

Geographical variation and taxonomy of the Dunlin *Calidris alpina* (L.).

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This study examines in detail morphometric variation in the Dunlin *Calidris alpina* throughout its breeding range, with a view to determining the extent of geographical variation, considers the evolutionary history of the various populations, and discusses the taxonomic implications.

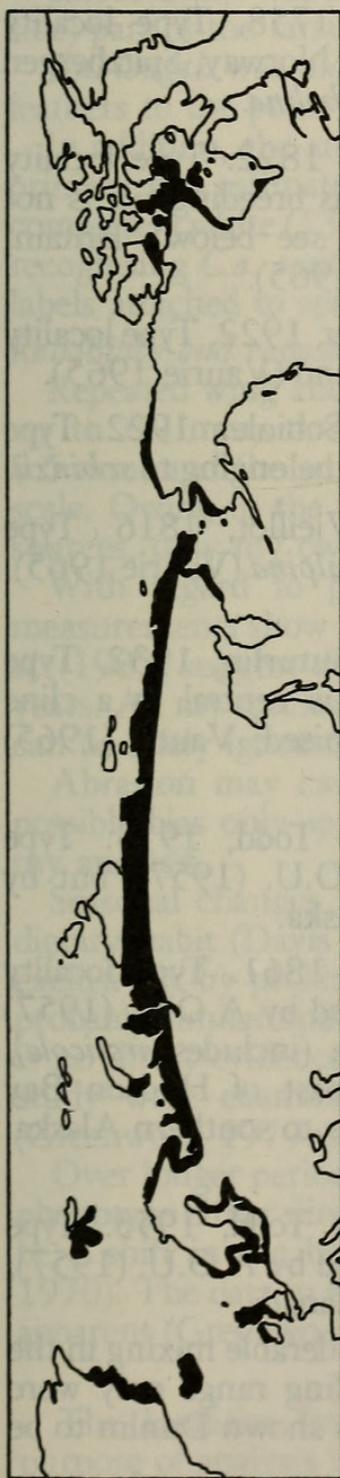


Figure 1. The breeding distribution of Dunlin *Calidris alpina*.

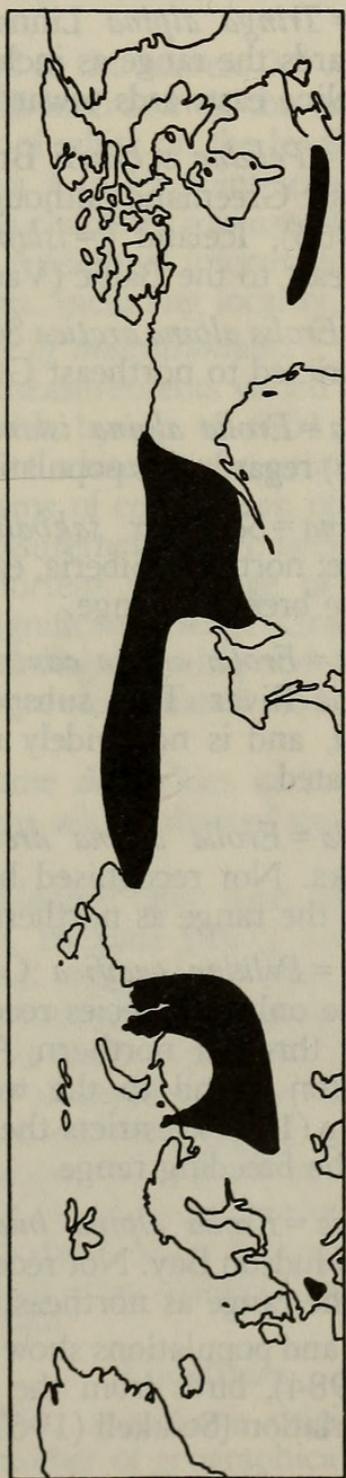


Figure 7. Tundra refuges that were utilised by Dunlin *Calidris alpina* during the last glaciation.

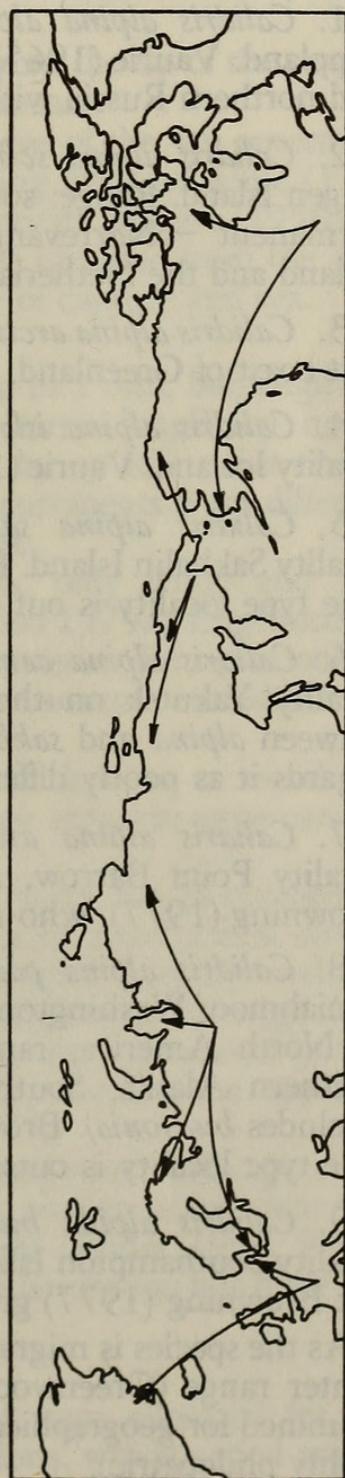


Figure 8. Movements of Dunlin *Calidris alpina* populations since the last glaciation.

