On Some Aspects of Spatial Pattern in Biological Populations

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The spatial pattern of distribution of the individual members of a population of organisms is obviously of importance in the analysis of population behavior. A knowledge of this pattern and of the forces responsible for it finds practical application, for example, in estimating the rate of spread of genetic mutations or in predicting the course of an epidemic. Such problems have attracted the interest of biometricians, and in recent years there have been numerous contributions to the statistical theory of distribution.

Recently, some attention has been given to the possibility of using distance between individuals as a variable in distribution analysis. Of the many distance relationships that exist, the most easily ascertained and the most amenable to mathematical treatment is the distance to nearest neighbor. Dice (*1*), Skellam (*2*), Moore (*3*), and Clark and Evans (*4*) have all made use of the distance to nearest neighbor in the study of spacing. Further reflection suggests that the nearest neighbor relationships in a population may in themselves reveal information about the distribution pattern that does not require measurement of the actual distances involved.

In natural populations, many individuals are spatially related to one another in a "reflexive" manner; that is, in many cases two individuals are closer to each other than either one is to any other individual. When the distance between two such individuals is small compared with distances to other individuals, there is an obvious occurrence of pairs, but in many situations this pairing tendency is much less readily apparent. It can be shown, however, that in a randomly distributed population the relation of nearest neighbor is reflexive for a definite proportion of individuals. Consider two individuals, I_1 and I_2, in a population of density ρ distributed at random in two-dimensional space, and let the distance between them be denoted by r. Then I_1 and I_2 may be regarded as the centers of two intersecting circles of radius r, to be designated as circle 1 and circle 2, respectively. The probability that I_2 is the nearest neighbor of I_1 involves the assumption that circle 1 contains no other individuals; this probability can be shown to be

$$dP = 2\pi r \rho e^{-\pi r^2 \rho} dr$$

Then, given the event that I_2 is the nearest neighbor of I_1, the probability that I_1 is also the nearest neighbor of I_2 is the probability that the portion of circle 2 not included in circle 1 contains no other individuals; this probability is

$$e^{-r^2 \rho (\pi/3 + \sqrt{3}/2)}$$

Now the probability that I_1 and I_2 are the nearest neighbors of each other is the product of the two probabilities just given. By taking the integral from $r = 0$ to $r = \infty$ of this joint probability, we find the proportion P of the population for which the relation of nearest neighbor is reflexive to be

$$P = \frac{6\pi}{8\pi + 3^{3/2}} = 0.6215$$

This expected proportion of reflexives has been verified empirically in a synthetically constructed random population of 1000 points (Table 1). The number of individuals for which the relation of nearest neighbor is reflexive was found to be 602 in this population, and the difference between this and expectation is not statistically significant.

It may also be observed that the individuals of a population differ with respect to the number of other individuals for which they serve as the nearest neighbor. Some members of a population may be so placed that they are not the nearest neighbors of any other individual. Others, however, may serve as nearest neighbor to several individuals. In a random population of infinite size, the proportions of individuals that are nearest neighbors to 0, 1, 2, or more other individuals form a definite distribution that is independent of the population density. We have not succeeded in deducing the probabilities for these proportions, but approximations to them were obtained empirically from the synthetic random population mentioned previously (Table 1). Nearly 30 percent of the points did not serve as nearest neighbor to any other point, and approximately 70 percent were nearest neighbors to 1, 2, or 3 other points. The probability of serving as nearest neighbor to 4 or more

Table 1. Proportions of reflexive distances to nearest neighbor and of individuals serving as nearest neighbor to 0, 1, 2, and 3 other individuals in various populations.

Nature of population	No. of individuals in population	Proportion of nearest neighbor relations that are reflexive	Proportion of individuals serving as nearest neighbor to				
			0	1	2	3	4 or more
Synthetic random	1000	0.602	0.297	0.453	0.225	0.025	0.000
Liatris aspera	197	.579	.289	.467	.208	.036	.000
Lespedeza capitata	184	.609	.315	.435	.201	.049	.000
Solidago rigida	89	.607	.315	.416	.258	.011	.000

individuals is evidently extremely small. It can be shown to be impossible for any individual to be nearest neighbor for more than 5 other individuals.

