

## The Relation between Variability and Abundance shown by the Measurements of the Eggs of British Nesting Birds

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### I—ORIGINS OF RESEARCH

For some years it has appeared to the author of importance to ascertain by collocation of direct observations whether, in fact, Darwin's generalization that "widely distributed, much-diffused and common species vary most", is well established; and, if so, whether we can form an idea of the quantitative relationship between variability and abundance. In a paper published nine years ago in collaboration with Mr E. B. Ford (1928), I examined the variability, shown by Mr Ford's observations, of thirty-five species of night-flying moths, mostly British, from which examination it appeared that the difficulties in the way of comparing variabilities could be overcome at the expense of some elaboration of the calculations. When a satisfactory basis of comparison had been obtained it appeared that in both sexes the group of species classified in entomological handbooks as "abundant" or "very common" were, in fact, on the average, some 60% more variable than the group of species classified as less than common, while the group of species classified as common held, in both sexes, an intermediate position. Within each of these three groups there was a wide range of variability and I should give an altogether false impression if I suggested that variability among these thirty-five species was closely associated with abundance, or that, if influenced by abundance, it is not also much influenced by other causes. Nevertheless, the apparent influence of abundance was, in this research, statistically significant, and encouraged me to think that other cases might be found in which the reality of the phenomenon could be tested and its numerical importance gauged.

For many years the Rev. F. C. R. Jourdain has made and compiled measurements of considerable numbers of the eggs of British nesting birds. At the suggestion of Mr Julian Huxley, I approached Mr Jourdain, proposing at the same time that, in order to ensure the preservation of the large number of individual measurements he had made, I could have them copied in my

department, in a form suitable for permanent preservation in the Archives, which the British Museum (Natural History) had established for the reception of bodies of original biological measurements. Mr Jourdain very kindly let me have his measurement sheets from time to time, and, over a period of 5 years, the primary reduction of each set of 200 measurements was carried out, species by species. It is the result of this undertaking that I wish here to put on record. I desire that it should be understood that I myself took no part in the collection or measurement, and could have undertaken no part of the work had not Mr Jourdain's measurements been generously placed at my disposal. I trust that the original data will eventually be made public, by being deposited at South Kensington: for my own enquiry is not the only one that might be based upon them, and it may be that I should have done better if, in some respects, I had treated the data somewhat differently.

Measurements of eggs have been used solely because they are available, and the data have the particular value that they allow a large number of species to be compared, each species being represented by a fairly considerable sample. The relative size of different individuals would certainly be better represented by measurements of representative bones, or by the total weight of the body. In undertaking the research I felt no assurance that the measurements of the eggs did not vary so greatly from causes unconnected with the size of the mother as to make them useless as a gauge of variability in the different species. Had that been the case, I should merely have failed to establish any association between variability and other factors. It was a ground for hesitating to undertake the enquiry, not for hesitating to accept any results to which it might lead.

Had the data been collected for the object I had in view, it would have been preferable to measure 100 eggs of different clutches, rather than a total of 100 eggs from a variable number of clutches which were much larger, for example, among the game birds than among the pigeons. On trial I find that measurements of eggs belonging to the same clutch very generally vary less than do eggs from different clutches, so that, had it been necessary to try to compare the variabilities of species of different orders, the comparison would have been appreciably more precise if only one egg had come from each nest. The available data, however, had not been collected in this way, and the varying size of the clutch thus provided only one more reason for restricting the comparisons within groups of related birds. I have not thought it necessary to apply the refinement of eliminating the variability within clutches, but have taken the series of 100 measurements available as representing each species. The similarity of the measurements of eggs

of the same clutch, while it has been thus a minor technical embarrassment, is satisfactory evidence that measurements of the eggs are, in a real sense, indirect measurements of their mothers.

## 2—THE EQUILIBRIUM OF MUTATION AND SELECTION

The theoretical reasons for anticipating a higher variability associated with a numerically larger population are recondite and by no means fully understood. They depend on the balance of selective and mutational agencies, by which the genetic variability of natural populations must be determined. It is because we cannot easily predict these *a priori* that direct empirical knowledge is of importance. In respect of variations conditioned environmentally, there is no reason to suppose that these would be greater or less in a dense than in a sparse population. The same is true of that fraction of the variability which is caused by deleterious mutations. To these all species appear to be exposed. It is important to note that these are the only mutations which can have an appreciable mutation rate. Some of them, in *Drosophila* and maize, have mutation rates of the order of one in a million in each generation, and a few are even more frequent. But no beneficial mutation, even if the benefit it conferred were almost infinitesimally slight, can have a mutation rate of this order, else it would long ago have established itself throughout the species concerned, and so would no longer appear as a mutation. We are therefore left to consider only "neutral" mutations, together with the beneficial mutations which must be exceedingly infrequent. In saying this I do not refer to the aggregate frequency; for the different kinds of mutations possible may be exceedingly numerous. Each of these kinds, however, must be so infrequent in its occurrence that, in the entire species, each occurs no more frequently, perhaps, than once in a thousand generations.

A perfectly neutral mutation is, of course, a mathematical fiction, like a perfect equipoise between the weights on the scales of a balance. Moreover it has been shown (Fisher 1930) that to be effectively neutral the equipoise between the selective advantages of the contrasted genes must be almost incredibly exact. It is difficult, therefore, to claim for this class of mutations any real importance. Its importance for us rests on the fact that, like other mathematical fictions, it affords a convenient basis for calculation.

If species of different populations were supplied at the same absolute rate with different neutral mutations, each occurring with extreme rarity, then calculation shows that the number of factors maintained in the

heritable variance of the species would be nearly proportional to the logarithm of the population. For example, if one appeared in each generation, this would be enough in a population of a million to maintain, on the average, 30.4 factors segregating. While in a population of a billion (a million million) it would be enough to maintain 58.0. The additional segregating factors in the more numerous species would, indeed, add little to its observable variance because of the very great inequality of the gene ratios with which, in such species, factors can be maintained. They would, on the other hand, be available to increase the observable variance whenever, by change of circumstances, the mutant gene happened to become slightly advantageous. When this occurs the gene ratio will shift slowly towards equality, and the contribution of the factor in question to the observable variability of the species will steadily increase, until the rival genes are equal in numbers. After this it will decrease again as the new gene replaces the old. Such a course of events must often take thousands of generations. It appears that only if the more numerous species, through its capacity for keeping a larger number of neutral mutations in store for future use, or because of the larger number of individuals exposed to the chance of very rare advantageous mutations, manages to maintain a larger supply of new genes, each gradually spreading throughout the whole population, that its observable variance will be larger than that of a species of smaller population. Hence, although I believe many unknown factors may largely affect the variation of different species, any consistent difference in variability, observable between more and less populous species, must be ascribed to that fraction of the specific variance contributed by those particular factors by means of which evolutionary progress is now taking place. It is for this reason that I believe the attempt to ascertain whether such a difference in variability can be measured is worth the very considerable computational labour which the attempt involves. It would be too much to claim that we have here a means of measuring the rate of evolutionary progress. What it does supply is the order of magnitude of the contribution to the observable variance, of those genetic factors by means of which evolutionary progress is now proceeding.

### 3—THE CALCULATION AND ADJUSTMENT OF VARIABILITY

Table I shows for each of 180 populations of birds the five statistics calculated from the measured lengths and breadths of, in nearly all cases, 100 eggs. If  $x$  and  $y$  stand for the length and breadth of any egg, these five statistics are the following:

(i) The mean length and mean breadth calculated from the formulae

$$\bar{x} = \frac{1}{n}S(x),$$

$$\bar{y} = \frac{1}{n}S(y),$$

where  $n$  stands for the number of eggs measured and  $S$  for summation over the observed values.

(ii) The mean squares and product of deviations from the means, namely the variance of length

$$\frac{1}{n-1}S(x-\bar{x})^2,$$

the variance of breadth  $\frac{1}{n-1}S(y-\bar{y})^2,$

and the covariance of length and breadth

$$\frac{1}{n-1}S(x-\bar{x})(y-\bar{y}).$$

The first four of these statistics are always positive, but the covariance, though in fact it is generally positive, may be of either sign. For example, among the thirteen gulls in the list, the covariance is positive in all cases save the Arctic skua (*Stercorarius parasiticus*) for which it has a small negative value.

