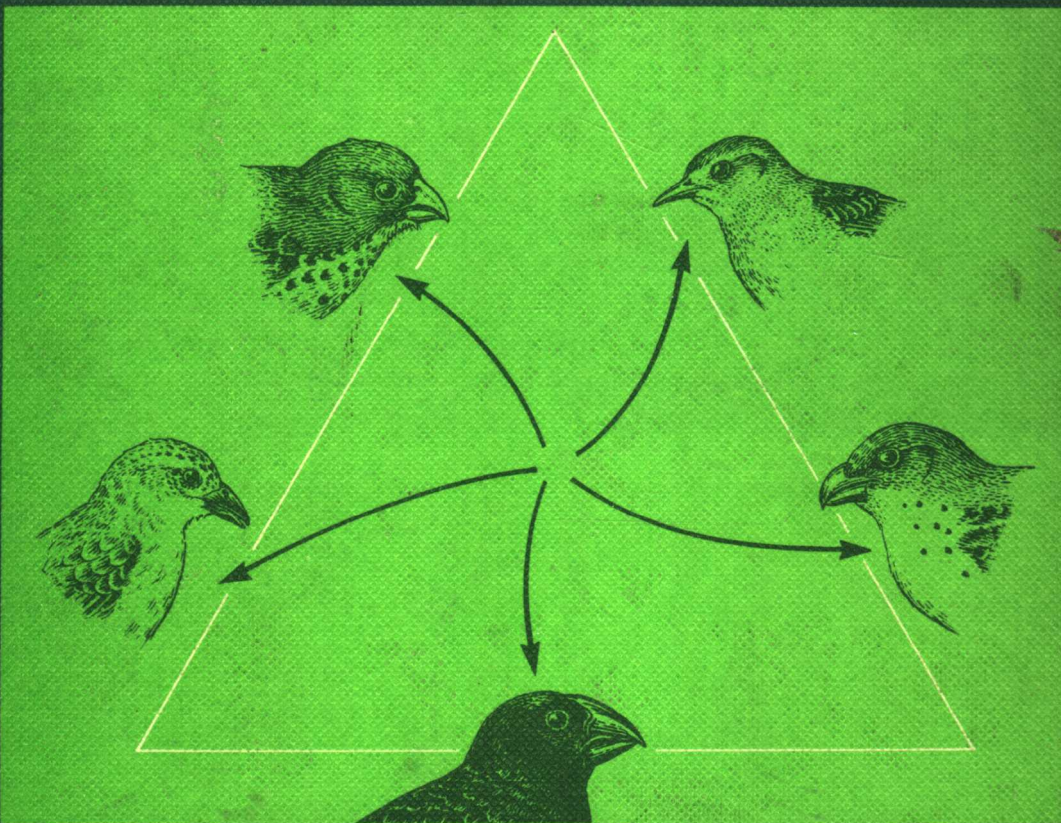


Population Biology and Evolution

Edited by
K. Wöhrmann and V. Loeschcke



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Preface

This volume contains the papers presented at a symposium on population biology sponsored by the Deutsche Forschungsgemeinschaft. It was held at the guest house of the University of Tübingen at Oberjoch on May 15-19, 1983.

Prior to this conference a small group of European biologists had met in Berlin (June 1981) and Pavia (September 1982) to discuss research problems on the borderline between population genetics and evolutionary ecology.

From the contributions and discussions at these meetings it became evident that the unification of approaches to evolutionary problems in population genetics and evolutionary ecology has not yet been successful and requires further efforts. It was the consensus that a larger symposium with international participation would be helpful to confront and discuss the different approaches to population biology in order to assess "where we are now" and "where we should be going."

As a result an organizational committee was formed (F. Christiansen, S. Jayakar, V. Loeschcke, W. Scharloo, and K. Wöhrmann) to identify topics that seemed, at least to them, to be fruitful in tackling problems in population biology. Consequently, a number of colleagues were asked to participate in the meeting.

