	0.50	0.82	3.33	4.47	2.75	1.39	0.99	1.81	1.32
Idaho, males; n=16																			
Mean	248.86	134.99	73.43	65.24	81.92	38.17	102.41	24.99	10.29	14.53	13.68	18.46	43.51	58.58	37.44	18.57	31.74	47.13	29.45
Min.	229.1	122.0	69.4	61.0	73.2	32.6	92.0	22.0	9.0	12.7	11.6	15.6	39.5	49.1	32.1	15.0	28.7	41.6	25.6
Max.	262.9	145.6	79.8	68.8	87.0	42.3	108.1	26.9	11.3	15.7	15.5	20.2	50.8	68.1	42.5	21.9	34.5	52.3	33.4
S.D.	9.71	6.33	2.87	2.80	3.61	2.69	4.63	1.49	0.64	0.86	0.89	1.47	2.94	4.58	2.71	2.14	1.68	2.76	1.95

MEASUREMENTS (con't)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Idaho, females; n=22																			
Mean	234.86	124.85	67.72	63.66	76.66	35.33	98.90	24.08	9.92	13.14	12.92	16.86	41.19	55.24	37.62	16.69	29.24	43.86	28.78
Min.	220.3	119.2	62.1	60.3	73.6	33.0	91.6	22.0	9.1	12.4	11.2	14.7	36.2	46.3	33.5	13.0	27.1	40.9	25.1
Max.	254.1	131.6	71.1	67.4	79.8	38.6	107.5	26.2	10.9	15.3	14.0	18.6	46.5	63.9	43.5	20.9	31.0	47.8	33.6
S.D.	7.43	3.78	2.58	2.01	1.79	1.51	3.33	0.99	0.52	0.66	0.80	0.99	2.88	4.43	2.67	2.04	1.13	1.85	1.79
Smithers, males; n=6																			
Mean	272.53	150.92	79.67	68.95	85.22	44.25	112.15	26.10	10.62	14.42	14.22	20.80	47.62	65.60	44.77	20.05	34.07	49.57	33.25
Min.	267.2	146.4	75.6	65.0	82.7	41.1	107.7	25.0	9.6	12.3	12.8	18.5	44.5	59.8	41.6	17.9	32.1	45.3	29.6
Max.	280.9	155.3	85.2	71.1	90.5	48.2	117.4	27.5	11.4	15.9	15.4	21.8	51.0	68.7	48.7	21.0	36.7	52.9	36.8
S.D.	4.75	3.66	4.04	2.27	2.86	2.37	3.40	1.16	0.71	1.22	0.85	1.21	2.50	3.36	2.92	1.16	1.50	2.72	2.40
Smithers, females; n=4																			
Mean	256.63	140.38	75.25	67.75	79.48	41.48	106.95	24.38	9.68	13.95	13.55	19.70	46.35	63.33	44.28	18.75	32.50	47.30	31.33
Min.	243.2	134.1	71.8	66.7	75.1	40.1	101.4	23.3	9.2	12.5	12.8	18.1	43.5	57.5	42.8	16.6	30.6	44.1	30.4
Max.	269.6	149.2	78.1	69.2	83.6	43.2	110.8	25.2	10.0	15.5	14.0	22.1	48.5	67.8	46.7	22.3	35.5	50.8	31.8
S.D.	10.78	7.02	2.79	1.05	3.59	1.35	4.02	0.93	0.40	1.43	0.53	1.92	2.37	4.31	1.78	2.64	2.13	3.17	0.64
Prince George, males; n=15																			
Mean	268.21	147.55	78.31	68.50	83.82	43.51	110.91	26.28	10.41	15.28	14.36	20.09	48.63	65.09	43.47	19.79	32.79	50.33	32.55
Min.	242.2	128.1	69.7	63.6	73.8	38.0	99.8	24.0	9.0	13.6	12.7	17.3	40.5	53.6	39.3	17.0	28.3	42.2	30.4
Max.	290.9	158.7	84.9	72.8	90.1	46.1	121.2	28.1	11.2	16.6	15.3	23.7	59.8	71.4	48.8	22.4	35.1	55.1	35.4
S.D.	12.33	8.07	4.59	1.95	4.21	2.22	5.41	1.35	0.64	1.01	0.81	1.66	4.52	5.74	2.69	1.48	2.04	3.34	1.60
Prince George, females; n=10 (1)																			
Mean	256.41	136.07	75.27	67.41	79.07	39.92	105.69	25.06	9.92	13.71	13.67	18.38	44.26	61.48	41.78	19.32	31.64	46.47	31.48
Min.	245.5	126.1	72.1	63.6	73.2	37.7	102.5	23.6	9.0	12.6	13.0	16.1	38.6	52.1	36.8	16.0	29.8	43.2	29.7
