ENTOMOLOGIA

A GENETIC STUDY OF WILD POPULATIONS AND EVOLUTION

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The determination of the scientific basis of heredity within the last two decades and the verification of the principal conclusions in many different plants and animals has made possible the application of analytical methods in the study of variations in wild populations. As with the physical and chemical sciences, genetics has been enabled to make use of mathematics to compound (often theoretically) out of simple units, the genes, the complexity known as an organism, much in the same way as a chemist compounds molecules with atoms and the physicist compounds atoms with protons and electrons.

The difficulties in dealing with living organisms are tremendous but the progress in this field has been great. Biological mathematicians as Wright, Fisher and Haldane have shown the way for the field worker to apply the laboratory information derived primarily from *Drosophila* and maize to problems of evolution in the wild.

It has seemed that the smaller the unit of organism with which we deal, the more difficult has become the process of analyzing evolution. Yet it is fundamental to understand the simple units before the more complex. Picturing in our mind the complete cellular nucleus of an organism as the ultimate hereditary complex, through decreasing complexity we pass through the chromosomes and come to the genes. Beyond the gene, the realms of chemistry and physics are encountered, an almost impossible task still.

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The taxonomist's work is with the complete organism, that is, with the final product of the total gene, chromosome and environmental action on growth. The cytotaxonomist or cytogeneticist deals with the form and differentiation of the chromosomes, In each of these fields it has been possible to observe directly the object studied. For the geneticist this is not possible. He can observe at the present day only the effect of the gene upon the organism and in certain cases to determine the position of the gene in the chromosome in relation to other genes.

The effects of all genes which an organism possesses are often not expressed in the completed organism and the effects of some may be different depending upon the genes with which they act in cooperation. A recessive gene has no effect unless it is present in duplicate. The geneticist, by making the proper intercrosses, is enabled to duplicate in the one organism such "hidden" genes and to determine the percentage of such genes in wild populations. Many aberrations, freaks or forms in wild populations have been shown to be instances in which two such recessive genes have become duplicated in the same organism. On the other hand, a dominant gene has its effect upon ontogeny whether present single or double, though in the latter case the double effect may be too strong and the organism dies (lethal gene).

With a knowledge of the hereditary character of a gene derived from the proper crosses, it is possible to determine the frequency of a gene in a wild population whether dominant or recessive. The simple genetic or algebraic formula first applied to wild populations in theory by Hardy is all that is necessary:

$$A^2 + 2Ab + b^2$$

A theoretical dominant gene can be designated by the capital letter A and its recessive counterpart by the small letter b. Then if we know that a form (let us say a color variation) existing in a wild population is dominant and represents by random count 75% of all individuals in a population, we can determine the frequency of homozygous dominant individuals (with two such genes present), of heterozygous individuals (with one dominant and one recessive gene present) and of the homozygous recessive individuals (with two recessive genes present). For example, the 75% will be distributed between the A^2 and 2Ab since both contain at least one dominant gene. The b^2 is 25% of all individuals and has only recessive genes. The recessive gene frequency is then cleary 50% of the whole (the square root of .25 is .50) and the dominant gene frequency comprises the other half:

	A^2	+ 2Ab +	b^2
genotype frequency (not visible)	25%	: 50% :	25%
phenotype frequency (visible)	75%	:	25%
ratio	3	:	1

gene frequency: 50% dominant
50% recessive

In some cases the heterozygote is visibly different from either homozygote and three visible forms are present in the populations. The phenotype frequency then would be the same as the genotype frequency above.

Few naturalists have not observed the rather close correlation between animal and plant form and specific environmantal factors in which the organisms live. Some of this body form is imposed directly during ontogeny upon the organism and is changeable when the environment changes. Other differences are controlled from within the body and are uninfluenced by a change in the external conditions. These are the gene controlled variations. Science knows no way by which the environment is capable of influencing the genes in a definite direction for the purpose of producing a complete organism better suited for life under those conditions. Therefore, the geneticist assumes it is by the selective survival of individuals carrying genes of definite value that an organism is evolved to fit an environment. *The entire process of evolution is thus left to chance change of genetic constitution and to environmental selection after the internal change*. Most. changes of genes or genetic systems are deleterious or lethal. This would be expected since the organisms of the present day have been selected for years and the chances of an advantageous change arising are very remote. Sturtevant, Dubinin and Dobzhansky have utilized modern genetic techniques possible only with the aid of the fly *Drosophila* for determining the frequency of "hidden" recessive lethal genes in wild populations. It is clear that until such a gene is present in duplicate it is not lethal and has no effect. Likewise, in the case of an advantageous recessive gene there is no selection except in those individuals in which it is duplicated.

The author has been studying a dominant gene in *Colias* butterflies which is indicated by a white color in the females which carry it. At least under some circumstances, this gene is lethal when homozygous.

