

**CRANIOMETRIC STUDY OF ALLOMETRY, ADAPTATION
AND HYBRIDISM OF RED DEER (*CERVUS ELAPHUS
SCOTICUS*, L.) AND WAPITI (*C. E. NELSONI*, BAILEY)
IN FIORDLAND, NEW ZEALAND**

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SUMMARY: Red deer and wapiti are sympatric in part of Fiordland National Park. Caughley (1971a), on the basis of Fisher's Discriminant Function of 22 skull measurements divided the mixed population of the eastern catchments into 38% red deer, 20% hybrids and 42% wapiti.

The same skulls were re-examined with 15 measurements, and re-evaluated against red deer from South Westland, wapiti from Montana and Canada, and further samples from the mixed population area. Separation was based on a polythetic agglomerative cluster analysis, and by comparing groups so shown with those indicated by step-wise 3-group discriminant analysis, 2-group discriminant analysis, and matching of length of skulls. The sample was concluded to comprise only 8% red deer, 52% hybrids and 40% wapiti. The use of North American specimens as controls was dismissed as invalid because they are larger and exhibit different patterns of growth to animals in Fiordland.

The Wapiti Area population is in poor physical condition. The wapiti show, compared with American conspecifics, proportionally high priority for growth of the neurocranium and maxillary region, and slower growth of the viscerocranium. Non-linear changes of most of the cranial bones, compared with length, show that growth occurs in well defined stanzas whereby from three to five years it is concentrated on length characters, after which the skull proportionally broadens. These changes of shape, associated with increase in size throughout life, blur the fidelity of discriminant analysis.

Hybridism in this population is attributed principally to dominant wapiti bulls mating with red deer, hybrid and wapiti females and thereby absorbing most of the red deer into a hybrid gene pool. The hybrid group is morphologically bimodal ("red-like hybrid" and "wapiti-like hybrid") and the range of forms is virtually continuous between the two parent species. Dominance of wapiti is probably reinforced by their breeding season being about two weeks earlier than that of red deer. Grouping of these forms by cranial analysis gives diagnoses which are highly correlated with morphological descriptions of type based on pelage, size and other external characteristics. Consistent with this result, culling of red deer and hybrids by experienced hunters is highly selective.

INTRODUCTION

European red deer (*C. elaphus scoticus*) and North American wapiti (*C. e. nelsoni*) have been found to breed and raise fully fertile offspring in most circumstances where cross-mating has been attempted (Whitehead, 1950). In the Fiordland region of New Zealand (Fig. 1), west of Lake Te Anau, where wapiti were liberated in 1905 (Donne, 1924) and into which red deer had dispersed by 1940 (Tustin, 1970, unpubl. report), hybrids were recorded within a decade of merging of the two varieties (Millais, 1928, Banwell, 1966). Subsequently, attempts were made to cull these from the mixed population (Ban-

well, 1966). When larger numbers of hunters began to visit the area after World War 2, concern began to mount at the frequency with which supposed hybrids were observed and after Murie (in Poole, 1951; also Murie, 1966) had confirmed from a study of skins and upper canine teeth that "hybridism can be accepted as fact", it began to appear as if introgressive hybridisation would eventually absorb the wapiti into a mixed population, and so destroy their status as the only free-living pure wapiti in the southern hemisphere.

Confident identification was acknowledged to be difficult. Murie did not identify boundaries between

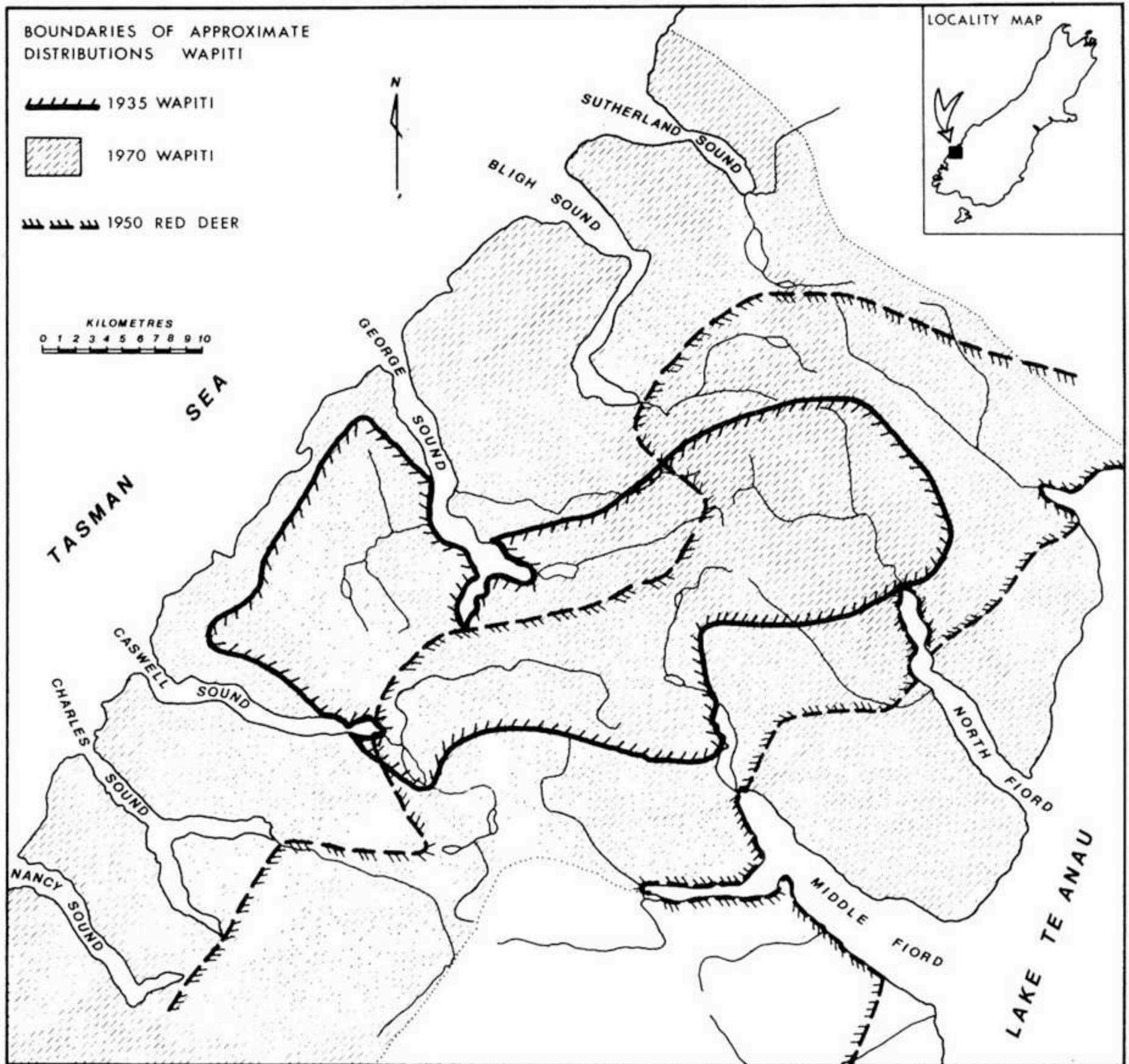


FIGURE 1. Map of the area in Fiordland National Park which is occupied by wapiti, with synopsis of information on history of spread of red deer and wapiti (Tustin, unpubl. report).

the pure animals and hybrids. A party of hunters collected a sample from the Large Burn in 1961 (Harrison, 1961). They recorded diagnoses of "type" from external examination, and the skulls were sent for an opinion on the question of hybridism to the Museum of Vertebrate Zoology, University of Cali-

fornia, Berkeley. There, McCullough (1969) concluded that "much of the population shows (unspecified) intermediate characteristics . . . They are genetically a single species" and that therefore "the specific name *elaphus*, Linnaeus, 1758 has priority over *canadensis*, Erxleben, 1777".

Caughley (1971a) and Anderson (1971) have published recent analyses. Caughley's, the most rigorous, and based on analysis of skull measurements, applied Fisher's Discriminant Function of 22 measurements of 50 adult female red deer and 30 adult female wapiti to 177 adult female skulls collected from the Wapiti Area of Fiordland. That analysis yielded a polymodal distribution which ranged between the upper limit of the red deer controls and the lower limit of wapiti controls (see reproduction, Fig. 2). Caughley accordingly split them subjectively into 38% red deer, 20% hybrids and 42% wapiti. He noted that this treatment placed the only available authenticated hybrid specimen into the putative red deer group. Neither transformation of the measurements into logarithms or ratios effected any improvement. To clarify these problems, the skulls collected by Caughley, supplemented by further collections from the Fiordland area, South Westland, Montana, and the Canadian Museum, have been re-examined.

MATERIAL

Seven samples of female skulls of three years of age or greater (fully erupted teeth) are considered.

1. Caughley Wapiti Area Sample. As described by Caughley (1971a), this sample was shot without regard to type during the austral summer 1966-67 in the mixed population area. Caughley's analyses included 177 specimens. In this paper, 189 specimens are considered. Caughley had rejected the remaining 12 because of damage to posterior

- parts of the skull, which were a focus of his measurements.
- 2. Caughley Grebe-Monowai sample. Fifty specimens were collected by Caughley as red deer controls for his analyses. Of these, five were rejected because they had been dissected for an unrelated study,
- 3. North American wapiti. This comprises 43 adult female skulls in the Montana State Fish and Game Department collection at Bozeman (principally from Yellowstone National Park) and 20 skulls collected from Canadian National Parks and stored at the Canadian National Museum, Ottawa.
- 4. 1970 Wapiti Area Sample. One hundred and two samples were collected during a selective culling operation in the south-west portion of the Wapiti Area. They were shot from a helicopter (Challies, 1974b), the crew of which included an experienced observer who directed the rifleman to avoid shooting wapiti-like animals.
- 5. 1973 Wapiti Area Sample. Two hundred and eighty-one skulls were collected from selective culling by helicopter over the entire Wapiti Area in February-March 1973. Animals judged to be wapiti or the "better class of hybrids" (J. H. McKenzie, pers. comm.), were not shot.
- 6. N.Z.D.A. Berkeley Museum Sample. Of the sample collected in the Large Burn and elsewhere, seven females were identified well enough to match skulls with field notes on their pelage and probable type made by the field party leader (A. R. Harrison, pers. comm.). A red deer in the collection was identified as coming from the Woodrow Burn. Notes on these specimens are included here as evidence of the correlation between external and skull characteristics.
- 7. Twenty one red deer skulls from the Haast-Arawata area, South Westland, which were selected as relatively large specimens of red deer from a commercial venison harvest (C. N. Challies, pers. comm.).

