

ADVANCES IN GENETICS

VOLUME 19

Edited by
E. W. CASPARI

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GENES, BEHAVIOR, AND EVOLUTIONARY PROCESSES: THE GENUS *Drosophila*

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I. Introduction

Research in behavior genetics largely began as a by-product of other investigations in a number of organisms including *Drosophila*. Not until the last 15 years have attempts been made to integrate this information (Fuller and Thompson, 1960; Hirsch, 1967; Parsons, 1967a). More recently, texts have appeared in this hybrid field (De Fries and McClearn, 1973; Ehrman and Parsons, 1976). In particular, Ehrman and Parsons (1976) argued that the special emphases of behavior genetics compared with other areas of genetics have warranted these recent developments. In brief, these emphases are (1) difficulty of environmental control, (2) the difficulty of objective measurement, and (3) the importance of the study of learning and reasoning. It must be stressed that *no unique genetic principles are required when we consider the mechanism of the inheritance of behavioral traits*. To date studies on mechanisms have been the predominant approach in behavior genetics, as shown by perusal of Ehrman and Parsons (1976). Even so, in the later chapters of this book evolutionary considerations assume progressively more importance. Indeed prophetically for behavior genetics, Caspari (1967)

wrote that "all biological phenomena can be considered from two points of view: mechanism and evolution." In agreement, the whole movement of the coverage of Ehrman and Parsons' book goes from the mechanism of the inheritance of behavioral traits to the evolutionary aspects of behavior. More recently the need to stress evolutionary principles was emphasized by authors such as Wallace (1974).

Mayr (1963) wrote that "the shift into a new niche or adaptive zone is almost without exception, initiated by a change in behavior." That is, there will initially be only minor changes at the structural level, and the evolution of morphological changes may follow behavioral changes. He returned to this theme again, in a perceptive article (1974) entitled "Behavior Patterns and Evolutionary Strategies," where he rightly comments that in recent years there has been a growing synthesis between behavioral biology and evolutionary biology. This has led "to the posing of a whole battery of new questions on the evolution of behavior patterns and on the impact of behavior on the course of evolution." With this comment in mind, it is logical to look at its application with respect to genetically well-known groups of organisms. This review will be concerned with *Drosophila*.

II. Closed and Open Programs and Sexual Isolation

Some behaviors are regarded as innate—that is they are predominantly determined by the genotype. These behaviors are based on genetic programs not allowing of appreciable modifications during the process of translation into the phenotype, and are called *closed programs* by Mayr (1974). Other genetic programs are modified during the translation into the phenotype, by input occurring during the life-span of its owner; they thus have an acquired component. Mayr refers to this as an *open program*. Closed programs are widespread among so-called lower animals, which to date must include *Drosophila*. But here we must be careful, since although many genotypes have been tested for a great variety of behaviors and closed programs appear to predominate, this does not mean that the use of appropriate testing procedures over a period of time would not reveal results ascribable in part to open programs—this point will be further considered later in this review.

One behavior where the evolutionary significance of a closed program is evident is mating. Male animals preferably display to females of their own species, and females normally respond to the displays of their own males. A female *Drosophila*, if kept in isolation until ready to mate, and then offered the simultaneous choice of males of several species in-

