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Title: GENETIC PARAMETERS OF THE HOUSE FLY (MUSCA DOMESTICA LINN.)

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Eight strains of housefly, Musca domestica Linn., from two laboratories were intercrossed to form a stock population. Virgin males and females from the stock were collected, and nine sets, each consisting of twelve males mated to five females, were successively done. Pupae weight, adult weight, emergence time and egg production of the first batch were measured on four male and four female offspring from each of two dams mated to the same sire.

Analyses of variance and covariance were made, and the heritability for each trait and genetic and phenotypic correlations among the traits were estimated.

Heritability estimates of pupae weight and adult weight, 0.32 ± 0.24 and 0.34 ± 0.19 respectively, are reasonable considering that they are growth traits and are comparable with similar estimates in some other organisms. Heritability of the emergence time,

0.72 ± 0.30, was high. Heritability of egg production was considered to be zero and was low when compared with estimates of egg production in the fowl.

Extimates of genetic correlations between pupae weight and adult weight, between pupae weight and emergence time, and between adult weight and emergence time were 0.91, 0.50, and 0.62, respectively. Genetic correlations between egg production and the other traits cannot be estimated in this experiment. Phenotypic correlations were 0.86, 0.03, 0.09, 0.05, 0.08, and -0.09 for between pupae weight and adult weight, between pupae weight and emergence time, between pupae weight and egg production, between adult weight and emergence time, between adult weight and egg production, and between emergence time and egg production, respectively.

Selection index has been proven to be a very effective method in selection. Selection indexes were:

$I = -0.0504Y_1 + 0.7651Y_2 + 0.1969Y_3 + 0.0050Y_4$ for all four traits and

$I = -0.0438Y_1 + 0.7648Y_2 + 0.1959Y_3$ for the first three traits

where Y_1, Y_2, Y_3 and Y_4 denote measurements of pupae weight, adult weight, emergence time, and egg production, respectively.

The findings from this experiment can serve as fundamental information for subsequent selection studies in this population.

Genetic Parameters of the House Fly (*Musca domestica* Linn.)

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INTRODUCTION

Almost all kinds of organisms, both plants and animals, from microorganisms to large livestock, have been used in genetic studies and most genetic parameters have also been established. For the purpose of developing concepts in livestock selection, smaller organisms are widely used for experimental purposes because of their advantages of shorter life-cycles and greater reproduction rates. The results can be obtained in shorter periods of time with small laboratory animals than with farm animals. Small laboratory animals, e.g., the rat, mouse, and Drosophila, are very popular as experimental subjects. In the insect class, Drosophila is most frequently used in various kinds of studies, including genetic studies. In contrast the housefly, Musca domestica Linn., being a carrier of several diseases that endanger human and livestock welfare, is mostly used in testing drugs, insecticides, and in the study of its ability to develop drug resistance. Despite its dangers to human and livestock health, the housefly can also be used in genetic studies. During the last decade there have been few genetic studies with the housefly. More genetic information is needed to promote genetic study in this organism. A certain population of the housefly, Musca domestica Linn, was used

in the present experiment. The object was to study some genetic parameters for pupae weight, adult weight, emergence time, and egg production. The parameters established were heritability estimates of each of the four traits, genetic and phenotypic correlations among the traits. These parameters can also serve as fundamental information for future studies in this population.

The first part of the experiment was directed toward the establishment of the population stock from eight strains of the housefly obtained from two laboratories. The latter part of the experiment was concerned with the collection of the data on each of the traits and the analysis of the data.

REVIEW OF LITERATURE

The discovery of houseflies, Musca domestica Linn., resistant to DDT by Sacca (1947) and Missirol (1947) has led to numerous investigations of resistance to insecticides in this and other insects. Genetic investigation of the organism involved is an important and fundamental step toward an understanding of the problem. According to Hiroyoshi (1961) the first attempts at the formal study of the genetics of Musca domestica Linn. may have been conducted by Sarkissian and Serebrovsky, Russian investigators, who listed the total of nine housefly mutants which occurred spontaneously or were induced by x-ray in 1941.

Perje (1948) bred flies from different parts of Sweden and studied their spermatogenesis. He discovered that M. domestica has the chromosome number 2n= 12; the autosomes are all metacentric. One of the autosomes has a secondary constriction with no connection to the nucleolus. The sex chromosomes consist of a long metacentric X chromosome and a small Y chromosome. These sex chromosomes are heterochromatic in spermatogonia and spermatocytes.

Some useful mutants have been reported by Milani (1954) and other investigators. Hiroyoshi (1960) reported some additional mutants including four eye color mutants, car(carnation), cm(carmine), rb(ruby), and w^{au}(auburn); an eyeshape mutant, ro(rough); a wing shape mutant, ct(cut); and a wing vein mutant, Lp(loop). By using

17 marker genes, 5 linkage groups which were assumed to represent all the autosomes of the housefly were demonstrated. No sex-linked mutant was detected.

Hiroyoshi (1961), by studying crossing of these 17 mutant markers, demonstrated the existence of all five autosomal linkage groups, numbered them, and prepared a linkage map.

Regarding genetics of insecticide resistance in the housefly, expecially DDT, much research work has been done by investigators and various conclusions have been reached.

Bruce and Decker (1950) reported that resistance was a multiple gene character and was carried by both male and female flies. Reciprocal crossing experiments between flies of non-resistant and DDT resistant NAIDM laboratory strains resulted in the F_1, F_2 and F_{15} generations having a resistance exactly intermediate between that of the parents.

Harrison (1951) made reciprocal crosses between resistant and susceptible strains of flies of Italian origin. The F_1 flies were slightly more resistant than the non-resistant strain. In the F_2 offspring, the proportion of non-resistant individuals was approximately 75 percent. Backcrosses between an F_1 female fly and a resistant male resulted in the 1:1--non-resistant to resistant flies. This led to the conclusion that DDT resistance was due to a single recessive gene.

Keiding (1953) crossed multiresistant and susceptible flies and

then exposed them to DDT. The F_1 showed 3 susceptible : 1 intermediate resistant. Backcrosses also showed 1:1 susceptible to intermediate offspring. He concluded that DDT resistance was mainly determined by one recessive gene.

According to LaFace (1952), and D'Alessandro and Mariani (1953), resistance was found to be multifactoral in inheritance.

Johnston, Bogart, and Lindquist (1954) experimented with two resistant fly strains, Bellflower and Orlando, and a colony of susceptible ones and found that resistance in both resistant strains declined after six to nine generations in a DDT-free environment. Accompanied by the results from crosses among these flies, they concluded that DDT resistance was developed in the cytoplasm as well as being inherited.

Maelzer and Kirk (1953) crossed a non-resistant "Canberra" with a "weak" resistant "Illinois" strain. There was only a little difference between F_1 and F_2 generations into "strong" and "weak" individuals. They suggested that high resistance in the Illinois strain is controlled by a dominant gene superimposed on the partially resistant constitution of the weak type.

Based on the work by Maelzer and Kirk (1953), Lichtwardt (1956) made mass crosses between the susceptible stock IS-1 and the resistant stock IR-1, which was derived from the same stocks used by Maelzer and Kirk (1953), and concluded that the resistance to DDT

was controlled by a single autosomal dominant gene designated as R and the R factor did not seem to reduce the fertility of the strain.

Tsukamoto and Suzuki (1965) reported that the 5th chromosomal dominant gene and 2nd chromosomal incompletely recessive gene are responsible for high levels of resistance to DDT. The R-DDT gene is near the carmine eye-color mutant (cm).

Genetical studies by Busvine (1953) using speed of action as a criterion indicated a single factor inheritance, whereas topical application studies indicated multigene inheritance. Busvine and Khan (1955) reported also that resistance to gamma benzine hexachloride was due to multiple allelomorphs.

With respect to resistance to other insecticides, Harris, Wearden and Roan (1961) stated that Malathion resistance in the housefly is inherited by two allelic groups exhibiting incomplete duplicated dominance epistasis; no sex-linkage is involved. According to Georghiou and Bowen (1966), the pattern of insecticide resistance in the housefly from six areas of California was found to reflect the different chemical control practices in each area. Major factors for resistance to parathion, malathion, isolan, and DDT in strains studied by Hoyer, Plapp and Orchard (1965) were all located in the same chromosome. According to Georghious et al. (1965), insecticides did not cause direct genetic change in insects, but served as selective agents. Flies resistant to one chemical acquire resistance to another

more quickly than normal flies (Decker and Bruce, 1952).