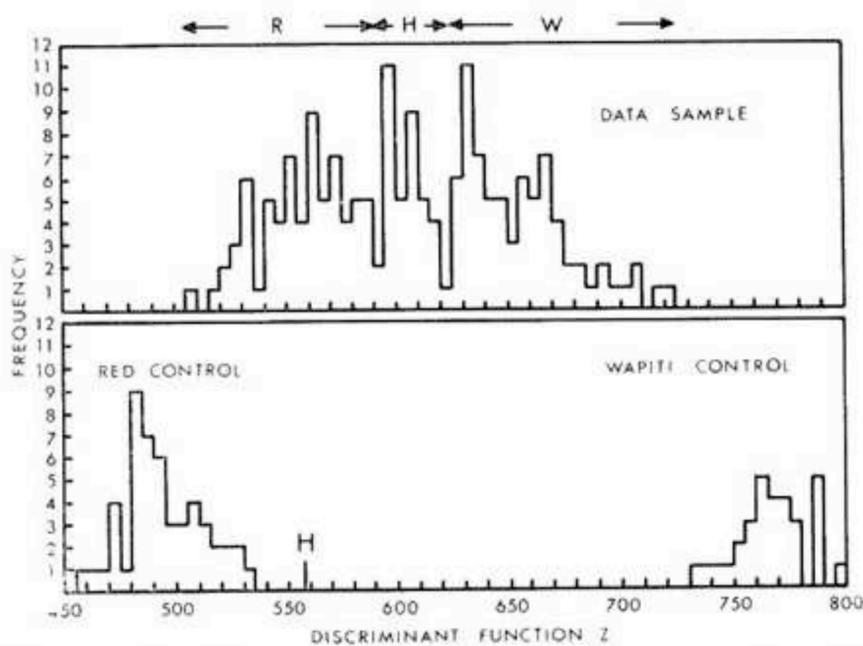


FIGURE 2. Comparison of Wapiti Area sample with Grebe-Monowai red and North American wapiti controls by 2-group analysis. Redrawn from Caughley 1971a, Fig. 4.

MEASUREMENTS

The specimens were aged from counts of cementum layers in the first molar tooth (Mitchell, 1963, Douglas, 1970). An etching and staining technique (Pekelharing, 1970) was used where necessary to reveal annuli. Measurements taken from the skulls are depicted in Fig. 3. In selecting them, we were guided by characters used by Mystkowska (1966) and Caughley (1971a), and, finally, by visual inspection of samples 1 and 2 which were spread out in rows to form a 2-dimensional array of age against

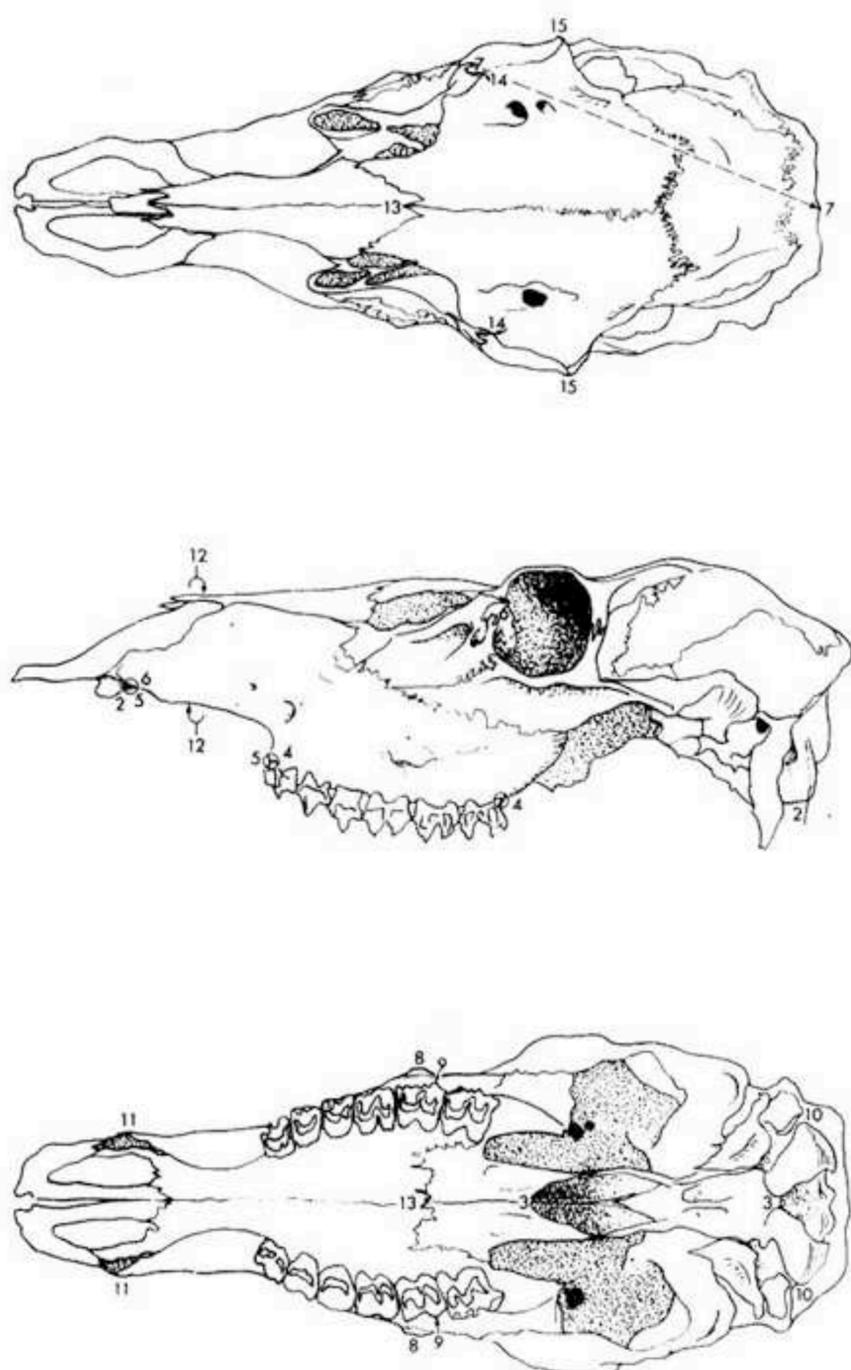


FIGURE 3. Three views of a Fiordland female wapiti skull showing the measurements used in this study.

size. Within the rows, wapiti (largest) and red deer (smallest) were distinctively different in size and form, and characters which appeared to consistently portray these differences were chosen. Measurements of, or including, the premaxillae were excluded because a high proportion of these were damaged or lost from the Fiordland collection. Linear measures were made with vernier calipers (0.1 mm) or tape (mm), uniformly to three significant figures. They are presented in centimetres. Equivalent measurements made by Caughley (1971a) and Mystkowska (1966) are indicated in the following list.

1. Cranial cavity. The volume of the cranial cavity (Mystkowska, 1966) was measured to the nearest 5 ml by plugging the foramina with modelling

clay and pouring sieved 0.4 cm water-rounded gravel (N.Z. specimens) or soya bean seeds (North American specimens) through the foramen magnum, shaking down, and measuring the volume in a graduated measuring cylinder.

2. Basal length. Ventral ridge of the occipital condyles to the posterior edge of the canine alveolus.
3. Ventral neurocranium. Median ventral lip of the foramen magnum to the posterior median edge of the palate (Mystkowska No. 10).
4. Maxillary tooth row length. Anterior rim of P2 alveolus to posterior rim of M3 alveolus (Caughley No. 1; approx. Mystkowska No. 15).
5. Margo-adentalis. Posterior rim of canine alveolus to anterior rim of P2 alveolus (approx. Mystkowska No. 14).
6. Lateral viscerocranium. Tip of pre-orbital process to posterior rim of canine alveolus (Caughley No. 19).
7. Lateral neurocranium. Median point of lambdoidal ridge to tip of preorbital process (approx. Mystkowska No. 5).
8. Facial tubers. Width of facial part of skull, across facial tubers (Mystkowska No. 19).
9. Maxillary tooth row width. Width from left to right buccal alveolus rim at second cusp of M2.
10. Occipital condyle width. Maximum breadth across the condyles (Mystkowska No. 26).
11. Canine width. Left to right buccal rims of canine alveoli (approx. Mystkowska No. 16).
12. Nasal cavity circumference. Around the mid-point of the adental region between C and P2.
13. Nasal cavity depth. Mid-dorsal fronto-nasal junction to mid-ventral palato-maxillary junction (approx. Mystkowska No. 28).
14. Anterior orbital width. Between fronto-lachrymal notches (caliper knife edge held perpendicular to long axis of the skull) (approx. Mystkowska No. 22).
15. Posterior orbital width. Maximum breadth across the zygomatic arch (Mystkowska No. 21).

ANALYTICAL METHODS

Background

Two-group discriminant analyses, using Grebe-Monowai red deer and North American wapiti control samples yielded a similar pattern to that found by Caughley (1971a, shown here as Fig. 2). But it was found in many cases by matching the basal length of these skulls with the calculated scores, that typical red deer scores had been assigned to specimens which exceeded the known size of the variety in New Zealand. Eighty three percent of the

North American wapiti skulls were larger than the limit of Fiordland deer, and, as shown by Caughley, their z-scores did not overlap. It therefore seemed prudent to work on the assumption that because of environmental and nutritional factors, ecotypic variation of the Wapiti Area population might invalidate use as discriminant controls of wapiti and red deer samples chosen from any other area. Changes of size and shape associated with age were also suspected to confound the analyses.