cluding her own, will almost unerringly accept the courtship of the male of her own species, as though there is innate knowledge of her own species. Quite clearly, if mating choice were more loose, considerable gamete and other wastage on the part of the female would ensue, so that natural selection for a closed system is to be expected. Even when we go to extremely closely related species, such as sibling species, isolation is normally perfect in the wild. For example, the sibling species *D. pseudoobscura* and *D. persimilis* are sympatric in some regions and are isolated by a complex of ecological and ethological factors (for references see Parsons, 1973) including temperature and food preference differences, activity and photoresponse differences, and sexual isolation associated with differing male courtship songs. In natural habitats, therefore, it is not surprising that interspecific matings are not found even though hybridization occurs relatively readily in the laboratory. In many laboratory experiments virgins were about 4 days old, but when flies of both sexes were placed together a few hours after emergence the proportion of hybrids was lower—a situation likely to pertain in the wild. Spieth (1958) suggests that the higher level of isolation under the latter situation may be due to individuals of both species maturing together, then acquiring the ability to discriminate between the species before sexual maturity. Furthermore, a *D. persimilis* female once having mated with a *D. persimilis* male, will not accept a *D. pseudoobscura* male subsequently. This shows that there may be a learned component in maintaining isolation in the wild. Laboratory experiments indicate other variables—for example, an environmental variable is that isolation is relatively low at 16.5°C (Mayr and Dobzhansky, 1945). A genetic variable is indicated, since isolation can be increased or decreased by selection (Koopman, 1950; Kessler, 1966). In conclusion, the program(s) leading to sexual isolation can be assumed to be closed in the wild, and only under the artificial laboratory condition is there any relaxation of this. Therefore efficient premating isolating mechanisms preventing copulation between closely related species are usually the rule.

For another pair of sibling species studied in depth (*D. melanogaster* and *D. simulans*), sexual isolation is even more extreme, again based on a complex of ethological (in particular) and ecological factors. Even so, a few hybrids can be obtained in the laboratory, and as for the above pair of sibling species, the level of hybridization is under both environmental and especially genetic control (Parsons, 1972, 1975a).

Drosophila paulistorum is a taxon that contains an extraordinary complex of geographic races or incipient species, endemic in Central and South America; six units are close to the status of reproductively isolated, but morphologically indistinguishable, species. They display pronounced,

in some cases nearly complete, sexual isolation associated with sterility of hybrid males. Observations of the courtship patterns involved show both qualitative and quantitative differences between races. A seventh race, called the Transitional one, occurs exclusively in Colombia. All strains of this race can be crossed and produce fertile hybrids with at least one of the other races; in fact, this is regarded by Dobzhansky *et al.* (1969) as a relic of the ancestral population from which the other races have differentiated. Therefore, we have a situation of an extremely dissected and differentiated gene pool, making it a near unique example of a situation where it is difficult to decide whether there are one or several species. Sexual isolation is determined by polygenic differences between the races (Ehrman, 1961). All stages of isolation occur in *D. paulistorum*, ranging from none to almost complete separation. The variations in sexual isolation have presumably arisen by natural selection occurring as a result of geographic separation and the accumulation of genetic differences in the course of adjustment to different environments.

Ehrman (1965) using multiple-choice tests compared given pairs of races that have been found to occur both sympatrically and allopatrically. In allopatric crosses, the average isolation coefficient was +0.67 and in sympatric crosses was +0.85 (Table 1). Thus pairs of races

TABLE 1
Numbers of Matings Observed and Isolation Coefficients Calculated for Sympatric and for Allopatric Crosses^a

Races	Origin	Matings	Coefficient ^b
1. Amazonian × Andean	{ Sym	108	0.86 ± 0.049
	{ Allo	100	0.66 ± 0.074
2. Amazonian × Guianan	{ Sym	104	0.94 ± 0.033
	{ Allo	109	0.76 ± 0.061
3. Amazonian × Orinocan	{ Sym	106	0.75 ± 0.065
	{ Allo	124	0.61 ± 0.070
4. Andean × Guianan	{ Sym	109	0.96 ± 0.026
	{ Allo	102	0.74 ± 0.066
5. Orinocan × Andean	{ Sym	100	0.94 ± 0.033
	{ Allo	111	0.46 ± 0.064
6. Orinocan × Guianan	{ Sym	104	0.85 ± 0.053
	{ Allo	100	0.72 ± 0.069
7. Centro-American × Amazonian	{ Sym	102	0.68 ± 0.072
	{ Allo	103	0.71 ± 0.070
8. Centro-American × Orinocan	{ Sym	110	0.85 ± 0.052
	{ Allo	103	0.73 ± 0.069

^a From Ehrman (1965). The total number of matings observed was 1695.

