

DOES BODY SIZE EVOLVE BY QUANTUM STEPS ?

Derek Roff
 Institute of Animal Resource Ecology,
 University of British Columbia,
 Vancouver, British Columbia,
 Canada, V6T 1W7.

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ABSTRACT. The hypothesis presented by Løvtrup (1976) that body size evolves by quantum steps is examined. It is concluded that the statistical method employed by Løvtrup *et al* (1974) to test this hypothesis is invalid. Even if this method is allowed it is shown that the results obtained do not differ from those expected by chance.

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In a recent issue of this journal (December, 1976) Søren Løvtrup suggested that the neo-Darwinian theory of evolution is deficient and cannot explain the processes that lead to the formation of species and higher taxonomic categories. In support of this thesis Løvtrup claimed that body size changes in quantum steps and not by small incremental changes as implied by the neo-Darwinian theory. The purpose of this note is to show that, whatever the merits of his other arguments, Løvtrup's contention that body size evolves in discrete increments is based upon a fallacious statistical analysis. Further, I shall show that even using this method of analysis the null hypothesis that the observed fit is fortuitous cannot be rejected.

Løvtrup's hypothesis is that 'when the species within a given taxon are arranged with respect to mean body size, a grouping will obtain such that the ratio of the mean values of two successive groups is a power of two, if reference is made to volume or weight, or of $\sqrt[3]{2}=1.26$, if the length is used to measure the body size' (Løvtrup *et al* 1974). To test this hypothesis Løvtrup and his colleagues used body length data on mammals, birds and extinct and living equidae. The data were separated into clusters by means of a cluster analysis devised by Engelman and Hartigan (1969). This method is designed to separate two normal populations with different means but equal variances. To use the technique to separate more than two groups is not justified unless the robustness of the technique to this change in the initial assumptions has been studied. Suppose, for example, that we have a sample consisting of observations from three normal populations differing in their means but not their variances. We require that a method such as that of Engelman and Hartigan that separates clusters by dividing the sample into two should first separate one normal distribution from the other two. However, the variances of these two clusters will not be equal and therefore the significance of this division cannot be correctly assessed. If the table of significance values given by Engelman and Hartigan indicates that the division is not significant this cannot be taken as correct because the assumption of equal variances may not

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TABLE 1

Maximum and minimum variances given by Løvtrup et al (1974).

FAMILY	MINIMUM VARIANCE OF GROUP	MAXIMUM VARIANCE OF GROUP
Bovidae	1024	14161
Cervidae	9409	184900
Sciuridae	144	2704
Cricetidae	9	576
Muridae	81	3600
Primates	1296	9216
Carnivora	1681	58564
Pinnipedia	15876	52900
Piciformes	1.7	4.4
Strigiformes	0.2	86.5
Equidae	32.5	6146.6

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be satisfied. On the other hand, if the table indicates that the division is significant but the variances are not equal we can assume that the sample consists of two or more populations but it is not clear that the division is the correct one. At the very least, if the method of Engelman and Hartigan is used the variances of each group must be tested for homogeneity after each division. Løvtrup et al do not indicate that this was done. The variances obtained in their groupings vary enormously (Table 1) and suggest that the assumption of equal variances is incorrect.

The second point I take issue with is the method Lovtrup and his colleagues adopt to decide when to stop subdividing groups: 'When the progress of the operation is analysed, it is found that the significance of the grouping increases with each subdivision up to a certain maximum, subsequently it falls off again. Except for some special cases to be discussed presently, the values shown in the following tables are those representing the maximum group significance' (Løvtrup et al 1974). If the subdivision results in two groups that are not statistically different there is no reason to suppose that the subdivision is valid and hence further subdivision is not warranted. Each subdivision is independent of previous subdivisions and subdivision should be continued until the significance of the grouping drops below a previously assigned significance level, which in general will be the 95% level. In this regard we should note that 28 of the 48 groups given by Løvtrup et al lie below the 95% level of significance; four of the eleven tables contain only groups whose significance is below 0.95! Therefore, the validity of the groups must be seriously questioned.

Thus far I have argued that the method of separating clusters is incorrect. Now I should like to consider whether the null

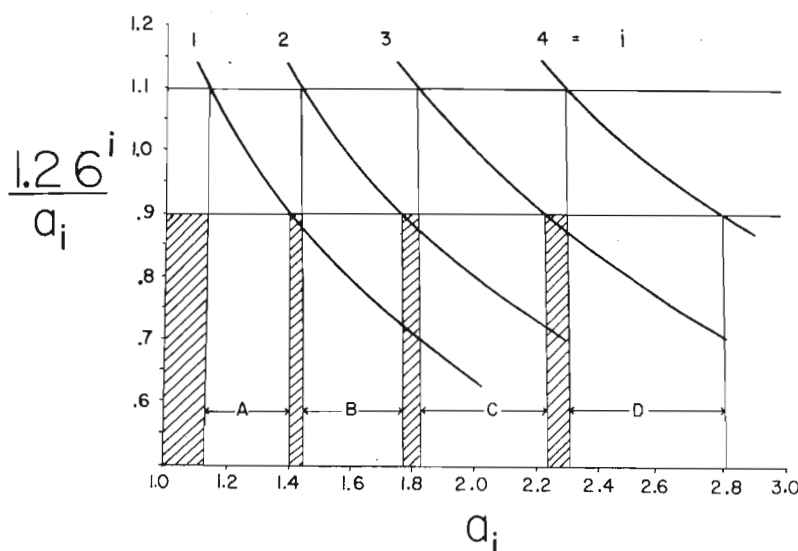


FIGURE 1

The relationship between the ratio Expected/Observed and the constant a_i , the amount by which the mean size of the first group must be multiplied to obtain the value of the i th group:

