11

ATTEMPT AT APPLICATION OF ANALYSIS OF VARIATION TO THE QUALITATIVE RICHNESS OF THE FAUNA OF TERRESTRIAL VERTEBRATES OF THE U. S. S. R.

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The Problem

The term "richness of fauna" may be understood in two ways: first, as a great number of species found in any one place, and second, as a large number of individual animals. For the first case, it is better to use the term "qualitative richness of fauna" and for the second, "quantitative".

The significance of topographic variation on qualitative richness of fauna is generally known. The majority of zoogeographers explain diversity by historical causes, although no one denies the influence of present-day ecological conditions. The relative importance of these two groups of factors is still uncertain.

Introduced to science by Fisher (Fisher, 1925, 1928) and rapidly developing now (Sheffe', 1959; Plokhinski, 1960), the method of "dispersion analysis" or otherwise called "analysis of variance" affords the opportunity to determine the relative significance of the influence of separate factors on the total variability of a phenomenon. Statistically eliminating contemporary ecological factors (in the first place, abiotic), it is possible to approach the determination of the magnitude of influence of historical factors. Will this be the same for different groups of organisms?

Methods

Inventories of the terrestrial vertebrates of the USSR have reached a stage which permits the application of quantitative methods. The icthyofauna has also been well studied, but the complex of basic ecological factors on land and in the water is so varied (Hesse, Allee, Schmidt, 1951) that it would be more reasonable to devote a special paper to the analysis of the icthyofauna.

The entire surface of our country was divided into 66 equal-sized quadrats, of 10° longitude (about 700 miles on a side). Then the number of species found in each quadrat was determined by the superposition of areas on this grid. The raw data for these compilations was obtained from the most complete summaries of the distribution of terrestrial vertebrates of our country (Bobrinski, Kyznetsov, and Kyz'akin, 1944; Denent'ev and Glavkov, 1951-1954; and Terent'ev and Chernov, 1949). In some individual cases from the data taken out of the aforementioned summaries, changes and additions were made according to more recent information. The entire labor-consuming task of the transposition of range maps into quadrats was completed by S. V. Kanep and D. N. Fugenov. Climatic and other indices of abiotic (physical) conditions for the separate quadrats were calculated on the basis of maps from the Bol'shoi Sovietskoi Encyclopedia (1957), the Bolshovo Sovietskoi atlas of the world (1937), and the book by A. A. Borisov (1948).

For the sake of standardization and generalization of present statistical treatment, the systematized scheme and designations of the book of N. A. Plakhensk (1961) were used, with the exception of the term "deviation" for which the more common term "variance" was substituted. Variance for each quadrat is the square of the deviation of that quadrat's value from the mean value for all quadrats; r-1 is the number of degrees of freedom of non-random factors; n-r is the number of degrees of random factors; η^2 is the correlation ratio for non-random factors; σ_x^2 is the factor's variance; σ_z^2 is the error's variance; F is the variance ratio (the confidence level of 95% is used). For condensation in the tables, the following abbreviations are made: M = mammals, A = birds, R = reptiles, and Am = amphibians.

Formal Indices

It stands to reason that latitude and longitude, taken by themselves, do not take into consideration "ecological factors", but when these are taken in combination with several real causal factors it is possible to consider several excellent summarizing indices. Rekliv (1901) noted that "animal and vegetable species become more numerous as one preceeds from the poles to the equator", and this is now known to be generally true with respect to latitude. Analogous views are contained in many other reports (Eccart, 1913; Jacobi, 1919; Dahl, 1921; Hesse, 1924). Romer devoted an entire speech on the 1st of December 1906 to the Zen Kenderyskon Society of Naturalists especially to the question of the dimunution of the numbers of animal species with the increase in geographic latitude (Romer, 1907). In the following years, work was devoted to the quantitative expression of the stated dependence for different animal groups (Terent'ev, 1946; Kusenov, 1957; and others). By a priori considerations one is forced to conjecture that the changes in dependence on longitude will be in great measure determined by historical, but not ecological, principles.

