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MULTIVARIATE GEOGRAPHICAL VARIATION IN THE WOLF *CANIS LUPUS* L.¹

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INTRODUCTION

Modern biology is subdivided in numerous disciplines dealing with particular aspects of life. But what lives and evolves in reality is not isolated characteristics, it is whole organisms or, even more exactly, populations of organisms. Nowhere else perhaps as much as in evolutionary studies has a synthetic approach become important. While this makes the theory of evolution the focus of biology, it also creates intricate problems. The student of evolution often has to compare groups of organisms with respect to multiple characters. Multivariate statistical techniques should be most efficient in such problems but comparatively little use has been made of them. The following analysis of geographical variation in the wolf (*Canis lupus* L.) is an attempt to evaluate these techniques in practice. Although only morphological characters are considered here, physiological, behavioral and

ecological data could be analysed in the same manner.

The last comprehensive taxonomic study of North American wolves was that of Goldman (Young and Goldman, 1944). It consisted primarily of qualitative skull and pelage descriptions and failed to show clearly the nature and the extent of geographical variation in the species as a whole. During the present study groups of specimens have been compared with respect to complexes of metrical characters. This has disclosed multivariate trends of variation between several Nearctic wolf populations. The techniques used and the results obtained are exposed and discussed in this paper.

MATERIAL AND DATA

Numerous wolf specimens were collected in northwestern Canada by the Canadian Wildlife Service and the Manitoba Game Department during recent predator control operations. This material was deposited in the Museum of Zoology of the University of British Columbia. In this study it has been compared with British Columbia, Alaska and Arctic material, some of which was bor-

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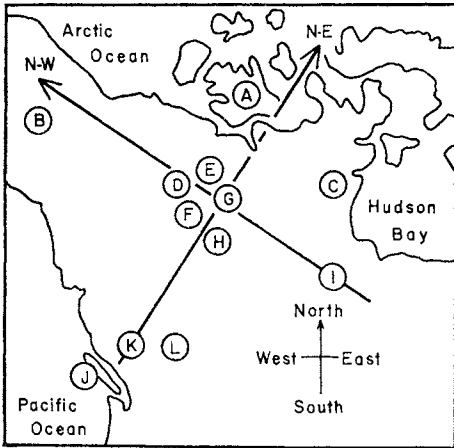


FIG. 1. Geographical origin of the samples.

rowed from the British Columbia Provincial Museum, the National Museum of Canada and Dr. R. Rausch, Anchorage, Alaska. Approximately five hundred specimens were studied. They were grouped according to sex and geographical origin as shown in figure 1 and table 1. Juvenile specimens were excluded as there was only half a dozen of them. Four general areas are represented by large samples: British Columbia (group K), Manitoba (I), and the Northwest Territories between Great Slave Lake and Great Bear Lake (groups D + E and group G). Two arrows have been lined up on these large samples in the map (fig. 1) and in a subsequent graph (fig. 10). They point

approximately northeastward and north-westward and help to refer biometrical differences to their geographical context.

Skulls were available for most specimens while there were pelage and body data for only part of the material. The analysis of geographical variation was therefore based primarily on skull dimensions. Photographic transparencies of the carcasses were available for four samples of the Northwest Territories and they were examined with respect to pelage coloration. Twelve skull dimensions were measured, in the manner illustrated (fig. 2). They are referred to hereafter by the following coded designations:

- L_1 : Condylobasal length
- L_2 : Palatal length
- L_3 : Postpalatal length
- W_1 : Zygomatic width
- W_2 : Palatal width outside the first upper molars M_1
- W_3 : Palatal width inside the second upper premolars Pm_2
- W_4 : Width between the postglenoid foramina
- W_5 : Interorbital width
- C_1 : Least width of the braincase
- C_2 : Width between the auditory bullae
- T_1 : Alveolar length of the upper carnassial Pm_1
- T_2 : Crown length of the first upper molar M_1

TECHNIQUES OF ANALYSIS

The advantages of multivariate statistical techniques for evolutionary problems have been discussed by Anderson (1954). Typically evolutionary studies lead to comparisons of groups of organisms with respect to numerous charac-

TABLE 1. *Size and sex-composition of the samples*

Locality	Group	Males	Females	Undetermined	Total
Arctic	A	11	8	—	19
Alaska	B	3	3	3	9
Keewatin	C	5	3	6	14
Northwest Territories	D	41	39	—	80
	E	41	40	—	81
	F	12	8	—	20
	G	33	33	—	66
	H	—	—	9	9
Manitoba	I	73	64	—	137
Vancouver Island	J	5	5	—	10
Mainland of B. C.	K	15	12	18	45
Rocky Mountains	L	6	3	—	9
					499

teristics. But in reality, as stressed by Olson and Miller (1958), the various aspects of living organisms distinguished by man are intimately associated. When comparing evolutionary groups of organisms it is therefore best to consider as many characters as possible simultaneously. Theoretically such joint comparisons call for multivariate analysis.

Practical reasons as well as theoretical ones make multivariate techniques desirable in evo-

lutionary studies. Groups of organisms may be entirely distinct with respect to several characters jointly and yet overlap with respect to every one of the same characters separately. Hypothetical examples of such cases are illustrated here. In figure 3 for instance two groups of specimens, represented respectively by open circles and solid dots, occupy readily separable portions of a bivariate scatter diagram. But the complete separation of these two sam-