The Dunlin's breeding distribution is mainly Holarctic, with intermittent gaps, and in some areas is sub-Arctic. Briefly, the range extends through northeast Greenland, Iceland, Britain, Ireland, the Baltic, southern Norway, Lapland, arctic Russia, northern and southern Alaska and northeast Canada (Fig. 1). Previous studies of geographical variation in Dunlin have concerned only restricted populations or only one or two characters: MacLean & Holmes (1971) and Browning (1977) examined variation in bill-length in North American populations, Väisänen (1977) egg dimensions in western Europe, Soikkeli (1966) bill-length and wing-length in western Europe, and Ferns & Green (1979) breeding-plumage variations of populations migrating through Britain.

Up to 9 subspecies of Dunlin are currently recognised.

1. *Calidris alpina alpina* = *Tringa alpina* Linnaeus, 1758. Type locality Lapland. Vaurie (1965) regards the range as including Norway, Spitzbergen and northern Russia with a cline eastwards towards *sakhalina*.

2. *Calidris alpina schinzii* = *Pelidna schinzii* Brehm, 1822. Type locality Rugen Island. Range: southeast Greenland (although this breeding site is not permanent – Nørrevang 1963), Iceland (= *islandica*, see below), Britain, Ireland and the Netherlands east to the Baltic (Vaurie 1965).

3. *Calidris alpina arctica* = *Erolia alpina arctica* Schiøler, 1922. Type locality east coast of Greenland. Restricted to northeast Greenland (Vaurie 1965).

4. *Calidris alpina islandica* = *Erolia alpina islandica* Schiøler, 1922. Type locality Iceland. Vaurie (1965) regards this population as belonging to *schinzi*.

5. *Calidris alpina sakhalina* = *Scolopax sakhalina* Vieillot, 1816. Type locality Sakhalin Island. Range: northeast Siberia, east of *alpina* (Vaurie 1965). The type locality is out of the breeding range.

6. *Calidris alpina centralis* = *Erolia alpina centralis* Buturlin, 1932. Type locality Yakutsk on the Lena River. This subspecies is central in a cline between *alpina* and *sakhalina*, and is not widely recognised; Vaurie (1965) regards it as poorly differentiated.

7. *Calidris alpina arcticola* = *Erolia alpina arcticola* Todd, 1953. Type locality Point Barrow, Alaska. Not recognised by A.O.U. (1957), but by Browning (1977), who gives the range as northern Alaska.

8. *Calidris alpina pacifica* = *Pelidna pacifica* Coues, 1861. Type locality Simiahmoo, Washington. The only subspecies recognised by A.O.U. (1957) in North America, ranging through northern Alaska (includes *arcticola*), southern Alaska, Southampton Island to the west coast of Hudson Bay (includes *hudsonia*). Browning (1977) restricts the range to southern Alaska. The type locality is outside the breeding range.

9. *Calidris alpina hudsonia* = *Erolia alpina hudsonia* Todd, 1953. Type locality Southampton Island, Hudson Bay. Not recognised by A.O.U. (1957), but Browning (1977) gives the range as northeastern Canada.

As the species is migratory and populations show considerable mixing in the winter range (Greenwood 1984), birds from the breeding range only were examined for geographical variation (Soikkeli (1967) has shown Dunlin to be highly philopatric).

Morphological characters examined

The following measurements of museum skins were used to examine geographical variation:

Wing-length. Maximum flattened primaries were measured to the nearest 0.5 mm. Both wings were measured and where there was a difference the longer measurement was used.

Bill-length. The upper mandible, from the tip to the beginning of the feathers was measured to the nearest 0.1 mm.

Tarsus-length was measured to the nearest 0.5 mm from the posterior aspect of the joint between the tarsometatarsus and tibiotarsus to the anterior aspect of the joint between the tarsometatarsus and the proximal phalange of the middle toe.

Tarsus-width was measured to the nearest 0.01 mm at the narrowest (side to side) part of the tarsus.

Tail-length was measured to the nearest 0.5 mm from the tip of the central feathers to the point of quill insertion on the undersurface.

In addition, the amount of white on the leading edge of the 4th outermost primary was estimated on a 1 to 13 point scale, rising from no white (1) to completely white (13). This character was used by Horvath & Keve (1956) for recognising *C.a. centralis*. Additional information was obtained from the data labels attached to specimens, including locality, date of capture and sex.

Reliability and repeatability of measurements

Repeated wing and tail measurements varied by up to 1 mm, bill-length by up to 0.1 mm, tarsus-width by up to 0.01 mm, tarsus-length by up to 0.5 mm, and the amount of white on the primaries by up to 1 point on the scale. Owing to the problems of comparison of measurements from different sources, only my own measurements have been used.

With regard to post-mortem shrinkage of skins, only wing- and tail-measurements show any significant change (Greenwood 1979a). Engelmoer *et al.* (1983) suggest that shrinkage of wing and tail continues for up to only 3 years. All my specimens were older than 3 years so this source of variable error can be safely ignored.

Abrasion may cause some difficulties in mensural data, so to avoid any possible bias only specimens which showed no feather abrasion were used in my analysis.

Seasonal changes in bill-length have been shown to be due to changes in dietary habit (Davis 1954, Packard 1967), but because Dunlin feed almost exclusively by probing at all seasons, the rates of abrasion and regrowth are probably similar and cause little seasonal change in bill-length, although there is no direct evidence of this from recaptured Dunlin. Measurements in this study were examined for seasonal change, but no trends were apparent (Greenwood 1979b), and so can be ignored.

Over longer periods, changes in the environment may cause a change in the phenotype either directly or by selection, genetic drift may occur, or there may be a shift in the breeding distribution of populations (Miller 1956, Power 1970). The data in this study were examined for secular change but none was apparent (Greenwood 1979b).