Table 1. Analysis of the degree of influence of latitude on the number of species.

	M	A	R	Am
r-1	5	5	3	3
n-r	60	60	42	42
η^2	0.74	0.84	0.68	0.25
σ_x^2	10028	77544	3035	67
σ_z^2	288	1382	104	14
F	35	56	29	4.8

Table 2. The mean number of species found at the various latitudes.

Latitude	M	A	R	Am
30-40°	87.0	229.5	47.5	4.5
40-50°	80.7	213.0	27.3	8.1
50-60°	67.3	207.1	7.9	6.7
60-70°	39.9	153.4	2.4	3.0
70-80°	16.4	42.0	0	0
80-90°	1.8	12.3	0	0

Four separate analyses of variance were made, one for each taxon and its dependence on latitude, and the parameters calculated are given in Table 1. The decreasing number of degrees of freedom for Reptiles and Amphibians are explained as follows: representatives of these taxa at latitudes above 70° are found only as exceptions. From the preceding table, it is obvious that latitude imparts its maximum influence on the richness of fauna of the birds, while the poikilotherms, apparently, are more influenced by other factors. The empirical significances of the regression of the number of species with latitude are given in Table 2. Attention is drawn to the fact that the number of species diminishes with increase in latitude in all cases except amphibians. The alien value for poikilotherms makes it foolish to search for interpreting formulas, whereas for homeotherms, the values are all alike (Figures 1 and 2).

Mammals: $y = 102.1050 + 0.2670x - 0.0178\,x^2$
Birds: $y = -24.4275 + 11.9590x - 0.1401\,x^2$

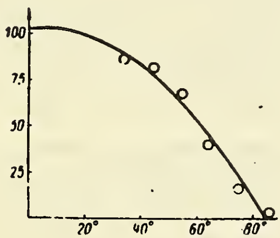

Figure 1. Regression of number of species of mammals on geographic latitude. The abscissa is graduated in degrees latitude, the ordinate in number of species.

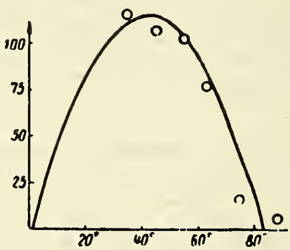

Figure 2. Regression of number of species of birds on geographic latitude (abscissa and ordinate are the same as in Figure 1).

The analyses of variance based on longitude give the figures presented in Table 3. The homeotherms show no correlation with longitude, but there is a weak correlation with longitude for the poikilotherms. Therefore, the detailed analysis of regression (Table 4) does not have meaning, although it does demonstrate the presence of two patterns: the number of species of homeotherms generally decreases from West to East (an artifact of the study?), whereas the

Table 3. Analysis of degree of influence of longitude on the number of species.

	M	A	R	Am
n-1	8	8	7	7
n-r	57	57	56	56
η^2	0.14	0.15	0.26	0.56
σ_x^2	1182	9026	541	95
σ_z^2	1017	6990	245	9.3
F	1.2	1.3	2.5	10.2

Table 4. The mean numbers of species ocurring at various longitudes.

Longitude	M	A	R	Am
20-40°	60.0	193.4	9.7	9.7
40-60°	57.9	162.9	22.1	6.1
60-80°	53.3	154.8	16.7	2.9
80-100°	51.9	141.5	5.5	2.8
100-120°	39.5	147.3	3.0	2.5
120-140°	47.4	149.4	4.4	3.6
140-160°	29.4	94.0	2.1	2.0
160-180°	18.4	79.6	0.2	0.6
180-200°	12.0	47.5	0	0

number of species of poikilotherms shows an East-West maximum (at roughly the Carpathians and the Caucasus on one side, and the Far East on the other side). These observations may be considered to be evidence that longitudinal distribution is dependent in Eurasia first and foremost upon historical factors (the glacial impoverishment of the Siberian fauna).