According to Barker (1960), an adult female housefly with a blackish body of 1/2 inch in length, lays her eggs in lots of about 125 each. Though the number of eggs is generally 500 in total, it was recorded that this insect is capable of laying as many as 5,000 eggs. Animal manure seems to be the preferred place for the eggs to hatch. If the weather is warm, the eggs hatch in eight or twelve hours, but if it is unseasonably cool, the hatching time may be two or even three days. After feeding for four or five days, the all-white larva, or maggot, is ready to pupate. The pupa stage takes another four or five days. After an interval that may last three to twenty or more days from emergence, the adult female is ready to lay her eggs. According to Imms (1948), the larva stage is divided into three stages; first, second, and third instar which last 24-36, 24, and 72-96 hours respectively, under a temperature of 25°-35°C. The developmental cycle, from egg to the eclosion of the imago, varies in different parts of the world according to variations in temperature and other factors. It varies from an average of 44.8 days at 16°C, to an average of 10.4 days at 30°C. As reported by West (1951), each female in her lifetime is capable of developing from four to six batches of eggs, which she deposits at intervals of two weeks, the intensity of such activity depending on environmental factors. Temperature and humidity are obvious factors affecting the housefly other than food.

During the larva stage, temperature along with humidity affects media condition. Developmental stages are prolonged when the temperature decreases and vice versa. The adult flies tend to be most active when the temperature is high and the humidity is low (Dakshinamurty, 1948). Life-history and factors affecting the housefly are discussed in detail by West (1951). According to Peterson (1964), a temperature of 80^{o}-86^{o}F and the humidity at 50 percent or higher were suggested for rearing flies in the laboratory.

Rogoff (1965) studied reproductive behavior of the housefly in the absence of light and observed successful oviposition and subsequent development of 2nd generation flies with normal sex ratio. An adaptive ability in Drosophila to mate in the absence of light was also reported by Spieth and Hsu (1950).

The life span of normal flies (Dauer, Bhatnagar and Rockstein, 1965), was found to be 13.2 days. Rockstein and Lieberman (1958) found different life spans in male and female flies. Mean length of life for males was 17 days, and for the female it was 29 days. They concluded that the survival of the male is governed by a relatively simple factor, which in the female, was more complex. Under control conditions, the duration of the developmental stages and the longevity of the adult were influenced by temperature and relative humidity (Ranade, 1965). Studies by Pimentel, Dewey, and Schwardt (1951) revealed that there are no significant differences between a highly

DDT resistant strain and non-resistant strain in the number of eggs laid, length of egg stage, hatchability, length of pupal stage, pupal weights, sex ratio, preoviposition period, or in length of the adult stage. Rockstein (1957) studied the longevity of the housefly at 80°F and 45% relative humidity, and found that the male lives 15 days average, 40 days maximum; the female lives 20 days average, and 45-55 days maximum. He also observed that when powdered whole milk was added to the original sugar and water fly feed, the flies lived 32 days on the average and 60 days maximum.

Michelsen (1960) found that at 28°C males reach sexual maturity from 18-27 hours after hatching from the puparium; this period varied from less than 24 hours to 60 hours at a temperature of 15°-30°C. When the male was kept at 34°C for more than 24 hours, sterility was observed. Murvosh, Fye and Labrecque (1964) reported that the male does not mate until he is 24 hours old. The course of copulation lasts one hour but sperm transferring was completed in the first ten minutes. The male has little sex recognition.

The effect of cholesterol deficiency on reproduction of the adult housefly was studied by Monroe (1960). He found that a cholesterol deficiency had no appreciable effect on adult survival or total egg production, but it caused nearly 80% reduction in egg hatching. The total viable egg production in 0.1% cholesterol was 30% greater than that found for flies on the control diet (sucrose:defatted dry milk 1:1).

Morrison and Davies (1964) showed that dry, chemically defined diets when fed to adult flies gave no significant difference from feeding with fresh milk.

In rearing housefly larva, West (1951) pointed out that bacteria and yeast produced essential accessory growth elements which must be present for proper development of the larvae. Greenberg (1954) has used CSMA moistened solely with tap water (400 cc media: 300 cc of water) and has obtained normal size flies. The result was also supported by other workers.

Methods of rearing houseflies have been described by Peterson (1964). A small room or a large insulated cabinet where the temperature can be maintained at 80°-86°F with a humidity of 50 percent or higher and good ventilation are desirable. The cage for adult flies is approximately one cubic foot in size with a wooden bottom and two wooden ends. The sides and top are covered with a continuous piece of No. 16 mesh wire screen stapled to the wooden ends, with an opening at one end, fitted with a cloth sleeve. The method of feeding the adult fly is also described. A 6" x 8" battery jar, two-thirds filled with mixed medium, will support approximately 2100 well developed larvae. To obtain 2100 larvae, it should be seeded with 2800 eggs, approximately 0.4 ml. in a graduate centrifuge tube. A mass of eggs about the size of a pea contains 500 to 600 eggs. A method of collecting puparia and other methods for rearing larvae have also been

described. As reported by Moreland and McLeod (1956), measuring eggs by the use of centrifuge tubes is preferred for routine mass rearing work.

Breeding the housefly can be done singly or in mass. According to Sacca and Benetti (1960), a male can fertilize up to 11 females. Usually one fertilization is sufficient for the entire egg-laying period of the female (Zingrone, Bruce and Decker, 1959). Sacca and Benetti (1960) also found that only three females out of 264 were mated more than once in a 25-day experimental period. The second time was with the same male because mating produces a change in the female genitalia rendering further acceptance of the male impossible. This was also confirmed by the result of the mating study by Zingrone, Bruce and Decker (1959). Breeding methods and methods for rearing the offspring of single pairs of houseflies were described and discussed by Lichtwardt, Bruce and Decker (1955), Smith (1961), and Nagasawa and Asano (1963).

Gene action and the heritability of quantitative characters have been discussed by Lush (1948). His definitions of heritability, in the broad and in the narrow sense, were given. The narrow sense estimate of heritability, the ratio of additive genetic variance to phenotypic variance, is used when the main emphasis is to express what fraction of the phenotypic differences between parents may reasonably be expected to be recovered in their offspring. Estimation of

heritability was also discussed by Lerner (1950) and Falconer (1964).

The use of a selection index has long been recognized for its value. Lush (1935) emphasized that permanent improvement from phenotypic selection is proportional to the additive genetic fraction of the observed variance and that this varies for different traits. Hazel and Lush (1942) presented formulas for selection. According to these workers, selection by use of an index, which gives proper weight to each trait, is more efficient than selection for one trait at a time or for several traits with an independent culling level for each trait. Smith (1936) developed an index designed for the selection of plant lines, using Fisher's concept of discriminant functions to derive a linear equation based on observable characteristics as the best available guide to the genetic value of each line. The principles of constructing and using selection indexes which permit the attainment of maximum genetic progress were given by Hazel (1943).

MATERIAL AND METHODS

Four strains of the housefly (Musca domestica, Linn.); Isolan Resistant, Orlando Susceptible, Sevin Selected, and Malathion Resistant were obtained from the Entomological Research Division, Agricultural Research Service, U. S. Department of Agriculture, Corvallis, Oregon. These strains were labeled; Stock numbers I, II, III, and IV respectively. Four more strains such as Deildrin Resistant, Naphthaline Resistant, Milan SRS Susceptible, and Orlando DDT Resistant were obtained from the Entomological Laboratory, Oregon State University, Corvallis, Oregon and were labeled as Stock numbers V, VI, VII, and VIII respectively.

About 500-600 flies of each strain were kept in a cage 11" x 11" x 11" with two sides, and the top was made of one piece of No. 16 wire screen. The bottom and back were made of plywood and a cloth sleeve stapled to the front was twisted and tied with a rubber band. A pint, wide-mouthed, fruit jar, filled with water, with a piece of paper toweling stuck through the lid and a petri dish filled with powdered skimmed milk mixed with powdered sugar, 1:1, were placed on the floor of the cage which was covered with a paper towel. The room in which the flies were reared was equipped with two automatic electric heaters set so that they would keep the room temperature at $75^{\circ} \pm 5^{\circ}$F. A fan was set to suck out the air every 12 hours; the fan

was kept running for a period of two hours each time.