Agglomerative Clustering

Accordingly, age classes three, four, five, six, seven and ≥ eight years of all samples (Nos. 1, 4 and 5) which could be presumed to represent the range of physical condition of the hybridising population, and the Grebe-Monowai red deer sample (hereafter called the "Fiordland sample"), were classified by agglomerative clustering. Each of the 15 characters were given equal weight by dividing each measurement by its corresponding median. Medianised data were used to calculate a matrix of Euclidean distances (Orloci, 1972) derived by comparison of each specimen with every other:

$$d_{ij} = \sqrt{\sum_{k=1}^c \left(\frac{x_{ik} - x_{jk}}{X_k}\right)^2}$$

where d_{ij} = distance between the i th and j th animals

c = the number of characters

X_k = median value of character k

x_{ik} and x_{jk} are the values of character k of the i th and j th animals.

Groups were then defined by a polythetic agglomerative clustering process (Gower, 1967). Three major groups defined by this procedure were interpreted as putative red deer, hybrids and wapiti.

Step-wise 3-group discriminant analysis

The three groups defined by agglomerative clustering were then analysed with BMD programme 07M (in Dixon, Editor, 1973) to investigate the congruence of group membership probabilities defined by the two methods, and to determine the order of importance of each character in the discrimination process in each age class.

Two-group discriminant analysis

The putative Fiordland red deer and wapiti which were congruently defined by agglomerative clustering and 3-group discriminant analysis (above), were

used as controls for computation of 2-group discriminant co-efficients (BMD 04M, Dixon, 1973) of the 15 characters, and 14 of the characters each divided by character 2 (ratioed data). For the run reported later in detail, age classes 3-7 inclusive were combined. The derived coefficients were then applied to all samples of all age classes.

Size analysis

The frequency distributions of sizes of the 15 characters, in 36 classes (the same number of classes used by Caughley for his most successful partitioning by Fisher's discriminant analysis) which span the range from the smallest Grebe-Monowai red deer to the largest North American wapiti, were calculated for the age groups 3-4, and ≥ 5 years. Results for basal length are given in this report.

Computer facilities

The initial 2-group analyses were run on an ICL 1902 package programme under the tutelage of T. P. Whiston of Forest Research Institute, Rotorua. All other analyses were run on the Burroughs B6718 computer at the University of Canterbury, using programmes written by the authors, except where specified.

TABLE 1. Summary of Classification by agglomerative clustering.

		3	4	5	6-7	8	Totals	%
Caughley Sample	R	3	1	7	1	3	15	7.98
	HR		6	6	9	13	(32)	
		12					97	51.60
	HW		13	4	13	21	(53)	
	W	10	10	12	17	27	76	40.43
	?	0	0	1	0	0	1	
TOTALS		25	30	30	40	64	189	
1970 cull Caswell/Charles)	R	5	4	5	11	1	26	25.74
	HR		6	2	11	25	(44)	
		5					71	70.30
	HW		1	9	4	8	(22)	
	W	1	0	1	0	2	4	3.96
	?	0	0	0	1	0	1	
TOTALS		11	11	17	27	36	102	
1973 cull	R	9	19	11	25	17	81	29.35
	HR		11	12	25	52	(100)	
		19					168	60.87
	HW		4	10	15	20	(49)	
	W	8	4	5	5	5	27	9.78
	?	2	0	1	2	0	5	
TOTALS		38	38	39	72	94	281	
							572	

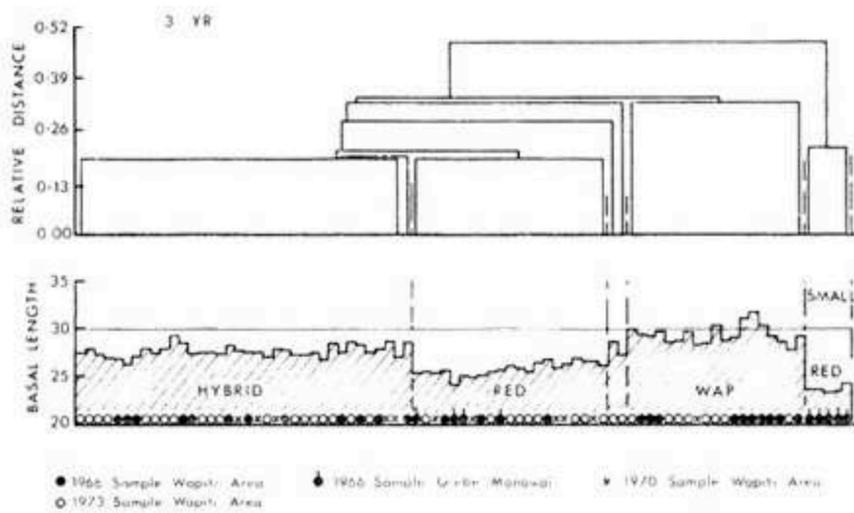


FIGURE 4. Dendrogram of 3-year old Fiordland animals, and bar diagram of basal length of specimens of the four samples in the interpreted groups. Known red deer split into two groups, one of these comprising five very small animals. The other red deer form a consistent group of small animals. Hybrids are intermediate in length between the red deer and wapiti.

RESULTS

Agglomerative Clustering

Analyses of the Fiordland sample in five age classes (3, 4, 5, 6-7, ≥ 8 years) indicated three identifiable patterns of splitting into the three major putative groups. The three year old cluster split wapiti from red deer and hybrids, and placed all hybrids into a single amorphous group; the 4, 5 and 6-7 year analyses partitioned the hybrids and red deer from wapiti, and then partitioned the hybrids into two forms, which we call "red-like hybrids" and "wapiti-like hybrids"; that for the ≥ 8 year old class partitioned wapiti and "wapiti-like hybrids" from red deer and "red-like hybrids", and subsequently split each of these groups. These patterns are accordingly described in detail by reference to dendrograms for only three age classes: 3, 4, and ≥ 8 years. The summary for all age classes is given in Table 1.

Three year pattern (Fig. 4)

The first vertical partition of specimens in the dendrogram separated five small known red deer (histograms below dendrogram show basal length of skulls); the second separated a group of large animals, and the third segregated a group of small animals which included four known red deer from a larger group of intermediate-sized animals. The consistency of association of the known red deer (except for the five very small ones) into one block,

along with other small animals, leaves little doubt that these are red deer. Likewise, the grouping of large animals identified the putative wapiti group. The intermediate-sized animals on the left of the dendrogram are accordingly interpreted to be hybrids.

Partitioning of the known red deer into two groups suggests there is a greater difference between 3 year old Grebe-Monowai red deer and those from the Wapiti Area, than there is between young wapiti and red deer in the mixed population area.

Four year old pattern (Fig. 5)

At four years, 14 large skulls (putative wapiti) are partitioned first; then a group containing all known red deer is partitioned from animals of intermediate size. Unlike the three year olds however, the intermediate group splits into two, one of which contains skulls 27-29 cm basal length, and the other skulls of 28-31 cm basal length.

On the basis of size and the different proportions obtained by random and selective sampling, they are interpreted as distinctive "red-like hybrids" and "wapiti-like hybrids". This interpretation is discussed in greater detail later.

Eight years and older pattern (Fig. 6)

The first separation in this group distinguished three large skulls (over 33 cm) from all others. The second distinguished wapiti and "wapiti-like hybrids" (right side of Fig. 6) from red deer and "red-like hybrids". These two major groups then split at small increments of similarity into wapiti (and four doubt-

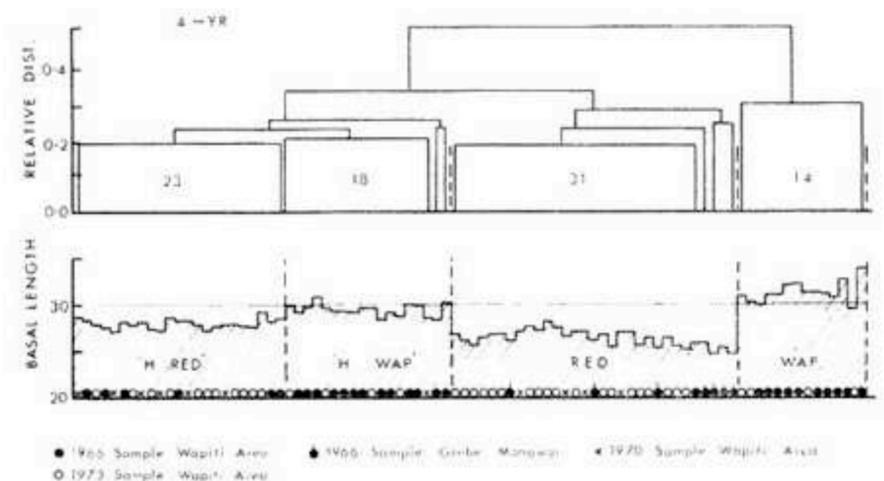


FIGURE 5. Dendrogram and bar diagram of skull lengths for 4-year old specimens. This pattern, splitting reds, wapiti and two groups of hybrids was found also among 5-7 year old animals. On the criterion of basal length, the smaller hybrids are described as "red-like", the longer as "wapiti-like". Known reds serve as markers of the red deer group.