We have divided this book into chapters corresponding to the eight topics chosen. The volume begins with the relation between genotype and phenotype and is followed by a chapter on quantitative genetics and selection in natural populations. Chapter 3 deals with theoretical aspects of density regulation and life histories followed by discussions of genetic heterogeneity and ecological factors. The next chapter concerns genetic structure and demography in plant populations and Chap. 6 covers population differentiation and asexual reproduction. These are followed by contributions on theoretical aspects of coevolution and concludes with some comments on models in population genetics and evolutionary ecology.

The papers are revised versions of those presented at Oberjoch. They were reviewed by participants of the meeting including colleagues who did not present papers. We wish to thank all the reviewers for their help and the members of the organizational committee for their support in arranging the conference.

Special thanks are due to the leaders of the evening discussions, W. Scharloo and P. Grant, and to the chairmen of individual sections. We are grateful to Mrs. M. Bullinger and Mrs. C. Rehm from the Institute of Biology II in Tübingen for assistance in organizing the conference and to Doth Anderson, Annie Jensen, Kirsten Petersen, and Marianne Szygenda from the Institute of Ecology and Genetics in Aarhus for editorial assistance.

Aarhus and Tübingen
April 1984

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Introduction: Genotype and Phenotype: Basic Concepts in Population Biology

V. LOESCHCKE¹ and K. WÖHRMANN²

An individual is characterized by its particular genotype. In sexually reproducing species two individuals rarely share a genotype. The phenotype of an individual is the result of the interplay between its genotype and its environment: of single gene effects, the interaction between its genes, and the interaction between the genes and the environment. The phenotype includes all aspects of the individual's morphology, physiology, behavior, as well as its ecological relationships to other individuals.

In practice, we use the concepts of genotype and phenotype in a more restricted sense by referring to a subset of the genotype and to a partial phenotype at some stage of the life history. In this restricted sense individuals of the same species commonly share genotypes and phenotypes. If we consider a specific partial phenotype, then generally we will find that several genes are relevant in the formation of particular characters. These genes are located on chromosomes and are therefore more or less linked to groups of other genes. Genes contributing to the determination of particular characters may well have pleiotropic effects on other characters, which in turn are affected by other genes. At the molecular level, they are coding for products that may be interacting functionally with other gene products.

It is the individual that survives and reproduces. Its success in doing so under specific environmental conditions is characterized by the fitness. Thus, fitness is a function of the phenotype and the environment. The differential success of distinct phenotypes in contributing to the next generation induces a change in the relative proportions of genes transmitted to the next generation (Fig. 1). Thus, essential features of evolutionary processes occur at two distinct levels. Selection is acting on phenotypes, but only genes record the history of the selective processes.

The processes that link genotype and phenotype are only known in a few cases and will hopefully be better understood in the future. So far, evolution has been considered by evolutionary ecologists mainly as changes in life history characters and other dynamically interesting phenotypes in relation to environmental conditions. On the other hand, population geneticists view evolution as changes in heritable phenotypic variation that can be traced back to genetic variation and as changes in the corresponding gene frequencies. Both disciplines have tried to characterize the evolutionary role of variation at each level in relation to environmental conditions. One of the major tasks of contemporary population biologists is to relate the processes that occur at both levels and, in addition, to differentiate concepts of the environment when

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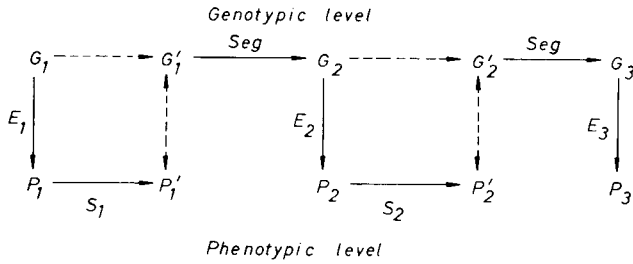


Fig. 1. Some basic processes within and between the genotypic and phenotypic levels. The phenotypes, P_1 , that correspond to the genotypes, G_1 , are influenced by the environment E_1 . Selection, S_1 is operating on the phenotypes, P_1 , and thereby conditions a change in the phenotypic composition of the population from P_1 to P_1' . Consequent upon this change there is a change in the genotypic composition from G_1 to G_1' . At the genotypic level segregation, Seg , occurs which determines the genotypic composition, G_2 , at the beginning of generation 2. The process continues in similar fashion in subsequent generations

describing these processes. The contributions to the symposium are attempts toward this goal using a variety of approaches which hopefully will provide an impression of the diversity within contemporary population biology.