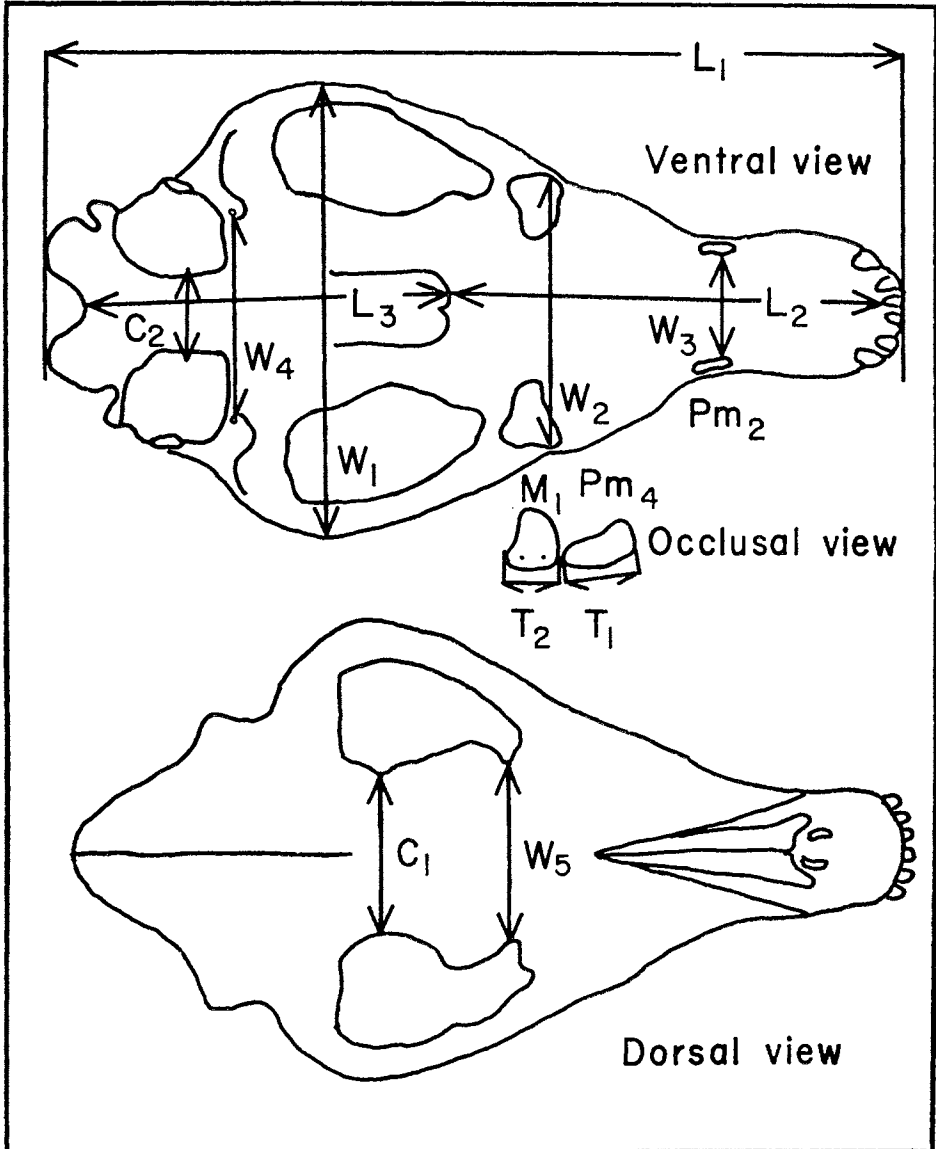


FIG. 2. Skull dimensions measured and coded designations; dorsal and ventral views of the skull and occlusal view of left upper teeth.

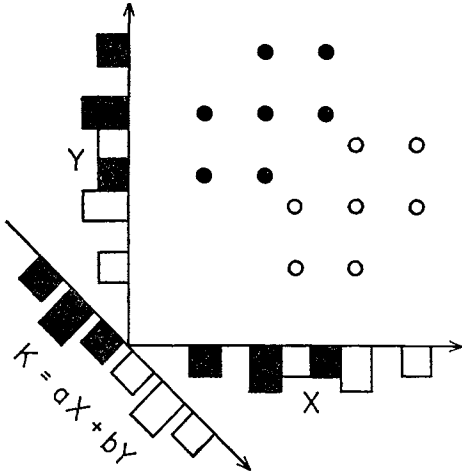


FIG. 3. Hypothetical example of discriminatory analysis for two characters. Scatter diagram and frequency histograms of characters X and Y and of discriminant function $K = aX + bY$.

ples would fail to appear if the two metrical characters X and Y were considered one after the other. This can be seen by projecting the bivariate diagram upon axes X and Y respectively; the black and the white frequency bars are interspersed in the resulting frequency histograms. The difference of the two samples could be fully expressed by a single variable though, the so-called *discriminant function* $K = aX + bY$; it corresponds to the projection of the graph upon axis K and its frequency histograms of the two samples are completely separated.

For three characters a scatter diagram assumes the form of a box within which groups of dots, circles and crosses are dispersed (fig. 4). The three edges OX, OY and OZ of the box are the coordinate axes of characters X, Y and Z. Bivariate diagrams of these data would correspond to perpendicular views of the tridimensional graph through faces XOY, XOZ and YOZ. However the true nature and magnitude of the differences between the groups would not show up well if the characters were considered one by one or two by two. The relative position of the samples appears much more clearly if the graph is viewed through the discriminant plane K_1OK_2 or projected upon it. This optimum two-dimensional representation of between-group differences is obtained by calculating the discriminant functions $K_1 = a_1X + b_1Y + c_1Z$ and $K_2 = a_2X + b_2Y + c_2Z$ and making their scatter diagram (fig. 5). The projections X, Y and Z of coordinate axes OX, OY and OZ upon the discriminant plane (fig. 5) indicate its signification in terms of the

original variables themselves, the three metrical characters.

But it is in joint studies of four or more characters that the efficiency of ordinary graphing methods are unequalled for ordinary graphing methods are impossible in more than three dimensions. Nevertheless multivariate procedures permit the analyst to examine optimum two-dimensional slices of the unexisting multidimensional graph (fig. 10, 11, 12). Much time can also thus be saved; no lengthy univariate or bivariate search is necessary for the most informative combinations of characters. There would be sixty-six different manners to associate twelve characters two by two for instance; but one or two discriminant graphs bring out almost all available information. Discriminant functions then are indispensable not only to disclose the true degree of distinctness of multivariate samples but also to condense the information relative to large numbers of characters in very few graphs.

Many samples of biometrical data follow the normal distribution at least approximately. Graphically they appear as elliptical clusters of points (fig. 8). In practice much of the information contained by such samples should be explicit in the scatter diagrams themselves. But comparisons involving several large samples would be likely to engender confusion. To avoid this, statistical summarization is necessary. *Equal frequency ellipses* are particularly effective for normal bivariate data; they

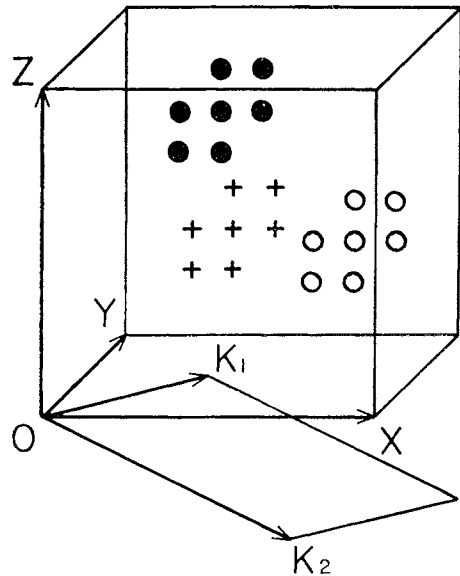


FIG. 4. Hypothetical example of discriminatory analysis for three characters. Scatter diagram of characters X, Y and Z and discriminant plane K_1OK_2 (see fig. 5).

have been used for instance by Kotaka (1953) on *Anadara granosa* (Pleistocene pelecypod from Japan). Their biometrical utilization has been thoroughly discussed by Defrise-Gussenhoven (1955). Confidence belts about regression lines and quadrilateral range diagrams have also been used to represent bivariate dispersion. However a regression line yields an estimate of the value of one character from others and this is not of primary importance in studies of evolution. As for the range diagrams utilized by Imbrie and Imbrie, (1956), they would be preferable to ellipses only for certain abnormal types of data; but departures from normality are often negligible in practice and, when important, they can frequently be corrected by using logarithmic instead of arithmetic values. In general then equal frequency ellipses are more suitable than any other current statistical device to outline the range of variation of bivariate specimens. And, used in conjunction with discriminant scatter diagrams, they are applicable to studies of any number of characters.