When the flies were ten days old, they were egged by placing, in the rearing cage, a 50 ml. beaker that contained CSMA media mixed with two parts of tap water and dashed with 5% ammonium hydroxide. After 8-12 hours, the eggs were transferred to a round, wide-mouthed, gallon jar filled three-fourths full with CSMA media mixed with water (1:2 by weight). The eggs were seeded one inch deep in the media. All stock flies were egged in as near to one day as possible. The rearing jars were placed near the floor at least six inches apart in order to allow adequate ventilation around the jars, thus reducing some amount of heat that was produced during fermentation of the media. Around the 8th to 12th day or when the pupae that gathered near the top layer of dry media were dark-reddish-brown (almost black) in color, they were transferred to half-pint jars or petri dishes and placed in emerging cages of 12" x 4 1/2" x 4 1/2", built in the same manner as previously described. The emerging flies were collected and sexed every 12 hours, or sooner, by means of a 2 1/2" x 12" long mailing tube operated by suction from a vacuum cleaner. The tube had a wire screen fitted inside near the middle of the tube, and this tube was attached to a vacuum cleaner. The tube was closed with a lid and detached from the vacuum cleaner. Carbon dioxide gas from a CO_2 tank was run into the tube for 30-60 seconds and the flies were poured into a sexing cup which had carbon dioxide gas flowing in continuously to keep the flies

immobilized until sexing was finished. These flies were supposed to be virgin (Murvosh and LaBrecque, 1964). From each stock, 50 males and 100 females were kept and crosses were made in the 12" d x 4 1/2" w x 1/2" h cages as follows (♂x♀):

I x II ⟶ F_1 I II

II x I ⟶ F_1 II I

III x IV ⟶ F_1 III IV

IV x III ⟶ F_1 IV III

V x VI ⟶ F_1 V VI

VI x V ⟶ F_1 VI V

VII x VIII ⟶ F_1 VII VIII

VIII x VII ⟶ F_1 VIII VII

The females were egged, reared, sexed and the F_1 virgins were obtained in the same manner as previously described. The F_1 flies (50 males and 100 females) were then crossed as follows:

♂		♀	
I II	x	III IV	⟶ F_2 I II III IV
II I		IV III	
III IV	x	I II	⟶ F_2 IV III II I
IV III		II I	
V VI	x	VII VIII	⟶ F_2 V VI VII VIII
VI V		VIII VII	
VII VIII	x	V VI	⟶ F_2 VIII VII VI V
VIII VII		VI V	

Then the F_2 virgins were obtained and crossed as follows:

♂ ♀

I II III IV V VI VII VIII
IV III II I × VIII VII VI V ——————> F_3 I II III IV V VI VII VIII

V VI VII VIII I II III IV
VIII VII VI V × IV III II I ——————> F_3 VIII VII VI V IV III II I

Then two types of the F_3 were placed together in a 11" x 11" x 11" cage and were allowed to interbreed for three generations. These flies were kept as a population stock for the experiment.

The stock flies were egged every four to five days, starting at the seventh day of age, to supply virgins for the entire experiment. Each of the 12 males was mated to five virgin females in a pint jar that was covered with paper toweling and fastened with a rubber band. A 50 ml. beaker filled with water and with a funnel made of a piece of paper towel placed on top and a small cup made of aluminum foil containing fly food (1:1 powdered skimmed milk and powdered sugar) were placed in the jar to provide food and water for the flies. At the tenth day or when a solid white lump (eggs) was observed in the females' abdomens, the females were individually placed in an egging vial after the flies were immobilized by running carbon dioxide gas into the jar. The egging vial was made from a 25 x 95 mm glass vial that had a piece of black cloth one square inch in size on the bottom and a small lump of mixed media (about the size of a pea) and a dash of five percent ammonium hydroxide placed in it. The flies were

visited every six hours and the date and time when the eggs were laid were recorded. Eggs from each female were then transferred into a quart jar filled two-thirds full with mixed CSMA media (1: 2 media: tap water). Only the eggs from two females mated to each of the males were needed, but eggs from three females were retained to insure offspring from two females. When the pupa were mature (became blackish red-brown), 12 pupa from each of the two females were weighed with a torsion balance of 500 mg. capacity, and each pupae was placed in an emerging vial made from a 25 x 95 mm vial containing a water-moistened cotton ball and plugged tightly with cotton wool. The vial was labeled according to sire, dam, and its number. These pupae were visited every six hours or more frequently during the day. The approximate time between the last visit and the previous visit was considered as the emerging time for the emerged flies observed at the last visit. The number of hours from egg to emergence was then recorded for each fly. The emerged flies were weighed after they were immobilized with CO_2 gas at three to six hours after emergence when the wings were fully spread and dried. Only four males and four females from each dam were weighed.

The females were individually mated to any males in a pint jar. When most females in the set were ready to be egged i.e., a white solid lump of egg is observed to occupy most parts of the abdomen, the flies were then transferred into an individual egging vial made from a

25 x 95 mm glass vial filled one inch high with fermented media and a piece of black cloth completely covering the entire surface of the media in the vial with the assumption that the fly would have the least chance to lay the eggs directly into the media. The black cloth with the eggs was removed from the vial; the eggs were spread out on the cloth and were counted under a magnifying glass with a press button counter. Number of eggs were then recorded for each fly. Nine sets of the same experiment were done successively with the virgins obtained from the stock and pupae weight, adult weight, emergence time (from egg to adult), and number of eggs laid were recorded for each offspring. To summarize, the entire experiment contained nine sets; twelve sires were involved in each set; two dames were mated to each sire, and four characters were measured from four male and four female offspring from each dam.

The data obtained were punched on cards and processed through the computer; heritability for each trait and correlations among the traits were estimated.

According to King and Henderson (1954), when the environment is random for all individuals in a population, the variance among full sibs is expected to contain one-half of the additive genetic variance plus all of the environmental variance ($\sigma^2_g/2 + \sigma^2_e$). The sire's component of variance, and the dam's component of variance are each expected to contain one-fourth of the additive genetic variance ($\sigma^2_g/4$).

The assumption must be made that no dominance or epistasis occurs, and that the sires and dams have equal additive genetic variance. Estimates of these components can be combined into an estimate of heritability:

$$h^2 = \frac{4(\sigma_g^2/4)}{\sigma_g^2/4+\sigma_g^2/4+\sigma_g^2/2+\sigma_e^2}$$

$$= \frac{\sigma_g^2}{\sigma_g^2+\sigma_e^2}$$

The method of estimation of the sums of squares and the form of the analysis of variance of the nested classification were also presented.

According to Van Vleck (1964), estimates of heritability can be obtained in three ways:

$$h_s^2 = \frac{4\sigma_s^2}{\sigma_s^2+\sigma_d^2+d_e^2}$$

$$h_d^2 = \frac{4\sigma_d^2}{\sigma_s^2+\sigma_d^2+\sigma_e^2}$$

$$h_{sd}^2 = \frac{2(\sigma_s^2+\sigma_d^2)}{\sigma_s^2+\sigma_d^2+\sigma_e^2}$$

Where h^2_s is the heritability estimated from paternal half sibs, h^2_d is estimated from maternal half sibs and h^2_d is estimated from full sigs. The σ^2_s may contain variance due to sex linkage and σ^2_d may contain variance due to maternal effects and variance due to interaction between the sire and dam genotypes. Genetic correlations can also be estimated in these three ways.

Analyses of variance and covariance for balanced nested designs were shown by Bogart (1959) including various methods to obtain estimates of heritability, phenotypic correlation, genotypic correlation, and environmental correlation.

In a random mating population, according to Bogart, 1959, heritability in a narrow sense is the ratio of the variance due to additive genetic effects divided by the total variance, or:

$$h^2 = \frac{\sigma^2_G}{\sigma^2_G+\sigma^2_D+\sigma^2_I+\sigma^2_E}$$

where σ^2_G, σ^2_D, σ^2_I, and σ^2_E are the variances due to additive genetic, dominance, epistatic, and environmental effects.

According to King and Henderson (1954), the statistical model for expressing the individual datum as a linear function of certain parameters and random variable is:

$$Y_{hijk} = \mu + a_h + s_{hi} + d_{hij} + e_{hijk}$$

where Y_{hijk} is the record for any trait of the kth progeny of the jth dam mated to the ith sire within the hth set. There are n_{hij} progeny of each dam. Thus:

$$\sum_{h}\sum_{i}\sum_{j} n_{hij} = N.$$

In order to estimate the variance components, the expected values of the sums of squares or expected mean squares need to be known as shown in the following analysis of variance table.

Source of variation	d.f.	Sum of squares	Expected sums of squares
Among sets	h-1	H-C	
Among sires/ sets	s-h	S-H	$(s-h)\sigma_e^2 + (k_1-k_3)\sigma_d^2 + (N-k_2)\sigma_s^2$
Among dames/ sires/ sets	d-s	D-S	$(d-s)\sigma_e^2 + (N-k_1)\sigma_d^2$
Among full sib-progeny/ sets	N-d	T-D	$(N-d)\sigma_e^2$

N = Total number of progeny record analysed.
h = Number of sets.
s = Number of sires by set subclasses.
d = Number of dams by set subclasses.
H = Uncorrected set sum of squares.
S = Uncorrected sire by set sum of squares.
D = Uncorrected dam by set sum of squares.