An examination of any group, such as the gulls, displays the first difficulty encountered in making any valid comparison of variability. The smallest bird of the group, the lesser tern (*Sterna albifrons*) has a variance in length just under 2 mm.<sup>2</sup>, and in breadth a little more than 0.5 mm.<sup>2</sup>, while the largest of the group, the greater black-backed gull (*Larus marinus*) gives 7.4 mm.<sup>2</sup> for length and 2.0 mm.<sup>2</sup> for breadth. Both values are nearly four times as great as those for the smaller bird. Obviously, in both cases the variance is much greater chiefly because the eggs are much larger. The mean length for the black-backed gull, 77 mm., is considerably more than twice that for the lesser tern, 33 mm., while the breadth also is greater in nearly the same proportion. It is clear that no valid comparison of variabilities can be made unless a method is found of making allowance for the average length and breadth observed in each species. Owing to the wide range in size in almost all the groups, these allowances will have to be considerable in magnitude, and the validity of the comparisons to be made must depend entirely on this process having been properly carried out, both as to principle and as to accuracy.

TABLE I—PRIMARY STATISTICS AND STANDARDIZED VARIANCES OF EGG LENGTH AND EGG BREADTH FOR  
180 POPULATIONS OF BRITISH NESTING BIRDS

	No. of eggs	Mean length mm.	Mean breadth mm.	Variances			Co- variance mm. <sup>2</sup>	Standardized variances	
				Length mm. <sup>2</sup>	Breadth mm. <sup>2</sup>	Length Breadth		Length	Breadth
Accipitres									
<i>Aquila chrysaetus</i> L.	100	77.020	59.485	15.708	6.9698	4.5164	83.81	125.55	
<i>Haliaeetus albicilla</i> L.	54	75.809	58.709	16.401	7.6514	9.5308	87.58	130.76	
<i>Buteo buteo</i>	100	56.798	45.445	4.8317	2.6469	2.8689	67.54	107.50	
<i>Milvus milvus</i>	58	56.978	45.090	6.8614	1.8381	1.6926	81.51	92.50	
<i>Falco peregrinus</i> T.	100	51.803	41.001	3.7375	1.6007	0.61182	65.12	95.09	
<i>Fernis apivorus</i> L.	23	50.383	41.717	3.2206	1.5224	1.1442	65.32	90.89	
<i>Circus cyaneus</i> L.	107	46.305	36.077	6.4417	2.0039	1.4445	99.26	116.60	
<i>Falco subbuteo</i> L.	100	41.573	32.732	2.1186	1.2276	0.40279	63.15	104.01	
<i>Accipiter nisus</i> L.	100	39.827	31.836	4.7697	2.3955	2.5186	104.14	135.41	
<i>Falco tinnunculus</i> L.	100	39.737	31.771	2.3015	0.95622	0.64694	72.75	95.72	
<i>Falco columbarius</i>	100	39.950	31.267	1.5714	0.88244	0.45833	53.87	93.88	
Alcae									
<i>Uria aalge</i>	100	81.726	50.063	8.4545	3.4302	1.5346	31.44	112.75	
<i>Uria aalge albionis</i> W.	100	81.466	49.671	12.865	3.2526	2.4427	49.63	111.20	
<i>Alca torca</i> L.	100	73.080	46.889	9.7063	2.9012	2.1057	53.05	110.92	
<i>Fratricula arctica</i> L.	100	60.802	42.297	4.3010	1.4227	0.02890	43.72	88.48	
<i>Uria grylle</i> L.	102	58.243	39.743	3.7772	1.3641	0.66939	41.02	92.48	
Anseres									
<i>Anser anser</i> L.	100	85.319	58.040	15.764	4.9455	3.9656	62.73	114.16	
<i>Somateria mollissima</i> L.	100	77.146	50.712	10.812	1.9449	1.9004	54.05	86.22	
<i>Tadorna tadorna</i> L.	100	65.813	47.594	3.2922	1.3453	0.14374	27.02	74.96	
<i>Meergus merganser</i> L.	100	66.383	46.409	2.7051	1.2447	0.54490	14.74	74.23	
<i>Meergus serrator</i> L.	100	65.559	45.120	4.3424	1.2273	-0.01150	35.35	76.31	
<i>Oedemia nigra</i> L.	72	65.226	44.849	5.5880	1.4361	0.36474	46.50	83.72	
<i>Nyroca ferina</i>	100	60.734	44.000	3.9004	1.1008	0.28869	42.97	73.34	
<i>Nyroca platyrhyncha</i> L.	100	57.177	41.031	3.4028	1.5405	1.0713	42.57	94.38	
<i>Nyroca fuligula</i> L.	100	57.787	40.525	3.1848	1.0338	-0.00280	36.68	78.41	
<i>Anas strepera</i> L.	100	54.268	39.063	2.3119	1.8858	0.76709	31.55	107.56	
<i>Anas penelope</i> L.	100	53.930	38.253	4.2631	2.0191	0.90567	57.55	112.58	
<i>Anas acuta</i>	100	54.199	37.440	3.8470	2.1984	0.85061	50.34	118.50	
<i>Spatula clypeata</i> L.	100	51.996	37.172	4.6959	0.85557	1.1913	66.20	77.82	
<i>Anas crecca</i>	100	45.478	33.449	2.8815	0.90778	0.69200	61.33	89.64	

TABLE I—(continued)

	No. of eggs	Mean length mm.	Mean breadth mm.	Variances			Co-variance mm. <sup>2</sup>	Standardized variances	
				Length mm. <sup>2</sup>	Breadth mm. <sup>2</sup>	Length Breadth		Length	Breadth
Columbae									
<i>Columba palumbus</i> L.	100	41.113	29.789	5.0292	1.1460	0.92368	94.97	110.38	
<i>Columba livia</i> Gmelin	100	39.375	29.167	2.4645	1.0372	0.69876	70.37	107.76	
<i>Columba oenas</i> L.	100	37.864	29.016	2.2138	0.96095	0.65624	72.63	104.57	
<i>Streptopelia turtur</i> L.	100	30.713	22.985	1.6817	0.51806	0.25090	80.70	99.08	
Colymbidae									
<i>Colymbus arcticus</i> L.	100	83.752	52.594	11.418	4.1769	2.3866	45.99	116.60	
<i>Colymbus stellatus</i>	100	74.968	45.332	10.729	2.5145	2.1405	49.78	108.39	
Gallinae									
<i>Tetrao urogallus</i> L.	100	57.320	41.475	2.8756	0.49018	0.16465	35.69	43.58	
<i>Lyrurus tetrix</i>	100	51.302	36.961	1.8242	1.5305	0.49745	27.22	103.51	
<i>Lagopus scoticus</i>	100	45.763	32.116	3.8658	0.64439	0.75484	69.64	78.92	
<i>Lagopus mutus</i>	100	43.590	31.027	2.9078	0.77674	0.49169	63.55	90.03	
<i>Alectoris rufa</i> L.	100	41.376	31.042	1.5846	0.62549	0.28839	45.65	80.03	
<i>Perdix perdix</i> L.	100	36.485	27.275	1.1482	0.45260	0.39790	45.97	77.71	
<i>Coturnix coturnix</i> L.	112	30.365	23.065	0.84283	0.54734	0.23175	53.13	100.98	
Gaviae									
<i>Larus marinus</i> L.	100	76.570	53.940	7.4137	2.0061	0.64230	44.16	81.27	
<i>Catharacta skua</i>	100	70.580	49.063	10.106	2.7195	0.54057	65.09	103.19	
<i>Larus argentatus</i> Gm.	100	69.780	48.220	11.306	4.0799	2.4162	70.68	122.44	
<i>Larus fuscus</i> L.	104	67.650	46.980	14.420	3.1829	1.3101	84.89	113.97	
<i>Larus canus</i> L.	100	57.648	41.385	7.0902	2.7718	2.2524	73.61	119.11	
<i>Stercorarius parasiticus</i>	100	57.201	40.254	5.8664	1.7914	—	0.07076	64.56	102.86
<i>Rissa tridactyla</i> L.	101	54.817	40.185	4.7244	1.5073	0.92907	63.02	95.08	
<i>Larus ridibundus</i> L.	102	51.930	37.170	4.2743	1.2463	0.45970	62.37	94.15	
<i>Sterna sandvicensis</i>	100	51.707	36.098	4.1075	0.88+04	0.37123	59.05	82.13	
<i>Sterna dougalli</i> Mont	100	44.055	30.041	2.7590	0.62669	0.27540	56.14	84.06	
<i>Sterna hirundo</i>	100	40.993	30.317	2.8841	0.80244	0.42830	72.84	93.13	
<i>Sterna paradisaea</i>	100	40.228	29.376	2.3069	0.84992	0.39088	64.07	98.61	
<i>Sterna albifrons</i>	100	32.993	23.870	1.9813	0.57606	0.30625	77.52	100.60	
Grallae									
<i>Fulica atra</i> L.	100	52.574	36.179	5.3397	1.9845	1.9019	67.47	117.19	
<i>Gallinula chloropus</i> L.	100	44.446	31.414	8.6241	2.6295	1.4181	108.16	141.93	
<i>Crex crex</i>	100	37.350	26.750	2.3445	0.84880	0.83900	70.94	107.24	
<i>Rallus aquaticus</i> L.	100	35.920	26.020	1.4851	0.45140	0.09960	56.16	82.22	
<i>Porzana porzana</i>	29	34.928	24.241	1.4121	0.27323	0.10311	53.36	67.23	
Herodiones									
<i>Ardea cinerea</i>	106	60.001	43.142	6.0025	2.7251	0.75065	62.30	114.58	