Multivariate calculations follow the same basic plan however many variables are analyzed jointly. The average value of metrical characters in a group of specimens is the mean; it is the center of the sample of points. The variation of the characters within this group of organisms is summarized numerically by a set of mean squared deviations and cross products, the so-called *within-group covariance matrix* W. Matrix W is generated by the elliptical dispersion of the individuals around their group mean and it figures in the equation of the equal frequency ellipses (or multidimensional ellipsoids) circumscribing the sample. The multivariate analysis of within-group variation consists in calculating the *principal axes* of such ellipses; to these directions of maximum variation (or *characteristic vectors*) correspond *principal variance components* (or *characteristic roots*). It is when biometrical samples are examined with respect to these principal trends of variation that their information content is the most explicit. Principal component analysis is closely similar in principle to factor analysis as applied by psychologists and, more recently, by biometricians.

As noted by Yates (1950), the analysis of differences between groups of specimens is analogous to that of within-group variation. The dispersion of group means around their grand mean is expressed by the *between-group covariance matrix* B. The so-called *discriminant functions* are the principal axes of matrix B after standardization by matrix W of within-group variation (pooled over all samples). Geometrically speaking the ellipsoid of within-group variation is taken as a yardstick for between-group variation. But, within ordinary

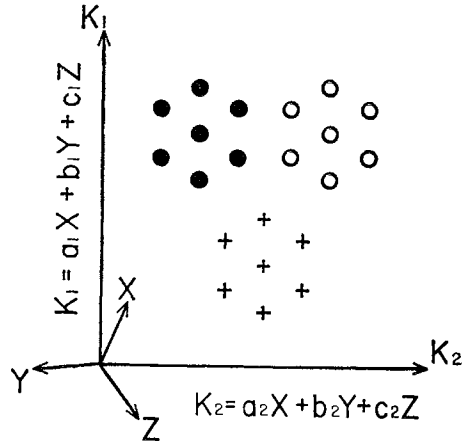


FIG. 5. Scatter diagram of discriminant functions K_1 and K_2 corresponding to plane K_1OK_2 of figure 4 and projections thereupon of axes OX, OY and OZ.

samples of living organisms, the greatest variation component of body dimensions is generally age and size (Teissier, 1955; Wright, 1932). Consequently the standardization of matrix B by matrix W emphasizes other factors of variation than age and size. The purpose formerly served by age classes and size-independent ratios is thus automatically fulfilled in discriminatory analysis. In multivariate group comparisons as in principal component analysis it is in the direction of the principal axes that the observations differ the most and that most of the information lies.

Several expositions of multivariate methods are now available (Hotelling, 1954; Kendall, 1957; Quenouille, 1952; Rao, 1952); to understand them elements of multidimensional algebra and geometry are indispensable; Murdoch's excellent introduction (1957) provides a relatively easy way to the latter. Most recent applications of multivariate analysis have unfortunately been too abstract; the graphical means of presentation utilized in this study make multivariate results just as easy to visualize as univariate or bivariate ones. As for the length of computations, it is no longer prohibitive thanks to the growing availability of electronic digital computers. Multivariate statistical techniques should be used more and more along with simpler methods when problems call for them. This appears to be the case in biometrical studies of evolution.

PELAGE COLOR VARIATION

The pelage coloration of wolves is very variable in intensity, in hue and in pattern. As detailed verbal descriptions are not

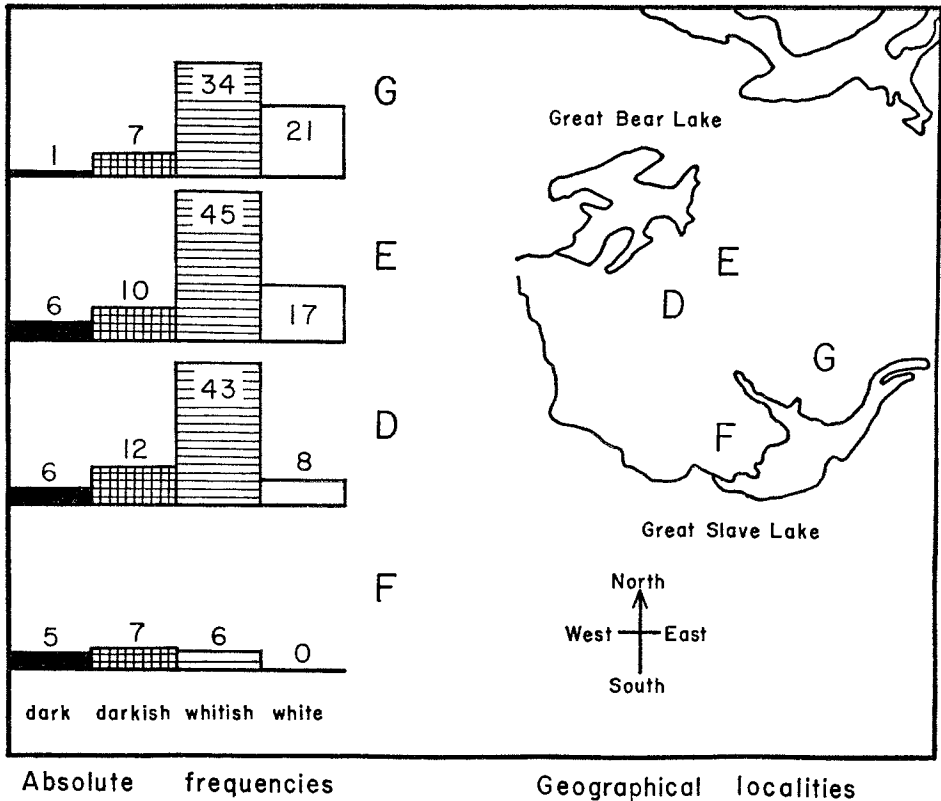


FIG. 6. Northeastward increase in the relative frequency of pale wolves toward the tundra between Great Slave Lake and Great Bear Lake.

suitable for large samples, the photographic transparencies examined were classified into four arbitrary classes according to the general darkness of pigmentation: dark, darkish, whitish and white. Such arbitrary classes do not correspond in the wolf to actually discrete color phases as in some polymorphic species. Such a classification is also only approximate and fits adequately only the present material. It does disclose however gradual differences in color-class frequencies analogous to the clines in color-phase frequencies of the red fox and the black bear (Cowan, 1938).

The relative frequency of pale wolves increases in a northeastward direction (toward the tundra) between Great Slave Lake and Great Bear Lake in the Northwest Territories (fig. 6). There are

gradually more white and whitish and fewer dark and darkish individuals in samples F, D, E and G successively. Samples D and E differ little from each other but differ significantly from the two extreme groups (95% chi-square). Seasonal variation is apparently not involved since specimens were collected at comparable dates. On the other hand, the environmental conditions of these four localities appear too similar for such pronounced differences to be phenotypical. Consequently the color frequency shift probably expresses a cline in gene frequencies. The extreme whiteness of tundra in winter is of course very well known and the higher frequency of pale wolves there is clearly a case of homochromy. The selective value of concealing coloration for a predator would pre-

sumably lie in the corresponding ease to approach preys. Pale pelage coloration may be just one facet of a physiological complex however and it is possibly related to other factors than homochromy.