Localities

The localities from which specimens originated were allocated for the purpose of analysis to a number of geographical regions, which varied greatly

TABLE 1
Measurements of Dunlin *Calidris alpina*, giving mean values, standard deviations and (sample sizes).

Locality (see text)	Wing length/mm male female	Tarsus length/mm male female	Tarsus width/mm male female	Bill length/mm male female	Tail length/mm male female	White vane male female						
1	111.59 2.14 (52)	115.52 2.23 (32)	22.79 0.64 (52)	23.94 0.91 (32)	1.44 0.07 (52)	1.48 0.08 (32)	26.07 1.11 (51)	29.45 1.09 (31)	47.56 2.44 (52)	48.27 2.83 (32)	5.88 1.91 (52)	6.66 2.90 (32)
2	113.08 2.43 (75)	115.83 2.63 (56)	24.34 0.73 (75)	25.26 0.87 (56)	1.46 0.06 (74)	1.50 0.07 (55)	28.71 1.35 (69)	31.99 1.87 (51)	47.31 2.57 (75)	47.74 2.53 (57)	4.97 1.65 (74)	5.05 2.17 (57)
3	111.10 1.91 (21)	114.88 2.54 (13)	23.81 0.93 (21)	25.23 0.90 (13)	1.47 0.08 (21)	1.49 0.06 (13)	28.48 2.03 (21)	31.06 1.45 (13)	45.93 2.89 (21)	48.08 2.44 (13)	5.00 1.92 (20)	4.92 1.98 (13)
4	110.67 2.40 (24)	114.29 3.26 (24)	23.77 0.85 (24)	24.90 0.88 (24)	1.48 0.06 (24)	1.51 0.06 (24)	26.95 1.37 (22)	30.91 1.89 (22)	46.67 2.76 (24)	47.69 1.69 (24)	3.70 1.29 (23)	4.78 1.57 (23)
5	110.70 2.19 (10)	113.14 3.02 (7)	23.85 0.47 (10)	24.36 1.25 (7)	1.51 0.05 (9)	1.50 0.05 (7)	28.01 1.30 (10)	30.13 1.60 (7)	47.22 3.04 (9)	47.00 1.32 (7)	4.30 1.77 (10)	3.57 1.51 (7)
6	111.50 3.29 (59)	114.06 3.17 (45)	23.91 0.90 (58)	24.92 0.87 (45)	1.45 0.06 (58)	1.49 0.06 (45)	28.73 1.99 (59)	31.85 1.98 (43)	46.69 3.00 (59)	46.67 2.39 (46)	5.12 2.02 (58)	4.98 2.11 (45)
7	113.23 2.78 (11)	117.00 5.57 (3)	24.59 0.86 (11)	26.17 1.89 (3)	1.47 0.07 (11)	1.44 0.12 (3)	29.65 1.25 (11)	34.10 2.52 (3)	47.71 1.90 (11)	48.17 2.36 (3)	6.09 3.21 (11)	6.33 2.08 (3)

8	112.68 3.07 (14)	116.72 2.64 (16)	24.14 0.63 (14)	24.94 0.68 (16)	1.48 0.04 (14)	1.47 0.06 (16)	28.11 1.84 (14)	31.62 2.14 (16)	45.89 2.54 (14)	48.13 1.58 (16)	5.29 2.23 (14)
9	112.17 4.17 (12)	116.71 4.54 (7)	23.33 0.71 (9)	24.58 0.66 (6)	1.47 0.09 (9)	1.51 0.06 (6)	28.39 2.47 (12)	33.70 3.13 (6)	45.75 2.77 (12)	47.64 3.52 (7)	6.17 2.37 (12)
10	116.04 2.13 (25)	118.08 2.31 (19)	24.18 0.79 (25)	25.74 0.82 (19)	1.52 0.09 (23)	1.53 0.07 (18)	29.76 1.42 (23)	33.68 1.32 (19)	50.20 3.93 (25)	49.63 3.02 (19)	5.84 2.53 (25)
11	114.78 1.83 (18)	117.43 3.66 (7)	24.50 0.64 (18)	25.21 1.11 (7)	1.49 0.05 (18)	1.51 0.04 (6)	30.85 1.06 (13)	32.67 1.80 (7)	47.44 3.23 (18)	47.07 3.66 (7)	6.00 2.45 (18)
12	113.79 2.55 (12)	115.50 2.89 (4)	24.67 0.94 (12)	25.75 1.04 (4)	1.52 0.07 (12)	1.56 0.04 (4)	31.74 1.61 (12)	34.20 3.09 (4)	49.54 3.88 (12)	51.88 4.52 (4)	5.36 3.35 (11)
13	118.14 3.19 (14)	119.06 2.99 (8)	25.61 0.84 (14)	26.25 0.53 (8)	1.50 0.08 (15)	1.54 0.10 (8)	32.01 1.74 (15)	35.09 2.47 (8)	47.96 3.90 (14)	47.56 3.45 (8)	10.33 3.45 (15)
14	121.36 2.44 (58)	124.99 2.88 (41)	26.56 0.96 (62)	27.54 0.78 (42)	1.54 0.06 (63)	1.57 0.06 (42)	36.69 1.93 (62)	40.19 1.45 (41)	51.37 2.90 (61)	52.44 3.01 (42)	8.78 3.01 (60)
15	121.76 2.59 (78)	125.08 2.07 (53)	26.19 0.77 (87)	27.13 0.83 (65)	1.54 0.05 (87)	1.56 0.06 (66)	33.78 1.71 (85)	36.59 1.98 (66)	51.20 2.88 (80)	51.70 2.85 (57)	12.29 1.50 (75)
16	120.28 1.62 (9)	121.57 2.13 (7)	27.39 0.60 (9)	27.63 0.64 (8)	1.58 0.06 (37)	1.59 0.03 (8)	32.26 1.08 (9)	39.03 1.44 (8)	48.72 2.53 (9)	48.56 1.94 (8)	10.25 1.17 (8)
17	119.55 2.44 (37)	122.15 2.22 (27)	27.01 1.10 (37)	27.44 0.76 (27)	1.55 0.06 (9)	1.58 0.05 (27)	36.38 1.84 (37)	39.06 1.69 (27)	48.96 2.43 (36)	50.26 2.44 (27)	9.36 2.40 (27)

in size, each having to be large enough to produce sufficient specimens for statistical analysis and yet small enough to show the fine detail of geographical variation. Each specimen was allocated to one of 17 localities:

1. NE Greenland.
2. Iceland.
3. Great Britain, north of 58°N.
4. Great Britain, 55°N–58°N.
5. Great Britain, south of 55°N, and Ireland.
6. S and SE Baltic.
7. Finland.
8. S Norway.
9. S Sweden.
10. Lapland.
11. W Siberia, east to the Ural Mts.
12. Siberia, from the Ural Mts to the Yenesei Valley.
13. E Siberia, west to the Yenesei Valley.
14. S Alaska, north to Cape Prince of Wales.
15. N Alaska, south to the Brooks Range.
16. NW Hudson Bay.
17. SW Hudson Bay.

Analysis of data

The specimens analysed were those obtained within the breeding range between May and July inclusive. Some specimens collected in April and August were regarded as breeders if they were obtained in areas where immigration from other localities was unlikely, and indeed, verification of breeding status was often found on the specimen's label. The sex of the individual, if known, was taken from the data label. In addition, birds were separated sexually in western Europe by slight variation in neck plumage (Soikkeli 1966), although this differentiation is not applicable to Alaskan populations (R. T. Holmes). The initial analysis determined the mean, standard deviation and sample size for all characters and both sexes at each locality.

The usual criterion of statistical significance is $P = 0.05$, which clearly presents problems when one is performing many significance tests simultaneously, as here, and there is no agreed solution, though it is generally accepted that one should adopt a more stringent significance criterion. I have therefore followed the recommendation of Cooper (1968) that this should be $\alpha - P = 0.05/n$, where n is the number of tests being performed.

RESULTS

Univariate analysis of inter-locality variation

The initial data are shown in Table 1. For all characters, the smallest means are generally found in Greenland and the western Palaearctic, and the largest in the eastern Palaearctic and the Nearctic. In order to examine the significance of this variation, I have used Gabriel's Sums of Squares Simultaneous Testing Procedure (SS-STP) (Gabriel & Sokal 1969). The test is used to detect significant differences between subsets of samples within the total number of samples. My analysis treated sexes separately because Dunlin are sexually dimorphic (Greenwood 1979b). Prior to using SS-STP, the data were analysed by Anova, and as 12 of these analyses were performed (2 sexes \times 6 characters) a modified significance level of $\alpha - P = 0.004$ was used. The anovas showed there was significant difference ($P < 0.001$) within males and females for all characters. Anovas enabled the calculation of coefficients of intra-class correlation and showed (Table 2) that wing-length, tarsus-length and bill-length are particularly important in describing inter-locality variation.

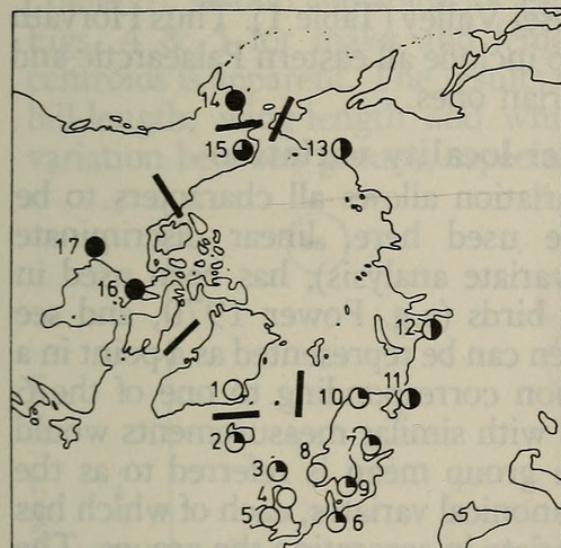
The results of the SS-STP provide the geographical patterns, and the all-important bill-lengths of males and females are shown in Figs. 2 & 3 respectively. The lines to the right of the means show those subsets within which the differences between samples are not significant, that is when the

TABLE 2

Univariate analysis of inter-locality variation in Dunlin *Calidris alpina*. Results of Anova. All F-ratios are significant at $P < 0.001$ for the degrees of freedom (d.f.) shown. A high coefficient of intra-class correlation indicates that the character is important in interpreting inter-locality variation.

Character	Sex	F-ratio	d.f.	Coefficient of intra-class correlation/%
Wing-length	M	91	16,512	75
	F	58	16,352	73
Tarsus-length	M	89	16,521	74
	F	48	16,365	69
Tarsus-width	M	14	16,519	29
	F	8	16,363	25
Bill-length	M	130	16,508	81
	F	85	16,355	80
Tail-length	M	15	16,515	32
	F	13	16,360	37
White vane	M	19	16,506	62
	F	35	16,353	62

samples are arranged in order of means and when subsets are omitted whose members are all contained in a larger subset. Maps of variation in the other characters can be inspected in Greenwood (1979b).



1	\bar{x}	s	n
1	26.07	1.11	51
4	26.95	1.37	22
5	28.01	1.30	10
8	28.11	1.84	14
9	28.39	2.47	12
3	28.48	2.03	21
2	28.71	1.35	69
6	28.73	1.99	59
7	29.65	1.25	11
10	29.76	1.42	23
11	30.85	1.06	13
12	31.74	1.61	12
13	32.01	1.74	15
15	33.78	1.71	85
16	36.26	1.08	9
17	36.38	1.84	37
14	36.69	1.93	62

Figure 2. Inter-locality variation of bill-length of male Dunlin *Calidris alpina*. Means (\bar{x}) are ranked in increasing order of magnitude, along with locality number (1), standard deviation (s), and sample size (n). Lines to the right of these data each represent a maximal non-significant subset resulting from comparisons using SS-STP (for further explanation see text). Occasional bars separating localities on the map indicate those adjacent localities which are significantly different mensurally from one another. The populations with the largest means for bill-length are represented by solid circles, the smallest by open circles. The intervals were obtained by dividing the range of means into 5 equal parts.