Genotype and Phenotype

Genetics of Adaptive Reactions

W. SCHARLOO¹

Neo-Darwinism is a theory which is completely focused on genes: evolutionary change is considered to be a change of gene frequencies. This view has its origin in the theory of population genetics. The mathematical theory bestowed prestige on evolutionary genetics. As a consequence this prestigious mathematical framework became more and more identified with the whole field.

Nevertheless, at the end of the fifties and the early sixties there was still a place for quantitative genetics in evolutionary biology [e.g., see SEB Symposium on Evolution (Brown and Danielli 1953) and the Cold Spring Harbor Symposium on Population Genetics (Demerec 1955)]. Quantitative genetics is not so much a theory of genes as a theory of phenotypes. Selection operating in quantitative genetics is selection on phenotypes as it is, of course, almost always in nature. Genetic effects of selection are determined by the developmental and/or physiological processes which connect genes and phenotypes.

In the early sixties quantitative genetics started (1) to identify and localize genes involved in quantitative variation (Thoday 1961) and (2) to analyze physiological and developmental processes underlying quantitative variation (Robertson 1959; Spickett 1963).

Electrophoretic Variation

The discovery of electrophoretic variation by Harris (1966) and Lewontin and Hubby (1966) stopped this almost completely. Experimental population genetics became electrophoresis. After the International Congress of Genetics in Berkeley in 1973 a well-known quantitative geneticist wrote to me: "Quantitative genetics is dead."

By a dogmatic inverted application of the dictum "one gene-one polypeptide" stained bands became equalled with genes, often without proper genetic analysis. Electrophoresis strengthened the gene frequency approach in evolutionary genetics. A positive interaction of the prestige of the mathematical theory of population genetics and the esteem for a molecular approach made this gene frequency approach to evolution the dominant tenet in evolutionary biology without much regard for what is beyond the genome.

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Revolutions

Since then, two revolutions have tended to restore the balance between genotype and phenotype in evolutionary theory. Paleontologists and ecologists were the revolutionaries. The paleontologists could not relate morphological evolution as it is revealed in the paleontological record with frequency changes of electrophoretic variants. Ecologists could not recognize change of frequencies of electrophoretic variants as underlying adaptive change of characters with ecological importance, e.g., rates and timing of reproduction.

These revolutions are genetic and sometimes even antigenetic.

Paleontologists proclaimed the theory of punctuated equilibria, indulged in coquetry with saltational events and promoted species selection as the directing force in evolution instead of individual selection in populations (Gould 1980, Stanley 1979).

Thereby they try to remove population genetics from its central position in the explanation of evolution. Some people see Marxism behind this revolution.

In contrast, ecologists staged a counterrevolution (see Stearns 1976) and went straight back to Darwin's gradualism. The optimalization of life history characters implies that the right selection will find suitable genetic variability to produce smooth gradual adaptation (perhaps some philosopher of science will relate this to Reaganomics or Thatcherism).

Phenotypic Aspects

Whatever their further merits, these developments have contributed much to a renewed interest for the phenotypic aspects of evolutionary genetics, in particular for phenotypic characters which have ecological significance. Such a genetics of ecology leads inevitably to a renewed interest in quantitative genetics (Van Noordwijk et al. 1980). This approach is complementary to what I would like to call the ecology of genes in which the ecological significance of variation on individual gene loci, e.g., alcohol dehydrogenase or amylase is investigated (cf. De Jong and Scharloo 1976, Scharloo et al. 1977).

However, simple quantitative genetics, i.e., quantitative genetics which deals only with statistical parameters is not enough. We have to go again into the developmental and physiological processes underlying quantitative characters. This was the message which I tried to convey when introducing what I called the Magic Triangle (M.T.) of evolutionary genetics (Scharloo et al. 1977).

The Magic Triangle

The angles represent three levels of observation on which genetic variation can be observed.