Recent barren-ground caribou studies (Banfield, 1954; Kelsall, 1957) have shown caribou to migrate more intensely through areas D and E than through areas F and G. The similarity of pelage coloration between wolf populations appears to be proportional thus to the local intensity of caribou migrations. This relationship could be expected if the movements of

wolves were correlated with those of caribou. The latter correlation is effectively suggested by field observations. Wolves are often seen with caribou herds (Rausch, 1951) and, statistically speaking at least, they probably follow them at migration (Banfield, 1951).

A relatively higher frequency of dark individuals has been reported in the Rocky Mountains (Cowan, 1947). The short-distance cline exhibited by the present material may therefore be part of a long-distance cline going at least from the Rockies to the Northwest Territories.

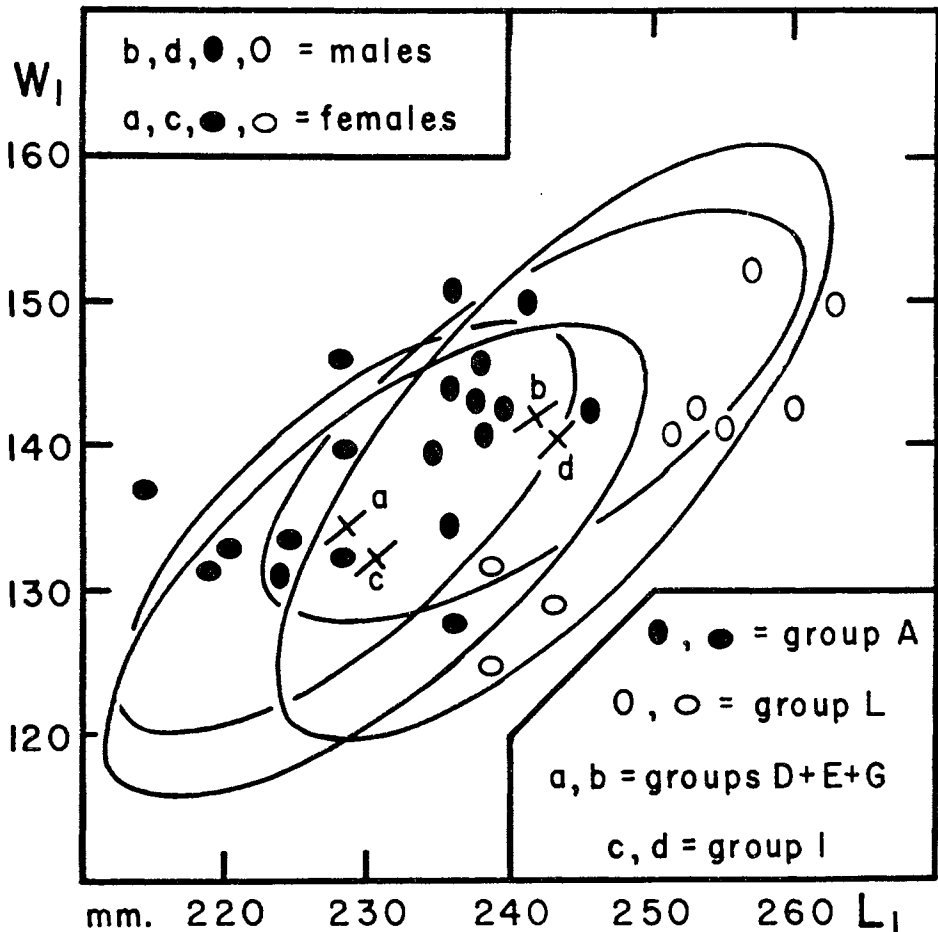


FIG. 7. Condylbasal length (L_1) and zygomatic width (W_1). Dots represent individual specimens; crosses and ellipses represent means and 95% frequency intervals respectively. Males have a larger skull than females and northeastern individuals are shorter and relatively broader-skulled than southwestern ones.

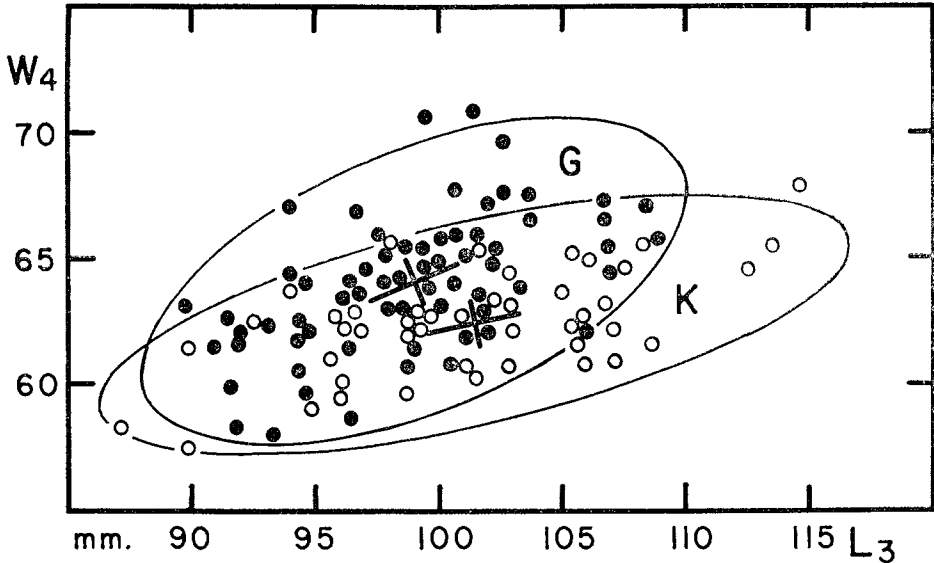


FIG. 8. The wolves of the Northwest Territories (G) have a higher growth rate of postglenoid width (W_4) relatively to postpalatal length (L_3) than those of British Columbia (K).

More data on the pelage coloration of wolves would perhaps show analogies with the geographical distribution of the color phases of the red fox and the black bear (Butler, 1947; Cowan, 1938).

BIVARIATE SKULL VARIATION

Overall skull size can be satisfactorily described by condylobasal length (L_1) and zygomatic width (W_1). Bivariate scatter diagrams of these two dimensions were made and 95% equal frequency ellipses were calculated following Defrise-Gussenhoven's procedure (1955). Figure 7 summarizes the most important information. Males are approximately 4% larger than females in linear skull dimensions. This agrees with Hildebrand's conclusions on the body size of Canidae (1952). Other facts brought out are the small skull size (close to the left lower corner of the graph) and the great relative skull breadth (close to the left upper corner) of northeastern wolves. Groups L, I, D + E + G, and A are successively closer to the left side of the graph. This ordering of samples according to skull size and relative breadth is strikingly simi-

lar to the ordering of the geographical localities of origin projected upon a line of northeastward direction. Such gradual geographic variation was termed *clines* by Huxley (1938).