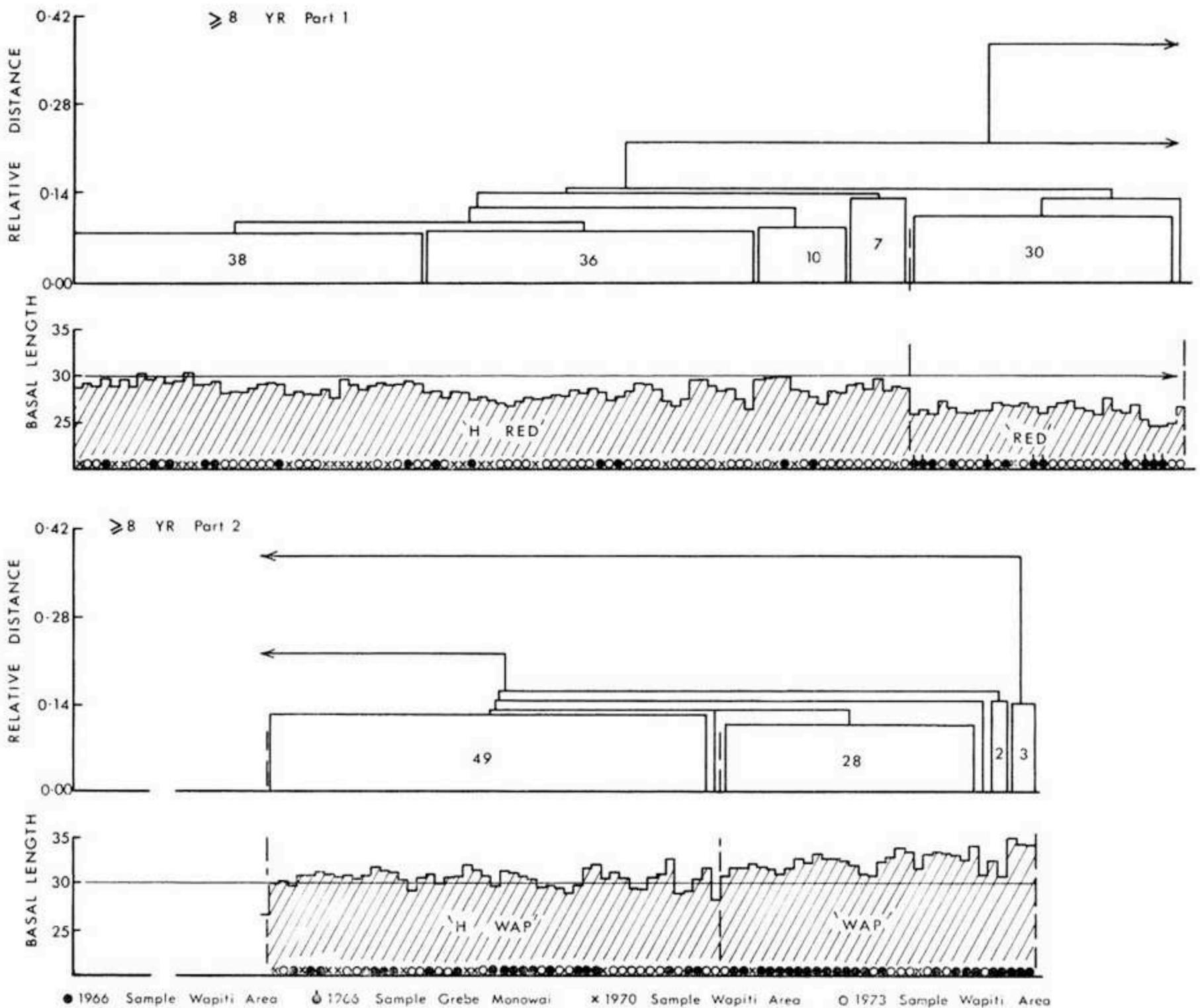


FIGURE 6. Dendrogram and bar diagram of skull lengths for animals over seven years. The three large specimens are discordant. Otherwise, the split is into wapiti and "wapiti-like" hybrids on the right, and red and "red-like" hybrids on the left. Known reds serve as markers of the red deer group.

ful cases) at 30-34 cm and "wapiti-like hybrids" at 28-32 cm, and red deer (25-27 cm - including all the known red deer) and "red-like hybrids" ranging from 27-30 cm.

Congruence of 3-Group Analysis and Agglomerative Clustering

Four hundred and sixty specimens from the Wapiti Area which were assigned to the three major taxon-

omic groups by clustering, (i.e., 10 doubtful specimens were rejected) were subjected to step-wise three-group discriminant analysis (BMD 07M) to: test congruence of classification; select only congruently assigned red and wapiti skulls from the Wapiti Area for determination of 2-group coefficients; and test the relative discriminatory importance of the characters.

Of these, 97 224 and 139 respectively were assigned

by clustering to red deer, hybrids and wapiti, whereas 3-group analysis gave corresponding maximum group membership probabilities as 103 red deer, 219 hybrids, and 138 wapiti (Table 2). Ninety seven per cent remained in the same groups by both classifications. If the 10 rejected doubtful specimens are included for consideration, the overall risk of misclassification therefore appears to be about 5.3%. No assignment was so incongruent with 3-group analysis that any specimen was reassigned from one variety to the other. These results indicate that the hybrid group, as deduced from agglomerative clustering, is truly intermediate in size and form between the parent species.

On average, 15% (68) of the classifications were incongruent when only the most important discriminating character was included in analyses (column 12, Table 3). As further characters were included, changes of group membership diminished in frequency, until about eight coefficients were included. Inclusion of the remaining seven effected only five fewer mis-matchings.

Therefore, in any age class, about eight characters appear to be adequate to discriminate the groups. But, as shown in columns 2-6 of Table 3, different characters appear among the first eight for each analysis, and their order of appearance is erratic.

TABLE 2. *Test of congruence of classification as red deer, hybrids and wapiti by 3 group step-up discriminant functions, against agglomerative clustering.*

Age Group	Assignment	R	H	W	Totals
3	R	12	0	0	12
	H	1	29	1	31
	W	0	1	17	18
4	R	21	0	0	21
	H	0	34	1	35
	W	0	0	14	14
5	R	16	0	0	16
	H	1	30	0	31
	W	0	0	17	17
6-7	R	28	0	0	28
	H	3	59	0	62
	W	0	0	22	22
8	R	18	2	0	20
	H	3	62	0	65
	W	0	2	66	68
All ages	R	95	2	0	97
	H	8	214	2	224
	W	0	3	136	139
Totals		103	219	138	460

Note: Cluster separation downwards; step-wise 3-group classes at head of columns.

TABLE 3. *Summary of classification by step-wise 3 group analysis of assignments from agglomerative clustering showing order of inclusion of character by age classes, and corresponding improvement in congruency.*

No. of characters included	Character No. included					Incongruent classif.					Total incongruent classifications	Reduction with extra character
	3	4	5	6-7	8	3	4	5	6-7	8		
1	11	2	12	2	7	7	7	10	13	31	68	
2	6	11	1	14	14	6	2	4	10	24	46	22
3	5	10	9	4	2	7	4	3	8	20	42	4
4	8	5	7	1	1	6	3	4	5	14	32	10
5	12	8	5	15	3	5	1	3	5	14	27	5
6	10	1	4	11	5	3	2	2	4	12	23	4
7	1	13	11	8	11	3	1	2	4	12	22	1
8	4	3	10	6	15	2	1	2	3	12	20	2
9	13	9	3	5	8	2	2	2	3	12	21	-1
10	7	15	2	13	6	2	2	2	3	11	20	1
11	3	7	14	3	4	4	2	2	3	5	16	4
12	2	14	13	9	3	1	3	2	3	8	17	-1
13	14	6	6	7	12	1	3	1	3	9	17	0
14	9	4	15	12	10	2	2	1	3	6	14	3
15	15	12	8	10	9	3	1	1	3	7	15	1

TABLE 4. Average sizes of characters of putative Fiordland red deer and wapiti as congruently defined by clustering and 3-group discriminant analysis, and size and ratio 2-group coefficients derived from 3-7 year old samples.

No.	Name	Units	SIZE			RATIOS		
			Group means P. red	P. wap	Coefficients	Group means P. red	P. wap	Coefficients
1	Cran. cav.	ml	311	393	-0.00288	11.74	12.36	-0.00639
2	Bas. length	cm	26.5	31.8	0.07102	—	—	—
3	Vent. neur.	cm	10.4	12.1	-0.08971	0.39	0.38	0.05893
4	Tooth r.l.	cm	10.0	12.0	-0.18955	0.37	0.38	0.19068
5	Marg. ad.	cm	5.4	6.2	-0.38380	0.20	0.19	0.36590
6	Lat. visc.	cm	13.6	16.6	0.04747	0.51	0.52	-0.29231
7	Lat. neur.	cm	15.7	18.1	-0.00120	0.59	0.57	0.36299
8	Fac. tuber	cm	10.9	12.2	-0.05797	0.41	0.38	0.27594
9	M2 width	cm	9.9	11.2	0.03945	0.37	0.35	0.22720
10	Occ. condyle	cm	6.0	7.3	-0.04730	0.23	0.23	-0.24310
11	Can. width	cm	4.9	6.0	-0.24645	0.18	0.19	-0.75850
12	Nas. cav. c	cm	16.4	19.7	0.04759	0.62	0.62	-0.09311
13	Nas. cav. d	cm	6.7	7.9	-0.01927	0.25	0.25	-0.00526
14	Preorb. w.	cm	9.7	11.6	-0.06113	0.37	0.36	-0.37212
15	Postorb. w.	cm	14.2	16.2	-0.03039	0.54	0.51	0.36872

Maxillary tooth row width (char. 9) is the only character which was excluded from the first eight in all five analyses. Cranial cavity (1), canine width (11), margo adentalis (5), basal length (2), maxillary tooth row length (4), facial tubers (8), and occipital condyle width (10) were each included in the first eight in three or more of the five analyses.

Two-group Discriminant Analysis of the Wapiti Area Samples

Initially, specimens from the Wapiti Area which were congruently identified as red deer or wapiti were investigated by 2-group discriminant analysis (BMD 04M) in the age classes 3, 4, 5, 6-7, 8-9 and ≥ 10 years. As with 3-group analysis, relative values of the coefficients were found to be erratic. Therefore, all age groups were pooled to determine general coefficients for raw size and ratios. This treatment was found to yield coefficients which effectively separated the young and aged classes, but gave poor separation for 4-7 years. Accordingly, use of 3-7 year samples (86 red, 39 wapiti) was examined, and found to give effective separation for all age classes. The coefficients (Table 4) were then used to calculate the discriminant z-scores of all available samples.