Computation of observed sums of squares can be done as follows:

$$T = \sum_h \sum_i \sum_j \sum_k Y_{hijk}^2$$

$$C = Y....^2/n...$$

$$H = \sum_h Y_{h...}^2/n_{h..}$$

$$S = \sum_h \sum_i Y_{hi..}^2/n_{hi..}$$

$$D = \sum_n \sum_i \sum_j Y_{hij.}^2/n_{hij.}$$

Coefficients of the variance components in the expected sum of

squares are calculated as:

$$k_1 = \sum_h \sum_i \frac{\sum_j n_{hij}^2}{n_{hi.}}$$

$$k_2 = \sum_h \frac{\sum_i n_{hi.}^2}{n_{h..}}$$

$$k_3 = \sum_h \frac{\sum_i \sum_j n_{hij}^2}{n_{h..}}$$

Once the observed sums of squares and coefficients of the variance components in the expected sums of squares are computed, the expected sum of squares can be equated to the observed sum of squares to obtain estimates of the components of variance, σ_e^2, σ_d^2 and σ_s^2 which are used to estimate heritability.

Heritability was estimated as:

$$h^2 = \frac{4\sigma_s^2}{\sigma_e^2+\sigma_d^2+\sigma_s^2}$$

Phenotypic, genetic and environmental correlations can be calculated from analyses of covariance as shown by Bogart (1959).

$$r_{y_1y_2} = \frac{\sigma_{e_{y_1y_2}} + \sigma_{d_{y_1y_2}} + \sigma_{s_{y_1y_2}}}{\sqrt{\left[\left(\sigma_{s_{y_1}}^2 + \sigma_{d_{y_1}}^2 + \sigma_{s_{y_1}}^2\right)\left(\sigma_{e_{y_2}}^2 + \sigma_{d_{y_2}}^2 + \sigma_{s_{y_2}}^2\right)\right]}}$$

$$r_{G_1G_2} = \frac{\sigma_{s_{y_1y_2}}}{\sqrt{\left(\sigma^2_{s_{y_1}} \times \sigma^2_{s_{y_2}}\right)}}$$

$$r_{E_{y_1}E_{y_2}} = \frac{\sigma_{e_{y_1y_2}} + \sigma_{d_{y_1y_2}} - \sigma_{s_{y_1y_2}}}{\sqrt{\left[\left(\sigma^2_{e_{y_1}} + \sigma^2_{d_{y_1}} - \sigma^2_{s_{y_1}}\right)\left(\sigma^2_{e_{y_2}} + \sigma^2_{d_{y_2}} - \sigma^2_{s_{y_2}}\right)\right]}}$$

Selection index was calculated according to Hazel (1943). The aggregate genotype, H, is:

$$H = a_1G_1 + a_2G_2 + \ldots + a_nG_n$$

where a_i are the relative economic values which measure the amount by which profit is expected for each unit change of the observed trait. The values of 1 were used here. The G_i are the sum of the additive effects of all genes influencing the ith trait. The object is to find a linear function of the observed traits (Y_i) which has maximum correlation with the aggregate genetic value, H, of the individual. The index is:

$$I = b_1Y_1 + b_2Y_2 + \ldots + b_nY_n$$

The b_i are multiple regression coefficients computed so as to maximize the correlation r_{IH}. The b_i is solved by

simultaneous equations:

$$b_1 V(Y_1) + b_2 \text{Cov } Y_1 Y_2 + \ldots + b_n \text{ Cov } Y_1 Y_n = \text{Cov } Y_1 H$$

$$b_1 \text{ Cov } Y_1 Y_2 + b_2 V(Y_2) \quad + \ldots + b_n \text{ Cov } Y_2 Y_n = \text{Cov } Y_2 H$$

$$\vdots$$

$$b_1 \text{ Cov } Y_1 Y_n + b_2 \text{ Cov } Y_2 Y_n + \ldots + b_n V(Y_n) \quad = \text{Cov } Y_n H$$

In matrix form:

$$P\underline{b} = G\underline{a}$$

where

P = matrix of phenotypic variances and covariances

G = matrix of genotypic variances and covariances

$\underline{a}$ = column vector of economic values (values of 1 were used)

$\underline{b}$ = column vector of index coefficients

or:

$$\begin{bmatrix} \sigma^2_{p_{y_1}} & \sigma_{p_{y_1y_2}} & \sigma_{p_{y_1y_3}} & \sigma_{p_{y_1y_4}} \\ \sigma_{p_{y_1y_2}} & \sigma^2_{p_{y_2}} & \sigma_{p_{y_2y_3}} & \sigma_{p_{y_2y_4}} \\ \sigma_{p_{y_1y_3}} & \sigma_{p_{y_2y_3}} & \sigma^2_{p_{y_3}} & \sigma_{p_{y_3y_4}} \\ \sigma_{p_{y_1y_4}} & \sigma_{p_{y_2y_4}} & \sigma_{p_{y_3y_4}} & \sigma^2_{p_{y_4}} \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix}$$

$$= \begin{bmatrix} \sigma^2_{s_{y_1}} & \sigma_{x_{y_1y_2}} & \sigma_{s_{y_1y_3}} & \sigma_{s_{y_1y_4}} \\ \sigma_{s_{y_1y_2}} & \sigma^2_{x_{y_2}} & \sigma_{s_{y_2y_3}} & \sigma_{s_{y_2y_4}} \\ \sigma_{s_{y_1y_3}} & \sigma_{s_{y_2y_3}} & \sigma^2_{s_{y_3}} & \sigma_{s_{y_3y_4}} \\ \sigma_{x_{y_1y_4}} & \sigma_{x_{y_2y_4}} & \sigma_{s_{y_3y_4}} & \sigma^2_{s_{y_4}} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \end{bmatrix}$$

Variance of aggregate genotype is:

$$\sigma^2_H = \underline{a}'G\underline{a}$$

Variance of index is:

$$\sigma^2_I = \underline{b}' P\underline{b}$$

and heritability of the index is:

$$h^2_{IH} = \frac{\sigma^2_I}{\sigma^2_H}$$

The efficiency of the index is:

$$r_{IH} = \sqrt{\frac{\sigma^2_I}{\sigma^2_H}}$$

RESULTS

Means of pupae weight, adult weight, emergence time, and egg production of the first batch by set and overall means are shown in Table 1. Overall means for pupae weight, adult weight, emergence time and egg production are 24. 51 mg., 18. 55 mg. 343. 60 hrs. and 122. 48 eggs respectively. Total observations for pupae weight, adult weight, and emergence time are 1343, and for egg production, 569 total observations.

Analyses of variances and variance components for pupae weight, adult weight, emergence time and egg production are shown in Tables 2, 3, 4, and 5. The heritabilities are 0. 3245 ± 0. 2362, 0. 34 ± 0. 19, 0. 72 ± 0. 30, and -0. 02 ± 0. 19 respectively for pupae weight, adult weight, emergence time and egg production.

Since the sire component and heritability of egg production have negative values, correlations between egg production and other traits can not be computed because a square root of a negative value is unidentified. According to the method used for computing correlations by a computer, different methods from the one previously described were employed. Raw data of two traits to be computed are added together, and then the sire's component of covariance is computed as:

$$\sigma_{G_{y_1 y_2}} = \frac{\sigma^2_{G_{y_1+y_2}} - \sigma^2_{G_{y_1}} - \sigma^2_{G_{y_2}}}{2}$$

where:

$\sigma_{G_{y_1 y_2}}$ is the sire component of covariance for pupae weight and adult weight,

$\sigma^2_{G_{y_1+y_2}}$ is the sire component of variance of pupae weight plus adult weight,

and $\sigma^2_{G_{y_1}}$ and $\sigma^2_{G_{y_2}}$ are sire components of variances for pupae weight and adult weight respectively.

Then genetic correlations among the traits are computed as:

$$r_{G_{y_1} G_{y_2}} = \frac{\sigma_{G_{y_1 y_2}}}{\sqrt{\sigma^2_{G_{y_1}} \sigma^2_{G_{y_2}}}}$$

Likewise, phenotypic covariances are obtained as:

$$\sigma_{p_{y_1 y_2}} = \frac{\sigma^2_{p_{y_1+y_2}} - \sigma^2_{p_{y_1}} - \sigma^2_{p_{y_2}}}{2}$$

where:

$\sigma_{p_{y_1 y_2}}$ is the phenotypic covariance for pupae weight and adult weight

$\sigma^2_{p_{y_1+y_2}}$ is the sum of the component variance due to sires, dams and full sibs for pupae weight plus adult weight

$\sigma^2_{p_{y_1}}$ and $\sigma^2_{p_{y_2}}$ are the sums of components due to sires, dams, and full sibs for pupae weight and adult weight respectively.