^b Average (sympatric) = 0.85; average (allopatric) = 0.67.

occurring sympatrically exhibit more sexual isolation than the same pairs occurring allopatrically, or races coexisting geographically tend to be reproductively more isolated than those that do not. This is reasonable as the production of a large number of hybrids would be very inefficient. These differences are presumably due to natural selection within this complex taxon. Because of the variations of sexual isolation from random mating to complete isolation, it would seem also likely that variations may occur according to whether flies of different races are isolated or otherwise before mating. Further, variations may occur for flies once having mated, with respect to subsequent mating. The likely situation is that for a fly of a given strain or race, having mated with that strain or race, subsequent matings would be more likely to be with that given strain or race—that is, isolation would be enhanced and eventually this would be fixed into the genome, thus increasing levels of sexual isolation by natural selection [L. Ehrman (personal communication) informs me that she has evidence in support of this]. Such variations would indicate a component of sexual isolation controlled by an open program. This would seem reasonable in a situation where levels of sexual isolation themselves are highly fluid, and may represent the situation characteristic of a series of races not yet quite with specific status. A number of experimental possibilities emerge that are testable; such testing may add insight into the processes whereby sexual isolation is enhanced or reduced—in the former case leading to speciation.

Within *D. pseudoobscura*, Pruzan and Ehrman (1974) found evidence indicating age and previous experience effects with respect to the now well-documented phenomenon of frequency-dependent sexual selection (Petit and Ehrman, 1969). All previous experiments studying this phenomenon had used exclusively young virgins. Pruzan and Ehrman found that 4-day-old virgin females confer mating advantages on all tested rare males as expected, but females who had a previous mating experience when younger award a rare-male advantage *only* when the rare male is of the same karyotype as their first mate, and matings are random when the first-mate type males are common. Equivalently aged 11-day-old virgin females mate significantly more than expected with minority males if they are of the same karyotype as the females themselves, whereas matings are near random when the males differ. Frequency-dependent mating is therefore both age and experience dependent.

Therefore variations in choice may occur within species according to previous experiences. It should be noted that degrees of sexual isolation *within* species can be modified by artificial selection, as shown by experiments in *D. melanogaster* where homogamic matings are favored at the expense of heterogamic ones (Wallace, 1954; Knight *et al.*, 1956; Hoenigs-

berg *et al.*, 1966; Crossley, 1974). In artificially isolated populations of both *D. melanogaster* and *D. pseudoobscura*, preferences for homogamic matings tend to develop over time (Koref-Santibañez and Waddington, 1958; Ehrman, 1964)—in this case sexual isolation has occurred as a by-product of genetic divergence.

In conclusion, levels of sexual isolation within species, between races within species complexes, and between species are under genetic control. Suggestions occur for previous experience effects. This latter phenomenon needs further exploration, but in conjunction with more experiments on the genetic basis of sexual isolation. Extrapolation to the wild is essential, since laboratory situations may be far from those pertaining in the wild. For example, to what extent do repeat matings occur in the wild, and how do they depend upon previous experience? In spite of previous experience effects, sexual isolation is mainly under the control of a closed program; in any case, the normal result of previous experience is likely to be toward isolation.

III. Deviations from Random Mating within Species

Random mating is commonly assumed in natural populations—and indeed the theoretical foundation of population genetics is based on this assumption. It must be admitted that this is partly because of the simplifications leading to simple mathematical modeling. In practice, random mating rarely occurs (Parsons, 1967b). The increased study of mating patterns within species should be encouraged, coupled with considerations of their evolutionary consequences. Such studies might be both theoretical and observational. The genetic and behavioral study of the benefits that secondary sexual characteristics confer on their bearers also needs more emphasis. In *Drosophila*, for example, sexual dimorphism for traits involved in courtship is well developed in some of the Hawaiian species (Carson *et al.*, 1970; Spieth, 1973a,b), but not elsewhere [for example, the endemic Australian species many of which belong to subgenus *Scaptodrosophila* (Bock and Parsons, 1975)]. There are two main types of benefits of such sexual dimorphism: (1) their bearers may have superior competitive ability against others of the same sex; or (2) they may increase sex appeal. In the first case, selection is within one sex; and in the second case, selection is made by the opposite sex.