The shortness and greater relative breadth of skull of northeastern wolves also shows up in a scatter diagram (fig. 8) of postglenoid breadth (W_4) and postpalatal length (L_3). The wolves of the Northwest Territories (G) are shorter and broader-skulled than those of British Columbia (K) with respect to these two dimensions. But here the difference of proportion increases with size; there is a difference of relative growth rate. Equal frequency ellipses fit the data satisfactorily; there is no obvious curvature of trend and no need for a logarithmic transformation.

A third bivariate association shows geographical variation (fig. 9): interbullar breadth (C_2) with carnassial length (T_1). The specimens of Manitoba (I) and the Northwest Territories (D + E) are at the center of this graph and constitute the average. The wolves of British Columbia (K) have shorter upper carnassial teeth

than the average and those of Vancouver Island (J) a narrower interbullar space. Simple examination of the skulls confirms what the graphical analysis summarizes. Distinct spaces show in between the small teeth of British Columbia wolves and the ten Vancouver Island specimens have markedly inflated auditory bullae with a narrow interval. Surprisingly in this graph the Vancouver Island wolves differ the most from those to which they are the closest geographically. Further discussion of this will follow the joint multivariate analysis of all twelve skull dimensions.

MULTIVARIATE SKULL VARIATION

Comparing biometrical samples with respect to complexes of characters requires the calculation of discriminant functions. The coefficients K of these functions and the components D of between-group variation for which they account are the solution of the following matrix equation: $KB = DKW$. Matrices B and

W are the *between-group* and the pooled *within-group covariance matrices* respectively and their signification has already been explained in these pages. As geographical variation in skull proportions was of primary interest here, sexes were kept together; sexual skull differences were mostly size differences (fig. 7) and separating males and females here would have spread the group means too much in the direction of size. The equation $KB = DKW$ was solved on an electronic digital computer by matrix operations (Murdoch, 1957: 165, 166) corresponding to the transformations suggested by Rao (1952: 357, 367). Matrices were diagonalized following the Jacobi method. The within-group variances and covariances of the discriminant functions were calculated to verify the computations; they were exact to two or three significant digits ($KWK' = I$) and this was considered acceptable.

The sum of the components D_i of between-group variance was 75.464; of this

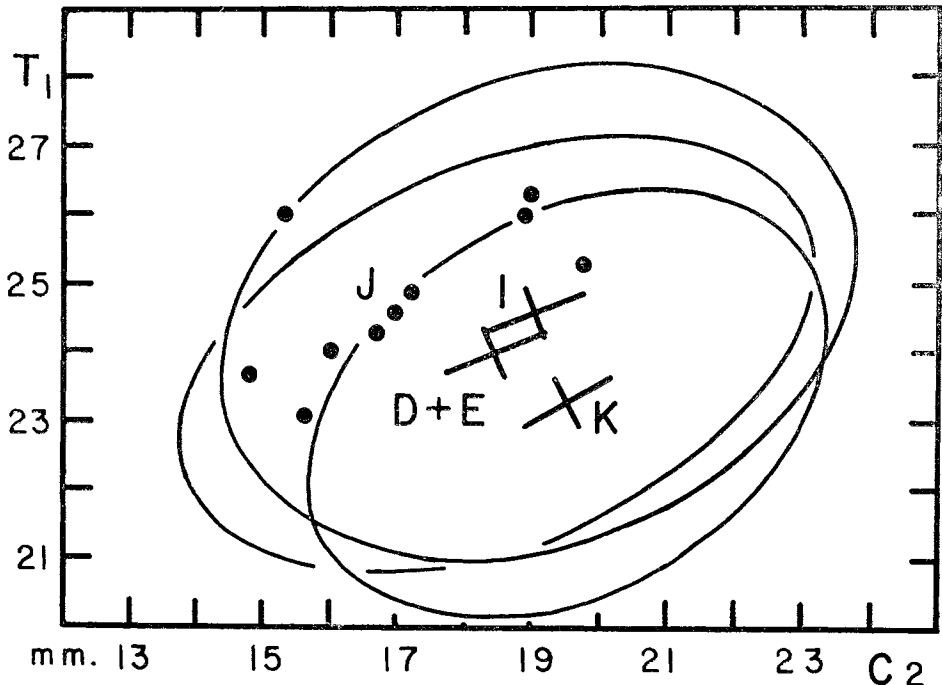


FIG. 9. The Vancouver Island specimens (J) have a narrow interbullar space (C_2) and those of British Columbia (K) short upper carnassial teeth (T_1).

TABLE 2. *Discriminatory analysis*

Variance component	D ₁	D ₂	D ₃	D ₄	D ₅
Magnitude	39.274	13.474	9.008	5.958	3.206
Per cent of total	52%	18%	12%	8%	4%
Probability	<.01	<.01	<.01	<.01	<.05

94% was accounted for by the first five functions (table 2). The statistical significance of these variances was tested as prescribed by Rao (1952: 372) for large samples. If the various samples came from a same population the probability of such large components would be less than 1% for the first four and less than 5% for the fifth. To each component correspond twelve coefficients for the skull dimensions in the discriminant functions; the numerical values of these coefficients are not given here for they could be deduced from the vectors of the discriminant graphs (figs. 10 and 12). The group means, the grand mean and the pooled within-group standard deviation

of the twelve skull dimensions are listed for reference (table 3); inspecting them rapidly confirms the reality of the multidimensional trends of variation disclosed by discriminatory analysis. Tabulating other statistics or raw data here would consume too much space without making anything explicit.

The pattern of dispersion of the groups in the plane of the first and second discriminant axes (fig. 10) presents similarities to the geographical disposition of the localities of origin. Northern samples tend to congregate in the left upper corner of the graph, eastern samples in the right upper corner and contrarywise for southern and western samples. The two ar-

TABLE 3. *Multivariate statistics (in mm.)*

Characters . .	L ₁	L ₂	L ₃	W ₁	W ₂	W ₃	W ₄	W ₅	C ₁	C ₂	T ₁	T ₂	
	Grand Mean												
	236.91	118.02	99.69	137.67	78.50	33.57	63.88	45.68	41.29	18.90	24.33	17.28	
	Pooled Standard Deviation												
	10.14	5.017	5.022	8.012	3.524	1.987	2.675	3.503	2.835	1.871	1.347	.8787	
	Group Means												
Group	N												
A	19	231.63	113.84	98.84	139.37	80.32	32.90	65.84	45.44	40.08	19.20	25.77	17.54
B	9	245.67	123.11	102.22	140.45	81.33	35.36	65.65	46.86	43.06	19.46	24.40	17.70
C	14	234.14	116.79	98.50	135.29	78.72	33.67	64.01	45.71	40.52	18.70	24.50	17.33
D + E	161	234.73	117.30	98.49	138.56	78.37	33.58	63.78	46.37	41.28	18.45	23.99	17.28
F	20	242.15	119.55	103.15	140.75	79.63	33.79	65.07	45.64	41.64	19.67	25.13	17.42
G	66	235.98	118.35	99.00	137.76	78.13	33.18	64.05	46.08	41.03	18.59	24.42	17.36
H	9	243.33	120.89	102.89	140.22	79.59	34.39	64.34	46.27	40.49	20.54	23.91	17.19
I	137	237.20	117.75	99.88	136.52	78.63	34.01	63.82	45.11	41.15	19.03	24.61	17.34
J	10	236.30	119.60	98.30	136.70	77.73	31.85	61.15	44.13	41.94	17.03	24.82	16.70
K	45	240.18	119.36	101.40	135.27	76.92	32.97	62.49	44.07	42.16	19.50	23.28	16.80
L	9	251.00	123.45	106.33	139.67	79.91	32.73	66.10	47.51	42.61	22.23	25.23	17.76