The Influence of Climatological Factors

The primary role of temperature and humidity amongst the physical factors is generally accepted. Unfortunately, it is difficult at this time to obtain satisfactory information on many parameters. Therefore, as a first approximation, three mean long-term quantities were used: air temperature in January (t_1), air temperature in July (t_7), and the sum of yearly precipitation in centimeters (S).

Analyses of variance using January temperatures gave the values presented in Table 5. A weak correlation is demonstrated for all four taxa, but comparisons of the taxa do not lead to clear-cut conclusions. The insignificance of the observed correlations makes it useless to calculate empirical lines of regression (Table 6), but it should be noted that in all cases the richness of fauna increases with increasing temperature. It is interesting also that the number of species of reptiles and amphibians is almost exactly equal at low temperatures, but that, at higher temperatures, the number of species of reptiles rapidly exceeds the number of species of amphibians.

Table 5. Analysis of degree of influence of the January temperature on numbers of species.

	M	A	R	Am
r-1	4	4	4	4
n-r	61	61	61	61
η^2	0.42	0.37	0.62	0.42
σ_x^2	7006	43600	2466	127
σ_z^2	646	4850	101	11
F	11	9	24	12

Table 6. The mean number of species found in areas with different mean January temperatures

t_1 in °C	M	A	R	Am
-50- -30	30.0	98.7	1.2	1.3
-30- -20	27.5	93.8	1.9	1.9
-20- -10	62.1	189.3	11.6	4.8
-10- 0	72.9	206.8	21.4	9.6
0- 10	90.0	227.3	55.0	5.3

An entirely different picture is obtained from the analyses of variance using mean July temperatures (Table 7): a very strong dependence is obtained for all taxa except amphibians, exceeding everything hitherto reported in this paper. Empirical lines of regression are given in Table 8. The dependence for mammals, birds and reptiles may be described with the following curvilinear equations:

Table 7. Same as Table 5, except for July temperatures.

	M	A	R	Am
r-1	6	6	5	5
n-r	60	60	45	45
^{2}	0.89	0.89	0.90	0 46
^{2}	11923	84066	3175	104
^{2}	127	836	32	11
F	94	101	100	9

Table 8. Same as for Table 6, except that the data is for July temperatures.

t_7 in °C	M	A	R	Am
0- 5°	8.4	28.3	0	0
5- 10°	27.6	85.6	0.2	0.7
10- 15°	41.4	159.1	3.2	3.4
15- 20°	70.7	215.5	8.8	7.5
20- 25°	97.0	253.8	29.3	9.3
25- 30°	88.0	212.0	52.8	5.0

Mammals: $$y = \frac{x}{0.2052 + 0.027276x - 0.002612x^2 + 0.000064x^3}$$

Birds: $$y = \frac{x}{0.1094 - 0.0048x + 0.000185x^2}$$

Reptiles: $$y = \frac{x}{13.0256 - 0.9828x + 0.0192x^2}$$

The graphs (Figures 3, 4, 5) indicates satisfactory correspondence between these curves and the empirical data. The question of the amphibians will be considered below.

Analyses of variance using the sum of the yearly precipitation gave the results presented in Table 9. It is seen that the total precipitation plays, even as was expected, a more significant

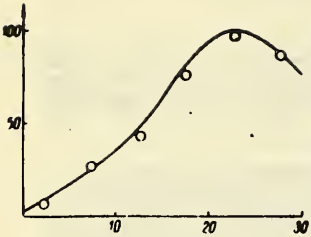

Figure 3. Regression of the number of mammal species on July temperature. The abscissa is graduated in °C, the ordinate in numbers of species.

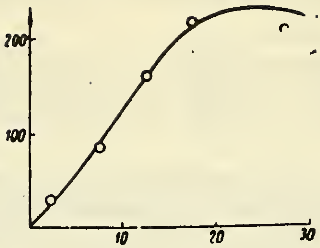

Figure 4. Regression of the number of bird species on July temperature (abscissa and ordinate same as in Fig. 3).