While there are difficulties in distinguishing these two components of sexual selection, in *Drosophila* when flies meet on food masses, each female has the opportunity of choosing among competing males, and because she effectively rejects some suitors, sexual selection—in this case

intersexual selection—can be inferred to have occurred. By using mutant flies, Sturtevant (1915) in a seminal paper showed sexual selection in *D. melanogaster*, as have many other investigators working on this and other species. Using karyotypes polymorphic in natural populations, the importance of heterozygosity on the effectiveness of the males has been clearly shown in species such as *D. pseudoobscura* (Kaul and Parsons, 1965; Spiess *et al.*, 1966) and *D. pavani* (Brncic and Koref-Santibañez, 1964). As discussed by Parsons (1974), a number of experiments suggest that male mating behavior is an important component of fitness; this agrees with early experiments of Merrell (1953), who found gene frequency changes in experimental populations of *D. melanogaster* to be predictable from male mating behavior variations. The need for more experiments of the type carried out in *D. melanogaster*, by Prout (1971a,b), who attempted to define a small number of fitness components that encompass the entire life cycle and are accessible to experimental evaluation, is clear—and indeed in his experiments, compared with other components of fitness, relative male mating abilities between genotypes were very important. The evolutionary significance of results of this type is, however, difficult to assess without extrapolation to nature. Emphasis for this comes from the observation that some of the experimental data in *D. pseudoobscura* show a dependence of relative mating speeds among karyotypes on the environment, such that there may be a tendency for heterokaryotypes to show less variability across environments (usually temperature changes) than homokaryotypes (for references, see Parsons, 1973, 1974). Therefore, we have the situation of possible genotype \times environment interactions affecting levels of sexual selection—but it is noteworthy that heterokaryotype advantage is greatest under conditions of environmental stress, which may be rarely effective in nature considering that flies can frequently move away from stressed microhabitats; specific evidence will be given later for Australian endemic *Drosophila*. Even so, it appears desirable to study sexual selection in all environments to which the population may be exposed.

In the Hawaiian Islands, in the region where many of the endemic species occur, the environmental extremes to which many of the cosmopolitan species must be subjected are unlikely to occur. The adults are able to distribute themselves into microhabitats suiting their ecological requirements, the main controlling factors being wind intensity, humidity, temperature, light intensity, food sources, and acceptable courting and oviposition sites. Of these, temperature is the most important factor. In the Hawaiian *Drosophila*, a courtship behavior pattern occurs that is not found elsewhere in the genus and has far reaching effects on its biology. In the field, flies of both sexes feed quietly with no male court-

ship activities. After a short period, males leave the food and each selects a territory or lek in the surrounding vegetation (Carson *et al.*, 1970), which is small in size and species specific in character. The lek occupant defends his territory against intruders and advertises his presence, so that sexually receptive females are attracted to advertising males. When she arrives at the lek she is treated agonistically until the male determines her sex. Then courtship occurs, but the male drives her from the lek if she finds his display unacceptable. Hawaiian lek *Drosophila* are sexually dimorphic associated with diverse and unique courtship patterns. In the remainder of the genus, other than male sex combs on the fore tarsi, which are not involved in producing courtship signals, visible dimorphism involved in courtship and mating does not occur. It can be inferred that the Hawaiian lek species have been subjected to intense sexual selection since the male does not court on feeding-ovipositing sites, but rather attracts sexually receptive females to his lek. Spieth (1974b) suggests that the insectivorous behavior of the honey-creepers, the fly-catcher, and the predatory muscoid genus *Lispocephala*, are responsible for powerful selection pressure upon the Hawaiian *Drosophila*. This selection has resulted in four discrete but interrelated events:

1. The selection of adults that are alert, wary and highly cryptic, both behaviorally and structurally
2. The drastic increase in size of some species
3. The abandonment of courtship on the feeding and ovipositional sites, thus eliminating the incessant courtship activity easily detectable by predators
4. The emergence of lek behavior and a concomitant drastic increase in sexual selection

For understanding the relationship between genes, behavior, and evolutionary processes, the comparative study of sexual selection among the various species of *Drosophila* must continue to be a fruitful area of study—in particular the genetic systems involved, with particular reference to the comparison between the sexually dimorphic and monomorphic species. Further, the complex behavioral patterns involved in achieving a successful mating would seem to indicate the unlikelihood, as can be shown in man (Ehrman and Parsons, 1976), that random mating is the rule as assumed by many population geneticists. It is the job of behavior geneticists interested in evolution to investigate the mechanisms leading to deviations from random mating and assess their effects on populations.

Considering the "laboratory" species, probably the most elegant proof of sexual selection is the phenomenon, already referred to, of frequency-dependent mating whereby rare males have an advantage compared with when they are common (Petit and Ehrman, 1969). From the population

point of view, the advantage of the rare male would be expected to lead to an increase in its frequency provided that there are no other selective forces acting against it. As the rare type of male increases, the mating advantage would slowly diminish, and it would appear that a number of gene and chromosomal polymorphisms in *Drosophila* are maintained by such frequency—balancing selection based on mating behavior. The mechanisms of frequency-dependence are still obscure, but it is clear that the females do discriminate subtle airborne cues from the initiating male—the cue being probably a lipid or steroid (Leonard *et al.*, 1974). Hay (1972) believes that the recognition of minority individuals is due to the existence of a colony order, such that the presence of this volatile male-borne material permits females to recognize when there are two types of males present, and thus modify their receptivity toward the minority males. Whatever the mechanism, the favoring of minority males in mating must ensure heterozygosity in the gene pool of the population, without the need to invoke classical overdominance.

In man, positive assortative mating (the tendency of like phenotypes to mate by choice) is found for numerous physical traits such as stature and arm span, and for many behavioral traits such as intelligence and personality (references in Ehrman and Parsons, 1976). Since these traits are heritable, then as Fisher (1930) argued, assortative mating is an agent important in modifying the genetic constitution of populations. A comparison with populations where matings are arranged would be of considerable interest. Evidence for positive assortative mating occurs between the color phases of the Blue Snow Goose and the Arctic skua (Cooch and Beardmore, 1959; O'Donald, 1959).

In *Drosophila*, few relevant experiments have been done, although Parsons (1965, 1973) found positive assortative mating for sternopleural and abdominal chaeta number in *D. melanogaster*. This could be a direct effect of fly size, as sternopleural chaeta number and fly size are positively correlated when fly size is altered by environmental means (Parsons, 1961). Alternatively, there may be behavioral differences between flies of different sizes leading to minor modifications in courtship behavior. For example, wing area, related to fly size, is a factor in determining male sexual success (Ewing, 1964). If assortative mating is general, as in man, evolutionary processes will clearly be affected.

The possible evolutionary significance of assortative mating was brought home meaningfully as a result of Gibson and Thoday's (1962) disruptive selection experiments for high and low sternopleural chaeta numbers in *D. melanogaster* in a single population maintaining gene flow between the high and low components. Within ten generations the population split into two subpopulations, which were characterized by high

and low chaeta numbers. As predicted by Mather (1955) therefore, the population became bimodal and polymorphic under disruptive selection. Maynard Smith (1962) considered on theoretical grounds that these results are difficult to understand unless there is positive assortative mating for sternopleural chaeta number in the base population, or unless there is selection favoring positive assortative mating during the experiment. While the base population was not tested, Thoday (1964) found strong positive assortative mating within the high and low lines. Hence the isolation developed by disruptive selection is associated with strong positive assortative mating within the subpopulations so constructed. In this way we have a laboratory model of the development of sexual isolation. These results therefore relate to the sexual isolation between races of *D. paulistorum*, and that developed by artificial selection for homogamy in *D. melanogaster* referred to at the end of Section II.