Limicolae										
<i>Numericus arquatus</i>	100	67-610	47-910	11-437	3-11109	2-3469	76-57	111-00		
<i>Numericus phaeopus</i>	85	58-485	41-706	4-2068	1-8620	0-59580	48-91	101-19		
<i>Haematopus ostralegus</i>	101	57-008	39-776	8-3329	2-5174	-0-31591	79-46	118-81		
<i>Burhinus oedinenemus</i>	100	53-788	38-436	9-2437	1-4850	-0-39391	92-02	98-74		
<i>Charadrius apricarius</i>	100	51-770	35-880	2-9360	1-0310	0-19000	43-71	89-42		
<i>Tringa nebularia</i>	100	51-434	34-811	5-0680	1-0510	0-66200	66-10	93-25		
<i>Vanellus vanellus</i>	100	47-090	33-710	5-0750	1-4320	-0-01600	80-14	109-00		
<i>Scelopax rusticola</i>	100	44-199	33-528	2-8865	0-71372	0-52298	67-07	78-67		
<i>Tringa totanus</i>	100	45-180	31-560	1-7930	0-86800	0-31100	37-26	93-49		
<i>Charadrius morinellus</i>	100	41-102	28-872	3-4911	0-65517	0-37844	76-57	89-27		
<i>Capella gallinago</i>	104	39-338	28-636	2-8690	1-1002	0-45483	75-62	112-17		
<i>Tringa hypoleuca</i>	100	36-418	26-277	2-4386	0-36058	0-07012	68-37	71-58		
<i>Charadrius hiaticula</i>	100	35-750	25-960	2-1430	0-51800	0-52300	72-77	88-35		
<i>Calidris alpina</i>	100	34-770	24-770	1-8600	0-35600	0-24700	67-96	76-51		
<i>Charadrius alexandrinus</i>	100	33-049	23-498	0-94800	0-30600	0-16600	43-85	74-74		
<i>Phalaropus lobatus</i>	100	29-957	21-000	1-2348	0-25434	0-19141	64-48	77-02		
Passeres										
Accentorinae										
<i>Accentor nodularis</i>	100	19-888	14-725	0-57682	0-24533	0-085152	79-98	107-02		
Alaudidae										
<i>Alauda arvensis</i> L.	100	23-770	17-057	0-92232	0-40369	0-028798	78-06	115-66		
<i>Lullula arborea</i>	101	21-612	16-348	0-61986	0-22732	0-075830	75-15	94-02		
Certhiidae										
<i>Certhia familiaris</i> L.	100	15-519	12-092	0-37059	0-077898	0-002139	90-03	74-51		
Cinclidae										
<i>Cinclus cinclus</i>	100	26-181	18-614	2-2276	0-59776	0-46956	105-41	124-91		
<i>Cinclus cinclus</i>	100	25-774	18-668	1-6064	0-46105	0-57832	94-41	113-17		
Corvidae										
<i>Corvus corax</i> L.	100	49-721	33-401	9-2116	2-2981	2-1536	95-04	131-04		
<i>Corvus corax</i> L.	100	43-560	30-360	5-7959	0-83420	0-54910	91-84	95-30		
<i>Corvus corone</i> L.	100	43-260	30-510	5-4377	0-76430	0-43970	90-77	90-94		
<i>Corvus frugilegus</i> L.	100	40-040	28-330	6-7420	0-75250	0-38810	108-50	96-94		
<i>Pyrocoryx pyrocorax</i>	100	39-410	27-940	1-4032	0-83590	0-06470	42-17	102-74		
<i>Coloeus monedula</i>	100	35-728	25-498	2-2774	0-75959	0-44894	74-05	106-79		
<i>Pica pica</i>	100	34-130	24-270	6-4464	0-87020	0-50120	123-77	117-18		
<i>Garrulus glandarius</i>	100	31-740	22-850	1-7130	0-64150	0-34200	74-85	109-28		



TABLE I—(continued)

	No. of eggs	Mean length mm.	Mean breadth mm.	Variances		Co-variance mm. <sup>2</sup>	Standardized variances	
				Length mm. <sup>2</sup>	Breadth mm. <sup>2</sup>		Length	Breadth
<b>Emberizinae</b>								
<i>Emberiza calandra</i>	100	23.805	17.728	1.8306	0.53860	0.41723	110.73	124.31
<i>Emberiza citrinella</i> L.	100	21.892	16.244	1.3981	0.35178	0.21611	104.30	113.77
<i>Emberiza cybus</i> L.	100	20.941	15.917	0.60426	0.32567	0.18839	77.76	112.01
<i>Emberiza schoeniclus</i> L.	100	19.879	14.657	0.55582	0.15904	0.07484	77.07	88.68
<b>Fringillinae</b>								
<i>Coccothraustes coccothraustes</i> L.	100	24.241	17.414	2.0820	0.47617	0.54023	111.42	120.96
<i>Passer domesticus</i>	100	22.514	15.673	1.1177	0.19755	0.13846	89.56	92.60
<i>Loxia curvirostra</i>	100	22.125	16.110	1.4265	0.29606	0.30884	105.72	107.23
<i>Loxia curvirostra</i>	100	21.644	15.912	0.91875	0.25138	0.04672	89.74	101.14
<i>Chloris chloris</i>	100	20.641	14.861	1.3532	0.36240	0.10990	109.79	123.44
<i>Fringilla coelebs</i>	100	19.863	14.594	1.0183	0.32340	0.19200	103.19	119.90
<i>Pyrrhula pyrrhula</i>	100	19.548	14.490	0.94616	0.17808	0.07564	102.39	94.55
<i>Passer montanus</i>	100	19.303	14.010	0.33484	0.21323	0.04532	77.18	105.65
<i>Carduelis cannabina</i> L.	100	18.045	13.317	0.69341	0.21476	—	96.90	110.39
<i>Carduelis flavirostris</i>	100	17.234	12.896	0.66227	0.24726	0.09145	100.90	119.26
<i>Carduelis carduelis</i>	100	17.035	12.841	0.72290	0.12143	0.10461	106.47	88.70
<i>Carduelis spinus</i>	100	16.479	12.347	0.69157	0.22171	0.12584	107.61	118.45
<i>Carduelis flammea</i>	114	15.737	12.213	0.49863	0.29053	0.13509	101.15	130.83
<b>Hirundinidae</b>								
<i>Hirundo rustica</i> L.	100	19.939	13.738	1.6008	0.32400	0.00241	117.07	126.13
<i>Delichon urbica</i> L.	100	19.417	13.378	0.97799	0.27163	0.22199	98.45	120.87
<i>Riparia riparia</i>	100	17.966	12.564	0.99459	0.14798	0.20119	108.55	100.03
<b>Laniidae</b>								
<i>Lanius collurio</i> L.	100	22.939	17.115	1.0125	0.28333	0.15012	89.06	99.88
<b>Motacillidae</b>								
<i>Anthus spinoletta</i>	100	21.295	15.916	0.89139	0.43792	0.12606	91.47	125.06
<i>Anthus trivialis</i>	100	20.725	15.556	0.80149	0.15198	0.09121	90.07	81.12
<i>Motacilla alba yarrellii</i>	100	20.565	15.290	1.0245	0.31889	0.08682	100.77	114.96
<i>Anthus pratensis</i>	100	19.778	14.634	0.47194	0.18520	0.10060	70.80	95.37
<i>Motacilla cinerea</i>	100	18.976	14.349	0.70280	0.22535	0.09780	94.23	105.47
<i>Motacilla flava raii</i>	100	19.086	14.160	0.90252	0.21322	0.12834	102.91	104.47
<b>Muscicapidae</b>								
<i>Muscicapa striata</i>	100	18.640	13.890	0.71010	0.20210	0.20660	95.37	103.83
<i>Muscicapa hypoleuca</i>	100	17.936	13.425	0.37223	0.29119	0.08727	90.40	122.73
<b>Panuridae</b>								
<i>Panurus biarmicus</i> L.	100	17.348	13.969	0.84414	0.15448	0.16554	116.85	90.84



