

Variation in the long-tailed field-mouse  
(*Apodemus sylvaticus* (L.)) in north-west Scotland  
II. Simultaneous examination of all characters

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(Communicated by L. H. Matthews, F.R.S.—Received 8 July 1963

—Revised 11 May 1964)

Measurements of ten characters were made on each of 156 specimens of *Apodemus sylvaticus* (L.) from eight islands in the Inner and Outer Hebrides and from two localities on the adjacent mainland of north-west Scotland. The characters were occipito-nasal length, weight, tail length, hind foot length, pectoral stripe length, tooth row length, values, chroma, incisor width and tooth wear. Tooth wear is a measure of age and a regression adjustment was used to bring all characters to a uniform age class. The pectoral stripe measurement was analysed using a logarithmic transformation.

An analysis into canonical variates was made, the object being to account for the largest possible part of the variation between groups using a limited number of linear combinations of the original measurements. Most of the variance was contained in the first two canonical variates and from the dispersion of the means of the samples it appeared that the populations of *Apodemus* separated into two main groups. The first contained animals from Raasay, Applecross, Laga, Mull and Lewis and the second those from Barra, South Uist and North Uist. The Rhum and Colonsay mice were to some extent distinct from both groups and from each other, with the former the more isolated.

The analysis confirms that differences between all the populations examined are small and that no distinct island species is readily recognizable. It appears that evolution has taken place on each island independently with no evidence of the island populations having been derived from one basic stock. It is proposed that the specific name *hebridensis* should be dropped, that *A. sylvaticus hamiltoni* (Hinton) be recognized as a large form from Rhum and that the remainder from the localities investigated should be referred to as *A. sylvaticus sylvaticus* (L.).

#### INTRODUCTION

In the preceding paper a study of variation in *Apodemus sylvaticus* (L.) from eight islands in the Inner and Outer Hebrides and two localities on the adjacent mainland of north-west Scotland, Delany (1964) obtained measures of the distinctness of various populations by making a series of comparisons of individual characters. The present paper utilizes many of these data but attempts, by the use of discriminant functions (Rao 1952), to handle all the measurements simultaneously. Linear functions are obtained which, characteristically, space out the means of the groups to a maximum. Further, the number of functions that account for the greater part of the variance can be ascertained and in the event of this being only two the results can be plotted in a diagram. This method was found by Ashton, Healy & Lipton (1957) to give good results in determining the affinities of certain anthropoid teeth. Foster (1963) used the same method in analysing the variation shown by populations of deer mice (*Peromyscus* spp.) isolated on islands off the west coast of Canada.

The analysis was made on a total of 156 mice, consisting of 25 from Applecross, 16 from Laga, 7 from Raasay, 6 from Rhum, 18 from Mull, 18 from Colonsay, 25 from Lewis, 16 from North Uist, 10 from South Uist and 15 from Barra. The Applecross mice were a random sample from a larger collection, but the others were all the animals available with complete series of measured characters. These characters included occipito-nasal length, weight, tail length, hind foot length, pectoral stripe length, length of tooth row, incisor width, tooth wear, values and chroma. Details of how they were obtained are given by Delany (1964).

#### STATISTICAL METHODS

The pectoral stripe measurement was, as previously (Delany 1964), transformed from a measurement  $x$  to  $\log_{10}(x+1)$ .

The statistical techniques used are basically those described by Rao (1952). In the present material, nine measurements were taken, and the set of measurements on each single animal can be represented by a point in a space of 9 dimensions. It is natural to enquire whether a diagram with fewer dimensions—ideally one or two—could depict the situation without the sacrifice of any essential information. For example, if we denote the nine measurements by  $x_1, x_2, \dots, x_9$ , we could choose coefficients  $c_1, c_2, \dots, c_9$  and plot the value of the linear function