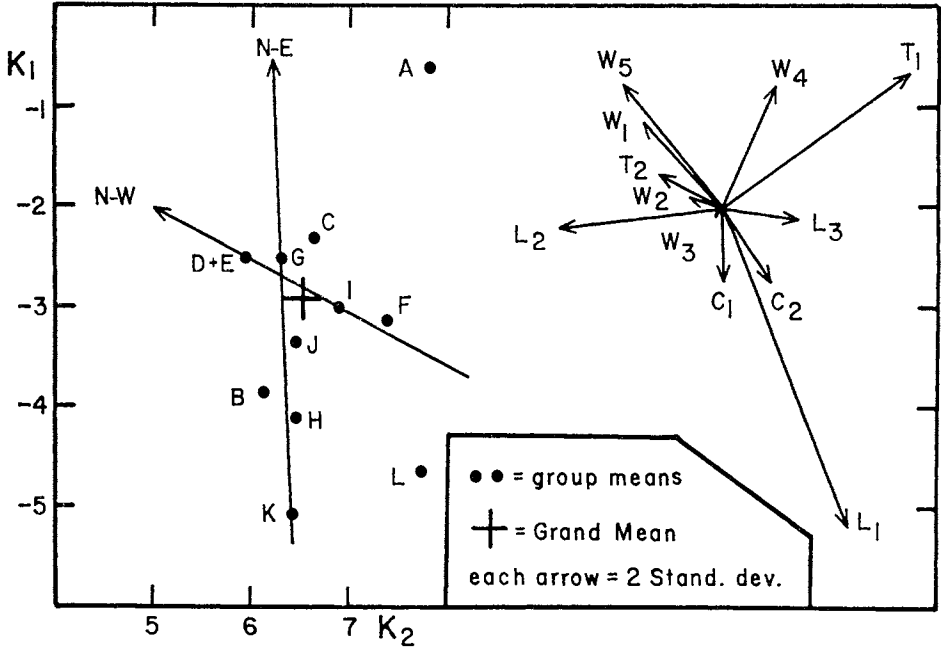


FIG. 10. Group dispersion (left) in discriminant functions K_1 and K_2 and variation of the skull dimensions (right); arrows N-E and N-W correspond to those of the map (fig. 1).

rows marked N-E and N-W correspond to those of the map (fig. 1) and help to evaluate the similarity of the pattern of biometrical dispersion to the pattern of geographical origin. Discrepancies come mostly from small samples; the most obvious one is the relative position of Alaska (B) and Vancouver Island (J) wolves. But this discrepancy is largely compensated for by the dispersion pattern of the third and fourth discriminant functions (fig. 12); here the average of the Alaska specimens diverges from the southern groups and the Vancouver Island individuals contrast sharply with all others. The first component of multivariate variance ($D_1 = 52\%$ of total), which corresponds closely to a northeastward direction, is markedly larger than the next one ($D_2 = 18\%$ of total). Geographical variation in skull dimensions would thus appear to be most pronounced northeastward. Ascertaining this last point would require more material however for the present samples are far from evenly dis-

tributed with respect to latitude and longitude.

As discussed previously, the full significance of discriminant scatter diagrams would not be explicit unless the coordinate axes of the original variables were projected thereupon. Sets of *vectors* (= arrows) bearing the coded designations of the skull dimensions indicate these projections in the discriminant graphs (figs. 10 and 12). Each vector shows the change in the discriminant functions that the corresponding dimension would generate if it varied independently. All skull dimensions are intercorrelated of course and these vectors must be considered jointly rather than separately. Northeastern wolves differ generally from southwestern ones (fig. 10) by a decrease in skull length (L_1) and in braincase development (C_1 and C_2) opposed to an increase in skull breadth (W_1, W_4 and W_5). Eastern individuals have longer upper carnassial teeth (T_1) and a shorter palate (L_2) than western ones. The wolves of

Vancouver Island (J) differ very much from the others (fig. 12) by six skull dimensions (greater T_1 and C_1 ; smaller T_2 , C_2 , W_4 and W_6) and very little with respect to the six others. The role of these

two groups of dimensions is contrasted not only by the directions but also by the lengths of their vectors. The Vancouver Island specimens are much further from the grand mean than the arrows (one