These proportions of nearest neighbor relationships prove not to be restricted to random distributions. They may also occur in populations marked by a considerable degree of aggregation or clumping. For example, as is shown in Table 1, similar proportions were found to exist in populations of the plants *Liatris aspera* Michx., *Lespedeza capitata* Michx., and *Solidago rigida* L. occurring in an old field on the E. S. George Reserve, Pinckney, Mich. All of these have been shown to exhibit marked clumping tendencies (*4*). It is evident, therefore, that these nearest neighbor relationships are not affected by all types of departure from randomness. The distributional forces responsible for the aggregation in these plant populations seem not to have influenced their nearest neighbor properties. The most important factors in their distribution appeared to be the patchiness of environmental conditions and the particular methods of reproduction and dispersal of each species.

It is clear, however, that the nearest neighbor properties of populations will respond readily to social forces affecting distribution. Any social force that promotes the formation of pairs or of other relatively small groups will tend to increase not only the proportion of reflexive relationships but also the proportion of individuals that serve as nearest neighbor to 1 or more other individuals. When these proportions are greater than expected, one can conclude that in some way the individuals have responded positively to one another.

These observations suggest a way of separating the consequences of social forces from other factors affecting the spatial patterns of distribution in biological populations.

References

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Direct Recording from the A-V Conducting System in the Dog and Monkey

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The functional properties of the cardiac purkinje tissue, like those of many anatomical entities, are known mainly from deduction and indirect methods. Older physiologists recognized that there is a delay between auricular and ventricular activity, and also that a bridge of special tissue connects these two divisions of the heart. They rightly concluded that the electric impulse is confined within this tissue during at least part of the delay. Lewis (*1*) in his work on the excitation of the heart correlated the peripheral distribution of the purkinje fibers in the ventricle with his findings relative to the sequence of cardiac excitation. Further, he and others found that cutting peripheral ramifications of the conducting system or destroying the A-V node caused changes in excitation. Recently Draper and Weidemann (*2*), using intracellular microelectrodes, have given an excellent picture of the electric characteristics of the portions of the conducting system that may be easily removed and studied, the false tendons. However, direct study of the tissue in the intact heart, particularly of the portions buried in the interauricular and interventricular septa, has not previously been available.

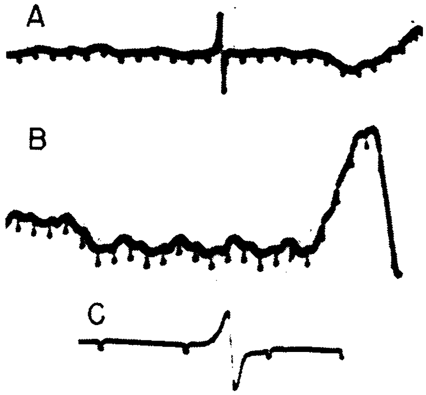

Fig. 1. Electric activity in conducting bundle of dog. (*A*) Records from electrode high in mid-interventricular septum under valve ring. Potential in center is from the bundle; slower potential changes at right show negative (receding) followed by positive (approaching) activity resulting from activation of ventricular myocardium. (*B*) Simultaneous Lead II ECG. P wave appears at left and QRS complex at right. It can be seen that biphasic bundle potential occurs about midway between auricular and ventricular activity. (*C*) Same potential as *A*, but faster sweep speed. Time pips were delivered simultaneously to both channels at 5-msec intervals. Bundle potential on *A* and *C* has peak-to-peak value of 3 mv.

During a continuing study of the pathway of normal ventricular activation, we had often taken records of excitation of the false tendons which cross the ventricular cavities, and it seemed possible to record from portions of the conduction system nearer to the A-V node and from the node iself.

Available apparatus consisted of a multichannel oscilloscope and multipolar needle electrode. These and the associated techniques have been described (*3, 4*). The multichannel apparatus facilitated scanning of many loci in a search for potentials. In the open-chested dog, exploring electrodes were inserted into the interauricular septum anterior to the coronary sinus in the area where Tawara (*5*) has located the A-V node. Other electrodes were pushed into the interauricular and interventricular septa along the pathway of the conducting bundle and its branches and into the apical ventricular cavity where preter-