For all the morphological characters, the correlations between male and female mean measurements were significant and can be taken as evidence for ordered geographical variation (Greenwood 1979b). Correlation coefficients were calculated between all pairs of characters, using sample means rather than individual measurements: all were positively correlated, and only 4 out of the 30 were not significant (Greenwood 1979b). Bill-length is the character that appears to show the most extensive variation (Figs. 2 & 3), and also shows the greatest discriminating power between localities (Table 2). Horvath & Keve (1956) suggested that a larger amount of white on the leading edge of the

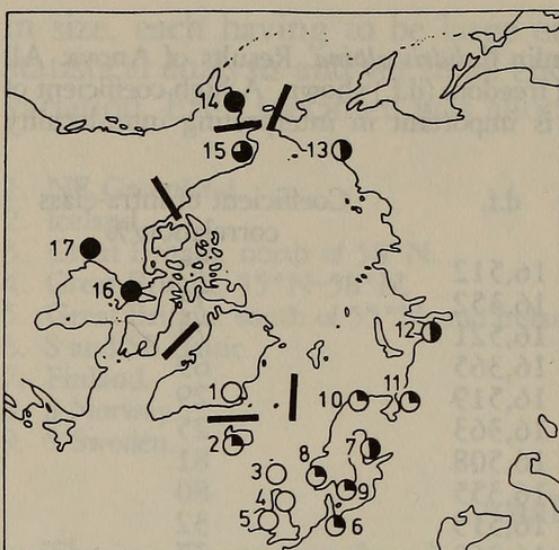


Figure 3. Inter-locality variation of bill length in female Dunlin *Calidris alpina* (see Fig. 2 for explanation).

fourth primary (white vane) could be used to separate central Siberian populations from those to the west which had less white. My results show that mean scores of less than 7 occur to the west of the Yenesei Valley, and mean scores above 7 occur to the east of the Yenesei Valley (Table 1). Thus Horvath & Keve's statement needs to be modified to include all eastern Palaearctic and Nearctic populations with the central Siberian ones.

Multivariate analysis of inter-locality variation

Multivariate analysis of geographical variation allows all characters to be examined simultaneously. The technique used here, linear discriminate analysis (LDA, also known as canonical variate analysis), has been used in other studies of geographical variation in birds (e.g. Power 1970, and see Greenwood 1979b.). An individual specimen can be represented as a point in a hyperspace of 6 dimensions, each dimension corresponding to one of the 6 measurements used. A group of specimens with similar measurements would be represented by a cluster of points. The group mean is referred to as the group centroid. LDA creates new axes or canonical variates, each of which has a value indicating the importance of that variate in separating the groups. The relative contributions of the characters to each canonical variate are represented by an 'eigenvector' (latent vector). Because LDA considers all characters together, specimens with data missing for one or more characters had to be omitted from the analysis.

A multivariate analysis of variance was performed in this way on the 6 Dunlin characters together, and the Wilks' lambda statistics for each character and for each canonical variate were converted for convenience to univariate F-ratios and chi-square respectively to test the significance of the inter-locality differences in the characters and in the canonical variates.

As in the univariate analysis, the sexes were considered separately, 474 males and 331 females. LDA requires that each sample contains at least one more specimen than the number of characters used, and some of the localities contained insufficient females for analysis. They were pooled with adjacent localities – locality 6 with 7, 8 with 9, and 11 with 12, since the univariate analysis showed no significant differences between pooled localities (except for tail-length between localities 11 and 12).

	1	\bar{x}	s	n
○	1	29.45	1.09	31
○	5	30.13	1.60	7
○	4	30.91	1.89	22
○	3	31.06	1.45	13
○	8	31.62	2.14	16
○	6	31.85	1.98	43
○	2	31.99	1.87	51
○	11	32.67	1.80	7
○	10	33.68	1.32	19
○	9	33.70	3.13	6
○	7	34.10	2.52	3
●	12	34.20	3.09	4
●	13	35.09	2.47	8
●	15	36.59	1.98	66
●	16	39.03	1.44	8
●	17	39.06	1.69	27
○	14	40.19	1.45	41

TABLE 3

Eigenvectors (see text) in a multivariate analysis of inter-locality variation in Dunlin *Calidris alpina*. The absolute value of each element measures the relative contribution of the relevant canonical variate.

Character	Sex	Canonical variates					
		1	2	3	4	5	6
Wing-length	M	-0.41	1.03	-0.24	-0.70	1.46	1.19
	F	-0.54	1.07	1.06	-0.40	0.62	1.20
Tarsus-length	M	-0.37	-0.35	1.70	-1.04	-0.12	-0.73
	F	-0.42	-0.33	-0.96	-1.54	0.25	-0.58
Tarsus-width	M	-0.13	-0.05	-0.05	-0.23	-0.93	0.69
	F	-0.10	-0.10	-0.20	-0.11	-0.96	0.60
Bill-length	M	-1.58	-1.54	-1.20	1.36	-0.06	-0.07
	F	-1.38	-1.38	0.41	1.52	0.21	0.06
Tail-length	M	-0.07	0.20	-0.58	-0.51	-0.54	-0.90
	F	-0.09	0.13	0.46	-0.18	-0.65	-0.94
White vane	M	-0.50	1.11	0.26	0.87	-0.48	-0.33
	F	-0.39	0.90	-0.89	0.61	-0.16	-0.39

There was significant inter-locality variation for all characters, greatest for bill-length in both males and females. The first and second canonical variates explain nearly 95% of the variation in males and nearly 96% in females, with bill-length, white-vane, and wing-length contributing most to these variates (Table 3). Group centroids for each locality sample are plotted graphically in Figs. 4 & 5 for males and females respectively; clustering of some group centroids is apparent. The results for LDA for the 2 sexes were clearly similar: bill-length, wing-length and white-vane being responsible for the greatest variation between groups, especially bill-length.