And the phenotypic correlations are computed as:

$$r_{p_{y_1y_2}} = \frac{\sigma_{p_{y_1y_2}}}{\sqrt{\sigma^2_{p_{y_1}} \sigma^2_{p_{y_2}}}}$$

Genetic correlations between pupae weight and adult weight, pupae weight and emergence time, and between adult weight and emergence time are 0.91, 0.50 and 0.62 respectively. Phenotypic correlations between pupae weight and adult weight, pupae weight and emergence time, and between adult weight and emergence time are 0.86, 0.03 and 0.05 respectively (Table 6).

Phenotypic correlations between egg production and the three other traits are computed from the data of female offspring that had egg production records only. The methods of computation were the same as the methods previously mentioned, except only the females with egg production records are involved. The phenotypic correlations

between pupae weight and egg production, adult weight and egg production, and between emergence time and egg production are 0.0884, 0.0759 and -0.0906 respectively (Table 6).

Heritabilities for the four traits, and genetic and phenotypic correlations among the traits are summarized in Table 7.

Selection indexes were computed and the results are:

$$I = -0.0504Y_1 + 0.7651Y_2 + 0.1969Y_3 + 0.0050Y_4$$

Variance of the index is:

$$\sigma_I^2 = 12.7171$$

Variance of the aggregate genetic value is:

$$\sigma_H^2 = 59.1497$$

and heritability of the index is:

$$r_{IH}^2 = \frac{\sigma_I^2}{\sigma_H^2} = \frac{12.7171}{59.1497} = 0.2150$$

Selection index for the first three traits is:

$$I = -0.0438Y_1 + 0.7648Y_2 + 0.1959Y_3$$

and the heritability of the index is:

$$r^2_{IH} = \frac{\sigma^2_I}{\sigma^2_H} = \frac{12.6858}{59.1497} = 0.2145$$

The efficiency of the index in both cases is:

$$r_{IH} = \sqrt{\frac{\sigma^2_I}{\sigma^2_H}} = .46$$

Table 1. Means of pupa weight, adult weight, emergence time and number of eggs.

Set No.	Pupa wt. (mg) Y_1	n	Adult wt. (mg) Y_2	n	Emergence T. (hrs) Y_3	n	Egg No. Y_4	n
1	26.42	131	19.88	131	395.75	131	113.94	59
2	22.49	155	17.17	155	383.22	155	120.41	61
3	23.49	125	17.54	125	381.14	125	117.71	48
4	22.35	119	17.23	119	322.21	119	107.69	48
5	23.68	161	18.11	161	346.61	161	123.56	72
6	24.59	152	18.97	152	347.90	152	131.77	69
7	25.61	170	19.51	170	326.34	170	129.72	74
8	26.12	158	19.88	158	337.06	158	137.52	69
9	25.20	172	18.30	172	272.11	172	111.99	69
Overall mean	24.51 ±0.08	1343	18.55 ±0.06	1343	343.60 ±1.08	1343	122.48 ±1.57	569

Table 2. Analysis of variance and variance component of pupae weight (Y_1).

Source	d.f.	S.S.	M.S.	Component
Sets	8	2610.25	326.28	2.0129
Sires/sets	88	2294.47	26.07	.4767
Dams/sires	89	1707.94	19.19	2.2439
Offs/dams	1157	3651.14	3.16	2.1557
Total	1342	10263.80	7.65	

Coefficients for Expected Mean Squares

	Offspring	Dams	Sires	Sets
Sets	1.0000	7.3667	14.2591	148.9393
Sires	1.0000	7.2809	13.8026	
Dams	1.0000	7.1458		
Offs.	1.0000			

Heritability - .32 S.E. - .24

Table 3. Analysis of variance and variance component of adult weight (Y_2).

Source	d.f.	S.S.	M.S.	Component
Sets	8	1364.64	170.58	1.0407
Sires/sets	88	1349.15	15.33	.3597
Dams/sires	89	910.04	10.23	1.0432
Offs/dams	1157	3205.60	2.77	2.7706
Total	1342	6829.44	5.09	

Coefficient for Expected Mean Squares

	Offspring	Dams	Sires	Sets
Sets	1.0000	7.3667	14.2597	148.9393
Sires	1.0000	7.2809	13.0826	
Dams	1.0000	7.1458		
Offs.	1.0000			

Heritability = .34 S.E. = .19

Table 4. Analysis of variance and variance component of emergence time (Y_3).

Source	d. f.	S. S.	M. S.	Component
Sets	8	1770825	221353	1474.7046
Sires/sets	88	147746	1679	47.6365
Dams/sires	89	89363	1004	128.3434
Offs/dams	1157	100617	87	86.9640
Total	1342	2108551	1571	

Coefficients for Expected Mean Squares

	Offspring	Dams	Sires	Sets
Sets	1.0000	7,3667	14.2591	148.9393
Sires	1.0000	7.2809	13.8026	
Dams	1.0000	7.1458		
Offs.	1.0000			

Heritability = .72 S. E. = .30

Table 5. Analysis of variance and variance component of egg number (Y_4).

Source	d. f.	S. S.	M. S.	Component (σ^2)
Sets	8	49290	6161	69.3508
Sires/sets	87	150849	1734	-6.0030
Dams/sires	89	153528	1725	191.5349
Offs/dams	384	445383	1160	1159.8529
Total	568	799050	1407	

Coefficients for Expected Mean Squares

	Offspring	Dams	Sires	Sets
Sets	1.0000	3.2827	6.2268	63.0510
Sires	1.0000	3.1818	5.8956	
Dams	1.0000	2.9508		
Offs.	1.0000			

Heritability = - 0.02 S. E. = .19

Table 6. Covariance and correlations among the traits.

		Y_1	Y_2	Y_3	Y_4
		Genetic Covariance			
Phenotypic Covariance	Y_1	--	0.38	2.40	--
	Y_2	4.24		2.56	--
	Y_3	1.35	1.50		--
	Y_4	7.27	5.15	-52.50	
		Genetic Correlation			
Phenotypic Correlation	Y_1		0.91	0.50	--
	Y_2	0.86		0.62	--
	Y_3	0.03	0.05		--
	Y_4	0.09	0.08	-0.09	

Table 7. Heritability, genetic and phenotypic correlations among the traits.

Heritability	Genetic Correlation			
	Y_1	Y_2	Y_3	Y_4
Phenotypic Correlation Y_1	0.32±0.24	0.91	0.50	--
Y_2	0.86	0.34±0.19	0.62	--
Y_3	0.03	0.05	0.72±0.30	--
Y_4	0.09	0.08	-0.09	-0.02±0.19

DISCUSSION

The mean of pupae weight for all flies in the present study was 24.51 ± .08 mg. which is comparable to pupae weights of 25.5 and 24.1 reported for the 4th and 8th generations by Ware and Teranova (1960). Pimental, Dewey, and Schwardt (1951) reported that the mean pupa weight for flies of a DDT resistant strain was 20.7 mg. while the mean for a non-resistant strain was 20.9 mg. Babers, Pratt, and Williams (1953) experimented with flies produced in standard CSMA medium, and the adults were fed with a 1:1 mixture of powdered whole milk and sucrose with water given separately, with the temperature of the rearing room at $26^{o} \pm 2^{o}C$; and they reported pupae weight of 23.74 ± 2.62 mg. for susceptible flies and 22.96 ± 4.28 mg. for DDT resistant flies.

The adult weight of flies in the present study was (Table 1) 18.55 ± .06 mg. Afifi and Knutson (1956) reported female body weight of susceptible NAIDM flies as 15.9, 19.5, and 21.9 mg. for F_1, F_2 and F_3 respectively. Body weights of flies 2-3 days old were reported by Alexander, Barker, and Babers (1958). The females of susceptible strains (NAIDM) weighed 21.7 to 20.2 mg., while females of the resistant strains (Orlando) weighed 13.0 to 22.8 mg. The body weight of males of susceptible strains ranged from 17.0 to 18.7 mg. while the body weight of flies of resistant strains were 11.4 to 19.0 mg. Generally speaking, the pupae and the adult weight of flies in the

present experiment are quite comparable to those reported by other investigators. This is not unexpected because the flies used were from a population derived by combining eight strains.