$$C = c_1x_1 + c_2x_2 + \dots + c_9x_9$$

for each animal in a single dimension, i.e. along a straight line. We would like this process to keep the groups as well separated as possible, and we accordingly choose the coefficients so as to maximize the ratio (mean square between groups)/(mean square within groups) in an ordinary analysis of variance of the quantity  $C$ . If  $\mathbf{B}$ ,  $\mathbf{W}$  are the dispersion matrices of the nine measurements between and within groups, and  $\mathbf{c}$  is the required vector of coefficients, this can be shown to require the solution of the matrix equation

$$(\mathbf{B} - \lambda\mathbf{W})\mathbf{c} = 0.$$

There are in fact nine values of  $\lambda$  for which the equation is soluble, and to each value corresponds a different vector  $\mathbf{c}$ .  $\lambda$  is precisely the variance ratio we wish to maximize, so that the optimum single linear function is that with coefficients given by the vector that corresponds to the largest value of  $\lambda$ . If a two-dimensional diagram is required, we can take two linear functions with coefficients given by the vectors corresponding to the largest two values of  $\lambda$ , and so on. These linear functions have the useful property of being uncorrelated within groups. The extent to which a limited number of linear functions exhaust the available information can be judged by comparing the sum of the  $\lambda$ 's used with the sum of all nine  $\lambda$ 's, which is  $(\text{trace } \mathbf{B})/(\text{trace } \mathbf{W})$ , i.e. the (between/within) ratio of the totals of the nine mean squares. The linear functions obtained by this method are a generalization of the better known discriminant function (Fisher 1938). Rao refers to them as *canonical variates*.

In the present material, the differences between groups were to some extent due to their different age-compositions. Similar adjustments using the tooth wear

character have, in consequence, been made as previously (Delany 1964). The results of this analysis are summarized in table 1. The values differ somewhat from those of table 2 of the preceding paper because of the omission of some animals.

TABLE 1. MEASUREMENTS ON *APODEMUS SYLVATICUS* (L.) FROM VARIOUS LOCALITIES IN NORTH-WEST SCOTLAND ADJUSTED FOR TOOTH WEAR

The adjustments tabulated are those to be added to measurements of animals in grades 1, 2 and 3 to make them comparable with grade 4 animals.

	o.-n. length (mm)	wt. (g)	tail (mm)	hind foot (mm)	pect. stripe (log <sub>10</sub> (mm + 1))	tooth row (mm)	incisors (mm)	value	chroma	no. in sam- ple
<i>Group means</i>										
Applecross	24.6	19.6	87.0	22.6	0.88	3.69	1.16	4.5	4.5	25
Laga	24.5	17.1	85.1	22.5	1.15	3.65	1.18	4.3	4.2	16
Raasay	24.1	19.7	81.7	22.9	1.17	3.73	1.13	4.5	5.4	7
Mull	25.5	21.0	85.9	22.6	0.92	3.78	1.25	4.3	3.9	18
Lewis	25.7	20.7	90.1	23.4	1.11	3.89	1.16	4.3	4.3	25
N. Uist	26.0	24.9	87.7	23.1	0.14	3.95	1.18	5.9	3.1	16
S. Uist	25.3	23.4	84.0	22.5	0.71	3.89	1.21	5.3	3.5	10
Barra	26.5	26.5	87.7	23.6	0.25	3.97	1.24	4.9	3.6	15
Colonsay	26.3	23.7	88.2	24.7	0.60	3.91	1.24	4.8	4.2	18
Rhum	27.1	26.7	98.4	25.9	1.34	3.98	1.25	5.0	5.1	6
<i>Standard deviations within group</i>										
	0.73	3.03	5.17	0.71	0.34	0.11	0.06	0.45	0.93	
<i>Correlations within groups</i>										
o.-n. length	1.00	0.76	0.60	0.52	0.08	0.21	0.58	0.22	0.22	
weight	—	1.00	0.57	0.31	0.03	0.11	0.41	0.25	0.15	
tail	—	—	1.00	0.44	0.08	0.13	0.36	0.17	0.09	
hind foot	—	—	—	1.00	-0.04	0.35	0.13	-0.07	0.02	
pect. stripe	—	—	—	—	1.00	-0.01	0.04	-0.16	-0.00	
tooth row	—	—	—	—	—	1.00	0.04	-0.04	-0.01	
incisors	—	—	—	—	—	—	1.00	0.22	0.27	
value	—	—	—	—	—	—	—	1.00	0.46	
chroma	—	—	—	—	—	—	—	—	1.00	
<i>Adjustments for tooth wear</i>										
grade 1	+ 1.25	+ 5.68	+ 5.52	+ 0.03	+ 0.11	- 0.12	+ 0.13	+ 0.32	+ 1.91	
grade 2	+ 0.64	+ 3.21	+ 2.28	+ 0.14	+ 0.02	- 0.08	+ 0.05	+ 0.51	+ 1.40	
grade 3	+ 0.03	+ 0.46	- 0.32	+ 0.15	+ 0.07	- 0.13	+ 0.00	+ 0.06	+ 0.35	

