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THE GENETIC BASIS OF AGGRESSION IN WILD HOUSE MICE: A DIALLEL ANALYSIS

by

Patrice Watson

A DISSERTATION

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In Partial Fulfillment of Requirements

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Under the Supervision of Professor James L. Connor

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TITLE

THE GENETIC BASIS OF AGGRESSION IN WILD HOUSE MICE:

A DIALLEL ANALYSIS

BY

Patrice A. Watson

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THE GENETIC BASIS OF AGGRESSION IN WILD HOUSE MICE: A DIALLEL ANALYSIS

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University of Nebraska, 1978

Adviser: James L. Connor

The genetic basis of a quantitatively varying behavioral trait can be described in terms of its genetic architecture: the proportions of the total phenotypic variation which are attributable to additive genetic variation, dominance genetic variation, and environmental variation; and the type of dominance variation, directional or ambidirectional. This is a study of the genetic basis of several measures of the aggressive behavior of male laboratory-bred wild house mice; for those measures found to have significant genetic determination, the genetic architecture was described.

The behavior of mice was observed in three testing situations, each designed to elicit a different type of aggression. In one test, mice were exposed to a nonaggressive male mouse. In another, mice were exposed to a live cricket. Each of these tests took place in the subject's home cage and lasted 7 min.; behavioral measures were the proportions of test time spent in: investigation, attention, approach, withdrawl, attack, tail rattle, box, eat (the intruder), exploration, and rest. Latency to attack was also measured. In the third test mice were restrained and subjected to mildly aversive tactile stimulation; behavioral measures were the frequency of jumping, biting, squealing, self-biting, grooming, and defecating.

The 240 subject mice were bred according to a diallel mating plan: samples of mice were tested from each of five inbred lines, all developed from

a single live-trapped population, and from all possible hybrid crosses among these lines. Each subject was given a score on each behavioral measure, that score being an average over four repetitions of each test. The results for each behavioral measure were separately analyzed to assess the significance of genetic effects and to estimate the genetic architecture. Fifteen of the twenty-six behavioral measures showed significant genetic variation.

The theoretical relationship between natural selection and genetic architecture was discussed: four specific types of natural selection (balancing, directional, stabilizing, and selective neutrality) have predictable effects on the genetic architecture of the traits influenced by the selection. All the behavioral traits showing significant genetic determination were classified by types of genetic architecture, and each type was related to the type of natural selection most likely to have produced it.

Inferences were made about the selective pressures which have influenced the aggressive behavior of this population of wild mice. Behavior in response to a cricket intruder was influenced by natural selection favoring short latency attack and minimal preattack contact with the insect. Aggressive/escape behavior in response to restraint and tactile stimulation was influenced by selection favoring moderate reactivity, or was selectively neutral. No inferences could be made about the action of selection on intermale aggression, since aggressive behavior in the intermale test was largely determined by environmental variation and/or genotype-environment interaction, and thus the genetic architecture of these variables was unspecifiable.

Acknowledgments

I am grateful to Dr. James L. Connor for his advice on all phases of this research; to Drs. Dan Bernstein, Connor, Frank Dudek, Donald Jensen, and Dwight Miller for serving on my supervisory committee; to Jose Inguanzo, Mike Munger, and Jeff Rehm for help with computer programming; to Jacqueline Smith for help in data collection; to Pat G. Lynds for advice on test procedures; and to Iota Chapter, Sigma Delta Epsilon - Graduate Women in Science and the managers of the Happold Student-Originated Studies Program for monetary awards which partially supported this research.

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Introduction

There is considerable interest in the evolution of aggressive behavior. The purpose of the research reported here was to determine the heritability of aggressive behavior in mice and to identify the selective pressures which have influenced this aggressive behavior.

Traditionally, inferences about the evolutionary advantages of behavior have been based on the differences between species or other, larger taxonomic categories (Lorenz 1958, Eibl-Eibesfeldt and Kramer 1958, Tinbergen 1960, Bitterman 1973). Dilger's (1962) study of behavioral variation among several African lovebird species exemplifies the successful use of this approach. However, such studies have been criticized (Hodos and Campbell 1969, Atz 1970, Lockard 1971) because they depend on the establishment of behavioral homologies (resemblance caused by inheritance from a common ancestor) among contemporary species in the absence of information about the behavior of ancestral species. The behavioral variation among contemporary species is the basis for inference about the action of evolutionary processes on the unknown behavior of the ancestors. Thus, in theory at least, "microevolutionary" studies of changes occurring within species should have advantages over "macroevolutionary" studies of changes within a genus (Dilger 1962) or within higher taxonomic categories (Bitterman 1973), since the behavior of the populations which are influenced by the evolutionary processes is available for study.

It has been recently suggested that inferences about the evolutionary advantages of behavior can be based on the variation within species. More specifically, there are putative causal relationships between the microevolutionary processes that have operated within a genetic population and the "genetic architecture" of that population (Breese and Mather 1960, Falconer 1960,

Bruell 1967, Broadhurst and Jinks 1974). Assuming that some trait shows quantitative variation along some dimension (a phenotypic scale) within the population, the "genetic architecture" is a way of describing the relative importance of the various factors which determine an individual's place on that dimension (an individual's phenotype). A simple division of the total phenotypic (or manifested) variation can be made: one part is the variation among individuals of the same genotype (environmental variation) and the remainder is due to genotypic variation. If there is genotypic variation (if the trait is heritable in the broad sense), this genetic component can be subdivided into two components. Additive or fixable variation is the component of phenotypic variation which is due to average gene effects and is assessed by the variation among homozygotes of different genotypes (i.e., AA vs. aa). Dominance variation is the component due to deviations of heterozygotes from the average value of their homozygote parents (i.e., Aa vs. ½AA+½aa). In an experiment in which several inbred strains are crossed, two types of dominance variation may be observed. Directional dominance occurs when the deviations of the heterozygotes from their average parental value are all in the same direction on the trait dimension; ambidirectional dominance occurs when the hybrids of some crosses deviate in a different direction than do hybrids of other crosses. The genetic architecture of a trait in a population, then, indicates what proportions of the phenotypic variation are due to additive variation, dominance variation, and environmental variation, and whether the dominance variation is directional or ambidirectional.