TABLE I—(continued)

	No. of eggs	Mean length mm.	Mean breadth mm.	Variances			Co- variance mm. <sup>2</sup>	Standardized variances	
				Length mm. <sup>2</sup>	Breadth mm. <sup>2</sup>	Length Breadth			
<b>Turdinae</b>									
<i>Turdus viscivorus</i> L.	100	31.198	22.338	3.2075	0.65753	0.33361	103.44	112.47	
<i>Turdus torquatus</i> L.	100	30.424	21.543	2.3093	0.44369	0.20057	90.59	98.78	
<i>Turdus merula</i> L.	100	29.390	21.483	2.7443	1.0445	0.29468	104.64	135.88	
<i>Turdus philomelos</i>	100	27.648	20.952	1.9245	0.64575	0.11839	98.62	116.90	
<i>Oenanthe isabellina</i> L.	100	21.211	15.907	1.2466	0.19641	0.20497	106.73	90.25	
<i>Luscinia megarhynchos</i>	100	21.066	15.641	1.9914	0.32406	0.30828	117.25	113.61	
<i>Eriothaca rubecula</i>	100	19.874	15.527	0.65144	0.44563	—	88.79	127.60	
<i>Saxicola rubetra</i>	100	19.158	14.473	0.67741	0.16098	0.08825	91.55	90.08	
<i>Saxicola torquata</i>	100	18.948	14.389	0.52494	0.20069	0.09690	82.05	100.14	
<i>Phoenicurus phoenicurus</i>	100	18.737	13.973	0.74599	0.19371	0.15121	97.01	101.44	
<b>Picariæ</b>									
<i>Picus viridis</i>	101	31.794	23.028	2.7972	1.2008	0.89137	96.48	135.74	
<i>Caprimulgus europæus</i>	100	31.879	22.464	2.6039	0.85081	0.48237	90.79	123.30	
<i>Dryobates major</i>	100	26.389	19.468	1.6541	0.93068	0.49631	94.74	139.70	
<i>Micropus apus</i> L.	100	25.004	16.325	1.2586	0.30856	0.03101	78.41	108.92	
<i>Alcedo isipda</i> L.	100	22.648	18.735	0.27202	0.39644	0.00073	41.91	104.92	
<i>Cuculus canorus</i> L.	102	22.600	16.893	1.3168	0.71787	0.77426	102.19	141.12	
<i>Lynx torquilla</i> L.	100	20.785	15.432	0.51523	0.33735	0.03867	69.65	116.60	
<i>Dryobates minor</i>	101	18.753	14.531	1.1165	0.34695	0.33414	118.75	122.82	
<b>Podicipedidae</b>									
<i>Podiceps cristatus</i>	100	54.875	36.757	7.2191	0.89318	—	12129	73.82	81.37
<i>Podiceps nigricollis</i>	100	43.086	29.794	3.5834	0.66421	0.56667	71.47	87.19	
<i>Podiceps nigricollis</i>	100	37.866	26.216	2.9910	0.76075	0.37126	77.30	104.63	
<b>Steganopodes</b>									
<i>Sula bassana</i> L.	100	78.063	49.111	14.797	2.8531	1.5739	62.82	106.25	
<i>Phalacrocorax carbo</i>	100	65.809	40.767	9.9172	2.4944	0.98666	62.06	117.40	
<i>Phalacrocorax aristotelis</i>	100	62.867	38.463	10.4327	1.9597	0.46867	68.04	112.32	
<b>Striges</b>									
<i>Syrinx aluco</i>	103	46.701	39.055	2.2254	0.85191	0.28200	58.09	71.54	
<i>Asio otus</i>	100	40.942	32.707	2.8194	0.76409	0.07435	78.35	83.35	
<i>Asio flammeus</i>	100	40.146	31.786	2.1861	0.55889	0.49863	68.66	72.45	
<i>Tyto alba</i>	100	39.740	31.572	2.6723	0.70103	—	78.73	82.85	
<i>Athene noctua</i>	100	35.628	29.576	1.7170	0.56063	0.30270	74.61	78.62	
<b>Tubimares</b>									
<i>Fulmarus glacialis</i> L.	100	74.030	50.613	11.027	3.4979	2.2767	62.50	111.47	
<i>Puffinus puffinus</i>	102	60.933	41.867	5.9234	1.5820	0.22261	56.35	94.14	
<i>Oceanodroma leucorhoa</i>	83	32.754	23.978	0.93276	0.36050	0.16466	47.43	79.72	
<i>Hydrobates pelagicus</i>	100	27.971	21.188	1.0920	0.45400	0.34894	72.78	100.58	

One obvious method of adjustment would be to divide each variance by the square of the corresponding mean, or, in other words, to use the so-called coefficient of variation, or its square, the relative variance, as a basis for comparison. The objection I feel to any procedure of this kind is that it is arbitrary, that is to say that it depends on the choice of the investigator. If his choice be wrong, he will make too great or too small an allowance for the size of the egg, and, in consequence, will make the smaller birds of each group appear more or less variable than they ought in comparison with the larger birds. For a comparison with abundance any such error would be fatal. Abundance is not likely to be independent of the size of the bird. In fact, in many groups the smaller species must be considerably more numerous in individuals than the larger species. We should thus, by making any such arbitrary choice, be liable to enhance or to diminish the effect we are seeking to detect, largely, and by an unknown amount.

The only adequate solution, as it seems to me, is to eliminate entirely any portion of the association between variability and abundance that may be due to the association of both these variables with the average length and average breadth of the eggs. It may be that, if some absolutely correct method of allowance for size could be imagined, large eggs would be found to be more or less variable than small eggs of related species. If so, this fact would, I hold, only be relevant to our enquiry as a disturbing factor, which we should wish to eliminate in studying whether, apart from size, variability is associated with abundance.

If this point of view is correct, the allowance we must make for the average length and breadth of the eggs of each species must be that provided by the data themselves, in such a way that, after allowance has been made, neither the larger nor the smaller birds of each group are on the whole the more variable. I have, therefore, first replaced the means and variances by their common logarithms, and then calculated, from the sums of squares and products within groups, the actual regressions of the logarithm of variance in length, the logarithm of variance in breadth, regarded as two dependent variates, on the logarithm of the mean length, and the logarithm of the mean breadth, as independent variates. If  $L$  and  $B$  stand for the logarithms of the mean lengths and breadths, and  $u$  and  $v$  stand for the logarithms of the variances of length and breadth, the allowances so found empirically from the data provided by 137 independent comparisons within groups are:

$$U = 4.327256L - 1.909220B,$$

$$V = -0.236169L + 2.320619B.$$

where  $U$ ,  $V$  may be regarded as corrections to be subtracted from  $u$ ,  $v$  in order to render them comparable. The exact procedure is shown in the Appendix on the Analysis of Covariance. These allowances differ greatly from what would have been used had the coefficient of variation been adopted. This would have been equivalent to using the formulae

$$U = 2L + 0B,$$

$$V = 0L + 2B,$$

and the comparison shows that the facts of nature are very different from those supposed in these last equations. An increase of size without change of shape would entail an equal increase in  $L$  and  $B$ . In the theoretical formulae this produces an increase twice as great both in  $U$  and  $V$ . In fact it is followed, as the two formulae show, by a relative increase of  $2.418 \pm 0.177$  in  $U$  and  $2.084$  in  $V$ . Both values show a higher allowance than that supplied by the coefficient of variation, though in the second case the deviation is not statistically significant. A change in size, even without change in shape, would not be adequately represented by the coefficient of variation.