Results for Grebe-Monowai red deer, Caughley's 1966 Wapiti Area sample, South Westland red deer and the North American wapiti are displayed as a set of telescoped scattergrams in Fig. 7. Numerals on

these scattergrams show the last digit of basal length in cm, from 3 (=23 cm) in the top left, to 7 (=37 cm) towards the bottom right. Raw z-scores are on the abscissae and ratios are on the ordinates.

These scattergrams show a direct positive correlation between z-scores derived from raw sizes and ratios (note that size scores are negative). Each shows an almost continuous series from putative and known red deer in the top left (of 23-28 cm), through hybrids (encircled symbols, of 26-33 cm), Fiordland wapiti (of 29-34 cm), and North American wapiti (of 33-37 cm).

The positions of the forms drift perceptibly towards the bottom right of the scattergrams with advancing age. For example, at 3 years, putative wapiti ranged between 29-33 cm and the mean raw z-score is approximately -6.1. At four years, sizes range from 30-34 cm, and the mean score is -6.4. By ten years, the corresponding figures are 30-34 cm and -6.6. Similarly, the mean scores for putative hybrids drift from -5.5 to -6.1 and those of putative red deer drift from -5.0 to -5.3.

The positions of South Westland red deer (box symbols) warrant particular notice on the scattergrams. At 3-4 years, they (with one exception) matched Grebe-Monowai red deer and Fiordland putative red deer in both basal length and z-scores. The exception was scored in the hybrid range. From 5 years, only one South Westland specimen was scored in the range of Fiordland red deer; nine were

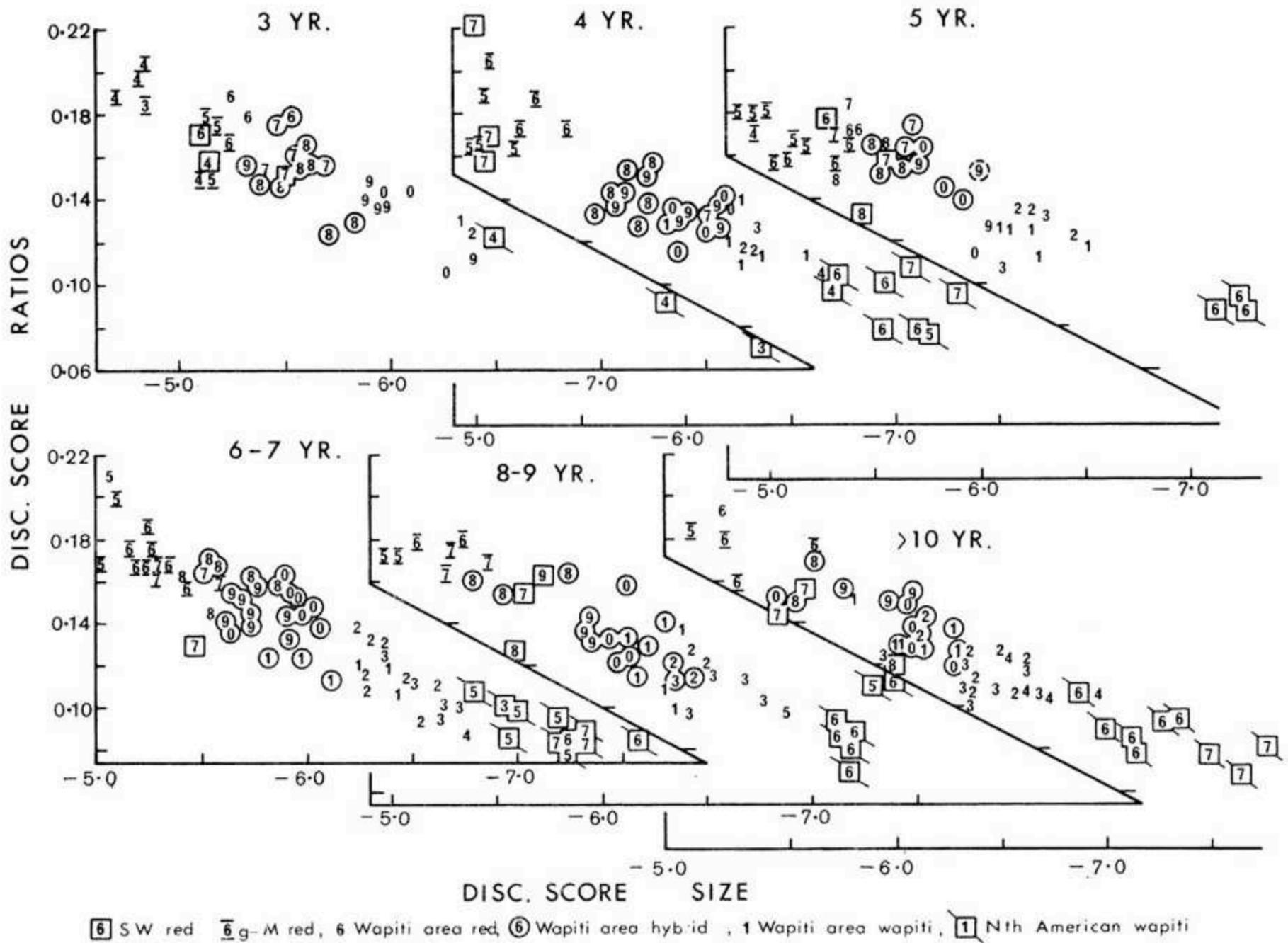


FIGURE 7. Telescoped scattergrams of the correlation between raw size z-scores (abscissae) and ratio z-scores (ordinates) for six defined age classes sampled in the Wapiti Area, South Westland and North America. The symbols show the origin of each specimen (see legend) and the last digit of its basal length in cm. Identity of Fiordland samples is derived from the agglomerative cluster analyses.

scored in the range of hybrids, and in most of these there is a tendency to score within the range of wapiti on the ratio axis and hybrids on the size axis. This suggests that the larger South Westland red deer are more "wapiti-like" in form than are the majority of Fiordland red deer.

Size Frequency Distributions

The distribution of size classes of all samples, in 36 classes (Fig. 8), shows the overall relationships between basal length and classification based on

agglomerative clustering, and permits easy comparison with the conclusions given by Caughley (1971a) (Fig. 2). When divided into age classes 3-4 and ≥ 5 years, putative Fiordland red deer match known red deer in classes 4 to 14, whereas putative wapiti, with 12 exceptions, are smaller than their American conspecifics. However, since the South Westland specimens are a biased sample of large red deer it is extremely unlikely that more than about 14 of Caughley's sample match the true range of Wapiti Area red deer. If only those which were congruently

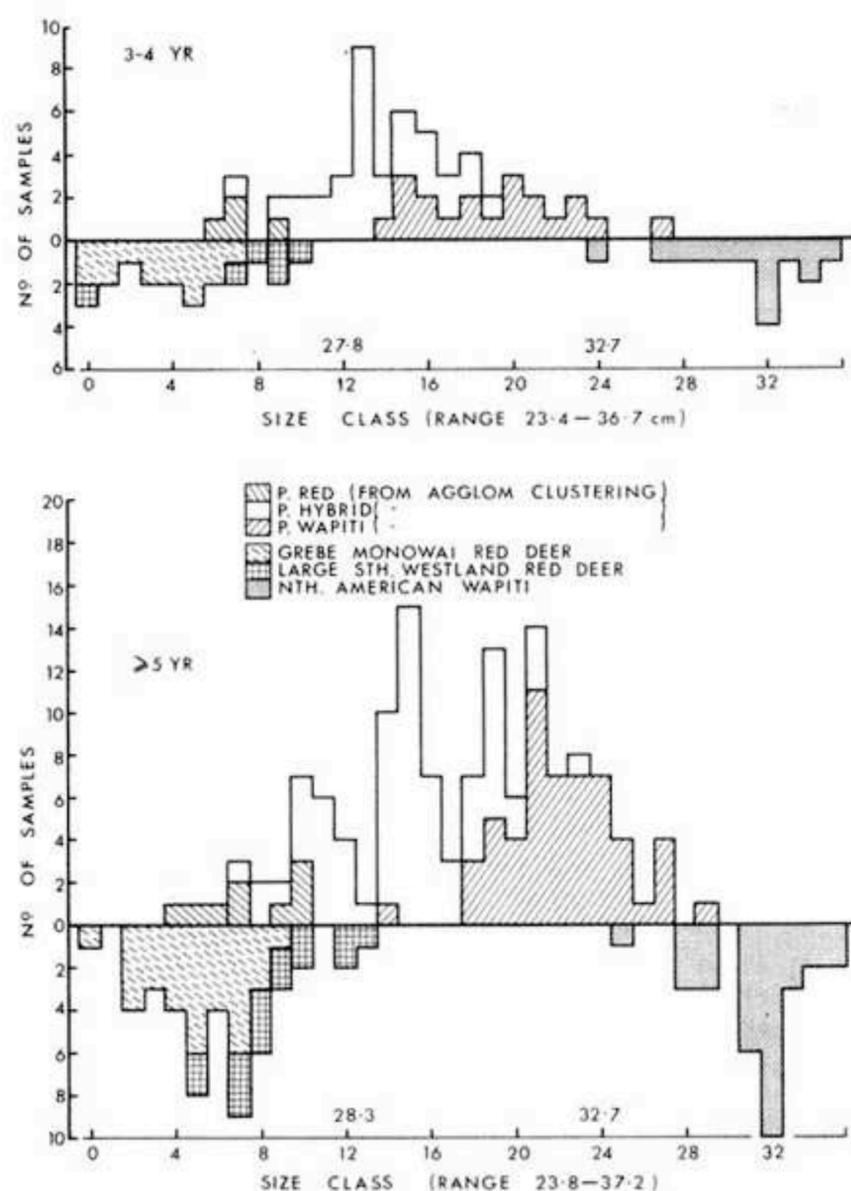


FIGURE 8. Basal length frequency distribution in 36 classes of Wapiti Area (above lines), and known red deer and wapiti samples (below lines), drawn in two broad age classes. Cross-hatching of Wapiti Area data is based on the identification by agglomerative clustering (compare with Fig. 2).

assigned to red deer by agglomerative clustering, 3-group analysis and basal length are accepted, the total number of red deer in the sample is 12. It is according pertinent that Caughley's diagram (Fig. 2) shows 13 skulls separated from other specimens by a narrow trough in the polymodal distribution, and for which the z-scores match red controls. Thus the totals of 12 from clustering, 14 by size matching, or 13 as deduced by reinterpretation of Caughley's diagram, suggests that the original Wapiti Area data sample contained no more than 14 red deer (8%).

