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BREEDING STRUCTURE OF POPULATIONS IN RELATION TO SPECIATION¹

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INTRODUCTION

THE problem of speciation involves both the processes by which populations split into non-interbreeding groups and those by which single populations change their characteristics in time, thus leading to divergence of previously isolated groups.

The first step in applying genetics to the problem is undoubtedly the discovery of the actual nature of the genetic differences among allied subspecies, species and genera in a large number of representative cases. Differences which tend to prevent cross-breeding are obviously especially likely to throw light on the process of speciation, but all differences are important.

Our information here is still very fragmentary. We know enough, however, to be able to say that there is no one rule either with respect to cross-sterility or to other characters. In some cases the most significant differences seem to be in chromosome number and organization. At the other extreme are groups of species among which gross chromosome differences and even major Mendelian differences are lacking, both cross-sterility and character differentiation depending on a multiplicity of minor gene effects. In general, there are differences at all levels (*cf.* Dobzhansky, 1937).

But even if we had a complete account of the genetic differences within a group of allied species, we would not necessarily have much understanding of the process by which the situation had been arrived at. A single mutation is not a new species, except perhaps in the case of polyploidy. The symmetry of the Mendelian mechanism

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is such that any gene or chromosomal type tends to remain at the same frequency in a population except as this frequency is changed either by some steady evolutionary pressure (such as that due to *recurrent* mutation, to various kinds of selection, to immigration and to differential emigration) or by the accidents of sampling, if the number of individuals is small. The elementary evolutionary process, from this view-point, is change of gene frequency.

It is to be expected that the nature of the process will be found to be affected by what I have called the breeding structure of the species, and it is this aspect of the matter that I wish to discuss here. Such a discussion involves at least three steps. First, there is the observational problem of determining what the breeding structures of representative species actually are. Naturalists are only beginning to collect the detailed information which turns out to be necessary, but that which we have indicates situations of great complexity. The second step is that of constructing a mathematical model which represents adequately the essential features of the actual situation while disregarding all unimportant complications. The third step is the determination of the evolutionary implications of a given breeding structure in relation to mutation and selection. As difficult problems of description and mathematical formulation are also involved in the cases of mutation and selection pressures, the whole problem is exceedingly complex. I can only discuss the implications of certain very simple models of breeding structure, chosen partly because they appear to correspond to situations which one might expect to find in nature, but partly also because of mathematical convenience.

EVOLUTION UNDER PANMIXIA

The simplest situation, under biparental reproduction, is that of a large population, breeding wholly at random (panmixia). If sufficiently large, variability due to accidents of sampling is negligible. Each gene frequency

shifts steadily under the pressures of selection and recurrent mutation. Mathematical formulations of these pressures have been given. Letting q be the frequency of a given gene, $(1 - q)$ that of its alleles, u and v the mutation rates respectively from and to the gene in question and \bar{W} the mean selective value of all possible genotypes, weighted by their frequencies, the change in gene frequency in a generation is given by the following formula (Wright, 1937) :

$$\Delta q = v(1 - q) - uq + \frac{q(1 - q)\delta\bar{W}}{2\bar{W}\delta q}$$

For a gene which causes the same difference from its allele in all combinations and which lacks dominance, the term for selection pressure reduces approximately to $sq(1 - q)$, where s is the selective advantage over the allele.

The numbers of generations necessary for any given shift in gene frequency, under various hypotheses, have been presented by Haldane (1932 and earlier). This sort of process has been taken as typical of evolutionary change by R. A. Fisher (1930), who has compared its unswerving regularity to that of increase in entropy in a physical system.

If, however, conditions are constant, this process comes to an end at an equilibrium point at which opposing pressures balance each other ($\Delta q = 0$). At this point there is stability of the species type in spite of continual occurrence of mutations, an extensive field of variability and continuous action of selection. On the other hand conditions never are wholly constant. It is possible that evolution, in each series of alleles, may consist of an unswerving pursuit of an equilibrium point, which is itself continually on the move because of changing conditions.