Average emergence time (Table 1) ranged from 272.11 hours in the 9th set to 395.75 hours in the 1st set, with the mean of 343.60 ± 1.08 hours, tending to decrease from the first to the last set. This may have been the result of outside temperature that affected the room temperature. The outside temperature was increasing from March to June which was the experimental period. As previously described, the experimental room was equipped with heaters to increase the room temperature up to $75^{o} \pm 5^{o}F$, but no provision was made to hold the temperature down when the outside temperature increased beyond $75^{o}F$. Imms (1948) has reported that temperature can vary the developmental period of the fly larvae. The mean of 343.60 ± 1.08 hours (14 days) is quite high compared to those reported by Babers, Pratt, and Williams (1953) which was about five days from egg to mid-point of pupation, approximately 8-9 days including the pupa period. The difference could be because the flies were reared at different temperatures, $26^{o} \pm 2^{o}C$ by Babers, Pratt, and Williams (1953).

The egg number (Table 1) ranged from 107.69 for the 4th set to 137.52 for the 8th set with the mean of 122.48 ± 1.57 which agrees with the average of 120 to 125 reported by West (1951) and Barker

(1960). The number of observations of egg production (569) was low in comparison with the number of observations on the other traits (1343). Not all female offspring have egg production records because all females in a set had to be egged at the same time and some were not ready to be egged at a given time; some had already laid their eggs. Once the flies are in the egging vials, they had to lay eggs within 2-3 days because water and food were not provided in the vials.

The heritabilities of pupae weight and adult weight, 0.32± 0.24 and 0.34 ± 0.19 respectively, are moderate when one considers that they are both growth traits. Bartlett, Bell, and Anderson (1966) reported heritability estimates of .34 ± .077 for random selection and .32 ± .055 for high selection lines both of which were large strains of Tribolium castaneum. Enfield, Comstock, and Braskerud (1966) reported a heritability estimate of .37 ± .025 in two populations. The heritability of adult weight was similar to estimates reported by many investigators: .22 and .23 for Drosophila body weight (Frahm and Kojima, 1966), .20 for Drosophila thorax length (Robertson, 1957), .35 for body weight at six weeks in mice (Falconer, 1955), .20 for body weight of White Leghorn chickens (Lerner and Cruden, 1951), .17 to .54 for nine week body weight of chickens (Godfrey and Goodman, 1956), .35 for sheep body weight (Morley, 1955), .30 for 180 day weight of swine (Whatley, 1942), and .14 (heifer) and .32 (bull) for birth weight of Hereford cattle (Pahnish et al, 1964).

A high estimate of heritability for emergence time, .72 ± .30,

was obtained in the present study. This indicates a high effect of additively controlled gene action. De-Fries, Touchberry, and Hays (1959) also reported a high heritability estimate of gestation length in Ayrshire cattle (. 708), and in Jersey cattle (. 704) while in Holstein-Friesian the heritability estimate was 0. 60 (Plum, Anderson, and Swiger (1965). The heritability of gestation length is generally high in most livestock as reported by many workers.

The negative value of heritability for egg production, -0. 02 ± 0. 19, which may be considered to be zero, indicates that egg production is probably a very lowly heritable trait. It is impossible for any trait to have a negative heritability, but by the method of computation employed, the negative value is unavoidable and, as pointed out by King and Henderson (1954), negative estimates of variance components may occur when the sample is small.

An accurate estimate of heritability is valuable in formulating breeding plans and predicting progress from selection. A character that is influenced strongly by environmental variations has a low heritability in a population in which the environment varies widely; consequently, great emphasis can not be placed upon mass selection. In low heritable traits, on the other hand, selection should be based on pedigree analysis, sib testing, and progeny tests (Lush, 1948). Emergence time is a trait of high heritability and should respond to individual selection, whereas egg production is of low heritability and

would not be expected to respond to individual selection but rather would require a different method of selection or crossbreeding as a means of improving the trait. In cases of pupae and adult weights which are considered moderately heritable, greatest progress can be made by employing both individual selection and progeny testing.

Heritability of egg production in Drosophila was 0. 2 as reported by Robertson (1957) while heritability of litter size in mice is 0. 15 (Falconer, 1955). Swine litter size was reported to be 0. 15 heritable by Lush and Molln (1942). Heritability of fowl egg production has been reported by many workers; . 18 ± . 052 for White Leghorns (Sheldon, 1956), . 28 for number of eggs laid in 69 trap days from the 23rd to 46th week of white gold meat-type chickens (Jaap, Smith, and Goodman, 1962), . 06 to . 36 for diallel crosses among light Sussex and Brown Leghorn laying fowl at different stages of laying (Hale and Clayton, 1964). Hill, Krueger, and Quisenberry (1966) reported . 22, . 25, and . 30 for eggs to date, eggs to 346 days and eggs to 522 days, respectively in white Leghorn chickens while Amer (1966) reported 0. 157 in Fayoumi, the native chicken of U. A. R.

Only the sire components were used in this study because the traits measured are unlikely to be associated with sex-linkage and maternal effects as pointed out by Van Vleck (1964), and it is assumed to be the best estimate available by King (1961). According to Falconer (1964), only the sire's component can be used to estimate the

heritability when the dam's component is much greater than the sire's component (Tables 2, 3, 4, and 5).

Genetic correlation between pupae weight and adult weight was very high, 0.91; consequently, one may assume that they are almost the same trait since the elapsed times when these two traits were measured were so close. At the time the pupae were weighed (when they have become a dark brown color) most of them are ready to emerge, and the adults were weighed three to six hours after emergence; thus, the time in which these two traits were measured may be as close as three hours and not more than three days. Of course, when the flies emerge, leaving behind the puparium enclosures, there is no doubt that the weight of the puparium enclosures varies within a certain range. The phenotypic correlation was also high (0.86) confirming the closeness of the relationship between these two traits. The genetic correlations between pupae weight and emergence time and between adult weight and emergence time are also high, 0.50 and 0.62 respectively. When two traits are genetically correlated, one should assume that, when artificial selection is made for a particular characteristic, the change in the average value of the genotype for the selected trait should result in an average change in the genotype for the unselected trait, and the change in the unselected trait should be proportional to the genetic correlation between the traits and the ratio of the genetic standard deviations of the selected and unselected

traits (Siegel, 1962). Bogart (1959) expressed changes involving two genetically correlated traits as:

$$\Delta G_{y_1} = r_{G_{y_1 y_2}} \frac{\sigma_{G_{y_1}}}{\sigma_{G_{y_2}}} \Delta G_{y_2}$$

where:

ΔG_{y_1} denotes the genetic change in selected trait

ΔG_{y_2} denotes the genetic change in unselected trait

$r_{G_{y_1 y_2}}$ is the genetic correlation between the two traits and

$\sigma_{G_{y_1}}$ and $\sigma_{G_{y_2}}$ is the genetic standard deviations of the two traits.

Since pupae weight, adult weight, and emergence time are displaying positive genetic correlations, genetic change in one should be accompanied by genetic changes in the others. If two traits should be negatively correlated, increasing one of the traits will result in decreasing the genetic value of the other. Improvement of both of these two traits by selection would be slow. Genetic correlation between gestation length and birth weight in Holstein cattle of 0.37 was reported by Plum, Anderson, and Swiger (1965) while a correlation of $0.44 \pm .28$ for Hereford cattle was reported by Lasley, Day, and

Comfort (1961).

A high phenotypic correlation between pupae weight and adult weight (0.86) was observed while the phenotypic correlations among all other traits was low; 0.03 for pupae weight and emergence time, 0.09 for pupae weight and egg production, 0.05 for adult weight and emergence time, 0.08 for adult weight and egg production, and -0.09 for emergence time and egg production.

Phenotypic correlations between adult weight and emergence time, and between pupae weight and emergence time are low while genetic correlations are high indicating the effects of environmental influences. Although phenotypic correlations are the actual characteristics which were directly observed, genetic correlations should be relied upon since they indicate the relationship of the genetic values among the traits. Dickerson (1957) found that genetic correlation between 18 week body weight and egg production to 72 weeks of age in chickens was -.16 while phenotypic correlation was .09. It appeared to be that, while the relationship was observed to be positive, it was genetically negative.

According to Hazel and Lush (1942), selection for a total score or index of net desirability is much more efficient than selection for one trait at a time or by the independent culling level method. But in practice, the index method is far more complicated than other methods since certain constants must be known in order to construct an

index (Hazel, 1943), and the calculations involved are complicated. In some cases, selection for one trait at a time permits earlier selection without waiting until all traits are mature.