Table 2 gives the results of the canonical analysis. Each canonical variate can be multiplied by an arbitrary factor; this factor has been chosen to give each variate unit standard deviation within groups. Since the variates are uncorrelated within groups, the contours of equal probability density for a pair of variates are circles.

It is a little difficult to assess the contribution of each separate measurement to a particular canonical variate. As a step in this direction, table 2*b* gives the coefficients when the original measurements are expressed each in terms of its own within-group standard deviation.

A plot of the group means for canonical variates I and II is given in figure 1, but this does not contain quite all the available information. Thus the Raasay and Lewis group means are quite close in these two dimensions, but are nearly 4 units

TABLE 2. CANONICAL ANALYSIS ON MEASUREMENTS ADJUSTED FOR TOOTH WEAR

a. Coefficients of canonical variates, standardized to unit S.D. within groups

	I	II	III	IV	V	VI	VII	VIII	IX
o.-n. length (mm)	+0.50	-0.12	+2.21	+0.29	+0.49	-0.35	+0.56	+1.14	-0.85
weight (g)	+0.09	+0.02	-0.29	-0.12	-0.33	+0.11	-0.18	-0.10	-0.14
tail (mm)	-0.08	-0.03	+0.07	+0.11	+0.04	-0.05	-0.16	-0.06	+0.11
hindfoot (mm)	-0.01	+1.44	+1.03	-0.16	+0.36	-0.35	+0.30	-0.40	-0.13
pect. stripe (log <sub>10</sub> (mm + 1))	-1.04	+0.69	-0.46	+0.80	+0.69	+2.35	+0.12	-0.01	-0.88
tooth row (mm)	+3.24	+0.27	+2.47	+1.03	-3.43	+4.49	+1.79	-1.78	+5.65
incisors (mm)	-0.85	+0.99	-6.96	-15.53	+7.89	+5.44	-3.70	-1.38	+8.44
value	+1.48	-0.82	-1.22	+1.20	+1.30	+0.45	+0.15	+0.50	+0.07
chroma	-0.66	+0.25	-0.02	+0.06	-0.66	-0.18	-0.02	+0.69	+0.35

b. Coefficients of canonical variates, measurements expressed as multiples of within-group standard deviations

o.-n. length	+0.36	-0.08	+1.61	+0.21	+0.36	-0.25	+0.41	+0.83	-0.62
weight	+0.28	+0.08	-0.88	-0.36	-0.99	+0.33	-0.56	-0.29	-0.43
tail	-0.39	-0.17	+0.34	+0.58	+0.19	-0.24	-0.81	-0.33	+0.55
hindfoot	-0.01	+1.02	-0.73	-0.11	+0.25	-0.25	+0.21	-0.28	-0.09
pect. stripe	-0.36	+0.24	-0.16	+0.27	+0.24	+0.81	+0.04	0.00	-0.30
tooth row	+0.37	+0.03	+0.28	+0.12	-0.39	+0.51	+0.20	-0.20	+0.64
incisors	-0.05	+0.06	-0.42	-0.94	+0.48	+0.33	-0.22	-0.08	+0.51
value	+0.66	-0.04	-0.54	+0.54	+0.58	+0.20	+0.07	+0.22	+0.03
chroma	-0.61	+0.23	-0.02	+0.06	-0.61	-0.17	-0.02	+0.64	+0.33