Wild populations of two forms of this butterfly (*Colias chrysotheme*) in North America have a higher frequency of white individuals in the north than in the south. This occurs nearly everywhere within the same race. In California, the frequency varies from 70% in the latitude of San Francisco to 13% in the latitude of the Mexican border (orange race). In the yellow race, the frequency is close to 100% in Alaska and drops to near 0% in the mountains of Utah, Colorado, etc. Climatic selection for the dominant gene form is assumed to be present in the north because of the regularities in the geographical distributions. Laboratory breeding has shown that changed environmental conditions have no effect in the determination during ontogeny of the white versus the orange or yellow forms. An attempt at discovering the selective advantage has not yet been possible, but some indications are that the white form is more rapid in development than the orange. This alone would be advantage enough to wholly change the gene frequency in favor of white throughout the range of the species. However, it has acting in opposition to this favored growth rate, the disadvantage of being lethal when homozygous under certain conditions. Apparently these conditions are those prevailing in the warmer climates.

A balance then exists between the advantage the white form has as a heterozygote and the disadvantage that it has as a homozygote under certain conditions. In both forms of *Colias chrysotheme* this balance is controlled by the enviroment so that in the far north either the climate renders the homozygote as not lethal or the faster development of the heterozygote counteracts the loss due to homozygote lethality.

A form of this butterfly exists in Colombia. Wherever white clover is found in considerable quantity (in the "Tierra Fría") this butterfly is found rather commonly. Preliminary observations have indicated that the frequency of the white female form is between 10%

and 15% in the savanna of Bogotá, at 2600 m. above sea level. With complete lethality of the dominant homozygote (as yet only conjectured) there is thus a gene frequency of 6.3% dominant and 93.7% recessive: (*).

	A^2 +	2Ab +	b^2
phenotype ♀	lethal	white	orange
phenotype ♂	lethal	orange	orange
genotype	WW	Wn	ww
%		12.5%	87.5%
ratio		1 :	8

Further research may indicate that within the climatic zone of Colombia in which this species exists, there may be found differences in the frequency of this gene. Of great interest would be a check on whether colder country is effective here in this country in developing a higher concentration of the gene. It may be possible to discover the factors controlling the balance between the three genotypes. With three zones of largely isolated Tierra Fría along the tops of the three Cordilleras, Colombia presents excellent terrain for this study.

In addition to the single gene difference as in the example above, in certain cases of gene segregation folowing fertilization, not all genes are separable as units. That is, genetic segregation is incomplete and chromosomes or portions of chromosomes are transmited as units. Where there is no genetic segregation at all, the line of species difference is drawn, for beyond this point there is completely independent evolution. In some other cases there may be only partial genetic segregation. Such a circunstance was found to be true in the case of the two North American races of *Colias chrysotheme*. Generally these would be considered two species but because of gene interexchange, these must be considered as intermediate between species and subspecies. There are a few known differences between them:

	yellow race	orange race
orange pigment on upper surface of the fore wing	absent	present

(*) In this case the males carry the gene but show no visible effect. The gene is called a sex-limited gene as contrasted with a sex-linked one since the gene is not present in the sex chromosomes but is transmitted normally.

diapause in the larvae	present	absent
food preference	white clover, red clover, etc.	alfalfa, Vicia Astragalus, white clover.
distribution (original)	Alaska to Guatemala at high elevations in the south. Atlantic Ocean to Sierra-Cascade divide.	Brit. Columbia to Mexico. Pacific ocean to the Mississippi Valley.

Except for the one minor color difference, there are no visible variations by which these races can be distinguished where they live in the same region. There is on the average about 10% of intermediates in the populations and considerable gene interexchange. Only where the races are separate in their geographical distribution are visible difference allowed to develop, for apparently, the high rate of hybridization with its subsequent gene exchange prevents environmental selection from being effective.

The hybridization in wild populations is constantly taking place at the expense of the species involved. Laboratory experiments indicate that there is high mortality in the interracial crosses and, owing to the food differences of the races, high mortality ensues from lack of proper food for the hybrid individuals.

With the present knowledge it is impossible to determine the status of *Colias dimera* with respect to the North American races. There are abundant differences between *dimera* and either race and they are apparently separated by an area uninhabited by Colias from Guatemala to Colombia. To the south *dimera* may connect along the Andes with *lesbia* of Argentina. Judging from food and color characteristics the latter may almost certainly be physiologically similar to the orange race. But these questions can not now be answered. *Colias lesbia* is an agricultural pest in the south and *Colias chrysotheme* (orange race) is an agricultural pest in the north. It is possible that alfalfa may some day be an important crop in Colombia. By tests of food preference it is possible now to determine whether or not *Colias dimera* could become a serious agricultural pest.