The postulate that variations in gene frequency due to accidents of sampling, are negligible calls for some comment. The variance in one generation is $\sigma^2_{\Delta q} = \frac{l(1 - q)}{2N}$ in a diploid population of effective size N . This is cumu-

lative and may cause wide divergence from equilibrium if the population is not too large. The systematic evolutionary pressures directed toward equilibrium and this sampling variance determine between them a certain distribution of values of the gene frequency instead of a single equilibrium point. The general formula can be written as follows (Wright, 1937) :

$$\varphi(q) = (C/\sigma^2_{\Delta q}) e^{q(\Delta a/\sigma^2_{\Delta q})^2}$$

For the values of Δq and $\sigma^2_{\Delta q}$ given above this reduces to

$$\varphi(q) = C \bar{W}^{2N} q^{4Ns-1} (1-q)^{4Nu-1}$$

In the special case of no factor interaction and no dominance, the term \bar{W}^{2N} becomes approximately e^{4Ns_a} . There is a marked tendency toward chance fixation of one allele or another if $4Ns$, $4Nv$ and $4Nu$ are all less than 1 while such variability is negligible if these quantities are large (*e.g.*, as large as 100).

The possible evolutionary significance of these random variations in gene frequency in a panmictic population has been considered elsewhere (Wright, 1931, 1932) and will not be discussed further here.

Mating never is wholly at random. It is important to determine whether departures from panmixia have significant effects on the evolutionary process and if so whether these consist merely in impeding the pursuit of equilibrium or whether they may not bring about progress of a different sort.

One limitation on the effectiveness of selection in a panmictic population is that it can apply only to the *net effects* in each series of alleles. It is really the organism as a whole that is well or ill adapted. A really effective selection pressure should relate to genotypes not genes. But in a panmictic population, combinations are formed in one generation only to be broken up in the next.

If a selective value (W) is assigned to every one of the practically infinite number of possible combinations of genes of all loci, the array of such values forms a surface in a space of at least as many dimensions as there are loci, more if there are multiple alleles. Because of non-

additive factor interactions, this surface in general has innumerable distinct peaks (*i.e.*, harmonious combinations) each surrounded by numerous closely related but slightly less adaptive combinations and separated from the others by valleys. Selection according to net effect can only carry the species up the gradient to the nearest peak but will not permit it to find its way across a valley to a higher peak. Evolution would have a richer field of possibilities under a breeding system that permitted exploration of neighboring regions in the surface of adaptive values, even at some expense in momentary adaptation.

A somewhat similar situation holds within systems of *multiple alleles* (*cf.* Timoféeff-Ressovsky, 1932). There is presumably a limit to the number of alleles that can arise from a given type gene by a single act of mutation. But each of these mutations presumably can give rise to mutations at two steps removed from the original type gene and so on in an indefinitely extended network. If there is approximate fixation of one allele (to be expected in general under pannmixia), only those mutations that are at one or two removes have any appreciable chance of occurrence. There will be continual recurrence of the same mutations without real novelty. A breeding system that tolerates a continually shifting array of multiple alleles in each series in portions of the population, gives the opportunity for a trying out of wholly novel mutations which occasionally may be of great value. The question then is whether there are breeding structures that permit trial and error both within each system of multiple alleles, and within the field of gene combinations, in such a way as to give a richer field of possibilities than under the univalent determinative process in a panmictic population.

EVOLUTION UNDER UNIPARENTAL REPRODUCTION

At the opposite extreme from the system of random mating is that in which there is uniparental reproduction.

Under vegetative multiplication, or under diploid parthenogenesis, each individual produces a clone in which all individuals are of exactly the same genotype, except for occasional mutations. Continued self fertilization also leads to the production of groups of essentially identical individuals.

Suppose that a highly variable panmictic population suddenly shifts to uniparental reproduction. Selection then would be between genotypes. Those combinations that are most adaptive would increase, including perhaps rare types that would have been broken up and lost under panmixia. The less adaptive combinations would soon be displaced. Selection would be exceedingly effective until only one clone was left in each ecological niche. But at this point evolution would come to an end, except for the exceedingly rare occurrence of favorable mutations.