c. Means of groups, adjusted to zero overall mean

Applecross	-1.79	-0.98	-0.26	+0.36	-0.18	-0.65	-0.30	-0.02	+0.03
Laga	-2.47	-0.95	-0.05	-0.08	+0.92	-0.21	+0.19	-0.06	-0.04
Raasay	-2.51	+0.08	-2.07	+0.28	-1.32	+0.25	+0.45	+0.13	-0.03
Mull	-0.86	-1.02	+1.01	-1.28	+0.33	+0.26	-0.10	+0.11	+0.01
Lewis	-1.14	+0.17	+1.82	+0.92	-0.28	+0.02	+0.22	-0.05	+0.01
N. Uist	+3.92	-1.26	+0.04	+1.13	+0.45	-0.35	+0.07	+0.08	0.00
S. Uist	+1.73	-1.36	-0.76	-0.46	+0.01	+1.02	+0.08	-0.14	+0.04
Barra	+2.36	-0.23	+0.79	-1.00	-0.85	-0.35	-0.18	-0.06	-0.03
Colonsay	+0.86	+1.67	-0.14	-0.76	+0.33	-0.59	+0.38	-0.02	+0.03
Rhum	-0.11	+3.87	-0.35	+0.90	+0.57	+0.58	-0.76	+0.02	-0.01
M.S. between groups	70.48	26.03	15.30	11.68	5.35	3.62	1.37	0.08	0.01
% of total variance	53	19	11	9	4	3	1	—	—

apart on variate III. We can define for each pair of groups a generalized distance (Mahalanobis 1936). This is not quite the same as the ordinary distance between the group means in the 9-dimensional space, but makes an allowance for the inter-correlations of the measurements. It is inversely related to the amount of overlap between the two groups. Rao (1952) has shown that the canonical variates can alternatively be defined as those linear combinations of the original measurements that maximize the sum of the generalized distances between all pairs of groups, thereby minimizing the total overlap. The generalized distances in our material are shown in table 3.

As is often the case, the individual canonical variates are not very readily interpretable in a biological sense. The first variate is to some extent a measure of overall size combined with an emphasis on high value and low chroma. The second is dominated by the hind foot measurement. It may seem surprising that the large

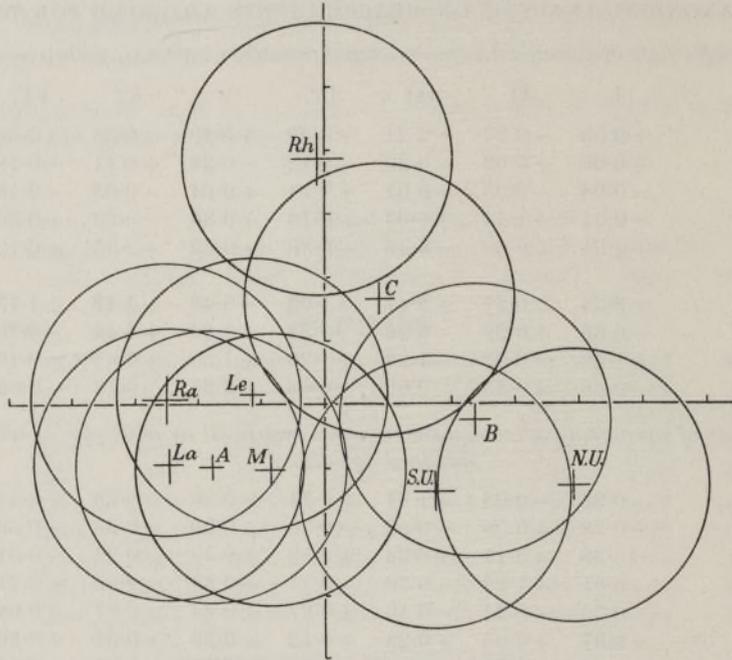


FIGURE 1. Disposition of ten groups of *Apodemus* with respect to the first two canonical variates. The circles are drawn to enclose 90% of the animals in each group; the bars extend for one standard error on either side of the group means. *A*, Applecross; *B*, Barra; *C*, Colonsay; *La*, Laga; *Le*, Lewis; *M*, Mull; *N.U.*, North Uist; *Ra*, Raasay; *Rh*, Rhum; *S.U.*, South Uist.