The further study of sexual selection and sexual isolation in the laboratory combined with field observations as carried out in Hawaii, is thus essential to ascertain the processes involved in mating success in diverse species groups and the degree to which they are modifiable by experience and by selection. A combined behavioral and genetic approach is needed for this important segment of the synthesis between behavioral and evolutionary biology. We have gone past the stage of proving that components of mating behavior are heritable—and experiments to do just that alone may well fall into Wallace's (1974) category of experimental data in behavior genetics no longer worth the effort needed to obtain them. For example, a question to investigate is Spieth's (1974a) conclusion that, for *Drosophila* in nature, males are primarily responsible for sexual isolation and females for sexual selection. Another neglected question is the frequency of multiple insemination in the wild—a point emphasized by Anderson's (1974) report in *D. pseudoobscura* that at least half of females in a sample from San Gabriel Canyon, near Riverside, California, carried sperm of more than one male. It is also known that multiple insemination is common in laboratory cultures of the same species (Dobzhansky and Spassky, 1967).

IV. Behavioral and Structural Phylogenies

If one constructs the phylogeny of a group of animals, such as ducks and pigeons, based on behavioral traits, that phylogeny is exceedingly similar to an independently designed one based upon strictly morphological traits. The interpretation of this parallelism is that both sets of characters are the product of the same genotype—representing a closed

genetic program (Mayr, 1974). Other examples given by Mayr include gulls and storks. The best insect example is the genus *Drosophila* (Spieth, 1952). Spieth's study encompassed 101 species and subspecies representing 21 species groups, and generally the evolution of mating behavior paralleled the morphological evolution of the group. Further, he concluded that divergence of the mating behavior between species occurs first at the physiological and behavioral levels, and that the visually observable morphological differences arise much later.

Brown (1965) quantified differences between 11 species of the *obscura* group for behavioral and morphological characters utilizing a measure of "Mean Character Differences" based on twenty behavioral and twenty-four morphological traits (Table 2), from which a high correlation between behavioral and morphological divergence emerged. Considering these data and the sibling species *D. melanogaster* and *D. simulans* (Bastock, 1956; Crossley and Zuill, 1970; Parsons, 1975a), it is clear that both behavioral and morphological differences between mutants within species are slight, those between sibling species are greater, and those between nonsibling species in the same division greater still. The same applies to the level of subgenera which show the major differences in behavior and morphology. Spieth (1974b) reiterated this general view after working on the Hawaiian *Drosophilidae*. Furthermore, Ewing and Bennet-Clarke (1968) analyzed the male courtship songs of species of the *D. melanogaster* and *D. obscura* species groups, and found pairs of sibling species to be more similar than pairs of nonsibling species.

It can therefore be presumed that behavioral differences in courtship *within* species could become, under suitable conditions, the prime traits differentiating closely related species—and eventually associated morphological differences would become apparent. What is needed is to see how such differences could have arisen during the course of evolution, and how the behavior serves to adapt the animal to its environment. This question in the more general sense—that is, extrapolating to behavior apart from courtship behavior—has been rarely posed, although mutants and evidence of genetic control affecting other behaviors are well known, e.g., affecting the central nervous system, the visual system, taxes such as geotaxis and phototaxis, and activity (for references, see Parsons, 1973). In the case of mutants affecting the central nervous system, studies with gynandromorphs have enabled the morphological localization of genetically controlled defects (Hotta and Benzer, 1972).

Another approach is to look at known morphological mutants with respect to their effects on behavior. Grossfield (1975) tabulated a number of such mutants and showed frequent and diverse behavioral changes, e.g., alterations in flight activity, wing-beat frequency, courtship and