It is obvious that a certain combination of the preceding systems should be much more effective than either by itself (*cf.* Wright, 1931). Prevailing uniparental reproduction, with occasional crossing would permit an effective selection by genotypes to operate in a continually restored field of variability. This combination is of course one that has been used most effectively by plant breeders. It is found in many plants and animals in nature and has presumably been an important factor in their evolution.

The demonstration of the evolutionary advantages of an alternation of periods of uniparental reproduction with cross-breeding may seem to prove too much, since it is not usual in those groups that are usually considered to have evolved the most, the higher arthropods and vertebrates. Perhaps, however, there are other systems which also bring about differentiation of types and thus a basis for selection based on type rather than mere net gene effect, and which have more stability than arrays of clones.

EVOLUTION IN SUBDIVIDED POPULATIONS

A breeding structure that happens to be very conveni-

ent from the mathematical standpoint is one in which the species is subdivided into numerous small local populations which largely breed within themselves but receive a small proportion of their population in each generation from migrants which can be treated as random samples from the species as a whole. The basis for the partial isolation may be geographical, or ecological or temporal (breeding season). In the latter two cases an adaptive difference is postulated. We are not here considering the origin of this but rather its consequences on other characters.

Whatever the mechanism of isolation, its evolutionary significance can be evaluated in terms of the effective size of population (N) of the isolated group, the effective rate (m) of exchange of individuals between the group (gene frequency q) and the species as a whole (gene frequency q_t) and the local selection coefficient. It will be convenient here to write s for the net selection coefficient and to ignore mutation pressure (Wright, 1931).

$$\Delta q = sq(1 - q) - m(q - q_t)$$

If s in a local population is much larger than m , we have approximately

$$\begin{aligned} \hat{q} &= 1 - \frac{1}{s} [m(1 - q_t)] && \text{if } s \text{ is positive} \\ \hat{q} &= \frac{mq_t}{(-s)} && \text{if } s \text{ is negative} \end{aligned}$$

If the values of s among local populations show differences greater than m , there will be marked adaptive differentiation of such populations. There is an approach toward fixation of the locally favored gene largely irrespective of the frequency in the species as a whole.

The importance of isolation in evolution seems to have been urged first by M. Wagner as permitting divergent evolution under the control of different environments. Wagner thought of environment as directly guiding the course of evolutionary change, when its effects were not swamped by those of cross-breeding. A similar view has been held by many others since his time who have considered such orderly clines among geographical races as

those described by the laws of Bergmann, Gloger, and Allen. While direct control over mutation is not in line with present knowledge of genetics, indirect control through differential selection seems probable enough in these cases (*cf.* Dobzhansky, 1937; Huxley, 1939).

Davenport (1903) and Goldschmidt (1934) have stressed the likelihood of the spreading of the range of species by the diffusion of preadaptive mutations into territories in which they are isolated from the first by the inability of the typical members of the species to live. Goldschmidt has interpreted the major differences among races of *Lymantria dispar* in this way. He finds these differences primarily in such physiological characters as developmental rate, length of diapause, etc. Mathematically, this would be a special case of the foregoing scheme.

Differential selection has been considered so far as a factor making only for divergence of groups within the species and thus tending toward splitting of the latter. There is a possibility, however, that it may be a factor making for progressive evolution of the species as a unit. Particular local populations may, by a tortuous route, arrive at adaptations that turn out to have general, instead of merely local, value and which thus may tend to displace all other local strains by *intergroup* selection (excess emigration). In terms of our multidimensional surface of adaptive values, a particular substrain may be guided from one peak to another by a circuitous route around a valley which would probably not have been found except by such a trial and error mechanism. As different alleles may approach fixation in different populations, mutations at two or more removes from the original type have more opportunity for occurrence than if the population were homogeneous. Thus there may be trial and error within series of alleles as well as between gene combinations.