TABLE 3. GENERALIZED DISTANCES BETWEEN GROUPS

	Apple- cross	Laga	Raasay	Mull	Lewis	N. Uist	S. Uist	Barra	Colonsay	Rhum
Applecross	—	—	—	—	—	—	—	—	—	—
Laga	1.53	—	—	—	—	—	—	—	—	—
Raasay	2.76	3.26	—	—	—	—	—	—	—	—
Mull	2.51	2.42	4.35	—	—	—	—	—	—	—
Lewis	2.67	3.00	4.32	2.75	—	—	—	—	—	—
N. Uist	5.83	6.53	7.21	5.48	5.62	—	—	—	—	—
S. Uist	4.05	4.56	4.99	3.38	4.50	2.59	—	—	—	—
Barra	4.62	5.36	5.89	3.59	4.22	3.22	2.66	—	—	—
Colonsay	4.00	4.35	4.71	3.57	3.70	4.66	3.63	2.92	—	—
Rhum	5.38	5.61	5.35	5.63	4.63	6.66	5.83	5.57	3.36	—

mice from Rhum are not distinguished on the first canonical variate but primarily on the second. One reason is the small number of mice in the group. A variate effectively dividing most of the material into two classes (such as the first canonical variate) gives rise to a larger variance ratio than one whose main result is to separate a numerically small group from the rest.

## RESULTS

The adjustments to each measurement for each grade of tooth wear are given in table 1, where it is apparent that certain characters, as found earlier (Delany 1964), vary more markedly with age than others. Occipito-nasal length, weight, tail length and incisor width appear to be most influenced by life history. For these characters the difference between animals with tooth wear grades 3 and 4 is small suggesting that the mice in the third category are almost fully grown. From the adjusted group means it appears that the Rhum mice are appreciably larger than the remainder. No other population stands out quite so distinctly, although the animals from the mainland and Raasay appear to be comparatively small with respect to occipito-nasal length, weight and length of tooth row. The correlations obtained between pairs of characters were generally not high; the greatest correlations, all positive, were between occipito-nasal length and weight, tail length, hind foot length and incisor width and also between weight and tail length.

In the canonical analysis (table 2) approximately 92% of the variation has been accounted for by the first four canonical variates with the first two responsible for 72%. The group means for the first two canonical variates have been plotted in figure 1 and circular contours enclosing 90% of the values inserted. Two main groupings appear, the mice from Applecross, Laga, Mull, Raasay and Lewis forming one group and those from North Uist, South Uist and Barra another. The Rhum animals are isolated from these two groups with the Colonsay mice occupying a position intermediate between those from Rhum and the group representing the three Outer Hebrides. These findings are largely confirmed by the generalized distances between the groups (table 3).

## DISCUSSION

It seems appropriate that the results obtained here should be considered, as far as possible, with those obtained by Delany (1964) as the two research projects represent different approaches to the same problem. From both analyses it is apparent that *Apodemus* is an animal displaying appreciable variation when separated into a series of isolated populations but that the magnitude of the variation is small. Also, critical examination is made difficult because the animal shows various distinct morphological changes during the course of its development. However, the existence of a distinct island species seems unlikely as all the evidence indicates closer affinity between populations of mice from some islands and the mainland than between those of several pairs of islands.

Both the analyses suggest that the mice from three of the Outer Hebrides in close geographical proximity are closely related and that the Lewis mice are relatively unlike those from any other island of the Outer Hebrides. The Rhum mice are very distinct. The Colonsay animals are interesting in that neither analysis shows them to be as readily distinguishable from the remainder as the Rhum mice, but both suggest that they have characters which separate them by an appreciable margin from the mice from certain localities, particularly Applecross, Laga, Raasay and North Uist. It is of interest that the two analyses should

produce such comparable results. The multivariate method is probably the better indicator of the main patterns of interrelationships whilst the univariate method permits more detailed study of the characters actually responsible for the differences.