The selection index that was developed is:

$$I = -0.0504Y_1 + 0.7651Y_2 + 0.1969Y_3 + 0.0050Y_4$$

for all four traits where Y_1, Y_2, Y_3 and Y_4 stand for the actual measurement of pupae weight, adult weight, emergence time, and egg production respectively. Pupae weight was weighted negatively while adult weight was highly positively weighted. Emergence time and egg production were weighted low. Since economic value of all traits were weighted the same (values of 1), the regression coefficients in the index are determined by their phenotypic and genetic variance and covariance among the traits. Because egg production has very low breeding value (heritability = 0), egg production can be deleted from the index. Therefore, the selection index, involving only the first three traits, was computed as:

$$I = -0.0438Y_1 + 0.7648Y_2 + 0.1959Y_3$$

Although egg production was deleted, the first three traits are still weighted almost the same as they were in the first index. The heritibilities of both indexes, 0.2150 and 0.2145 for the first and second

index respectively, are almost the same since there were no great differences in weighting the same trait in both indexes. The efficiency of the index in both cases was .46; therefore, 46% as much gain could be made as with a perfect index (where $R_{IH} = 1$). Hazel (1943) constructed selection indexes for 180 days weight, market score, and productivity in pigs and found that efficiency of the indexes were 36.1 to 40.4%.

SUMMARY AND CONCLUSION

Means of pupae weight, adult weight, emergence time, and egg production; 24.51 ± 0.08 mg., 18.55 ± 0.06 mg., 343.60 ± 1.08 hours, and 122.48 ± 1.57 eggs respectively in the present study agreed well with those reported by many workers except for emergence time which was higher than the results from previous studies. This is probably due to the fact that this experiment was done under a lower temperature range.

Heritability estimates for pupae weight, adult weight, emergence time, and egg production were 0.32 ± 0.24, 0.34 ± 0.19, 0.72 ± 0.30, and -0.02 ± 0.19 respectively. Heritability estimates of pupae weight and adult weight were moderate, considered as the growth traits, and agreed with those of similar growth traits in other organisms reported by other investigators. Heritability of emergence time was high compared with gestation length in cattle. The small negative heritability value of egg production which was considered as zero, was low compared to the heritability estimate for egg production in Drosophila and poultry. However, it indicates that the egg production trait in Musca domestica L. is greatly affected by environment.

The genetic correlation between pupae weight and adult weight, pupae weight and emergence time, and adult weight and emergence time were 0.91, 0.50, and 0.62 respectively. It indicates that

genetic change in any of the three traits will result in genetic change in the other two in the same direction. This is ideal for selection breeding in livestock provided that the direction of the changes are desirable.

The phenotypic correlations between pupae weight and adult weight, pupae weight and emergence time, pupae weight and egg production, adult weight and emergence time, adult weight and egg production, and emergence time and egg production were 0.86, 0.03, 0.09, 0.05, 0.08, and -0.09 respectively. The correlation between pupae weight and adult weight was very high as might be expected. This means that when the phenotypic change of one trait is observed, phenotypic change in the other trait is expected to be observed. The other correlations were very low; thus, the phenotypic change in one trait has little effect on the phenotype of the other trait. The phenotypic correlation between emergence time and egg production was negative and non-significant. There was a high genetic correlation between pupae weight and emergence time and between adult weight and emergence time, but their phenotypic correlations were low.

The selection indexes were computed as:

$$I = -0.0504Y_1 + 0.7651Y_2 + 0.1969Y_3 + 0.0050Y_4$$

for all four traits, and:

$$I = -0.0438Y_1 + 0.7648Y_2 + 0.1959Y_3$$

where Y_1, Y_2, Y_3, and Y_4 denote the measurement of pupae weight, adult weight, emergence time and egg production respectively. The second index can be used and the other three traits are still weighted almost the same as in the first index. The efficiency of both indexes is 0.46 and 46%.

More investigation of genetic parameters of the housefly is still needed to widen the use of this organism in genetic study.

BIBLIOGRAPHY

Afifi, Saad E.D. and Herbert Knutson. 1956. Reproductive potential, longevity, and weight of house flies which survived one insecticidal treatment. Journal of Economic Entomology 40:310-313.

Alexander, B.H., Roy J. Barker and Frank H. Babers. 1958. The phosphatase activity of susceptible and resistant house flies and german cockroaches. Journal of Economic Entomology 51:211-213.

Amer, M.F. 1966. Heritability of egg production and egg weight in the Fayoumi. Poultry Science 46:32-35.

Babers, Frank H., John J. Pratt, Jr. and Michele Williams. 1953. Some biological variation between strains of resistant and susceptible house flies. Journal of Economic Entomology 46:914-915.

Barker, Will. 1960. Familiar insects of America. New York, Harper. 236 p.

Bartlett, Alan C., A.E. Bell and V.L. Anderson. 1966. Changes in quantitative traits of Tribolium under irradiation and selection. Genetics 54:699-713.

Bogart, Ralph. 1959. Improvement of livestock. New York, Macmillan. 436 p.

Bruce, W.N. and G.C. Decker. 1950. Housefly tolerance for insecticides. Soap and Sanitary Chemicals 26(3):122-125, 145-147.

Busvine, J.R. 1953. Laboratory investigations with insecticide-resistant houseflies. In: Transactions of the Ninth International Congress of Entomology, Amsterdam, August 17-24, 1951. Vol. 2, Symposia. Amsterdam. p. 335-339.

Busvine, J.R. and N.H. Khan. 1955. Inheritance of BHC-resistance in the housefly. Transactions of the Royal Society of Tropical Medicine and Hygiene, 49:455-459.

Dakshinamurty, S. 1948. The common house fly, M. domestica, L. and its behaviour to temperature and humidity. Bulletin of Entomological Research 39:339-357.

D'Alessandro, G. and M. Mariani. 1954. Osservazioni sulla eredita' dei caratteri resistenza e sensibilita al DDT in Musea domestica L. . Rivista di Parassitologia 15:85-94.

Dauer, Maxwell, Prem Lata Bhatnagar and Morris Rockstein. 1965. X-irradiation of pupae of the house fly, Musca domestica, L. and male survival. Journal of Gerontology 20:219-223.

Decker, George C. and Willis Bruce. 1952. House fly resistance to chemicals. American Journal of Tropical Medicine and Hygiene 1:395-403.

DeFries, J.C., R.W. Touchberry and R.L. Hays. 1959. Heritability of the length of the gestation period in dairy cattle. Journal of Dairy Science 42:598-606.

Dickerson, G.E. 1957. Genetic covariation among some economic characters of Leghorn-type chickens (Abstract). Poultry Science 36:1112-1113.

Enfield, F.D., R.E. Comstock and O. Braskerud. 1966. Selection for pupa weight in Tribolium castaneum. I. Parameters in base populations. Genetics 54:523-533.

Falconer, D.S. 1955. Pattern of response in selection experiment with mice. Cold Spring Harbour Symposia on quantitative Biology 20:178-196.

Falconer, D.S. 1964. Introduction to quantitative genetics. New York, Ronald. 365 p.

Frahm, Richard R. and Ken-ichi Kojima. 1966. Comparison of selection responses on body weight under divergent larval density conditions in Drosophila pseudoobscura. Genetics 54:625-637.

Georghiou, G.P. and W.R. Bowen. 1966. An analysis of house fly resistance to insecticides in California. Journal of Economic Entomology 59:204-214.

Georghiou, G. P. et al, 1965. The present status of housefly resistance to insecticides in California. California Agriculture 19 (10):8-10.

Godfrey, George F. and Billy L. Goodman. 1956. Genetic variation and covariation in broiler body weight and breast width. Poultry Science 35:47-50.

Greenberg, B.A. 1954. Method for the sterile culture of housefly larvae. Canadian Entomologyist 86:527-528.

Hale, R.W. and G.A. Clayton. 1965. A diallel crossing experiment with two breeds of laying fowl. British Poultry Science 6:153-174.

Harris, Robert L., Stanley Wearden and Clifford C. Roan. 1961. Preliminary study of the genetic of house fly (M. domistica, L.) resistance to malathion. Journal of Economic Entomology 54: 40-45.

Harrison, C. Marry. 1951. Inheritance of resistance to DDT in the housefly, Musca domestica, L. Nature 167:855-856.

Hazel, L.N. 1943. The genetic basis for constructing selection indexes. Genetics 28:476-490.

Hazel, L.N. and J.L. Lush. 1942. The efficiency of three methods of selection. Journal of Heredity 33:393-399.