Let us now turn to the case in which the local selection coefficient is smaller instead of larger than m . The local equilibrium frequency (\hat{q}) is approximately as follows.

$$\hat{q} = q_t + \frac{sq_t}{m}(1 - q_t)$$

The values in different local populations in which s is smaller than m are clustered closely about the mean gene frequency, q_t . Selection causes no important differentiation. There may however be variability of each local population due to accidents of sampling if N is small and, consequently, much non-adaptive differentiation among such populations at any given moment.

$$\varphi(q) = Ce^{4Nsq} q^{4Nm} q_t^{-1} (1-q)^{4Nm(1-q_t)-1}$$

Figure 1 shows the form of the distribution for various values of Nm , taking $q_t = \frac{1}{2}$ and assuming no selection ($s = 0$). The variance in this case is as follows.

$$\sigma_q^2 = \frac{q_t(1-q_t)}{4Nm+1}$$

The distribution of gene frequencies is U shaped, implying random drifting from fixation in one phase to another if m is less than $\frac{1}{4Nq_t}$ and $\frac{1}{4N(1-q_t)}$. This again would permit trial within each series of alleles, and also between gene combinations.

The latter at least would be important even with larger values of m relative to $\frac{1}{4}N$. With $Nm = 5$, the standard deviation of values of q is 22 per cent. of its limiting value $\sqrt{q(1-q)}$. Such variability tends to become unimportant however if Nm is much larger.

Gulick seems to have been the first to point out the possible significance of isolation in bringing about a non-adaptive differentiation of local races. He has been followed by others, notably recently by Kinsey in his studies of the gall wasps of the genus *Cynips* (1929, 1936). A study of eleven isolated mountain forests in the Death Valley region by Dobzhansky and Queal (1938) showed a close approach to random mating with no appreciable selection within localities. Between localities on the other hand, frequencies ranged from 51 per cent. to 88 per cent., 2 per cent. to 20 per cent., 8 per cent. to 39 per cent. with standard deviations which can be accounted for by an effective value of Nm of about 5.1. The much greater standard deviation for the range of *D. pseudobscura* as a whole shows that this differentiation is cumulative with distance.

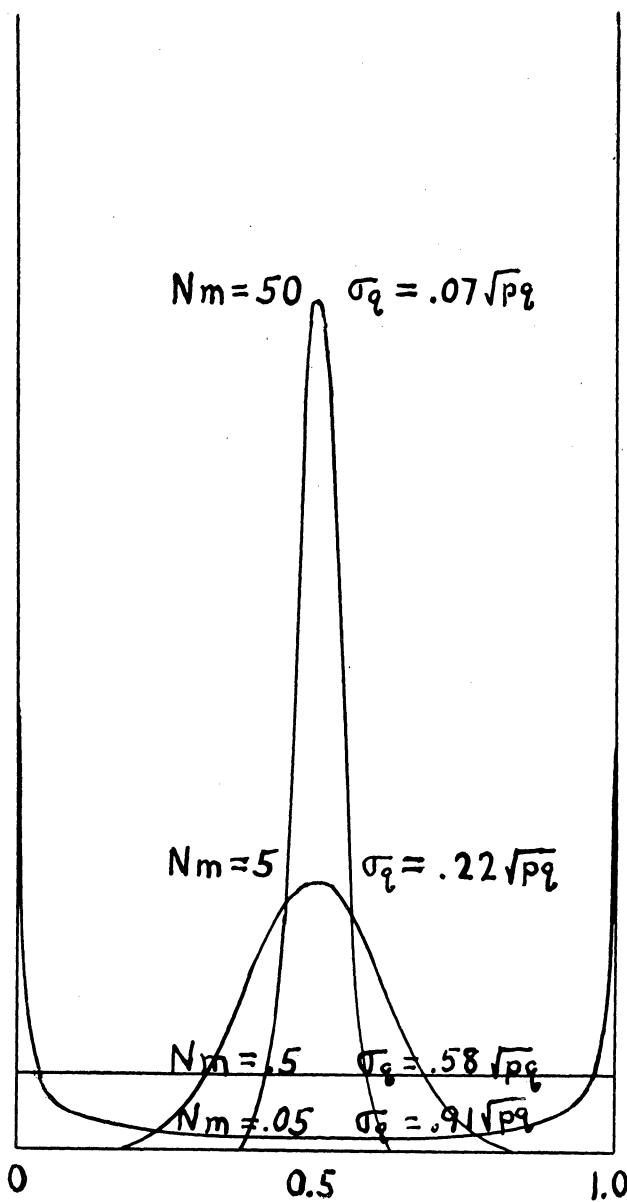


FIG. 1. The distribution of gene frequencies for various values of Nm , taking $q_t = \frac{1}{2}$ and assuming no selection. The symbol p is used for $1-q$.