The agreement is still more unsatisfactory if we consider a change in shape without change of volume, such as would be produced by decreasing  $B$  by one unit, and increasing  $L$  by two. The theoretical change in  $U$  is then 4. But the observed coefficient is 10.544, with a standard error 3.538. For  $V$  the deviation is less, but in the opposite direction, for instead of  $-2$  we obtain  $-2.793$ , with a standard error 4.209. The difference  $V - U$  is increased by 13.357, with a standard error 2.946, whereas the theoretical increase is only 6. It appears, therefore, that, with increase of size within groups of related birds, variability in length at least increases more rapidly than if the coefficient of variation were constant; and that, with change of shape, e.g. broadening and corresponding shortening, the relative variability of breadth to that of length increases still more rapidly.

The method of adjustment adopted has been designed for use in comparisons within groups, and has been obtained from the mean squares and products within these groups only, ignoring all differences from one group to another. The corrected values may not be thought, therefore, ideal for making comparisons of group with group, yet it is not without interest to see how the averages of the adjusted variances of the different groups compare with one another. In making these and other comparisons it will be convenient to multiply the numerical values of  $u - U$  and  $v - V$  by 100 to obtain a more convenient unit of comparison. Since common logarithms

to the base 10 were used, this new unit is equivalent to a difference of 2.3026 % ( $\log_e 10$ ).

The average values for adjusted variances in length and breadth are shown simultaneously in fig. 1. Families or subfamilies of passerine birds are marked with a cross, the non-passerine orders being shown by circles. The number of species averaged in each group is indicated.

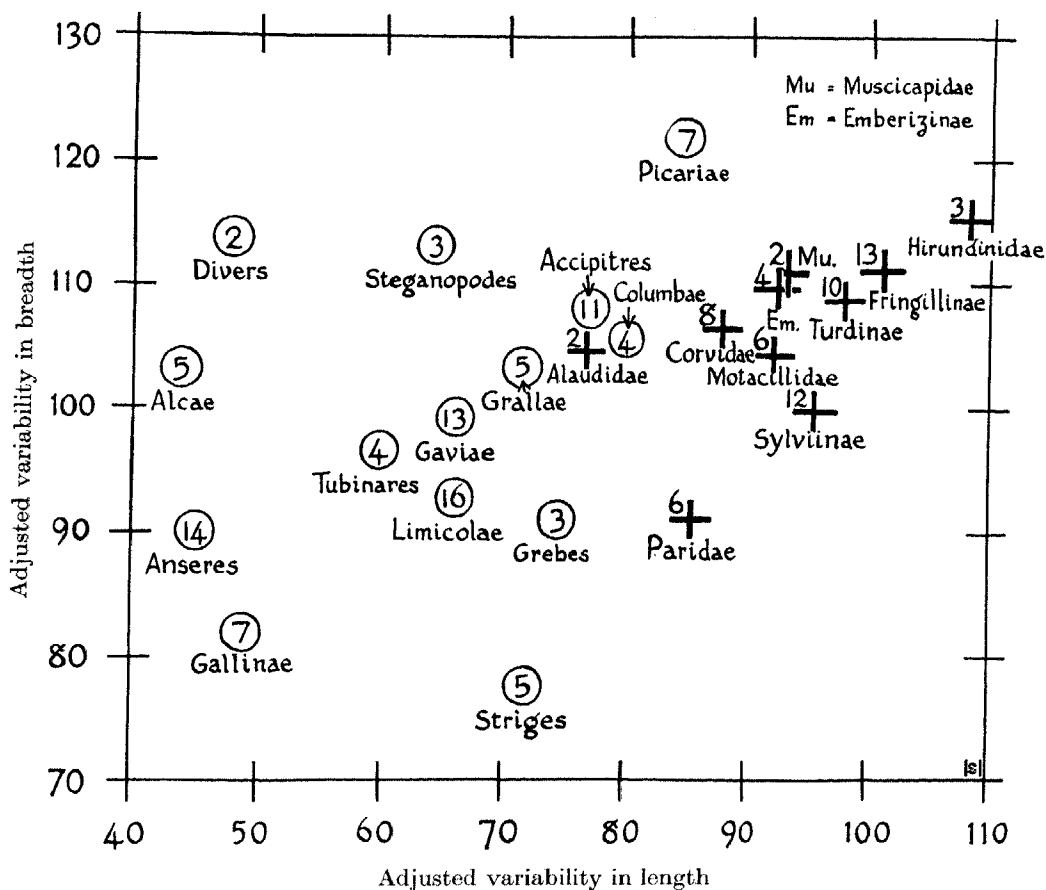


FIG. 1—Mean corrected variance for length shown from left to right, and for breadth upwards. Non-passerine groups are shown by circles, and passerine groups by crosses. The numbers indicate the number of species averaged in each group. The positions of the smaller groups have little accuracy. Each unit represents 2.3026 %.

One very obvious fact brought out by this diagram is the generally greater variability of the passerine species. If we judge by the variance figure for length, only the two larks, the least variable of the passerine groups, fall among the non-passerine orders, while among these the picarian

birds stand out as exceptionally variable. For the latter I have shown the average of seven species, excluding the cuckoo, which, if it had been included, would have further raised the average in both respects. The comparison is, probably, to some extent influenced by size, though it should be noted that the tits and the wren are among the least variable of the passerine birds. It seems not unreasonable to suggest that the difference in variability is connected with more recent evolutionary modification among the passerine groups.

#### 4—COMPARISONS WITHIN GROUPS

The purpose of the adjustments to which the variances have been subjected has been to render them comparable within groups, and in these to make comparisons between species believed to be more and those believed to be less numerous. To obtain estimates of relative abundance which should be entirely uninfluenced by the variability figures with which they were to be compared, I have had recourse to Mr Alexander, who has had much experience in the estimation of bird numbers, and in consultation with colleagues in this country and abroad has subdivided all the groups I submitted to him into two, three, or four classes, representing abundance in the world population, so far as it can be estimated. In spite of the great care which has been given to this classification, I cannot hope that in every case the species have been arranged in the best order, still less that large differences in real abundance have not, in some cases, passed unrecognized. All that I can claim is to have used the best indications of abundance available and that, where species have been assigned to the wrong abundance classes, this had been done without knowledge of the figures for variability. Misclassification might, therefore, diminish the apparent contrast in variability between more and less abundant species. Indeed, if misclassification is frequent it must have led to a serious under-estimate of this contrast. It could not, however, possibly have produced any consistent difference in the average variabilities of the species judged to be more or less abundant.

Table II gives the groups classified in only two abundance classes. These are the five guillemots and two divers among non-passerine birds, two larks, two flycatchers, six wagtails and pipits, and three martins among passerine birds. Of these twenty species, ten fall into the class judged to be rarer and ten into the class judged to be commoner than other members of their group.

The table shows for each species deviations from the mean values for each group, of the adjusted variances in length and breadth. The average

TABLE II—COMPARISON OF DEVIATIONS FROM GROUP MEANS OF ADJUSTED VARIABILITIES IN LENGTH AND BREADTH OF EGG, FOR GROUPS DIVISIBLE IN TWO ABUNDANCE CLASSES