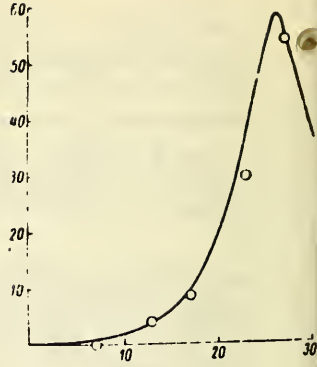

Figure 5. Regression of the number of reptile species on July temperature (abscissa and ordinate same as in Figure 3.

role only for the amphibians, but that even this is not great. Thus, the problem is not to look for an equation for the corresponding regressions, but to give these empirical meaning.

Table 9. Analysis of the degree of influence of total precipitation on the number of species.

	M	A	R	Am
r-1	6	6	6	6
n-r	60	60	60	60
η^2	0.20	0.28	0.18	0.42
σ_x^2	2658	26305	575	103
σ_z^2	902	5652	219	12
F	3.0	4.6	2.6	8.6

Discussion

The previous evidence shows without doubt that the number of species of the fauna is primarily a function of the presently operating factors (ecological), whereas the historical factors are responsible for the basic form of the specific composition of species. In other words, history determines how much of the potential size of the fauna is filled (saturated), which itself is determined by contemporary ecological conditions; i.e., in itself, the quantitative richness of the fauna (species diversity) is 80-90% a product of the present day conditions. By these means, the old zoogeographers-ecologists (Schmarde, 1853) have been shown to be correct, as are the contemporary zoogeographers, in giving attention to basic historical principles. The above is reasonable and correct only for faunas of a more or less substantial area; for, if we consider areas of small size, in the first place, stationary features and local perturbations arise. It is difficult to determine that minimum area, above which zoogeographical conformity prevails over local patterns (of diversity). It is reasonable to assume that the above findings hold for quadrats of the order of $n \times 10^4$ or $n \times 10^5$ kilometers^2. Amphibians, and very likely many groups of invertebrates, present exceptions: the numbers of these animal species depends, in general, rather strongly upon the general local situation, on microclimate rather than upon the macro-climate. Obviously, the minimal area necessary for zoogeographical regularity for mammals must be considerably larger--of the order of $n \times 10^6$ kilometers^2. Further investigation will be required to verify these suppositions and tentative findings.

As far as the correlation between latitude and temperature, localities (in soviet Russia) show a strong correlation - of the order $\eta = .84 \pm .01$ (Terent'ev, 1946); considering the shortage of information concerning local climates, it is possible to infer these from latitude. As mentioned earlier (p. 1), Rekliv was the first to note the latitudinal increase in total number of species. Thus, we may call this phenomenon "Rekliv's Rule". Furthermore, the increasing numbers of species associated with increases in temperature may be called "Schmarda's Rule", inasmuch as this author clearly noted the decrease in number of species with decreased annual temperatures.

Mere recognition of a positive or negative correlation does not definitely determine its form. Examination of the graphs of the present paper shows that some (Figures 3 and 4) appear to have two slopes: after the achievement of some optimum, the curve begins to descend. (Translator's note: here Terent'ev is referring to his mean values for the numbers of species--the data points.) One may examine other plots (Figures 1, 2, and 5) as parts of two-sloped curves. Given such a form, it is possible to make a more exact "Schmarda's Rule", taking the peak as the "optimum value". In the territory of the USSR, the greatest numbers of mammal, bird, and reptile species are found in quadrats with long-term mean July temperatures around 20-26°C. It is interesting to note that there is no difference in the optimum for amphibians, either.