The distribution of basal lengths of putative hybrids and wapiti overlap extensively in both the age groups shown. Accordingly, size alone cannot be used to evaluate the results from agglomerative clustering and 3-group analysis. However, Caughley's analysis and the results of both clustering and

discriminant analysis, all indicate that wapiti constitute about 40-42% of the data sample. Caughley gave estimates of 80 and 76 (of 178) from arithmetic and ratioed analyses (Caughley, 1971a, Table 2). Here (Table 1) 76 (of 189) were assigned to wapiti by clustering. We therefore regard 40% as a reliable estimate of wapiti in the data sample. The balance, 52%, are therefore considered to be hybrids.

Importance of the Characters in 2-group Discrimination

The importance of the measured characters in discriminating members of Caughley's data sample was estimated by calculating the averages of each of the 15 raw sizes and 14 ratios and multiplying them by their corresponding discriminant coefficients. This procedure gave average scores of -6.011 for raw sizes and 0.139 for ratios (Table 5).

On average, each character contributed 0.958 to the raw score (ignoring sign) and, as shown in Table 5, six of them (basal length, cranial cavity, ventral neurocranium, canine width, maxillary tooth row length, and margo adentalis) each contributed more than average to the total score. These six characters are therefore relatively important. Five of them also emerged among the most important in the series of 3-group analyses.

The relative contributions made by the ratio coefficients gave radically different emphasis to the characters. Basal length is of course lost. Among the remaining 14, lateral neurocranium, post-orbital width, facial tubers, anterior orbital width, canine width and lateral viscerocranium each contributed more than average. Canine width is the only character of more than average importance in both treatments (Table 4).

Among these ratioed characters, the relatively large contributions made by the six important characters (Table 5) appear to arise because these proportions (rather than absolute sizes) are most different in putative red deer and wapiti. Ratioed scores for red deer are larger than those for wapiti (Fig. 7). Consistently, the discriminant coefficients of the characters are positive for ratios which are larger among putative red deer, and negative for ratios which are larger among putative wapiti. Notably, in red deer, relative to basal length, the brain case (ventral and lateral neurocranium) is long and the post-orbital region and facial tubers are wide; the prominent features in Fiordland wapiti are, conversely, the relatively long facial area (lateral viscerocranium), greater span across the canine alveoli (canine width) and anterior edge of the orbits, and larger cranial cavity.

The average ratios for each age class, compiled for

TABLE 5. Contribution of character \times discriminant coefficient to average discriminant score of wapiti area sample 1966.

Absolute (raw) Size					
Char. Rank	Char. No.	Char. name	Mean Contribution	% of total - or + contribution	Mean diff. p.w., p. reds
1	2	Bas. length	2.136	51.1	20.0
2	12	N. cav. circ.	0.883	21.1	20.1
3	6	Lat. visc.	0.738	17.7	22.1
4	9	M2 width	0.423	10.1	13.1
5	7	Lat. neur.	-0.021	0.2	15.3
6	13	N. cav. depth	-0.145	1.4	17.9
7	10	Occ. condyle w.	-0.325	3.2	21.7
8	15	Postorb. wid.	-0.469	4.6	14.1
9	14	Ant. orb. wid.	-0.665	6.5	19.6
10	8	Fac. tubers	-0.683	6.7	11.9
11	1	Cran. cavity	-1.034	10.2	26.4
12	3	Vent. neur.	-1.053	10.3	16.4
13	11	Can. w.	-1.383	13.6	22.5
14	4	Maxill. T.R.L.	-2.140	21.0	20.0
15	5	Marg. ad.	-2.273	22.3	14.8
Total			-6.011		
Size/character 2 (ratio)					
1	7	Lat. neur.	0.209	27.7	-3.39
2	15	Postorb. wid.	0.190	25.2	-5.56
3	8	Fac. tubers	0.108	14.3	-7.32
4	9	M2 width	0.081	10.7	-5.41
5	4	Maxill. T.R.L.	0.073	9.7	0.00
6	5	Marg. ad.	0.071	9.4	-5.00
7	3	Vent. neur.	0.023	3.0	-2.56
8	2	Basal length—Ratio base			
9	13	N. cav. depth	-0.001	0.2	0.00
10	10	Occ. condyle w.	-0.056	9.1	0.00
11	12	N. cav. circ.	-0.058	9.4	0.00
12	1	Brain vol.	-0.077	12.5	+5.13
13	14	Preorb. wid.	-0.132	21.5	+2.70
14	11	Can. w.	-0.141	22.9	+5.56
15	6	Lat. visc.	-0.151	24.5	+1.96
Total			+0.139		

putative red deer, Fiordland wapiti and North American wapiti show these differences in greater detail (Fig. 9). Clearly, the most important discriminating characters (Fig. 9, A, B, C, M and N) are most different and are relatively consistent throughout life. But in the remaining characters there is either little difference between the species and/or the principal stanzas of growth are not uniformly related to the chronology of increasing basal length.

Four principal patterns are evident: bones which maintain a constant relationship to basal length; a "U" form, of decline from three years to a trough at

about 5-6 years, followed by a period of relatively rapid growth; declining proportion, such that through either relatively slow growth or reduction of size, proportional size is lower with advancing age; growth is consistently more rapid than that of length, and the proportion increases. There are also interesting cases where Fiordland wapiti show markedly different proportions and patterns from North American wapiti.

Maintenance of constant proportions is more commonly observed in the putative red deer skulls. It principally concerns length characters, as is to be expected because basal length is the factor against

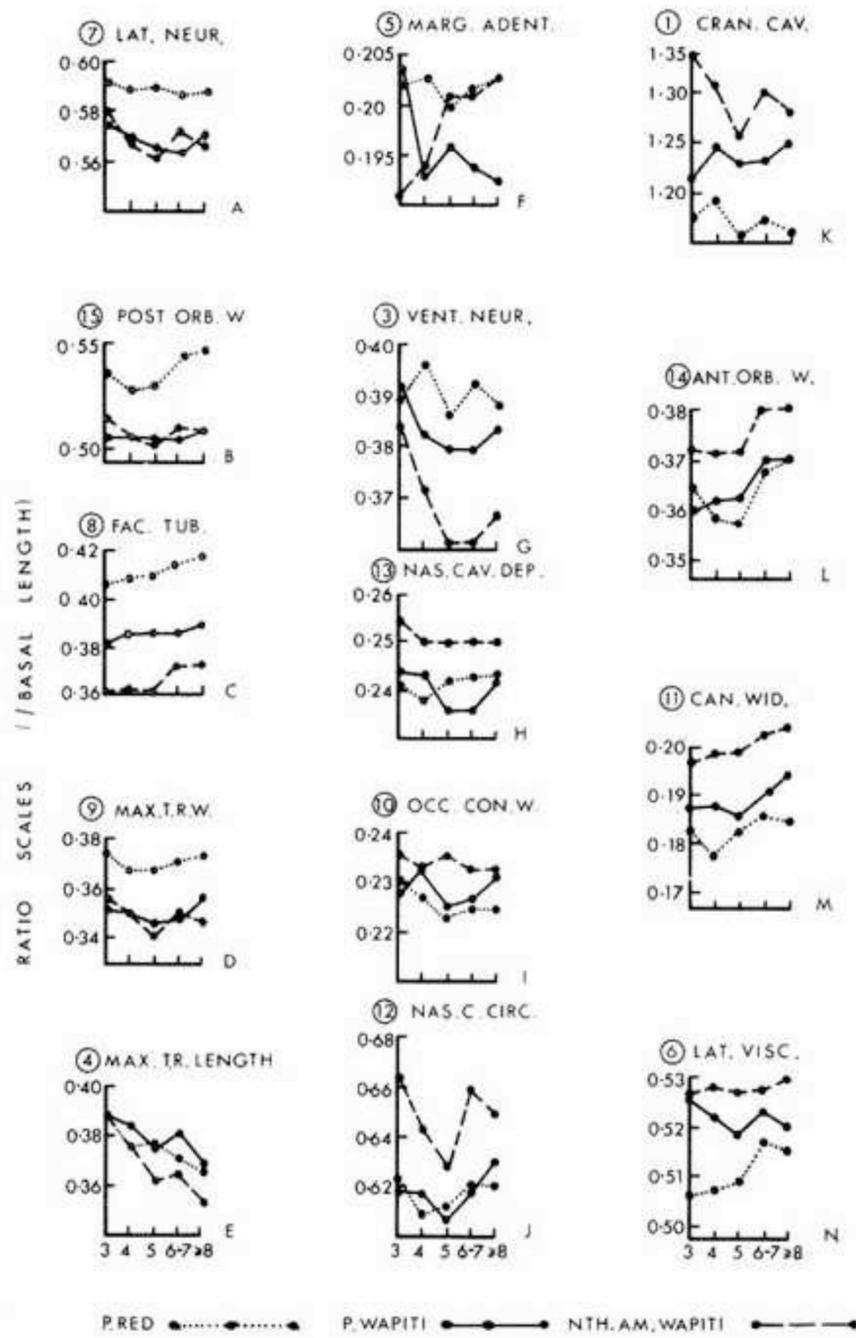


FIGURE 9. Average ratios of size of 14 characters divided by basal length, in the same age-classes as used for agglomerative clustering and 3-group analysis, of North American wapiti and putative Fiordland wapiti and red deer. The order of presentation from A to N, the same as in Table 5, shows the important ratios are relatively consistent at all ages. Those in the middle of the series were found to contribute little to discrimination (Table 5). The four different patterns of growth discussed in the text are clear in these diagrams.

which all others have been compared. The "U" form appears nine times in width characters (lateral neurocranium, and ventral neurocranium in both samples of wapiti). Decline of relative length occurs in the tooth row of both species, and the margo-adentalis of red deer. Continuous increases in proportions throughout life appear in 11 of the lines, notably those for the facial tubers and canine width

of both species, and the anterior orbital width of wapiti.