	Rarer	Variability in		Commoner	Variability in	
		Length	Breadth		Length	Breadth
<b>Alcae</b>						
	Razorbill	9.28	7.75	Southern guillemot	5.86	8.03
	Black guillemot	-2.75	-10.69	Northern guillemot	-12.33	9.58
				Puffin	-0.05	-14.69
	<b>2 Alcae</b>	<b>6.53</b>	<b>-2.94</b>	<b>3 Alcae</b>	<b>-6.52</b>	<b>2.92</b>
<b>Alaudidae</b>						
	<b>1</b> Wood lark	<b>-1.45</b>	<b>-10.82</b>	<b>1</b> Skylark	<b>1.45</b>	<b>10.82</b>
<b>Muscicapidae</b>						
	<b>1</b> Pied flycatcher	<b>-2.48</b>	<b>9.45</b>	<b>1</b> Spotted flycatcher	<b>2.49</b>	<b>-9.45</b>
<b>Motacillidae</b>						
	Grey wagtail	2.52	1.06	Meadow pipit	-20.91	-9.04
	Water pipit	-0.24	20.65	White wagtail	9.06	10.55
	Tree pipit	-1.64	-23.29	Yellow wagtail	11.20	0.06
	<b>3 Motacillidae</b>	<b>0.64</b>	<b>-1.58</b>	<b>3 Motacillidae</b>	<b>-0.65</b>	<b>1.57</b>
<b>Hirundinidae</b>						
	House martin	-9.58	5.20	Swallow	9.04	10.46
	Sand martin	0.52	-15.64			
	<b>2 Martins</b>	<b>-9.06</b>	<b>-10.44</b>	<b>1 Swallow</b>	<b>9.04</b>	<b>10.46</b>
<b>Colymbidae</b>						
	<b>1</b> Black-throated diver	<b>-1.90</b>	<b>4.11</b>	<b>1</b> Red-throated diver	<b>1.89</b>	<b>-4.10</b>
<b>10</b>	Totals	<b>-7.72</b>	<b>-12.22</b>	<b>10</b>	<b>+7.70</b>	<b>+12.22</b>
	Means	<b>-0.772</b>	<b>-1.222</b>		<b>+0.770</b>	<b>+1.222</b>

for the ten commoner species exceeds that for the ten rarer species by 1.542 in length and by 2.444 in breadth. These differences correspond to average differences of about 3.6 and 5.6% in the variances. The differences are small, but both are in the direction indicated by Darwin's law. If only these twenty species were available, the law would only be supported, it could not be said to be demonstrated by the data.

Table III gives the groups for which three abundance classes are available. These are the woodpeckers, owls, doves, cormorants, plovers, game-birds, rails, grebes, and petrels, together with the tits, buntings, and finches. Out of seventy-three species, twenty are placed in the rarest of three classes, thirty-two in the middle class and twenty-one among the commonest. The rarest class shows a variability less than the average in both length and breadth. The same is true to a less extent of the middle class, while the commonest class is above the average in both respects. In length the average value of the commonest class exceeds that for the rarest class by



TABLE III—COMPARISON OF DEVIATIONS FROM GROUP MEANS OF ADJUSTED VARIABILITIES IN LENGTH AND BREADTH OF EGG, FOR GROUPS DIVISIBLE IN THREE ABUNDANCE CLASSES

Rare	Variability in		Mid	Variability in		Common	Variability in	
	Length	Breadth		Length	Breadth		Length	Breadth
<b>Picariæ</b>								
Green woodpecker	1.57	7.03	Lesser spotted wood- pecker	23.84	5.89	Great spotted wood- pecker	0.17	10.99
<b>1 Picarian</b>	<b>1.57</b>	<b>7.03</b>	<b>2 Picarians</b>	-25.26	-12.11	<b>1 Picarian</b>	-	<b>0.17</b>
<b>Striges</b>								
Little owl	2.92	0.86	Long-eared owl	6.66	5.59	Short-eared owl	-	3.03
Tawny owl	-13.60	-6.22	<b>1 Owl</b>	<b>6.66</b>	<b>5.59</b>	Barn owl (white)	7.04	5.09
<b>2 Owls</b>	<b>-10.68</b>	<b>-5.36</b>				<b>2 Owls</b>	<b>4.01</b>	<b>-0.22</b>
<b>Columbæ</b>								
Stock dove	-7.04	-0.88	Rock dove	-9.30	2.31	Turtle dove	1.03	-6.37
<b>1 Dove</b>	<b>-7.04</b>	<b>-0.88</b>	<b>1 Dove</b>	<b>-9.30</b>	<b>2.31</b>	Wood pigeon	15.30	4.93
<b>Steganopodes</b>								
<b>1 Gannet</b>	<b>-1.49</b>	<b>-5.74</b>	<b>1 Shag</b>	<b>3.73</b>	<b>0.33</b>	<b>1 Cormorant</b>	-	<b>2.25</b>
<b>Paridæ</b>								
Crested tit	-18.14	-1.15	Long-tailed tit	0.33	-6.09	Great tit	-	4.29
			Marsh tit	8.79	-4.33			14.66
			Coal tit	1.34	1.73			
			Blue tit	11.95	-4.81			
<b>1 Tit</b>	<b>-18.14</b>	<b>-1.15</b>	<b>4 Tits</b>	<b>22.41</b>	<b>-13.50</b>	<b>1 Tit</b>	-	<b>4.29</b>
<b>Limicolæ</b>								
Stone curlew	25.72	6.04	Whimbrel	-17.39	8.49	Redshank	-29.04	0.79
Dotterel	10.27	-3.43	Ringed plover	6.47	-4.35	Curtlew	10.27	18.30
			Red-necked phalarope	-1.82	-15.68	Sandpiper	2.07	-21.12
			Kentish plover	-22.45	-17.96	Snipe	9.32	19.47
			Golden plover	-22.59	-3.28	Lapwing	13.84	16.30
			Greenshank	-0.20	0.55	Dunlin	1.66	-16.19
			Woodcock	0.77	-14.03			
			Oystercatcher	13.16	26.11			
<b>2 Limicolæ</b>	<b>35.99</b>	<b>2.61</b>	<b>8 Limicolæ</b>	<b>-44.05</b>	<b>-20.15</b>	<b>6 Limicolæ</b>	<b>8.12</b>	<b>17.55</b>

TABLE III—(continued)

	Variability in		Mid	Variability in		Common	Variability in	
	Length	Breadth		Length	Breadth		Length	Breadth
Rare								
<b>Emberizinae</b>								
Reed bunting	- 15.39	- 21.01	Girl-bunting	- 14.70	2.32	Common	18.27	14.62
<b>1 Bunting</b>	- 15.39	- 21.01	Yellowhammer	11.84	4.08	Common	18.27	14.62
<b>Fringillinae</b>								
Twite	- 0.12	8.26	Crossbill	4.70	- 3.77	House sparrow	- 11.46	- 18.40
Siskin	6.59	7.45	Redpoll	0.13	19.83	Chaffinch	2.17	8.90
Bullfinch	1.37	- 16.45	Greenfinch	8.77	12.44			
Hawfinch	10.40	9.96	Linnet	- 4.12	- 0.61			
			Tree sparrow	- 23.84	- 5.35			
			Goldfinch	3.45	- 22.30			
<b>4 Finches</b>	<b>18.24</b>	<b>9.22</b>	<b>6 Finches</b>	- <b>8.91</b>	<b>0.24</b>	<b>2 Finches</b>	- <b>9.29</b>	- <b>9.50</b>
<b>Gallinae</b>								
Capercaillie	- 13.00	- 38.53	Ptarmigan	14.86	7.92	Quail	4.44	18.87
Red grouse	20.95	- 3.19	Black grouse	- 21.47	21.40			
			Red-legged partridge	- 3.04	- 2.08			
			Partridge	- 2.72	- 4.40			
<b>2 Game birds</b>	<b>7.95</b>	- <b>41.72</b>	<b>4 Game birds</b>	- <b>12.37</b>	<b>22.84</b>	<b>1 Game bird</b>	<b>4.44</b>	<b>18.87</b>
<b>Grallae</b>								
Spotted crane	- 17.86	- 35.93	Corn crane	- 0.28	4.08	Coot	- 3.75	14.03
Water rail	- 15.06	- 20.94				Moor hen	36.94	38.77
<b>2 Rails</b>	- <b>32.92</b>	- <b>56.87</b>	<b>1 Rail</b>	- <b>0.28</b>		<b>2 Rails</b>	<b>33.19</b>	<b>52.80</b>
<b>1 Great-crested grebe</b>	- <b>0.38</b>	- <b>9.69</b>	<b>1 Black-necked grebe</b>	- <b>2.73</b>	- <b>3.87</b>	<b>1 Little grebe</b>	<b>3.10</b>	<b>13.57</b>
<b>Tubinares</b>								
Storm petrel	13.02	4.10	Maux shearwater	- 3.41	- 2.34	Fulmar	2.74	14.99
Fork-tailed petrel	- 12.33	- 16.76						
<b>2 Petrels</b>	+ <b>0.69</b>	- <b>12.66</b>	<b>1 Petrel</b>	- <b>3.41</b>	- <b>2.34</b>	<b>1 Petrel</b>	<b>2.74</b>	<b>14.99</b>
<b>20</b>	- 21.60	- 136.22	<b>32</b>	- 52.53	- 16.07	<b>21</b>	+ 74.20	+ 152.30
Means	- 1.080	- 6.811		- 1.612	- 0.502		+ 3.533	+ 7.252

4.613, corresponding to an average difference in variance of 10.6%. In breadth the difference is 14.063, corresponding to 32.4%. Taking the average of the figures for length and breadth, the mean values for the three classes are -3.946, -1.072 and 5.392. The difference between the common birds and the middle class is thus more than twice the difference between the middle class and the rarer birds. Owing to the considerable number of species in this classification, the totals and averages seem to possess some regularity.