Is it possible to express the mathematical dependence of the qualitative richness of fauna on temperature with such equations? An extension of this method gives the parabolic interpretations: $y = a + bx + cx^2 . . . .$ Theoretically, with such equations it is possible to express the course of any curve, if one includes a sufficient number of terms. Such a flexible function is adequate for a first approximation but is not devoid of basic shortcomings. The parabolas, in smoothing the mean of the curves, can give negative ordinates and may descend to approach zero. A negative quantity of species appears senseless, but the character of the region empirically analyzed has the meaning of a different function. Therefore, making use of the parabola, it fits the system to specify the limits of significance of the argument within which it is justified. For example, the parabolas of Figures 1 and 2 take on the meaning of an independent variable between 26° and 80° latitude. Presently there is no determining the ideal formula for the expression of the rule of the optimum ("Schmarda's Rule"). The important conditions which such a theoretical curve must possess are (1) that it must not allow the dependent variable to take on any negative values, and (2) that the asymptotes must approach the observed (empirical) values at each end of the curve. The necessary equations must take the following general form:

$$y = \frac{1}{a + bx + cx^2 + ...} \quad \text{and} \quad y = \frac{x}{a + bx + cx^2 . . . .}$$

The second formula is the preferred one, which even with only a second degree term in the denominator of the parabola, still shows the asymmetry so peculiar to the curved reaction in ecological factors. In practice, it is recommended to compute the ratios $\frac{x_1}{y_1}, \frac{x_2}{y_2}, \frac{x_3}{y_3}, . . .$ from the empirical data, and then to smooth these with a parabola of suitable degree (first, second, third, etc. . . .).

What do we obtain, in any given case, from such equations of regression? First of all, they make our theoretical ideas more precise, and secondly, they allow us to predict the value of data concerning the number of species, found in any given place. In making use of such standards, it is taken for granted that inevitably there will be scatter of empirical points about the predicted line of regression. It makes sense to look for causes only for those factors which show significant correlations. For example, the long-term mean air temperature in Leningrad is about 17.5°C (Syelyaninov, 1937). From this, it follows that we should expect about 211 species of birds in the Leningrad region. V. Bianki (1907) counted 237 bird species in this region, but noted that of these 237 species, 16 were rare, and another 24 were rather uncommon. This is very good agreement between the number of species predicted and the actual number occurring in the Leningrad region. On the other hand, if we try our prediction in the Crimea, we estimate that there will be from 39 to 46 species of reptiles. In fact, there are, according to old data, 15 species (Nikolski, 1905), and according to the latest investigations of N. N. Scherbak, only 14 reptile species in this region. Clearly, this particular fauna appears to be impoverished, which is precisely what N. N. Scherbok considers to be the case for the Crimea.

The amount of impoverishment carries with it a guiding character. On such areas it is desirable to check and to make our estimates more precise, with more detailed investigations in the separate regions of the USSR; and on the other hand, it is desirable to make further, more vast studies, taking in even other countries.

Summary

A number of species may be named "Qualitative Richness of Fauna", in opposition to the number of individuals, termed the "Quantitative Richness of Fauna".

The USSR territory was divided into 66 rectangles (10° latitude by 10° longitude). For each rectangle separately the number of Mammal species (M) was determined, the same for Birds (A), for Reptiles (R), and for Batrachians (Am). Deviances, estimates, variance-ratios (Tables 1, 3, 5, 7, 9) and regressions (Tables 2, 4, 6, 8) were calculated. Equations are given for the dependence of mammal and bird species numbers on geographical latitude, and for the dependence of mammal, bird, and reptile species numbers on the local mean July temperature. Dependence on geographical longitude and mean rainfall is insignificant. The number of species of amphibians is determined more strongly by micro-, rather than macroclimatic conditions.

Conclusions

(1) The number of species in a fauna is primarily determined by the mean temperature of the warmest month of the year (July).

(2) The greatest number of species of mammals, birds and reptiles in the territory of the USSR are found in areas with a July temperature on the order of 20-26°C.

(3) The quantity of species of amphibians is determined chiefly by microclimatic factors.

(4) An expression for the approximation of the "rule of the optimum" for species diversity is the following equation: $y = \frac{x}{a + bx + cx^2 + \ldots}$