Figure 1 summarizes the theoretical relationship between genetic architecture and microevolution. Several types of natural selection are listed on the left; these are illustrated by curves of the preselection phenotypic distributions

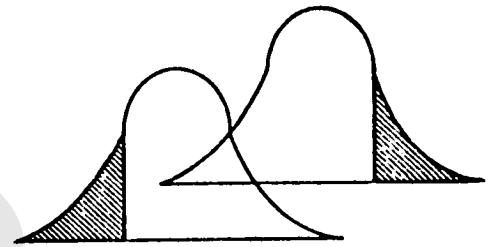
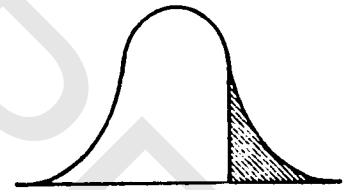
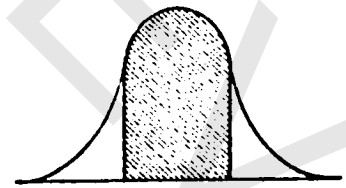
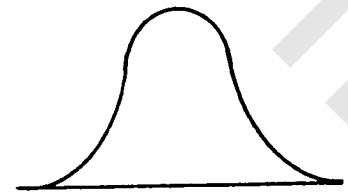
TYPE OF SELECTION		TYPE OF GENETIC ARCHITECTURE
I Balancing Selection		I High V_A; high V_D (directional)
II Directional Selection		II Low V_A; high V_D (directional)
III Stabilizing Selection		III Moderate V_A; low V_D (ambidirectional)
IV Selective Neutrality		IV High V_A; high V_D (ambidirectional)

Figure 1. Four types of selection and their effects on genetic architecture. The curves show the location of favored phenotypes in the preselection population distribution along the trait dimension.

showing the location of the phenotypes to be favored. On the right are the expected results in terms of genetic architecture.

The relationship depends on two very general effects of selection (Falconer 1960, Bruell 1967, Broadhurst and Jinks 1974). Selection favoring an extreme phenotype produces directional dominance in the direction of the favored end of the phenotypic scale; and selection, whether favoring an intermediate or extreme phenotype, depletes additive variation, unless some process acts to preserve the additive variation. In selective neutrality (Type IV), the phenotype for a particular trait has no effect on the biological fitness of the individual. Thus neither effect of selection occurs; random changes in the genetic material affecting the phenotype are not selected out, and high degrees of additive and ambidirectional dominance variation are expected. When selection favors individuals with intermediate phenotypes (stabilizing selection, Type III), both additive and dominance variation will be systematically decreased, producing a Type III architecture: low or moderate degrees of additive and ambidirectional dominance variation. When one extreme of a trait dimension is favored over other phenotypes by natural selection, directional dominance will result. In the absence of any counter-acting process, additive variation will decrease. Thus this directional selection (Type II) produces an architecture low in additive variation and high in directional dominance variation. However, when a counter-acting process is operating in addition to selection favoring a phenotypic extreme (balancing selection, Type I), the resulting architecture has high additive and directional dominance variation. Balancing selection may occur, for example, when two trait dimensions, both of which are affected by directional selection, are determined by the same genetic material. Heterozygotes, by virtue of dominance, may be in the favored extreme of both dimensions, and thus may

have a selective advantage over homozygotes. A specific and well-known example of a Type I genetic architecture produced by balancing selection is the case of a hemoglobin variant (sickle-cell) frequent in populations exposed to malaria. In some human populations, directional selection on two trait dimensions (oxygen carrying capacity of the blood and malaria susceptability), both affected by the same genetic material, results in overall heterozygote superiority and a Type I genetic architecture for each of the two traits.

The object of the research reported here is the classification of several behavioral variables, observed in a polymorphic (or variable) population, by the type of genetic architecture; and, on the basis of this classification, to infer the mode of selection which has affected the population distribution of the variables. To do this, a standard genetic experimental design, the diallel cross, was employed. In this design, several inbred lines are tested along with all possible crosses among them. This design has been frequently used in the investigation of the genetic architecture of behavioral traits using mammalian subjects. However, serious criticisms of previous uses of this method have arisen. The model assumes that the inbred lines used in the diallel cross, when pooled, constitute a gene pool that is representative of some single, coadapted founding population; it is the action of natural selection on this founding population that is to be inferred. To make this assumption plausible, two conditions not present in previous studies are required.

1. The gene pool of the stocks used must not be radically changed during domestication and inbreeding. Most, if not all, previously reported diallel studies of mammalian behavior have used domestic rodents; most have used housemice. Laboratory housemice descend from mice bred in captivity for hundreds of generations (Bruell 1970, Wahlsten 1972). Artificial selection