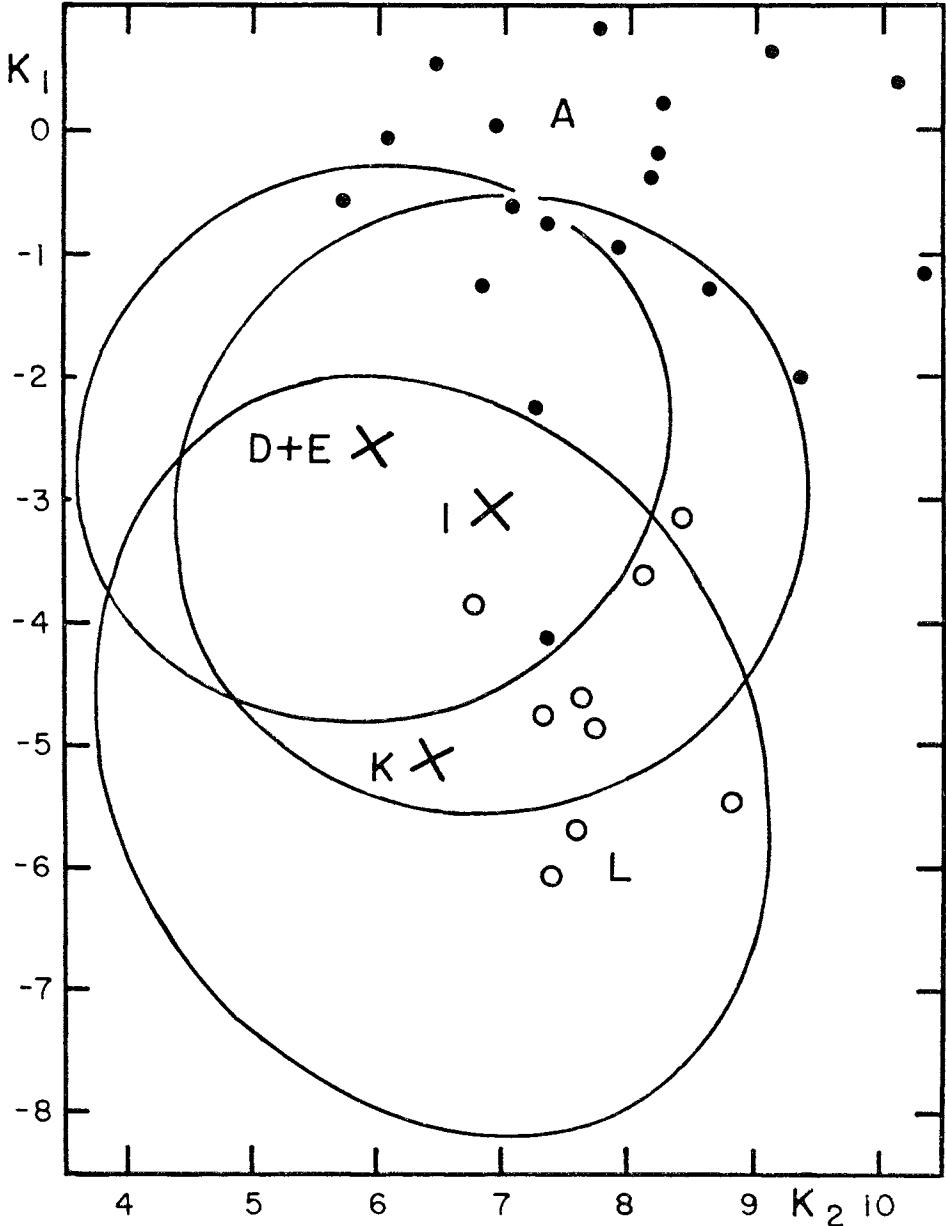


FIG. 11. Overlapping of groups in discriminant functions K_1 and K_2 ; dots represent individuals, mean crosses and 95% equal frequency ellipses represent samples; letters refer to closest symbols.

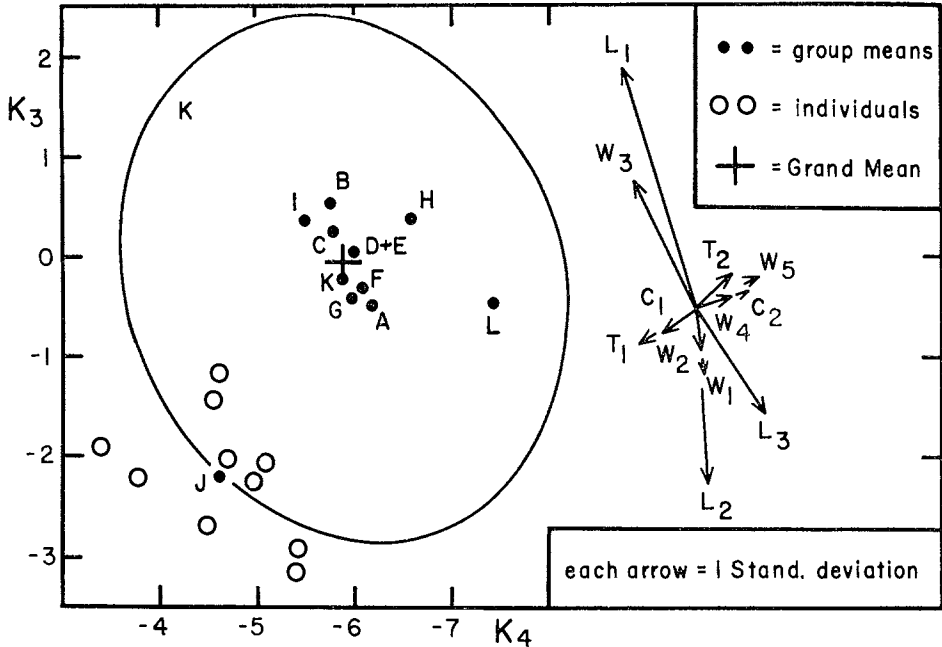


FIG. 12. Group dispersion (left) in discriminant functions K_3 and K_4 and variation of the skull dimensions (right); 95% equal frequency ellipse of group K.

standard deviation) of their discriminators are long.

The amount of overlapping of groups of specimens in discriminant graphs can be illustrated adequately with individual dots for small samples and equal-frequency ellipses for large samples. To evaluate overlapping exactly all discriminant dimensions should be considered jointly and the peripheral decrease in frequency within the samples should be taken into account. But for the sake of simplicity *biometrical overlapping* is defined here as the *percentage of common area between samples in a two-dimensional scatter diagram*. Following this definition the British Columbia wolves (K) overlap by approximately 50% (fig. 11) with those of Manitoba (I) and the Northwest Territories (D + E). The individuals of the Rocky Mountains (L) are intermediary and overlap largely both with those from British Columbia and those from Manitoba. The Arctic specimens (A) overlap by approximately 50% with those of the mainland. The lowermost point of sample

A represents a subadult female from Coronation Gulf (mainland) which should apparently have been grouped with mainland specimens and is relatively narrow-skulled. This individual excepted, the Arctic wolves do not overlap with those of the Rockies. Larger samples would probably do so to some extent however. The Vancouver Island specimens (J) overlap by approximately 50% with the others (fig. 12).

To sum up, the present material shows northeastern wolves to have shorter and relatively broader skulls than southwestern ones and eastern wolves to have a shorter palate and longer upper carnassial teeth than western ones. Such a generalization is only approximate however; the pattern of biometrical differences does not correspond exactly to the pattern of geographical origin and the first two discriminant functions account for only 70% of the variance between the groups. More variance is associated with a north-eastward direction than with any other one. The Vancouver Island wolves differ mark-

edly from the others with respect to six skull dimensions but very little with respect to the six others. The amount of biometrical overlapping and separation between all groups corresponds approximately to the degree of geographical separation by distance, insularity, etc.

INTERPRETATIONS AND CONCLUSIONS

The approximate correspondence of biometrical differences to geographical separation could readily be interpreted in terms of population genetics. Theoretically genetic differentiation within an incompletely panmictic population should increase with geographical distance and other factors of isolation (Li, 1955: 306-310). In the case of wolves, genetic differentiation should have been promoted by the immensity of their area of distribution and its subdivision by Pleistocene glaciers (Rand, 1954); but these influences should have been counteracted by the high mobility of such a large cursorial predator. The magnitude of biometrical differences between populations could be taken as indications of genetical differentiation.

The genetical interpretation of geographical variation is not the only possible one however. The specimens studied represent phenotypes and the latter have been exposed to highly varied environmental conditions. In fact environmental conditions vary throughout the area of distribution of the wolf. Arctic winters are gradually colder, darker and longer northward or northeastward for instance; and taiga is gradually replaced by tundra in a general northeastward direction. Such environmental differences might induce gradual phenotypical variation directly as well as genotypical variation indirectly. Direct effects of the environment on physiological processes and morphological characteristics are well known. Seasonal changes in temperature, illumination, humidity and food supply affect the reproductive cycles and migrations of various vertebrates. Molts and coat-color changes of weasels were controlled photoperiodi-

cally by Bissonnette and Bailey (1944), apparently through the pituitary gland. Prairie and tundra wolves could be particularly affected by seasonal periodicity as they cannot evade the climatic extremes of their habitat by seeking microclimates as small mammals do. The circumstances in which local populations live might induce modifications of growth processes, including those involved in skull development.