predicted value of the i th group = $1.26^i x$

observed value of the i th group = $a_i x$

Therefore, Expected/Observed = $1.26^i / a_i$

The shaded regions indicate values of a_i which give an unacceptable fit between observed and expected sizes. If two groups lie within the same region (A, B, C, D etc) one must be assigned to another region and hence its E/O ratio will lie outside the range 0.9-1.1.

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hypothesis can, in principle or practice, be falsified by this method. Lovtrup predicts that body size will vary according to the series

$x, 1.26x, 1.26^2x, 1.26^3x, 1.26^4x, \dots, 1.26^n x$
which equals

$x, 1.26x, 1.59x, 2.00x, 3.18x, \dots$

Where x is the mean body length of the first group. In matching up the expected and observed body sizes Lovtrup *et al* assume that some groups may be missing and make the best match possible. The difference between adjacent members of the predicted series is so small that a good fit is to be expected. To assess the accuracy of the fit Lovtrup *et al* suggest using the ratio Expected/Observed. They do not give a value of E/O which they consider acceptable but their results suggest a value between 0.9 and 1.1 (several of their values fall outside this range). Now consider the series

$x, a_1x, a_2x, a_3x, a_4x, \dots, a_nx$

where $a_1, a_2, \dots, a_n$ are arbitrary constants. Can this series be distinguished from that proposed by Lovtrup *et al* ? If the

TABLE 2'

Comparison between the results obtained by Løvtrup *et al.* (1974) for the Bovidae (A) and those obtained by random generation of groups (B-f).

A				B			
GROUP	MEAN	EXPECTED	E/O	GROUP	MEAN	EXPECTED	E/O
1-3	565	565	(1.0)	1-16	699	699	(1.0)
4-8	770	712	0.93	-	-	881	-
-	-	897	-	-	-	1110	-
9-28	1146	1130	0.99	17-24	1439	1398	0.97
29-36	1463	1424	0.97	25-32	1868	1761	0.94
37-40	1728	1794	1.04	33-38	2341	2220	0.95
41-45	2030	2261	1.12	39-60	2793	2797	1.00
46-49	2725	2848	1.05				

C				D			
GROUP	MEAN	EXPECTED	E/O	GROUP	MEAN	EXPECTED	E/O
1-4	584	584	(1.00)	1-30	1285	1285	(1.00)
-	-	736	-	-	-	1619	-
5-10	1026	927	0.90	-	-	2040	-
-	-	1168	-	31-60	2305	2571	1.12
11-40	1486	1471	0.99				
-	-	1854	-				
41-52	2166	2336	1.08				
53-60	2872	2943	1.02				

E				F			
GROUP	MEAN	EXPECTED	E/O	GROUP	MEAN	EXPECTED	E/O
1-40	1226	1226	(1.00)	1-20	716	716	(1.00)
-	-	1545	-	-	-	902	-
-	-	1947	-	-	-	1137	-
41-60	2519	2453	0.98	21-26	1403	1433	1.02
				27-44	1774	1805	1.02
				-	-	2274	-
				45-60	2617	2865	1.09

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predicted size is $1.26^i x$ and the observed size is $a_i x$ the E/O ratio is $1.26^i / a_i$. In fig 1 I have plotted the relationship between $1.26^i / a_i$ and a_i for values of i from 1 to 4. It can be seen that, providing no two values fall within the same range designated A, B, C or D, there are very few values of 'a' that produce an unacceptable fit. If two clusters both fall within the same range of 'a' (A, B, C, D etc) the E/O ratio of one will be outside the range 0.9-1.1. However, to detect clusters this close would require either a large sample size or small variances. The data of Løvtrup *et al.* satisfies neither of these requirements. Thus, in principle, it would be very difficult, given their data and criterion for an acceptable fit to find a series which did not fit the predicted series very well. This can be demonstrated by a

simulation experiment. I generated 60 data points by taking 15 sets of 4 observations from 15 normal distributions. All distributions had the same variance, 60, but their means were chosen at random from a range 500 to 2500. These values were selected to roughly match the values for the Bovidae given in Table 1 of Løvtrup et al. I analysed the simulated results according to their method. This procedure was repeated 5 times, the results of which are given in Table 2. The average E/O ratio of the simulated data is closer to unity than that for the Bovidae (1.006 compared to 1.017). The mean E/O ratio of all the groups given by Løvtrup et al is 1.002 compared to 1.006 for the random assembly and the difference is not significant. Thus the fit obtained by Løvtrup et al (1974) between observed and expected body sizes is no greater than might be expected from a random assembly of normal populations. Therefore, the contention that 'against all odds, the recorded finds happen to fit closely a geometrical scale of two', and that 'the Darwinian notion of small-step evolution is falsified with respect to body size' (Løvtrup 1976) is without foundation.

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