Concordance Between Skull and External Characters

Sample 6. These specimens were described by A. R. Harrison (pers. comm.) and the skulls were examined at the Berkley Museum in 1974 by C. L. B. Eight mature females were measured, and the z-scores were compared with the field descriptions.

Results. In the following notes, Harrison's reference number, our own series number and U. C. Berkeley catalogue numbers are given in that order. Shoulder height (S) and total body lengths (L) are in cm; Harrison's comments are given without change, and size and ratio scores are given in brackets.

—60 NZ 360. U. C. Berkeley catalogue cites as from Harrison and shot in Woodrow Burn (outside Wapiti Area), but collector unknown. Skull bas. lgth, 26.7 and undoubtedly a red deer (-5.45, 0.155). 21 64 NZ 295. S 112, L 198. Typical red deer (-5.39, 0.171). 7 62 NZ 340. S 112, L 198. Red hind (-5.67, 0.164). 22 65 NZ 355. S 126, L 207. $\frac{1}{4}$ red, $\frac{3}{4}$ wapiti hybrid, body colouring mouse shade, rump patch yellow (-6.11, 0.129). 19 61 NZ 405. S 130, L 215. Hybrid; red deer colouring, small tail, dark stripe round rump patch. Legs and head more of wapiti type (-6.18, 0.119). 14 66 NZ 430. S 140, L 224. A magnificent example of a wapiti cow. Rump patch dark yellow on tips of hair, otherwise white. Black margin to rump patch (-6.49, 0.099). 6 63 NZ 441. S 138, L 224. Pure wapiti. Greyish colour, with summer pelage almost gone (-6.71, 0.111). 16 67 NZ 425. S 140, L 217. Wapiti cow. Identical colouring to number 14 (-6.7, 0.091).

These records show complete congruence between the diagnoses given by Harrison and those based on craniological analyses.

Cull samples 4 and 5. Because the helicopter crews were instructed to avoid shooting wapiti or "the better class of hybrids" (J. H. McKenzie, pers. comm.) there should be smaller proportions of "wapiti-like hybrids" and wapiti in the cull samples than occur in the random sample taken by Caughley. Also, the diagnoses made by the autopsy crews in 1973 from morphological characters should concur with those based on the skulls.

Results. Table 1 records a summary of the agglomerative clustering classification by age classes of Caughley's 1966 sample and the culls of 1970 and 1973. Whereas Caughley's sample comprised 60% red deer and hybrids, these comprise 90% of the culls. Eight percent were identified as wapiti, with some indication ($\chi^2=3.25_{1df}$, $P<0.10$) that more frequent mistakes were made in 1973 (summer

pelage) than in 1970 (in winter pelage). Since only two of them exceeded 32.5 cm basal length, a size exceeded by 42% of Caughley's sample of putative wapiti, it is clear that most wapiti taken in the culls were small. They were presumably animals judged to be in poor condition or atypical by the helicopter crews.

Identification at the airstrip was rather inconsistent with the skull diagnoses (Table 6). The observers provisionally named 229 specimens which were congruently defined as red deer, hybrids or wapiti by clustering and 3-group discriminant analysis. Comparison of these shows that the crews often confused red deer and hybrids, and failed to recognise most of the wapiti. Of 71 identified as red deer by quantitative analysis, 24 (34%) were recorded as hybrids; of 139 hybrids, 42 (30%) were called red deer and two (1%) were called wapiti; of 23 wapiti, 20 (87%) were described as hybrids. Overall, they correctly named 62% of this sample.

TABLE 6. Comparison of identification of animals by cluster analysis and autopsy crews. 1973 cull.

		Identified by autopsy crew			Total
		R	H	W	
Identified by cluster analysis	R	47	24	0	71
	H	42	91	2	135
	W	0	20	3	23
Total		89	135	5	229

DISCUSSION

This study and its predecessors by Caughley (1971a) and Murie (1967) amply demonstrate the occurrence of a series from small red deer through a continuous range of intermediate forms to wapiti. Thus, they confirm the justification for trinomial classification as varieties of *C. elaphus*, viz. *C. e. scoticus* (L) and *C. e. nelsoni* (Bailey) (McCullough, 1969). But, retrospectively, the analyses brought out the need for careful consideration of the causes of adaptive differences and their effects on the cranial characteristics of a species. Nutrition, environmental characteristics and the competitive relationships between red deer, wapiti and their hybrids are believed to be important in the present case.

There is considerable evidence for the conclusion that the deer of the Wapiti Area are in relatively poor physical condition. Kidney fat levels are low (Smith, 1974, Challies, 1971). Body weights, antler size, and limb bones of animals presumed to be *nelsoni* by Smith (1974) are all less than averages of

North American populations. The change from winter to summer pelage, normally completed in well-conditioned deer by November, is often incomplete in Fiordland by February (J. H. McKenzie, pers. comm.). During this study, it was evident that the skulls in American collections are more robust than those from Fiordland. The frontals of many Fiordland specimens transmit daylight when viewed through the foramen magnum. American skulls, however, are opaque. Many have a thick, apparently "secondary" deposit of bone on the interior surface of the cranial vault and by Fiordland standards they are extraordinarily heavy. These differences are probably related to relatively low calcium and phosphorus levels in Fiordland forage plants (ref. J. A. Mills (pers. comm.) and Williams *et al.* (1976) pertaining to the diet of *Notornis mantelli* in the Murchison Mountains).

The essential point of these observations is that, as remarked by Smith (1974), and as was confirmed by comparisons of data from this study with measurements given by McCullough (1969), putative wapiti in Fiordland now more closely resemble the smaller Californian tule elk (*C. e. nannodes*) rather than *nelsoni*. Accordingly, it is concluded to be invalid to use North American samples of *nelsoni* skulls as discriminant controls of Fiordland samples.

This conclusion greatly influenced the course of this investigation. In essence, red deer were identified among the cluster-derived groups by their consistent smaller size and using the known red deer as "markers" (Fig. 4-6). Putative wapiti were identified by their greater average size, and putative hybrids were initially defined as those of intermediate size. Secondly, the high degree of congruence between these cluster-derived groups and those given by 3-group discriminant analysis demonstrated that the choice of boundaries from the cluster dendrograms was good (Table 2). Thirdly, application of the derived 2-group coefficients from 3-7 year old putative red deer and wapiti established a series within which the cluster-identified hybrids are intermediate in form and size between red deer and putative wapiti, and in which from both raw size and ratioed data, the North American specimens emerge as a "gross" extrapolation of the form of putative Fiordland wapiti (Fig. 7). Thus, within some limit which is also suggested by the discordant positions of the well-conditioned South Westland red deer (Fig. 7), "wapiti-ness" is to some extent an exaggerated expression of characters associated with their more exuberant growth. Finally, concordance of the skull diagnoses with the field decisions made by A. R. Harrison (pers. comm.) and the evidence of selection by the helicopter crews during the culls of

1970 and 1973, show that cranial and other characters are well linked and in accord with published descriptions of wapiti in North America.* Thus there is no doubt that a considerable proportion of the Fiordland population are indeed pure wapiti.

Discrimination is easiest when the animals are in winter pelage. Throughout the year however, rump patch characters, in addition to the typical dun or grey-white (winter) pelage, dark brown to black brisket and legs, larger size and distinctive gait, appear to be the simplest and most consistent field guide to identification of pure wapiti. The white disk always extends anteriorly to the tail; it is invariably bordered laterally and often dorsally, by a black margin; there is never a distinct red tint in the guard hairs of the disk (except among calves, Dr V. Geist, pers. comm.) or a dark or reddish dorsal stripe or patch extending posteriorly from the anterior border of the disk towards or onto the tail; the tail is distinctly shorter. Illustrations of North American *nelsoni* (Murie, 1951, Flook, 1970, Moran, 1973, Kirsch and Greer, 1968) and the attributes of a small captive herd at Te Anau (E. Meredith, pers. comm.) indicate that these characters distinguish pure wapiti from hybrids and red deer, but we are unable to recognise equivalent boundaries which separate red deer from the hybrids. Haziness of this boundary is also indicated by the large number of incongruent identifications of red deer and hybrids made by the autopsy personnel.

Interpretation of Caughley's data sample as comprising 8% red deer, 52% hybrids and 40% wapiti differs markedly from the figures given by him—38, 20 and 42% respectively. The difference in the two estimates of wapiti is minor. But the differences in proportions allocated to the red and hybrid groups are important. In Caughley's data sample, only 36 skulls were of equal or shorter basal length than the largest red deer available from South Westland. Therefore, basing judgement upon comparison with the Grebe-Monowai sample and the assessed poor physical condition of the Fiordland population, we consider it extremely unlikely that more than 12-14 in the sample are red deer (Fig. 8). Thus, we consider that Caughley erred by including approximately 54

"red-like hybrids" of less than 29 cm basal length in his putative red deer group. This interpretation also suggests that the only authenticated hybrid measured by Caughley correctly matches "red-like hybrids" as defined by this study (Fig. 2).