EFFECTIVE SIZE OF POPULATION

There appears to be the difficulty here that the number of individuals in such a form as *Drosophila* is so enor-

mous that it is difficult to conceive of a limitation in numbers as having any appreciable sampling effects. However, the effective N may be very much smaller than the apparent N (Wright, 1938).

If the number of the two sexes (N_m males, N_f females) is unequal, it can be shown that effective $N = \frac{4N_m N_f}{N_m + N_f}$. With unequal numbers, the effective size of population depends more on the smaller number than on the larger number. Thus with N_m males but an indefinitely large number of females, $N = 4N_m$.

Again, different parents may produce widely different numbers of young. If σ^2_κ is the variance in number of gametes contributed by individuals to the following generation in a population (N_0) that is maintaining the same numbers ($\bar{\kappa} = 2$), $\sigma^2_\kappa = \frac{\sum (\kappa - 2)^2}{N_0}$

$$N = \frac{4N_0 - 2}{2 + \sigma^2_\kappa}$$

The effective size of population is twice as great as the apparent in the highly artificial case in which each parent contributes just two gametes. Effective and apparent size of population are the same if the number of gametes contributed by different parents vary at random (Poisson distribution). If, as would often be the case, most of the offspring come from a small percentage of the mature individuals of the parental generation, the effective size would be much less than the apparent size.

A population may vary tremendously in numbers from generation to generation. If there is a regular cycle of a few generations ($N_1, N_2 \dots N_n$) an approximately equivalent constant population number can be found.

$$N = \frac{n}{\sum_{x=1}^n [1/N_x]}$$

This is controlled much more by the smaller than by the larger numbers. Thus if the breeding population in an isolated region increases ten-fold in each of six generations during the summer (N_0 to $10^6 N_0$) but falls at the

end of winter to the same value, N_0 , the effective size of population ($N = 6.3N_0$) is relatively small.

In such a cycle, certain individuals in favorable locations are likely to start reproduction earlier than others, perhaps getting a start of a whole generation. In a rapidly breeding form, these few individuals would contribute overwhelmingly more than the average to all later generations. Thus, by a combination of the two preceding principles, the effective size of population may be very small indeed.

The possible evolutionary significance of periodic reduction in the size of natural populations has been discussed by a number of authors. Elton (1934) especially has maintained that chance deviations in the characteristics of survivors at the time of least numbers may have important effects of this sort.

An important case arises where local populations are liable to frequent extinction, with restoration from the progeny of a few stray immigrants. In such regions the line of continuity of large populations may have passed repeatedly through extremely small numbers even though the species has at all times included countless millions of individuals in its range as a whole (*cf.* Fig. 2).

Such mutations as reciprocal translocations that are very strongly selected against until half fixed seem to require some such mechanism to become established. There is an exceedingly deep valley in the surface \bar{W} representing the mean adaptive value in populations with given frequencies of old and new chromosomes, and the term \bar{W}^{2N} in the formula for the joint chromosome frequencies is so small, where N consists of more than some half-dozen individuals that fixation is virtually impossible. Yet translocations have been noted between *Drosophila* species (*e.g.*, *D. pseudoobscura* and *D. miranda*, Dobzhansky and Tan, 1936) although they are far less common than inversions. The difficulty referred to here does not, of course, apply in species that reproduce vegetatively or by self-fertilization.