Max.	264.7	146.4	78.6	70.6	81.7	42.7	109.6	25.9	10.7	14.7	14.5	20.3	48.6	69.7	44.6	22.6	35.4	51.2	33.1
S.D.	6.93	5.69	1.95	2.28	2.86	1.78	2.37	0.85	0.50	0.73	0.49	1.41	3.18	6.06	2.80	2.15	1.65	2.63	1.18
Cariboo, males; n=10 (3)																			
Mean	262.85	138.95	77.99	67.59	79.45	41.90	108.07	25.51	9.90	14.62	13.59	18.87	45.55	61.73	42.14	19.17	31.95	48.46	33.01
Min.	249.4	128.3	73.9	65.3	75.3	37.1	102.0	24.0	9.0	13.2	12.6	16.3	41.0	54.4	40.0	17.3	28.1	43.4	31.0
Max.	274.0	151.7	82.1	70.2	87.5	46.3	112.0	28.5	10.7	16.3	14.2	21.1	50.1	69.8	45.1	21.1	35.3	52.8	35.8
S.D.	8.66	7.34	2.75	1.67	3.59	3.14	2.84	1.26	0.59	1.04	0.47	1.83	2.41	4.26	1.93	1.38	2.03	2.76	1.56
Cariboo, females; n=10 (1)																			
Mean	255.35	136.71	76.08	66.41	79.26	41.21	103.53	24.58	10.19	14.17	13.78	18.49	45.80	61.85	42.19	19.37	30.58	46.93	32.53
Min.	236.6	125.2	70.8	64.2	71.3	36.4	94.5	22.9	9.1	12.2	12.7	15.8	41.8	56.3	39.5	16.8	28.1	43.5	30.5
Max.	276.5	147.9	83.0	68.7	85.9	44.6	112.3	26.3	12.0	15.5	15.3	20.6	51.5	69.9	44.6	21.5	32.1	50.1	35.3
S.D.	12.33	7.52	4.24	1.49	4.78	2.87	5.05	1.06	0.94	1.06	0.87	1.57	3.53	4.10	1.61	1.41	1.39	2.27	1.64
Horseranch, males; n=14																			
Mean	269.69	147.14	79.76	69.29	84.02	42.89	108.81	25.76	10.42	14.85	14.31	20.06	48.66	67.18	44.17	20.46	32.62	49.22	32.39
Min.	257.5	139.7	76.4	65.6	80.9	39.6	102.7	24.1	9.6	13.3	13.0	17.3	43.2	61.4	39.0	16.9	30.9	44.9	30.1
Max.	278.3	157.9	83.6	75.2	88.1	47.5	113.9	27.7	12.0	17.7	15.6	23.3	53.2	77.0	48.7	23.1	34.0	54.7	35.4
S.D.	7.02	4.75	2.38	2.86	2.04	2.08	3.33	0.99	0.69	1.08	0.76	1.79	2.99	4.61	2.55	1.96	0.92	2.38	1.49
Horseranch, females; n=12																			
Mean	252.32	137.37	75.32	67.33	79.44	40.08	103.78	24.08	9.79	13.53	13.76	18.21	45.96	63.48	42.74	18.27	31.14	45.73	31.92
Min.	237.6	122.7	70.8	63.2	74.7	36.5	98.4	22.9	9.0	11.4	12.1	15.1	39.6	55.2	37.2	14.9	28.1	41.4	28.9
Max.	267.3	147.2	84.1	70.2	84.5	43.3	108.5	25.2	10.7	15.9	15.0	21.0	51.6	70.4	48.6	24.2	34.2	49.4	34.8
S.D.	9.48	8.40	3.77	2.19	3.35	2.42	3.21	0.62	0.52	1.25	0.85	2.12	4.15	5.32	2.67	2.85	1.78	2.68	1.42

MEASUREMENTS (con't)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Kechika Valley, males; n=19																			
Mean	274.14	145.56	81.49	67.66	85.36	44.25	111.75	26.25	10.74	14.78	14.77	21.40	49.31	66.34	44.52	21.42	32.44	49.89	32.25
Min.	255.2	130.3	73.8	65.6	78.7	40.1	105.2	24.1	10.1	13.1	13.7	18.5	42.5	60.1	40.9	18.6	29.5	45.2	30.2
Max.	286.6	156.6	87.5	70.6	90.1	47.5	116.5	27.7	11.7	16.2	16.3	23.8	53.8	72.2	48.5	25.2	35.7	53.0	35.8
S.D.	8.55	6.36	3.27	1.57	3.15	2.09	3.46	1.15	0.44	0.84	0.67	1.63	2.98	3.26	2.32	1.63	1.78	2.32	1.71
Kechika Valley, females; n=18																			
Mean	256.46	136.40	75.49	67.43	80.54	40.70	106.55	24.68	10.16	13.32	13.92	19.36	45.52	61.61	43.14	20.26	30.76	47.15	31.75