- M: molecular variation, i.e., variation in single genes as observed by electrophoresis and by analysis of amino acid sequences in proteins or base sequences in DNA (review Lewontin 1974).
- P: phenotypic variation, variation in physiological, morphological, or behavioral characters under control of a large number of genes. Its genetic basis is revealed by artificial selection (see Falconer 1960).
- F: variation in fitness, the ultimate parameter in population genetics, one could almost say, the parameter of the last judgement which determines the selective forces acting on phenotypes and genes. This type of variation has been revealed when chromosomes of *Drosophila* were made homozygous and by inbreeding (see Dobzhansky 1970).

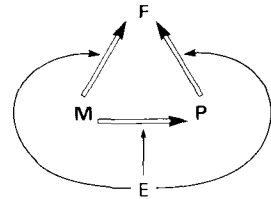


Fig. 1. The Magic Triangle of evolutionary genetics. *M*: molecular variation; *P*: phenotypic variation; *F*: variation in fitness; *E*: environmental effects. Further explanation in text

On all levels of observation we have abundant evidence for the presence of genetic variation. However, evidence on the connection between the variation on the three levels is limited. This is even the case for the connection $M \rightarrow F$, the relation between properties of proteins and fitness (see Koehn et al. 1983), let alone for the route $M \rightarrow P \rightarrow F$ where both arrows represent mainly ignorance. Because genetic effects of selection depend on these connections, the essential problems of evolutionary genetics are the sides of our Magic Triangle which form the links between genes and fitness, between genes and phenotypes, and between phenotypes and fitness.

The M.T. concentrates on what happens within organisms. However, fitness is dependent on environmental factors as well as on properties of the organism.

Environmental Interference

The M.T. is not a closed system. The environment interferes

1. When a character (either a molecule *M* produced by one gene or a phenotypic character *P* generated by the joint action of many genes) has obtained its final shape; fitness depends on the interaction of the character and the environment.

When there is no malaria, sickle cell heterozygotes have no advantage; when there are no thrush predators (as some suppose to be the case in France), there is no selection on snail color and banding.

2. However, the environment does not only affect fitness by its interaction with a character, morphological, physiological, or behavioral, when it is fully formed. The environment often already affects the making of a character, it interferes in the processes between genes and phenotype.

These environmental effects on the formation of characters are not necessarily random; they are often adaptive. The environmental factor causes a change in the character which promotes fitness under selection by the same environmental factor.

Adaptive Significance

A major problem is to decide whether an environmental effect can be considered to be an adaptive reaction. Schmalhausen (1949) in his book *Factors of Evolution* recognizes two types of reaction: (1) morphoses, phenotypic reactions on environmental factors which are not a normal part of the environment; (2) adaptive phenotypic reactions caused by environmental factors which regularly occur in the habitat.

Morphoses show considerable variation and are often monstrosities, phenotypes with considerably lower fitness. Adaptive reactions would be performed by all individuals of the population: the uniform reaction would produce phenotypes with improved fitness under the conditions which caused the reaction.

However, the uniformity criterion has its pitfalls: if the change caused by the environmental factor is a mechanical or physicochemical necessity, there is no reason to call it an adaptation.

Recently, Smith-Gill (1983) proposed a new criterion: adaptive reactions would involve the switching on of a coordinated set of genes. Morphoses would imply only the activation of one or a few uncoordinated genes. In our present state of ignorance concerning the processes of gene regulation and development, this criterion will be difficult to apply. Moreover, switching on a set of coordinated genes is just what happens when phenocopies of homeotic mutants are obtained by such abnormal environmental factors as heatshock or ether treatment (Garcia-Bellido 1977). Having a leg instead of an antenna is surely not an adaptive reaction.

Uniformity of Adaptive Reactions

The relative uniformity in reaction to environmental change is, of course, a necessity when the usual uniformity of wild phenotypes, the relative limited variation in normal phenotypes, is considered. This limitation of variation in wild populations is particularly striking when it is compared with the variety of phenotypes and reaction norms revealed in morphological mutants or in populations submitted to an abnormal environmental factor (see Waddington 1957, Scharloo 1962).

Origin of Adaptive Reactions

The Neo-Darwinian explanation of the uniform adaptive reactions is, of course, fixation of one type of adaptive reaction by natural selection acting on a variable array