Foster (1963) observed the deer mouse, *Peromyscus*, to display considerable variation in size when its populations have been isolated on islands. His multivariate analysis shows the first canonical variate, which is probably associated with size, to be more significant than the other nine combined. However, it is possible in this case that the importance of genetical size is exaggerated as no allowance was made in the original data for size variation due to age.

Except for an indication that the mice from the Uists and Barra are similar, the mice of no island group, such as the Inner Hebrides, seem uniform and consequently there is little evidence that the island populations have evolved other than from separately isolated groups of animals. Those islands such as Mull, Raasay and Lewis, where differences from the mainland mice are small, may have had their faunas isolated comparatively recently; alternatively, they may be subject to more frequent introductions from the mainland. These views could be consistent with those of Corbet (1961) who is of the opinion that the small mammal faunas of the Hebrides have largely been introduced by man. That evolution has taken place on the islands is suggested from some animals being larger or lighter in colour than any from the mainland. The increased size on several islands is not a feature peculiar to this archipelago, as similar or greater increases are witnessed on Foula (Delany 1963), Fair Isle (Delany & Davis 1961) and Sark (Bishop 1962). Corbet (1961) suggested that increased size in small rodents on small islands reflects increased intraspecific competition when freed from ground predators. On the islands studied, ground predators occur only on Mull, where there are stoats (*Mustela erminea* L.), and on Raasay where there are weasels (*Mustela nivalis* L.) (Harrison 1937). *Apodemus* on Mull shows a tendency to large size, whereas on Raasay it does not. Raasay, by way of contrast, has the largest subspecies of British bank vole (*Clethrionomys glareolus erica* (Barrett-Hamilton & Hinton)). These observations are not in complete accord with Corbet's views, which can only be regarded as very tentative.

The recognition of the many described subspecies of *Apodemus* is difficult to justify. Many of the differences are so small as to be unsuitable for critical identification. One of the most obvious island forms, that from Rhum, is large and has a long pectoral stripe. For this form it is suggested that the name *A. sylvaticus hamiltoni* (Hinton) be retained. The pale coloration of the animals from North Uist and Barra makes them fairly distinctive. Barrett-Hamilton & Hinton (1910-21) suggested that the Barra animals were a subspecies of *A. hebridensis* but because few individuals were examined felt unable adequately to describe a new subspecies or assign the animals to one that already existed. The differences between these mice and those from elsewhere is small and it is not proposed, at this stage, to give them a new name. For the remainder, differences are so small and the overlap so considerable between island and mainland populations that identification of individuals becomes impracticable. It is proposed that they should be referred to as *A. sylvaticus sylvaticus* (L.). That considerable doubt has existed

about the nomenclature of Hebridean mice is suggested by Barrett-Hamilton & Hinton (1913) originally describing a number of island forms as *A. s. sylvaticus* and later Hinton (1914) making the same animals subspecies of *A. hebridensis*. Matthews (1952) suggested that differences have been overemphasized and samples too small. Unfortunately, the present work has not included all the islands from which named forms have been obtained and therefore, strictly, the subspecific names of these island forms should be retained. However, it seems probable that as in the foregoing analyses, if examined critically, the magnitude of their differences would prove to be small. An exception is the St Kilda field mouse (*A. sylvaticus hirtensis* (Barrett-Hamilton)) which is undoubtedly larger than any recorded from elsewhere in north-west Scotland (Boyd 1959) and which would appear a valid subspecies.

*Apodemus* in the area studied is apparently showing first signs of differentiation or incipient subspeciation. It would be of further interest to trace the extent of differentiation in various places on the mainland as well as on the larger islands and see if populations there could be related to any peculiarity of the local habitat. This would be of particular interest in the Outer Hebrides where this animal appears to be distributed in localized pockets (Delany 1961).

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