Wapiti entered Caughley's eastern watershed sampling area by 1921 (Banwell, 1966). Red deer, spreading mainly from the south (Tustin 1970 unpublished report) and secondarily from the north-east (J. McL. Ward and J. H. McKenzie pers. comm.) had occupied most of the wapiti range by 1950 (Fig. 1). By the late 1940's, they were considered to be more numerous than wapiti in many parts of the eastern range (Wiseley and Kean, 1951, Murie, 1951 (in Poole, 1951)). Despite this early abundance, their scarcity in Caughley's sample suggests that most red deer have been absorbed into the hybrid gene pool, whereas pure wapiti remain relatively numerous. To discriminate this from the concept of random introgressive hybridisation we will refer to this pattern as "one-way hybridisation".

One-way hybridisation in a mixed Cervid population, in which few mature males dominate in mating, is probably the consequence of social dominance of wapiti bulls over red deer stags during the rut. K. H. Miers and P. C. Logan (pers. comm.) have described instances where wapiti bulls have taken command of harems previously held by red deer stags. Logan once witnessed an episode in which bugling by a wapiti bull put a stag to flight out of an alpine basin, even without visual contact between the animals. Such observations indicate that the high hierarchical status conferred upon individual male red deer by large antler and body size (Lincoln *et al.* 1972) is equally applicable to mixed populations which include wapiti.

The chronology of breeding, as reviewed by Smith (1974), would also tend to reinforce dominance of wapiti. Gestation averages about 250 days, whereas in red deer it is about 235 days. The season of births, as deduced from meagre Fiordland data, is about the same, or slightly earlier (Caughley 1971c). Thus the median date of conception of wapiti is probably about two weeks before that of red deer. Consistently, earlier maximum libido among the bulls is indicated by frail evidence (Smith 1974) that their testes reach maximum average weight about two weeks earlier than those of stags in the Wapiti Area.

It seems reasonable to suppose that the small size of Fiordland wapiti sampled in the past 20 years is related to their ability to survive on a poorer plane of nutrition than is demanded by the rigours of their native range in North America. There, mean temperatures in winter are in the order of -10°C to -15°C for at least four months annually, with

* The low success-rate of identifying animals at the airstrip in 1973 suggests that considerable experience of wapiti is necessary to enable observers to identify them, that identification of the groups is enhanced by the opportunity to observe living groups of animals from close range (as is routinely the case from a helicopter), and that there is some risk of bias of identification if observers are informed that there should be few if any wapiti in the sample.

extremes below -40°C and severe wind-chill conditions. In Fiordland, average temperatures in the valley refuges are probably above freezing point throughout the year, and extremes are unlikely to be below -15°C . There is not therefore the imperative demand for high growth rates in summer and accumulation of large fat depots in autumn which are implied by Bergman's Rule in *nelsoni's* North American range. This argument suggests that under excellent range conditions, Fiordland wapiti can display equal growth to their North American conspecifics (as the high quality of trophy antlers secured from the 1920's to the late 1950's shows they have done in past years) but, as the habitat is degraded by overbrowsing, they can survive on a much lower plane of nutrition.

The calculated differences of skull form of the Fiordland and American wapiti (Fig. 9) probably reflect these nutritional differences. The proportionally long neurocranium and broader facial tubers and maxillary tooth row, coupled with smaller occipital condyles, viscerocranium, nasal cavity, pre-orbital width and canine width suggest that under the poor nutrition regime, the highest priorities for growth are in the neurocranium and maxilla. That is, the highest priority is associated with maintenance of brain size and the dental arch.

These differences appear to be muted by advancing age. As shown in Fig. 7 (and was confirmed by fitting polynomial curves of basal length, raw score and ratioed score on log age), Fiordland wapiti average 14% shorter at three years age, and 9% shorter by 10 years. Raw size scores are 15% smaller at three years, and 11% smaller at 10 years. Ratio score differences trended from 36 to 33% smaller with age. Thus North American wapiti appear to grow relatively rapidly up to 3-4 years, whereas those in Fiordland grow less rapidly as juveniles but continue to grow more persistently, and carry relatively juvenile characters into old age.

Smith (1974), working with measurements of the lower jaw, suggested that the gradual increase of skeletal size associated with age of Fiordland wapiti should be interpreted as a consequence of deteriorating condition of the habitat at the time samples were collected. Under such a hypothetical regime, each successive cohort would display slower growth; each would therefore be somewhat smaller than its predecessor. A growth curve compiled from a sample collected over a short period of time would thereby suggest an illusory pattern of continuous growth throughout life.

We consider this interpretation to be inadequate to explain the present observations. Challies (1973),

Pekelharing (1973 unpubl. report), Lambert and Bathgate (1977) and Batcheler (unpubl. data) have recorded continuous growth of jaws in New Zealand ungulates which span high to low and deteriorating to improving conditions. The pattern is thus more general than Smith implies. Since studies of red deer in Europe, and of moose, caribou, and wapiti in North America generally show little increase in skeletal size beyond 3-5 years (see Smith's 1974 review, Miller, 1974, Flook, 1970), it seems more likely that the extremely high growth rates of young deer in the higher latitudes expresses a "die young or live well" adaptive imperative of their capacity to withstand long periods of negative energy balance during the winter. It can be sacrificed to some degree in Fiordland because the winter climate is relatively mild.

A curious feature of the Fiordland data is that whereas the skulls of the wapiti are smaller than their North American conspecifics (Fig. 8), those of the red deer are larger than those in the Grebe-Monowai sample. Like Smith (1974, remarking on body weights of Fiordland and European populations of red deer), we do not construe this apparent anomaly to mean that red deer are better adjusted to conditions in the Wapiti Area. Since the Grebe-Monowai sample (Caughley, 1971b) and those assumed to be red deer in the south-western portion of the Wapiti Area (Challies, 1970 unpubl. report) had similar fat reserves and fecundity rates, it would be expected that, other factors being equal, the minimum length of Grebe-Monowai skulls should be about the same as of those taken from the Wapiti Area. However, as shown in Figs. 4-6 and Fig. 8, both minimum and average basal length of the Grebe-Monowai sample are about 2 cm smaller. We consider the discrepancy must therefore be a consequence of the unique competitive situation facing red deer in the Wapiti Area. It seems reasonable to suppose that in the overbrowsed habitat competition would select rigorously towards those red deer which are large enough to compete with the larger animals. This hypothesis implies that there should be a very high mortality rate among the genetically less-fit (smaller?) red deer—which is consistent with the absence of any exceeding seven years age in Caughley's sample—compared with their longevity (Caughley, 1971b) without competition in the Grebe-Monowai. Further, it implies that increase of the minimum viable size of red deer in the Wapiti Area, coupled with reduction of that of wapiti, has squelched their potential size difference and so to some degree has removed size as a reproductive barrier between the two varieties. Hybridisation would thus be enhanced if, as suggested by Millais (1929), the much

greater weight of a well-conditioned wapiti bull is the only apparent deterrent to mating by a red deer hind. Collectively, therefore, we conclude: That competition for food resources and the social and physiological factors which comprise one-way hybridisation are the mechanisms which account for the small proportions of red deer taken from the eastern catchments in the past decade and; that the rate of hybridisation has accelerated during the past three decades as depletion of the habitat has stimulated intense competition between red deer and wapiti.

In addition to ecotypic variation related to nutrition, it is evident that application of multivariate techniques must take cognizance of the influences of age. As described in relation to Fig. 7, the 2-group z-scores drifted throughout life and as shown in Fig. 9, drift is associated with complex changes of shape and size of the skull. These complexities probably underly the rejection of use of 2-group coefficients derived from all age classes. In the test described, they effectively discriminated groups within the young and old animals, but not those between four and seven years. Conversely, use of 3-7 years samples gives greater discriminatory weight to those of "average" condition in the ontogeny of the deer skull. The range pivots around the five year age class which, as shown in Fig. 9, is the period when relatively rapid growth along the axis of the skull gives way to increasing breadth.

The use of ratios does not appear to have generated a spurious pattern of separation between forms. Discriminant analysis of both the 15 sizes and 14 derived ratios gave comparable and highly significant discrimination between the putative pure Fiordland forms as defined by clustering and 3-group discriminant analysis. (Respective F ratio values: sizes = $99.41_{(15,109 \text{ df})}$, ratios = $96.94_{(14,110 \text{ df})}$). The linear relationship of the size and ratio scores (Fig. 7) shows that animals were consistently identified by both methods. However, the ratio analysis appears to be more conservative in identifying taxonomic affinity of the skulls than that based on absolute size. As shown by the y axes plots of Fig. 7, the ratio z-scores of wapiti overlap strongly with those of the North American samples. But raw size z-scores, with only one exception, do not overlap. It is therefore clear that although ratios may not totally eliminate size from consideration (Aitchley *et al.* 1976), they emphasise different attributes of the skull (Table 5) and so should not be ignored in studies of closely related forms of biological material.

We cannot suggest with confidence a genetic basis for the appearance of two groups of hybrids in the

Wapiti Area (Figs. 5 and 6; Table 1). The pattern of splitting in the dendrograms indicates that they are relatively homogeneous at three years (Fig. 4); they appear then to discriminate into "red-like" and "wapiti-like" forms from the fourth year, and are more closely associated with red deer than with wapiti, to about the seventh year. Beyond that age, they appear to be more closely aligned with the "parent" variety than with each other (Fig. 6). This suggests that, with continued crossing and back crossing for 10 or more generations, the important components of phenotype are associated with few genes and dominance is more clearly expressed with age. Distinctive differences between these forms are also suggested by the proportions at which they occurred in the random (Caughley's) and cull samples. Caughley's sample of hybrids over 3 years of age occurred in the ratio 32 "red-like" to 53 "wapiti-like". In the cull samples, they occurred in almost the reverse proportions, 144:71 ($\chi^2=21.6, 1 \text{ df}$). It is apparent that the helicopter crews could discriminate between "red-like" and "wapiti-like" animals with reasonable certainty (i.e. they avoided shooting the "better class of hybrids"), and were able to recognise wapiti from "wapiti-like" hybrids with high confidence.

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