Hill, A.T., W.F. Krueger and J.H. Quisenberry. 1966. A biometrical evaluation of component parts of eggs and their relationship to other economically important traits in a strain of White Leghorns. Poultry Science 45:1162-1185.

Hiroyoshi, T. 1960. Some new mutant and linkage groups of the house fly. Journal of Economic Entomology 53:985-990.

Hiroyoshi, T. 1961. The linkage map of the house fly, Musca domestica, L. Genetics 46:1373-1380.

Hoyer, Richard F., Frederick W. Plapp, Jr. and Richard D. Orchard. 1965. Linkage relationships of several insecticide resistance factors in the house fly (Musca domestica, L.). Entomologia experimentalis et applicata 8(1):65-73. (Abstracted in Biological Abstracts 47:40325. 1966)

Imms, A. D. 1948. A general textbook of entomology. New York, E. P. Dutton. 727 p.

Jaap, R. G., J. H. Smith and B. L. Goodman. 1962. A genetic analysis of growth and egg production in meat-type chickens. Poultry Science 41:1439-1446.

Johnston, E. F., Ralph Bogart and A. W. Lindquist. 1954. The resistance to DDT by houseflies. Journal of Heredity 45:177-182.

Keiding, J. 1953. Development of resistance in the field and studies of inheritance. In: Transactions of the Ninth International Congress of Entomology, Amsterdam, August 17-24, 1951. Vol. 2, Symposia. Amsterdam. p. 340-345.

King, Steven C. 1961. Inheritance of economic traits in the Regional Cornell Control population. Poultry Science 40:975-986.

King, Steven C. and C. R. Henderson. 1954. Variance components analysis in heritability studies. Poultry Science 33:147-154.

LaFace, Lidia. 1952. Sul comportamento ereditario della resistenza ad alcuni insetticidi in Musca domestica. Rivista di parassitologia 13:57-60. (Abstracted in Biological Abstracts 27: 8538. 1953)

Lasley, J. F., B. N. Day and J. E. Comfort. 1961. Some genetic aspects of gestation length, and birth and weaning weight in Hereford cattle. Journal of Animal Science 20:737-741.

Lerner, I. M. 1950. Population genetics and animal improvement. Cambridge, England, Cambridge University. 342 p.

Lerner, I. M. and D. Cruden. 1951. The heritability of egg weight: the advantages of mass selection and of early measurement. Poultry Science 30:34-41.

Lichtwardt, E. T. 1956. Genetics of DDT-resistance of an inbred line of houseflies. Journal of Heredity 47:11-16.

Lichtwardt, E.T., Willis N. Bruce and George C. Decker. 1955. Note on the inbreeding of housefly. Journal of Economic Entomology 48:301-303.

Lush, J. L. 1935. The inheritance of productivity in farm livestock. Part V. Discussion of preceeding contributions. Empire Journal of Experimental Agriculture 3:25-30.

Lush, J. L. 1948. Heritability of quantitative characters in farm animals. Proceedings of the International Congress of Genetics 8:356-375.

Lush, J. L. and A. E. Molln. 1942. Litter size and weight as permanent characteristic of sows. Washington, D. C. 40 p. (U. S. Department of Agriculture. Technical Bulletin No. 836)

Maelzer, D. A. and R. L. Kirk. 1953. A preliminary study of the genetics of DDT resistance in houseflies. Australian Journal of Biological Sciences 6:244-256.

Michelsen, Axel. 1960. Experiments on the period of maturation of the male housefly, Musca domestica, L. Oikos 11:250-264.

Milani, R. 1953. The genetics of the house-fly, preliminary note. In: Proceedings of the 9th International Congress of Genetics, Billagio, Italy, 1953. Pt. 2. Florence, 1954. p. 791-796. (Caryologia Vol. 6, supplement)

Missiroli, A. 1947. Riduzione o eradicazione degli anofeli. Rivista di Parassitologia 8:141-169.

Monroe, R. E. 1960. Effect of dietary cholesterol on house fly reproduction. Annals of the Entomological Society of America 53:821-824.

Moreland, C. R. and W. S. Mcleod. 1956. Housefly egg measuring technique. Journal of Economic Entomology 49:49-51.

Morley, F. H. W. 1955. Selection for economic characters in Australian merino sheep. V. Further estimates of phenotypic and genetic parameters. Australian Journal of Agricultural Research 6:77-90.

Morrison, P. E. and D. M. Davies. 1964. Feeding of dry chemically defined diet, and egg production in the adult house-fly. Nature 201:104-105.

Murvosh, Chad M., R. L. Fye and G. C. Labrecque. 1964. Studies on the mating behaviour of the housefly, Musca domestica, L. Ohio Journal of Science 64: 264-271.

Nagasawa, Sumio and Shoji Asano. 1963. An inbreeding method of rearing the house fly. Journal of Economic Entomology 56: 714.

Pahnish, O. F. et al. 1964. Genetic analyses of economic traits measured in range-raised Herefords at preweaning and weaning ages. Journal of Animal Science 23: 562-568.

Perje, Ann-Margret. 1948. Studies on the spermatogenesis in Musca domestica. Hereditas 3: 209-232.

Peterson, Alvah. 1964. Entomological techniques. Ann Arbor, Michigan, Edwards. 435 p.

Pimentel, David, J. E. Dewey and H. H. Schwardt. 1951. An increase in the duration of life cycle of DDT-resistant strains of the housefly. Journal of Economic Entomology 44: 477-481.

Plum, Morgans, Henry Anderson and L. A. Swiger. 1965. Heritability estimates of gestation length and birth weight in Holstein-Friesian cattle and their use in selection indexes. Journal of Dairy Science 48: 1672-1675.

Ranade, D. R. 1964. Developmental anatomy of Musca domestica nebulo, Fobr. I. Life history of the imago and external morphology of the larval instars. Journal of Animal Morphology and Physiology 11: 245-256.

Robertson, F. B. 1957. Studies in quantitative inheritance. XI. Genetic and environmental correlation between body size and egg production in Drosophila melanogaster. Journal of Genetics 55: 428-443.

Rockstein, M. 1957. Longevity of male and female house flies. Journal of Gerontology 12: 253-256.

Rockstein, M. and H. M. Lieberman. 1958. Survival curves for male and female house flies. Nature 181: 787-788.

Rogoff, W. M. 1965. Mating of the house fly, Musca domestica, L. in monitored darkness. Journal of Medical Entomology 2: 54-56.

Sacca, G. 1947. Sull'esistenza di Mosche domestiche resistenti al DDT. Rivista di Parassitologia 8(2/3):127-128. (Abstracted in Biological Abstracts 22:10355. 1948)

Sacca, G. and M. P. Benetti. 1960. Experimental research on the mating and sexual behaviour of Musca domestica, L. (Diptera, Muscidae). Rendiconti dell'Istituto Superiore di Sanita' 23(5): 423-432. (Abstracted in Biological Abstracts 36:24587. 1961)

Sheldon, B. L. 1956. Genetic parameters associated with characters affecting egg production in the domestic fowl. I. The heritability of total egg production during the pullet year. Australian Journal of Agricultural Research 7:625-629.

Siegel, P. B. 1962. A double selection experiment for body weight and breast angle at eight weeks of age in chickens. Genetics 47:1313-1319.

Smith, A. G. 1961. Notes on breeding house flies (M. domestica, L.). New Zealand Journal of Science 4:292-295.

Smith, H. Fairfield. 1936. A discriminant function for plant selection. Annal of Eugenics 7:240-250.

Spieth, Herman T. and T. C. Hsu. 1950. The influence of light on the mating behaviour of seven species of the Drosophila Melanogaster species group. Evolution (New York) 4:316-325.

Tsukamoto, Masuhisa and Reiko Suzuki. 1965. Genetic analysis of DDT-resistance in two strains of housefly, Musca domestica, L. Botyu Kagaku 29(4):76-89. (Abstracted in Biological Abstracts 47:90372. 1966)

Van Vleck, L. D. 1964. Genetic parameters of five month lactation records. Journal of Dairy Science 47:421-425.

Ware, George W. and Andrew C. Teranova. 1960. The effects on house flies of adding wheat germ and corn oil to fly media. Journal of Economic Entomology 53:325-326.

Whatley, J. A. 1942. Influence of heredity and other factors on 180 day weight in Poland China swine. Journal of Agricultural Research 65:249-264.

West, Luther S. 1951. The housefly. Ithaca, N. Y., Comstock, 584 p.

Zingrone, Louise D., Willis N. Bruce and George C. Decker. 1959. A mating study of the female house fly. Journal of Economic Entomology 52:236.