Min.	242.2	122.7	67.2	62.2	74.6	36.6	101.0	23.4	9.4	12.7	11.8	16.1	38.2	52.6	39.5	17.6	27.1	43.5	29.0
Max.	275.5	150.4	82.0	72.5	85.3	45.1	111.6	26.0	11.9	14.1	15.4	21.7	51.5	68.7	46.7	24.4	34.8	52.8	35.1
S.D.	8.60	6.46	4.17	2.22	3.33	2.13	2.98	0.73	0.60	0.42	0.84	1.78	3.11	4.25	2.01	1.70	2.04	2.28	1.54
Peace River, males; n=9																			
Mean	276.24	147.88	81.38	69.40	86.94	44.72	111.06	26.89	11.36	15.99	14.86	20.93	50.13	67.04	44.01	21.31	32.61	51.04	33.64
Min.	259.3	133.0	73.7	66.6	82.2	41.0	106.7	25.4	10.3	13.8	13.9	18.5	44.9	58.8	41.3	19.1	30.9	48.8	31.7
Max.	281.9	155.9	87.1	71.7	91.3	46.8	115.1	28.6	13.2	17.5	16.0	24.8	55.0	77.1	47.2	24.1	36.1	53.6	36.0
S.D.	6.60	6.53	4.47	1.88	3.15	1.95	3.14	1.23	0.91	1.18	0.70	1.88	2.88	5.48	2.31	1.53	1.61	1.42	1.48
Peace River, females; n=8																			
Mean	257.80	136.90	74.63	67.06	81.29	40.38	105.73	25.81	10.21	14.44	14.18	19.14	45.60	61.30	41.54	19.66	31.51	47.56	30.66
Min.	249.3	129.2	71.3	64.4	78.3	37.7	103.1	22.9	9.4	13.6	12.6	17.5	42.7	57.1	39.2	18.3	30.1	44.1	26.8
Max.	275.4	145.1	78.9	69.4	85.1	46.3	110.6	27.1	10.7	15.8	15.5	21.5	50.6	66.7	43.2	21.2	34.0	51.6	33.1
S.D.	8.16	6.37	2.94	1.65	2.26	2.79	2.38	1.34	0.47	0.90	0.92	1.30	2.36	3.54	1.16	1.02	1.43	2.40	2.02
Jasper, males; n=12																			
Mean	273.97	146.87	81.16	69.33	85.80	44.40	111.12	27.12	10.86	15.51	14.42	20.93	48.87	66.87	43.29	21.74	33.03	50.85	32.06
Min.	261.6	136.6	77.3	63.3	82.9	41.8	105.6	25.6	10.2	13.9	13.1	18.9	44.2	60.4	40.2	18.2	30.7	48.8	26.0
Max.	283.7	156.8	85.7	72.9	89.9	49.4	117.2	28.8	11.7	16.6	15.3	24.9	54.4	71.5	48.0	26.1	36.7	54.8	36.8
S.D.	7.39	6.21	2.39	2.55	2.47	2.54	3.07	0.85	0.48	0.71	0.72	1.61	2.49	3.91	2.35	2.11	1.93	1.76	2.89
Jasper, females; n=12																			
Mean	257.76	134.98	75.24	67.38	78.93	40.54	105.49	25.18	9.79	13.63	13.78	18.71	44.39	59.41	42.26	20.73	29.84	46.28	30.92
Min.	249.8	128.3	70.6	64.8	75.3	38.4	102.2	23.6	8.8	12.7	12.7	16.8	39.7	53.5	39.4	18.3	26.7	43.7	26.8
Max.	265.8	143.3	78.2	70.2	81.5	43.1	109.2	26.0	10.3	14.6	14.9	20.7	49.4	65.3	45.0	23.6	33.0	48.5	33.3
S.D.	5.25	5.32	2.25	1.77	1.92	1.64	2.46	0.73	0.43	0.63	0.73	1.10	2.54	3.40	1.90	1.56	1.80	1.61	1.79
Domestic dogs; n=39																			
Mean	227.25	120.25	70.34	59.53	74.15	37.03	93.10	20.68	8.22	12.07	11.81	16.60	44.29	64.44	40.82	20.93	32.47	45.04	26.52
Min.	194.0	102.6	57.5	52.5	64.2	30.5	83.6	18.2	6.7	9.1	10.0	11.9	36.4	50.4	34.5	16.1	25.5	37.0	20.6
Max.	279.5	146.0	90.6	67.1	86.1	46.5	109.6	23.1	9.8	15.7	13.5	22.3	62.0	81.3	49.5	29.2	41.1	52.8	31.1
S.D.	19.21	10.34	7.87	3.12	5.76	4.21	6.44	1.33	0.81	1.38	0.84	2.31	5.94	7.58	3.33	2.81	3.60	4.36	2.35

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