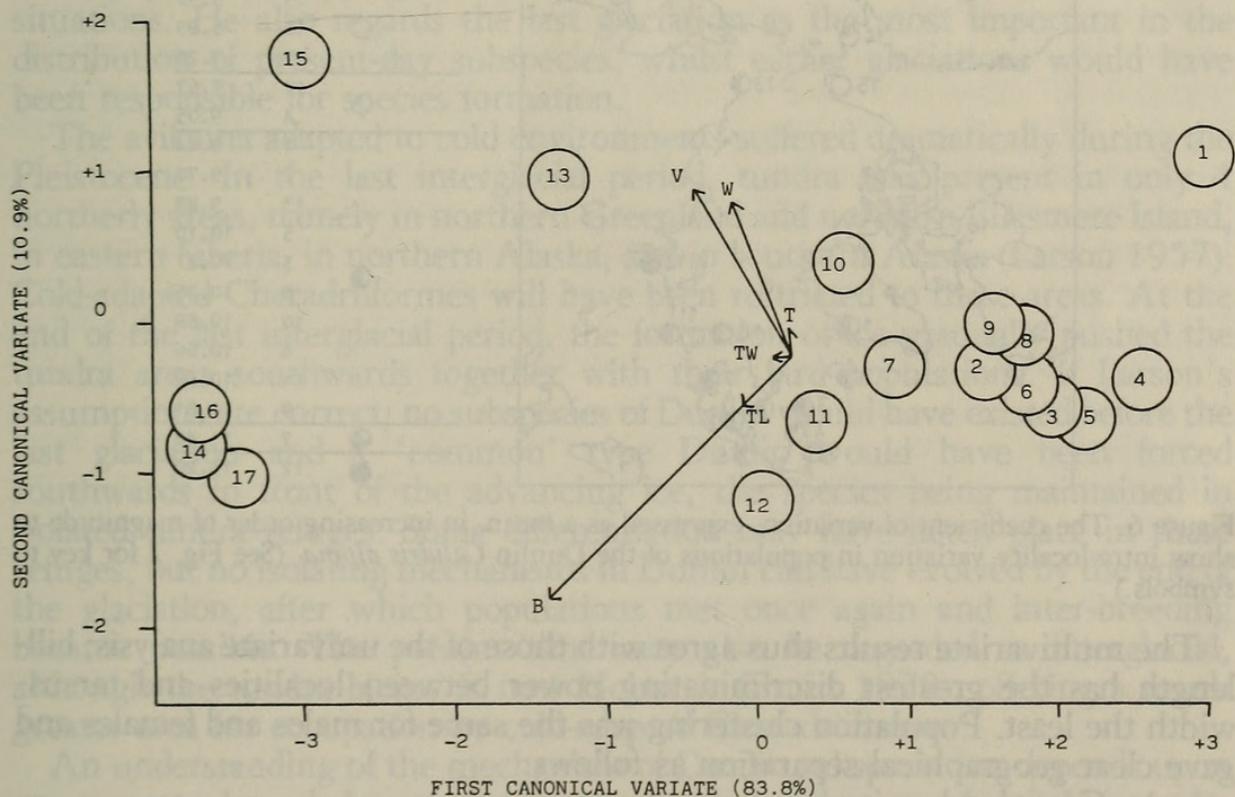


Figure 4. Linear discriminant analysis for samples of male Dunlin *Calidris alpina*. Group centroids for each locality are plotted on the first two canonical variates. The superimposed vectors emanate from the grand mean and their lengths reflect their contributions to the variation accounted for by these canonical variates, and their angles their relative contributions to the two variates. The characters are abbreviated; W, wing-length; TL, tarsus-length; TW, tarsus-width; B, bill-length; T, tail-length; V, white-vane.