There are sixty-eight species in the groups classified into four classes, namely the ducks, hawks, and gulls, together with the crows, thrushes, and warblers. Of these only eleven fell in the rarest class, sixteen in the next, twenty-two in the next and nineteen in the most common. For variation in length and breadth together the average values from the totals shown in Table IV are -0.900, -2.750, -2.104 and +5.272. As eleven species are rather a small number for a class, the two least numerous classes may be thrown together with an average of -1.996. This differs from the value for the most abundant class by 7.268, or 16.7%. In the orders divisible into three abundance classes the average difference was 21.5%. It would seem at the least that differences in population size only, apart from the many other factors at work, must account for difference of variability of the order of 20%.

As in the case of the division into three classes, the greatest contrast appears between the most abundant species and the next class, while among the rarer species differences in abundance are little associated with differences in variability. In our previous work with moths a similar phenomenon appears. The ten "abundant" species are more variable than the twelve "common" species by 42%, while the twelve common species exceed thirteen species classed as less than common by little more than 14%. The phenomenon may, therefore, be a real one. If so, it indicates a very important conclusion, namely that rapid evolutionary progress is somewhat strictly confined to a small minority of very abundant species, from which evolutionary radiation may later take place.

It is, however, at present possible that this inequality in the increase in variability as we pass from the less to the more abundant species is due to the defects of our knowledge. It is possible that the rarer species, though seldom taken to be very abundant, are more liable to be misclassified as to order of abundance among themselves. Such misclassification would greatly diminish the apparent increase in variability with increasing population. It is not impossible, likewise, even if relative abundance were well determined among the rarer species, that their order of abundance is less

TABLE IV—COMPARISONS OF DEVIATIONS FROM GROUP MEANS OF ADJUSTED VARIABILITIES IN LENGTH AND BREADTH OF EGG, FOR GROUPS DIVISIBLE IN FOUR ABUNDANCE CLASSES

Rarest	Variability in		Less rare	Variability in		Less common	Variability in		Commonest	Variability in	
	Length	Breadth		Length	Breadth		Length	Breadth		Length	Breadth
<b>Anseres</b>											
Shelduck	- 17.96	- 15.17	Eider	9.07	- 3.91	Wigeon	12.57	22.45	Mallard	- 2.41	4.25
Graylag goose	17.75	24.03	Scoter	1.52	- 6.41	Pochard	- 2.01	- 16.79	Teal	16.45	- 0.49
			Goosander	- 30.24	- 15.90	Gadwall	- 13.43	17.43	Pintail	5.36	28.37
			Red-breasted merganser	- 9.63	- 13.82	Tufted duck	- 8.30	- 11.72	Shoveller	21.22	- 12.31
<b>2 Ducks</b>	- 0.21	<b>8.86</b>	<b>4 Ducks</b>	- 29.28	- 40.04	<b>4 Ducks</b>	- 11.17	<b>11.37</b>	<b>4 Ducks</b>	<b>40.62</b>	<b>19.82</b>
<b>Accipitres</b>											
Golden eagle	7.08	17.56	Kite	4.78	- 15.49	Merlin	- 22.86	- 14.11	Kestrel	- 3.98	- 12.27
Sea eagle	10.85	22.77	Honey buzzard	- 11.41	- 17.10	Peregrine	- 11.61	- 12.90	Sparrow hawk	27.41	27.42
						Hobby	- 13.58	- 3.98	Buzzard	- 9.19	- 0.49
						Hen harrier	22.53	8.61			
<b>2 Accipitres</b>	<b>17.93</b>	<b>40.33</b>	<b>2 Accipitres</b>	- 6.63	- 32.59	<b>4 Accipitres</b>	- 25.52	- 22.38	<b>3 Accipitres</b>	<b>14.24</b>	<b>14.66</b>
<b>Gaviae</b>											
Great skua	- 0.91	3.91	Great black-backed gull	- 21.84	- 18.01	Black-headed gull	- 3.63	- 5.13	Kittiwake	- 2.98	- 4.20
Arctic skua	- 1.44	3.58	Little black-backed gull	18.89	14.69	Common gull	7.61	19.83	Herring gull	4.68	23.16
Roscaie tern	- 9.86	- 15.22	Sandwich tern	- 6.95	- 17.15	Arctic tern	- 1.93	- 0.67			
			Little tern	11.52	1.32	Common tern	6.84	- 6.15			
<b>3 Gulls</b>	- 12.21	- 7.73	<b>4 Gulls</b>	<b>1.62</b>	- 19.15	<b>4 Gulls</b>	<b>8.89</b>	<b>7.88</b>	<b>2 Gulls</b>	<b>1.70</b>	<b>18.96</b>

TABLE IV—(continued)

Rarest	Variability in		Less rare	Variability in		Less common	Variability in		Commonest	Variability in	
	Length	Breadth		Length	Breadth		Length	Breadth		Length	Breadth
<b>Corvidae</b>											
Chough	-45.45	-3.54	Jackdaw	-13.57	0.51	Carrion crow	3.15	-15.34	Rook	20.88	-9.34
<b>1 Crow</b>	-45.45	-3.54	<b>1 Crow</b>	-13.57	<b>0.51</b>	Hooded crow	4.22	-10.98	Magpie	36.15	10.90
						Raven	7.42	24.76	Jay	-12.77	3.00
<b>Turdinae</b>						<b>3 Crows</b>	<b>14.79</b>	- <b>1.56</b>	<b>3 Crows</b>	<b>44.26</b>	<b>4.56</b>
Ring ouzle	-7.21	-9.94	Mistlethrush	5.34	3.75	Redbreast	-9.31	18.88	Blackbird	6.54	27.16
Nightingale	19.15	4.89				Stonechat	-16.05	-8.58	Thrush	0.52	8.18
<b>2 Thrushes</b>	<b>11.94</b>	- <b>5.05</b>	<b>1 Thrush</b>	<b>5.34</b>	<b>3.75</b>	Whinchat	-6.55	-18.64	Wheatear	8.63	-18.47
<b>Sylvinae</b>						<b>3 Thrushes</b>	- <b>31.91</b>	- <b>8.34</b>	Redstart	-1.09	-7.28
Dartford warbler	-17.16	-7.52	Reed warbler	-4.71	1.71	Blackcap	-21.95	9.33	Willow warbler	-7.49	-12.76
			Wood warbler	10.26	8.55	Garden warbler	-10.76	4.13	Whitethroat	14.62	7.26
			Marsh warbler	-1.80	8.58	Sedge warbler	6.01	-24.62	Lesser white-	5.93	9.74
			Grasshopper warbler	17.59	1.86	Chiffchaff	9.44	6.22	throat		
<b>1 Warbler</b>	-17.16	-7.52	<b>4 Warblers</b>	<b>21.34</b>	<b>20.70</b>	<b>4 Warblers</b>	- <b>17.26</b>	- <b>17.38</b>	<b>3 Warblers</b>	+ <b>13.06</b>	+ <b>4.24</b>
Total	-45.16	+25.35	16	-21.18	-66.82	22	-62.18	-30.41	19	+128.48	+71.83
Means	-4.105	+2.305		-1.324	-4.176		-2.826	-1.382		+6.762	+3.781

stable with the passage of time than is that of the really dominant species. For proportionate changes in numbers among the rarer species must be followed by far less important reactions on the ecological balance, than when dominant species are concerned. It would, for these reasons, be premature at present to assume that the association of genetic variability with abundance is so strongly confined to the more abundant species as would at first appear.