We have discussed various considerations that make

effective N much smaller than at first apparent. The effective amount of cross-breeding may also be much less than the actual amount of migration seems to imply. Most of the immigrants are likely to come from neighboring groups, differing less from the receiving population in gene frequency than would a random sample from the

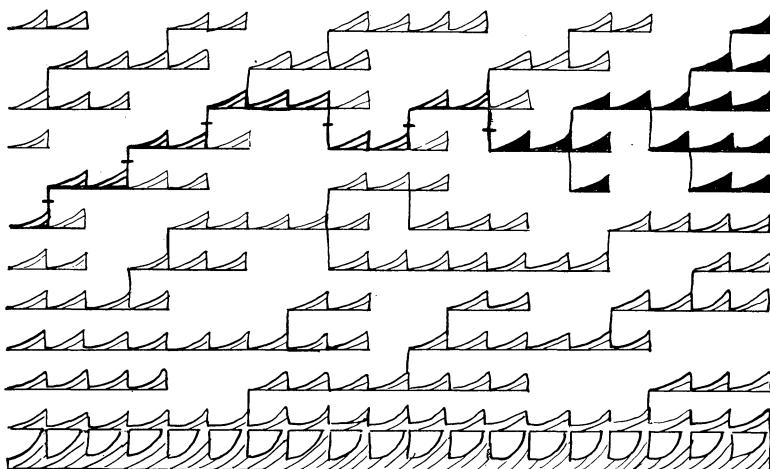


FIG. 2. Diagram of breeding structure in a species in which the populations in certain regions are liable to frequent extinction with reestablishment by rare migrants. Different territories are distinguished vertically. Generations proceed from left to right horizontally. The heavily shaded group represents a large population the entire ancestry of which has passed through small groups of migrants six times in the period shown.

species. If there is a correlation, r , between immigrants and receiving group, the m of the formula must be replaced by $m(1 - r)$ if m is to continue to be the actual amount of replacement by immigration.

In the case of *Drosophila pseudoobscura*, it has been noted that Dobzhansky and Queal (1938) found variability in gene frequency among mountain forests of the Death Valley region which implied an effective value of Nm of about 5. For the species as a whole, variability is such that effective Nm must be only about one tenth as large as this (0.5).

ISOLATION BY DISTANCE

This last case leads to another model of breeding struc-

ture which may be of considerable importance (Wright, 1938). Suppose that a population is distributed uniformly over a large territory but that the parents of any given individual are drawn from a small surrounding region (average distance D , effective population N). How much local differentiation is possible merely from accidents of sampling? Obviously the grandparents were drawn from a larger territory (average distance $\sqrt{2} D$, effective population $2N$). The ancestors of generation n came from an average distance $\sqrt{n} D$ and from a population of average size nN . It is assumed that the variance of the ancestral range, either in latitude or in longitude, increases directly with the number of generations of ancestry.

Fig. 3 shows how the standard deviation of gene frequencies for unit territories of various effective sizes increases with distance. If $\sigma_q = .577\sqrt{q_t(1-q_t)}$ and $q_t = 1 - q_t = \frac{1}{2}$ all values of gene frequency are equally numerous ($\phi(q) = 1$). Any larger value implies a tendency toward fixation of one or the other allele in different local populations.

If the parents are drawn from local populations of effective size greater than 1,000, the situation differs little from pannmixia even over enormous areas. There is considerable fluctuating local differentiation of unit territories where their effective size is of the order of 100, but not much differentiation of large regions unless effective N is much less.

Kinsey's (1929) description of the gall wasp, *Cynips pezomachoides erinacei*, conforms fairly well to the above model for the case of moderately large N . This subspecies ranges over some 500,000 square miles in northeastern United States. Both the insects and their galls may differ markedly and consistently in collections taken from different trees or small groves at short distances apart, but the same variability is found throughout the range. There is little regional differentiation in this enormous territory, although at still greater distances