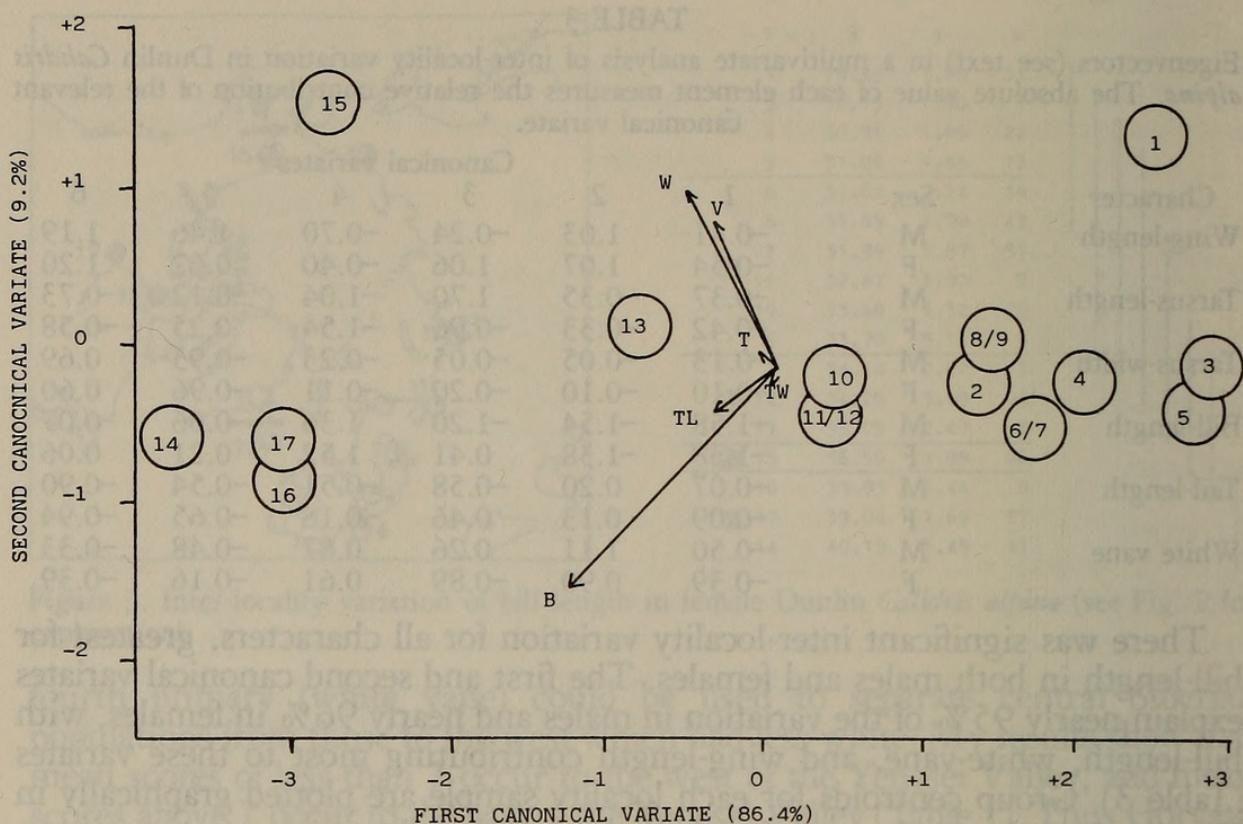
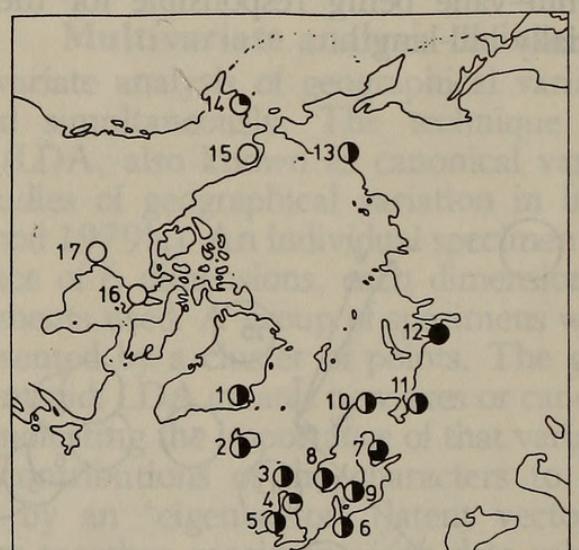


Figure 5. Linear discriminant analysis for samples of female Dunlin *Calidris alpina* (see Fig. 4 for explanation).



	1	\bar{x}
○	15	5.55
○	16	5.89
○	17	7.28
○	14	7.67
○	4	9.05
●	1	9.64
●	2	9.77
●	13	9.87
●	5	10.10
●	3	10.21
●	8	10.35
●	10	10.58
●	6	10.66
●	11	10.99
●	9	11.31
●	7	11.38
●	12	15.20

Figure 6. The coefficient of variation, expressed as a mean, in increasing order of magnitude to show intra-locality variation in populations of the Dunlin *Calidris alpina*. (See Fig. 2 for key to symbols.)

The multivariate results thus agree with those of the univariate analysis; bill-length has the greatest discriminating power between localities and tarsus-width the least. Population clustering was the same for males and females and gave clear geographical separation as follows:

1. Greenland;
2. Iceland, the British Isles, and the Baltic coasts;
3. Lapland, western and central Russia;
4. Eastern Russia;
5. Northern Alaska;
6. Southern Alaska and Canada.

Intra-locality variation

The coefficient of variation was used to express the character variation at each locality, and was calculated for each character; although the magnitudes varied with each character, the pattern of variation between localities was similar for all 6 characters both for the sexes combined and separate, thus demonstrating ordered geographical variation. A mean coefficient of variation was calculated for each locality to show up the geographical patterns (Fig. 6). The greatest intra-locality variations were in Finland and central Russia, the least variable were in Canada and northern Alaska; geographically intermediate populations showed intermediate levels of variation.

DISCUSSION

Evolution of Geographical Variation

It is generally recognised that the glacial and interglacial events of the Pleistocene have been important in speciation and subspeciation of birds and other organisms by causing geographic isolation of populations and thus opportunity to diverge. Such geographic isolation does not necessarily lead to the formation of new species (Mayr 1970) and when isolated populations meet once again the secondary contact may cause no more than clines. However, such clines may form the basis for subsequent speciation (allo-parapatric), while if populations remain differentiated after secondary contact then allopatric speciation has taken place (Endler 1977).

Larson (1957) regards the Charadriiformes as having evolved during the tertiary period, many species being adapted then to living in cold tundra situations. He also regards the last glaciation as the most important in the distribution of present-day subspecies, whilst earlier glaciations would have been responsible for species formation.

The avifauna adapted to cold environments suffered dramatically during the Pleistocene. In the last interglacial period, tundra was present in only 4 northerly areas, namely in northern Greenland and northern Ellesmere Island, in eastern Siberia, in northern Alaska, and in southern Alaska (Larson 1957). Cold-adapted Charadriiformes will have been restricted to these areas. At the end of the last interglacial period, the formation of ice gradually pushed the tundra areas southwards together with their bird populations. If Larson's assumptions are correct, no subspecies of Dunlin would have existed before the last glaciation and a 'common' type Dunlin would have been forced southwards in front of the advancing ice, the species being maintained in isolated tundra refuges. Some differentiation may have taken place in these refuges, but no isolating mechanisms in Dunlin can have evolved by the end of the glaciation, after which populations met once again and inter-breeding became possible. The present time may also be regarded as interglacial, although the tundra biome is now Holarctic (Pruitt 1978), offering a much greater area for occupation by cold-adapted Charadriiformes.