The growth of the various parts of the mammalian skull is neither perfectly synchronous nor isometric. The facial region reaches full development much later than the braincase (Baer, 1954). This was noted in Canidae at least as early as 1880 (Huxley). Because of this asynchronism and anisometry, temporary physiological disturbances might have very different effects according to their time of occurrence. Young northeastern wolves enter their first cold and dark arctic winter at an age (5 or 6 months) at which their facial growth potential is presumably still very high; their undersized face as adults is perhaps largely due to a metabolic and/or hormonal imbalance during this period of low temperature and illumination. Mice with the pituitary dwarf genotype differ from normal ones by "*their smaller size, their shorter snout, the short fleshy ears, and the relatively shorter tail*" (Gruneberg, 1952: 122). As for juvenile sheep with thyroid deficiencies, they grow skulls with normal braincase and teeth but with an underdeveloped facial region (Todd and Wharton, 1934); the descriptions of the latter would fit surprisingly well indeed the skulls of northeastern wolves with large teeth cramped in a short palate. The possible influence of low winter illumination on endocrine balance and growth is suggested by the effects of darkness on the teleost *Astyana: mexicanus* (Rasquin and Rosenbloom, 1954); darkness led to a loss of calcium from the bones and resulted in shorter and deeper-bodied fish than normal; skeletal changes were not repaired after return of the survivors to light.

Baer (1954) was led to postulate the existence of two major and relatively independent developmental processes in the postnatal mammalian skull; the expansion of the braincase on one hand, and the elongation of the face and the base of the skull on the other hand. It would be of great interest to see how much of variation in relative skull breadth in the present material could be ascribed to alterations of the equilibrium between two such growth processes. Very much of skull variation between the various breeds of domestic dogs (Stockard, 1941) could probably also be accounted for in this way. According to Scott's discussion (1957), the elongation of the mammalian skeleton is due to cartilage growth and promoted by pituitary growth hormones while its massiveness is due to subperiosteal growth and depends primarily on function and robustness factors. Although such a distinction seems most applicable to the postcranial skeleton, it appears to correspond also with trends of skull variation.

Whether or not the biometrical characteristics of wolves can be ascribed to specific growth processes however, the most important evolutionary problem is the extent to which such characters are genotypical or merely phenotypical. Bringing up and breeding captive animals from various localities under controlled conditions would be informative in this respect but such data are not available at present. Gradual phenotypical variation induced directly by environmental conditions is possibly present along with genotypical variation in the skull dimensions of wolves.

Taxonomical conclusions can be based on geographical variation only inasmuch as the latter is hereditary. How much of biometrical variation is inherited in the present material is unknown. Even if the biometrical differences were entirely genetical however, the overall pattern of variation between the populations sampled is more suggestive of an incompletely panmictic continuum than of distinct sub-specific units. Only one population seems

sharply different from its immediate neighbours, probably as a result of insular isolation, that of Vancouver Island. In fact, it resembles northern wolves more than those presently on the mainland of British Columbia. It is perhaps with northern populations that Vancouver Island had its most intense recent biotic contacts. It seems doubtful that such a small insular population would have a major long-term evolutionary significance however. Ascertaining the taxonomic relationships of northwestern Nearctic wolves would require more material from Vancouver Island, Alaska, Alberta and the regions in between. An adequate analysis of variation is of course desirable for the species as a whole or at least for all its North American representatives. There are most likely far too many sub-specific designations in use (Miller and Kellog, 1955).

As far as multivariate statistical techniques are concerned, their application to the present problem has probably already made their value apparent to many readers. One last comment is made in conclusion. Discriminant scatter diagrams of contemporaneous groups of organisms are closely analogous to what sections of phylogenetic trees at given time levels should be like. Discriminatory analysis may well prove an ideal tool in phylogenetic studies. Multivariate statistical techniques may make eventually possible the exact calculation of horizontal slices of the tree of Evolution.

SUMMARY

An analysis is made of pelage and skull variation in five hundred wolf specimens from northwestern Nearctic localities. Pale wolves are relatively more frequent toward the tundra. Males are 4% larger than females in linear skull dimensions. Northeastern specimens are shorter- but relatively broader-skulled than southwestern ones. Multivariate biometrical differences between populations appear approximately proportional to geographical separation. This may express genetic

differentiation through imperfect panmixia. But direct environmental influences may be involved. Formal taxonomic conclusions are postponed but it seems probable that far too many sub-specific designations are now in use. Multivariate statistical techniques are very efficient for evolutionary comparisons with respect to complexes of characters.

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APPENDIX

Multivariate Statistical Formulae³

Value of *i*th character measured on an individual specimen: X_i

Set of values of the *p* characters measured on an individual specimen: $X = (X_1, \dots, X_p)$

Mean of a sample: $\bar{X} = (\bar{X}_1, \dots, \bar{X}_p)$

Variance of *i*th character within a sample: W_{ii}

Covariance of *i*th and *j*th characters within a sample: $W_{ij} = W_{ji}$

Variance-covariance matrix of a sample:

$$W = \begin{pmatrix} W_{11} & \dots & W_{1p} \\ \dots & \dots & \dots \\ W_{p1} & \dots & W_{pp} \end{pmatrix}$$

³ A more detailed note on the calculation of discriminant functions is being prepared by S. W. Nash and P. Jolicoeur.

Equation of 95% equal frequency ellipse:
 $(X - \bar{X}) W^{-1} (X - \bar{X})' = 5.99$

$X' = X$ transposed; W^{-1} = inverse matrix of W ; only the elements of X and W corresponding to the two characters are included here in X and W ; 5.99 = 95% chi-square with 2 degrees of freedom; see Defrise-Gussenhoven (1955).

Covariance matrix of sample means around their grand mean:

$$B = \begin{pmatrix} B_{11} & \dots & B_{1p} \\ \dots & \dots & \dots \\ B_{p1} & \dots & B_{pp} \end{pmatrix}$$

Matrix of the coefficients K_{ij} of the discriminant functions:

$$K = \begin{pmatrix} K_{11} & \dots & K_{1p} \\ \dots & \dots & \dots \\ K_{p1} & \dots & K_{pp} \end{pmatrix}$$

Matrix of the components D_i of between-group variance corresponding to the discriminant functions:

$$D = \begin{pmatrix} D_1 & \dots & 0 \\ \dots & \dots & \dots \\ 0 & \dots & D_p \end{pmatrix}$$

Matrix equation yielding K and D : $KB = DKW$

Coordinate of any point $X = (X_1, \dots, X_p)$ upon the *i*th discriminant axis: $K_i = K_{i1}X_1 + \dots + K_{ip}X_p$

Within-group variances and covariances of the discriminant functions: KWK'

$K' = K$ transposed

$$KWK' = I = \begin{pmatrix} 1 & \dots & 0 \\ \dots & \dots & \dots \\ 0 & \dots & 1 \end{pmatrix} \text{ for the pooled}$$

within-group covariance matrix.

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