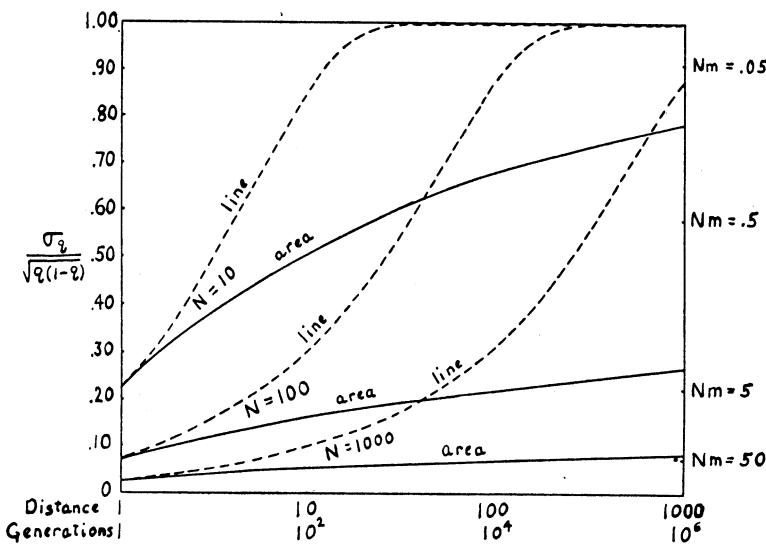


FIG. 3. The standard deviation of the mean gene frequencies of unit random breeding territories ($N = 10$; $N = 100$; $N = 1000$), in relation to mean distance. The case in which the population is distributed uniformly over an area is represented in solid lines, that in which it is distributed along one dimension by broken lines.

the species complex *C. pezomachoides* is subdivided into eight intergrading species.

In a species whose range is essentially one-dimensional (shore line, river, etc.) the ancestors of generation n come from an average distance of $\sqrt{n} D$ as before, but the effective size of population is $\sqrt{n} N$ instead of nN . Differentiation increases much more rapidly with distance than in the preceding case. This principle was suggested in qualitative terms by Thompson (1931) in his study of differentiation within species of river fish in relation to water distance. In weak swimmers (*e.g.*, Johnny Darters) there was marked increase in average difference in number of fin rays with increased distance in spite of a continuous distribution. The differentiation with distance was not as rapid, however, as that in several species with discontinuous distribution (restricted to the smallest stream). On the other hand the strong swimmers of the rivers showed little or no differentiation throughout their entire ranges.

Such uniformity in breeding structure as implied above is not likely to be closely approximated in nature. Even where there is apparent continuity of a population, it is likely that conditions vary from place to place in such a way that there is excess multiplication at certain centers separated by regions in which the species would be unable to maintain itself permanently were it not for immigration (as in the breeding structure of Figure 2). Moreover, even with complete uniformity of conditions, local differentiation should result in the accidental attainment of more adaptive complexes in some regions than in others. As before, incipient nonadaptive differentiation may lead to a more important adaptive differentiation. The centers in which population is increasing most rapidly will become increasingly isolated from each other by the mere fact that they are centers of emigration.

A process of this sort has been postulated by Sumner (1932) in the case of subspecies of *Peromyscus*. Within subspecies, he found statistical differentiation of most local populations which may well have been of the type due merely to distance. But at the subspecies boundaries there was typically a zone of relatively rapid change. These boundaries were not necessarily along natural barriers to migration. Sumner compared them with the distributions which would result "if a collection of spherical rubber bags were placed in rigid containers and then strongly but unequally inflated."

The breeding structure of natural populations thus is likely to be intermediate between the model of subdivision into partially isolated territories and that of local inbreeding in a continuous population. In so far as it is continuous, it is likely to be intermediate between area continuity and linear continuity.

Summing up, we have attempted to show that the breeding structure of populations has a number of important consequences with respect to speciation. Partial isolation of local populations, even if merely by distance is important, not only as a possible precursor of splitting of the species, but also as leading to more rapid evolu-

tionary change of the population as a single system and thus more rapid differentiation from other populations from which it is completely isolated. Local differentiation within a species, based either on the nonadaptive inbreeding effect or on local conditions of selection or both, permits trial and error both within series of multiple alleles and between gene combinations and thus a more effective process of selection than possible in a purely panmictic population.

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