An understanding of the mechanism of Dunlin subspeciation depends upon an accurate knowledge of the geographical distribution of suitable tundra refuges during the last glaciation. Earlier deductions regarding differentiation (Johansen 1956, 1958, Larson 1957) were based upon less knowledge of positions and extents of refuges than is now available. Further Palaeobotanical research has provided fresh information (Frenzel 1968) which, together with the earlier work (Larson 1957), shows that 4 tundra refuges existed during the

last glacial period: one in France, the second in central Siberia, the third, the Beringian, extending from eastern Siberia across the Bering Sea to Alaska, and the fourth in North America extending east from the Rocky Mountains (Fig. 7). On the assumption that at the height of the last glaciation, some 25 000 years BP, Dunlin populations were isolated in these 4 tundra refuges, and if modern characteristics of Dunlin reflect evolutionary history to some extent, then the course of differentiation may be reconstructed with the acceptance of these 4 tundra refuges, together with the existence of 6 geographical groups of Dunlin as shown by the results of LDA.

During the next 15 000 years the ice retreated to a distribution similar to that today (Moreau 1954). It seems likely that the Dunlin population in the small, very isolated French refuge spread northwards on the retreat of the ice, eventually colonising Greenland. The central Siberian population spread westwards and formed a zone of secondary contact in northwestern Europe with Dunlin from the French refuge. The Beringian population became divided by the rising sea-level at the end of the glaciation causing the Bering land bridge to disappear: the population isolated in eastern Siberia remained there and possibly advanced westwards to form a zone of secondary contact in central Siberia with birds from the Siberian refuge, while the eastern Beringian population remained in northern Alaska. The Dunlin from the North American refuge will have spread north and diverged into 2 groups, one westwards into southern Alaska, the other into northeast Canada (northwest Canada holds no Dunlin). Fig. 8 illustrates these postglacial events.

This account of events suggests that 2 zones of secondary contact were formed, one in northwest Europe and the other in central Siberia. The analysis of intra-locality variation gives support to this: it is generally recognised that populations show increased variability in areas of secondary intergradation (Endler 1977, Mayr 1969) and the 2 localities with the highest coefficients of variation are around the Baltic and in central USSR. In probable zones of secondary contact in Redshank *Tringa totanus*, Hale (1971) found that full breeding plumage was often not assumed. Although the extent of full breeding plumage was not quantified in this study, it is known that Dunlin from western Europe assume only an incomplete black belly-patch in their pre-nuptial moult (Witherby *et al.* 1940). This has not been noticed in skins of central Siberian populations.

Evidence of a zone of secondary contact in western Europe has come from other studies of Charadriiformes, including both northern and temperate species, e.g. Ringed Plover *Charadrius hiaticula* (Taylor 1978), Golden Plover *Pluvialis apricaria* (Hale 1980) and Black-tailed Godwit *Limosa limosa* (Rynn 1982).

Taxonomy of *Calidris alpina*

The analysis of Dunlin morphometrics clearly shows the existence of 6 geographical groups. Birds from Greenland are geographically isolated from all other groups and may be distinguished by their short bills. A second group of Dunlin from Iceland, the British Isles, the Baltic and southern Scandinavia are also geographically isolated. A third group shows obvious clinal variation from Lapland eastwards to central Siberia, a cline shown mainly by increasing bill-length. There is a step in the cline, with populations east of the Urals starting post-nuptial primary moult on the breeding grounds and populations to the west of the Urals as far as Greenland starting this moult away from the

breeding grounds (Greenwood 1983). A fourth group, which is contiguous with the third, is apparent in eastern Siberia: it is distinguished from more westerly populations by its longer wings. A fifth group is spatially separated from all others in northern Alaska. The final group concerns birds from southern Alaska and Canada. Although the members of this group are morphometrically similar, they may be separated into 2 component populations which have separate ranges on both the breeding and the wintering grounds (Greenwood 1984). Based upon this I accept 7 subspecies.

arctica: range, northeast Greenland;

schinzii: range, Iceland, the British Isles, western Europe, the Baltic and southern Scandinavia;

alpina: range, Lapland and northwest USSR – the precise eastern limit is difficult to determine as so few skins were available for examination from northern Russia, but the range may well include the Taimyr peninsula;

sakhalina: range, eastern USSR. The precise western limit is difficult to determine due to lack of specimens, but probably extends to the Lena valley;

arcticola: range, northern Alaska;

pacifica: range, southern Alaska;

hudsonia: range, North West Territories, Canada.

I reject 2 subspecies: *islandica*, because the population is morphometrically similar to others from the hybrid zone of *schinzii*; and *centralis*, because the evidence for a zone of secondary contact in northern Siberia between *sakhalina* and *alpina* is so slight. Studies of Dunlin in the region of the Khrebet Orulgan Mountains may help to determine whether such a zone exists.

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Notes on Philippine birds, 8. A collection from Mindoro revisited

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Blasius (1897a, b) published only abbreviated results of the collecting carried out in Mindoro by Dr Platen and his wife from April to November 1890, and did so in a relatively obscure journal, perhaps because by that time the results of 3 later collections had been published and the Platens had lost the credit for 42 forms that they had in fact been the first to collect in Mindoro (see Appendix 1). Hartlaub (1899) made a reference to the reports of Blasius but subsequently virtually no author dealing with the Philippines in general or Mindoro in particular has referred to them. In consequence, although Blasius



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