It has been essential, in order to demonstrate objectively the increase of variability with increasing population, that the variability should be unknown when the order of abundance within each group was assigned, and when the grouping was determined. One alteration has been made later, namely the separation of the grebes from the divers, which Mr Alexander advised me should not be regarded as of the same natural order. This change diminishes the apparent effect, since the grebes are, on the whole, the more variable as well as the more numerous of the two groups. Once, however, the general effect has been demonstrated, it is permissible to consider what factors may have contributed to the more striking exceptions to the general rule. One such cause which should be noted as probably effective is change of population during the human period, for it is difficult to conceive theoretically that the variability should change much in response to change of population in a period so short as 10,000 generations. Any changes, therefore, in the relative frequencies of different species of the same groups, consequent upon the occupation and cultivation of land by men, may have produced comparatively large deviations from the general tendency.

Among rare species, showing relatively large variation, the most prominent is the graylag goose and the sea eagle. These seem, not improbably, birds which may have been relatively more abundant in the distant past. Without these two birds the least abundant class would be much the least variable. On the other side, almost the largest discrepancy among common birds is the house sparrow, which is less variable than the average of the finches, and must certainly have increased greatly in population with the increase in human buildings. The only other deviation so large among the common birds is the meadow pipit, but I do not know that this bird has been favoured by cultivation in comparison with the other pipits and wagtails.

With respect to classification, I have tried to restrict the comparisons in the tables of variability to birds which are really closely related. Of the picarian birds I have only used the woodpeckers and wryneck, since the kingfisher, swift, and nightjar seem to be insufficiently comparable with them, and the cuckoo must also certainly be excluded.

5—SUMMARY

Primary statistics and adjusted measures of variability are given for the length and breadth of eggs of 180 populations of British nesting birds.

Comparisons within natural taxonomic groups show that the more abundant species are generally more variable than the less abundant species, in accordance with Darwin's generalization.

The magnitude of the differences observable in the egg measurements of British birds is about 20 %.

The excess variability *appears* to be strongly concentrated among the few most numerous species of each group, suggesting that evolutionary progress is much more rapid among these than among other species. This important indication may, however, be due to our comparative ignorance of the real relative numbers of the populations of the less numerous species.

6—APPENDIX ON THE ANALYSIS OF COVARIANCE

The 161 species available for comparison within groups fall into twenty-four groups, and leave, therefore, 137 degrees of freedom for each of the four variates. The two independent variates  $L$  and  $B$  stand for the logarithms of the mean length and mean breadth for each species. The sums of squares of these, within groups, together with their sum of products, supply the Information Matrix for the regressions, the elements of which are the coefficients of the equations of estimation by which the regressions are obtained.

$$\begin{aligned} S(L - \bar{L})^2 &= 0.9322847, & S(L - \bar{L})(B - \bar{B}) &= 0.8546502, \\ S(L - \bar{L})(B - \bar{B}) &= 0.8546502, & S(B - \bar{B})^2 &= 0.7961181. \end{aligned}$$

Inverting this matrix we have the Multiplier Matrix

$$\begin{array}{cc} c_{11} & 67.57225, & c_{12} & -72.54029, \\ c_{12} & -72.54029, & c_{22} & 79.12968. \end{array}$$

If  $u$  and  $v$  stand for the two dependent variates, the logarithms of the variances of the lengths and breadths, the regressions of  $u$  on  $L$  and  $B$  will be given by

$$c_{11}S(L - \bar{L})(u - \bar{u}) + c_{12}S(B - \bar{B})(u - \bar{u})$$

and

$$c_{12}S(L - \bar{L})(u - \bar{u}) + c_{22}S(B - \bar{B})(u - \bar{u})$$

respectively; while those of  $v$  on the same pair of independent variates will be given by

$$c_{11}S(L - \bar{L})(v - \bar{v}) + c_{12}S(B - \bar{B})(v - \bar{v})$$

and

$$c_{12}S(L - \bar{L})(v - \bar{v}) + c_{22}S(B - \bar{B})(v - \bar{v}).$$

The sums of products of  $u$  with  $L$  and  $B$  within groups are

$$2\cdot4025188 \text{ and } 2\cdot1783253,$$

giving the regressions

$$+4\cdot327256 \text{ and } -1\cdot909220.$$

The sums of products of  $v$  with  $L$  and  $B$  within groups are

$$2\cdot2034949 \text{ and } 2\cdot0493293,$$

giving the regressions

$$-0\cdot236169 \text{ and } +2\cdot320619.$$

The sum of squares of  $u$  within groups accounted for by variation of  $L$  and  $B$  is found by multiplying the regressions by the corresponding sums of products, and adding. The same method gives the sum of squares of  $v$ , and the sum of products of  $u$  and  $v$ , we have therefore the following analysis of variance:

	Degrees of freedom	$u^2$	$uv$	$v^2$
Regression	2	6·237411	4·487663	4·235315
Remainder	135	2·642530	2·274683	3·739038
Total within groups	137	8·879940	6·762345	7·974354

The mean squares and mean product from this table are

	$u$	$v$
$u$	0·0195743	0·0168495
$v$	0·0168495	0·0276966

which it is convenient to refer to as the matrix of residual covariance.

It appears that whereas before correction the variance in length is more variable than that in breadth, after correction the reverse is true. Moreover, after full allowance has been made for the mean length and breadth, the variability of length and breadth is still highly correlated, showing that species more variable in egg length are also generally more variable in egg breadth. For 100 eggs measured, sampling error will give to the logarithms (to the base 10) of the variances in length and breadth the sampling variance

$$\frac{2}{100 (\log 10)^2} = 0\cdot003772,$$

while the contribution to the sampling covariance will be smaller by reason of a factor  $\rho^2$ , the square of the correlation coefficient between the lengths and breadths of individual eggs, a factor which seldom exceeds 0·2. Even in the case of  $u$ , therefore, the sampling error accounts for only about one-fifth of the variance observed; this is, however, a sufficiently large proportion



to show that any much smaller number of eggs might have been insufficient to display the real differences in variability.

The standard errors of the regression coefficients, and of any linear compounds of them, are derived from the multiplier matrix, and the matrix of residual covariance. Thus the sampling variance of the regression of  $u$  on  $L$ , 4.327, is

$$0.0195743c_{11} = 1.3227,$$

giving a standard error 1.150, so that the regression is on the verge of being significantly greater than 2.

For the sum of the regressions of  $u$  on  $L$  and  $B$ , 2.418, we use instead of  $c_{11}$  the factor  $c_{11} + 2c_{12} + c_{22} = 1.62135$ , and obtain the standard error 0.1781. The significance of the small excess 0.418 is thus higher than that of the large excess 2.327 in the single regression. Equally, for change of shape without change of volume we need the *difference* between twice the regression on  $L$  and the regression on  $B$ , for which the appropriate factor is  $4c_{11} - 4c_{12} + c_{22}$ , or 639.57984. We may thus combine the independent variates in any way we please.

Combination of the dependent variates is carried out by means of the residual covariance matrix. Thus to test the significance of the sum of the regressions of  $u$  and  $v$  we should use the residual variance of  $u + v$

$$0.0195743 + 2(-0.0168495) + 0.0276966 = 0.0809699,$$

while for the difference we have the higher precision represented by the residual variance of  $u - v$

$$0.0195743 - 2(-0.0168495) + 0.0276966 = 0.0135719.$$

Thus, whereas the sum of the regressions of  $u$  is  $2.418 \pm 0.1781$ , so that the excess over the value 2.0 is significant, the regressions of  $v$  amount only to 2.084, with about the same precision, which is certainly not a significant excess. Adding the two together we have  $4.502 \pm 0.3623$ , where the standard error is derived from the sampling variance

$$0.0809699 \times 1.62135.$$

The regressions of  $v$ , though together exceeding 2.0, do not do so sufficiently to increase the significance of the discrepancy.

With regard to change of shape without change of volume, we shall need twice the regression on  $L$  less the regression on  $B$ . For  $u$  this is  $10.564 \pm 3.538$ , where the sampling variance is

$$0.0195743 \times 639.57984,$$

so that the value for  $u$  does not significantly exceed 4. For  $v$  similarly we

have  $-2.793 \pm 4.209$ , showing a quite insignificant difference from the value  $-2$ . Using the difference  $u - v$  we have consequently  $13.357 \pm 2.946$ , since the sampling variance is

$$0.0135719 \times 639.57984.$$

The excess over 6, being 7.357, is thus considerably greater than twice the standard error, and is clearly significant.

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