THE INFLUENCE OF TEMPERATURE ON VARIATION AND INHERITANCE OF BODILY DIMENSIONS IN DROSOPHILA MELANOGASTER 1.

By

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With 10 figures in the text.

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Introduction.

The fruit fly, *Drosophila melanogaster*, has been the outstanding material for genetic study for more than 20 years. MORGAN and his school have made many contributions in this field, out of which has been developed the modern theory of the gene. There are several hundred known mutations which follow the MENDELIAN scheme in inheritance

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 $(MorGAN, BRIDGES and STURTEVANT [1925]).$ In spite of this great mass of work on mutations, very little is known about the variation of inheritance of the dimensional characters of *Drosophila melanogaster.*

Castle et *al.* (1906) measured the tibia of *Drosophila* males as an index of the size of the flies, and studied the relation between size and number of teeth in the sex-comb. The conclusions were that: 1. inbreeding does not affect the variability in number of teeth in the sex-comb of the male, nor the variability in size; 2. size of the male individuals is closely correlated with number of teeth in the sex-comb.

LuTz (1911) showed that disuse of the wings of *Drosophila* for generations did not affect either wing length or wing breadth.

LuTz (1913) studied the sexual dimorphism of wing length and femur length of the middle leg in *Drosophila.* Sex differences in absolute size, as well as differences in the ratio between wing length and femur length in the two sexes were found to be significant. This difference in the ratio is further confirmed by the finding that in each sex the ratio is relatively constant without any relation to the absolute sizes involved. LvTz's conclusion about sexual dimorphism is that the sexes are built on different plans. He further studied the cross between normal females and wingless and miniature males. Their progeny showed the same sexual dimorphism.

Lurz (1915), in a study of natural selection, measured wing breadth of *Drosophila in* connection with the correlation between wing breadth and length of adult life in starvation. He found positive correlation between them. He also found higher means and lower variabilities of wing breadth in general populations and long-lived populations than in short-lived (living less than 66 hours) populations. The correlation between length of posterior cell and wing breadth was found to be higher in short-lived than in long-lived populations, particularly in males. Also, with other characters studied, he produced evidence of the action of natural selection during the course of the life of the flies.

Body dimensional characters under different conditions, such as temperature and starvation, have been the subject of study in recent years. ALPATOV and PEARL (1929) studied the dimensional changes of the body in normal wild type *Drosophila melanogaster* reared at different temperatures, 18⁰ C. and 28⁰ C. They found that in 7 characters out of 9 which were measured, the lower temperature groups were significantly larger than the high temperature groups, both in male and female.

ALPATOV (1930), in connection with the study of the relation between wing size and cell size at different temperatures, 280 C. and 180 C., and under starvation, found that:

1. Sex differences in the size of the wing were significant under all conditions studied.

2. The relative breadth of the wing was greater in males than in females, particularly those reared at 280 C.

3. The relative breadth of the wing of both females and males of underfed and 18° C. flies seemed to be less than in 28° C. flies

4. The sex differences were greater in 28° C. flies than in underfed or 18° C. flies.

Among other studies on the change in size effected by starvation may be cited those by SMIRNOV and ZHELOCHOVYSEV (1927), and GAUSE (1931). The former found in *Drosophila funebris* that shortening of the lengths of different portions of longitudinal vein IV as well as of the length of the posterior cross vein occurred in different proportions in the case of larval starvation. The variation of individual characters as well as the coefficient of correlation between 2 characters was increased significantly in underfed flies as compared with normal flies. GAUSE in *Drosophila]unebris* and *Drosophila ~nelanogaster* studied the variation of wing length in connection with egg length. Underfeeding produced a shortening of length of egg to a lesser degree than in the case of wing length.

EIGENBRODT (1930) with homozygous red, forked, bar stock of *Drosophila melanogaster* studied the effect of temperature on weight, thorax length, wing length and breadth, head breadth, etc., and showed that:

1. All characters measured except the number of teeth in the sex-comb varied inversely with temperature.

2. Sexual dimorphism in size was more striking at higher temperatures than at low.

Recently HERSH and WARD (1932) also studied the effect of temperature on the female wing length in homozygous long-winged and vestigial-winged flies of *Drosophila melanogaster* and their reciprocal heterozygotes and concluded that:

1. Wing length and area were exponential functions of the temperature.

2. The reciprocal heterozygotes with long-winged mothers had on the average larger wings at all temperatures than did those with short-winged mothers.

The effect of temperature on vestigial wings is the reverse of its effect on long wings. The higher the temperature, the longer the vestigial wing. This result has been reported by ROBERTS (1918), NADLER (1926), STANLEY (1928) and HARNLY (1930).

As to facet number, SEYSTER (1919), ZELENY (1917), KRAFKA (1920), HERSH (1924), LUCE (1926), HERSH (1930), E. DRIVER (1931) and O. DRIVER (1931) have shown that in bar, ultra bar, and full eye the facet number varies inversely with temperature, while in infra and double infra bar it varies directly with temperature.

As to mutations affecting the size of *Drosophila,* 2 mutant genes have been reported. BRIDGES and MORGAN (1923) found a dwarf mutation of *Drosophila melanogaster* in the cross between arc and speck, and determined the locus of the gene. BRIDGES and GABRITSCHEVSKY (1928) reported a giant mutation which shows a striking difference in size from wild type. Its locus was also determined. The giant mutation was studied under different conditions such as low temperature and exposure to X-rays, but without any significant effects. It was found, however, that the phenotypic expression decreased in proportion to the amount of food available, as expressed by number of offspring under standard food conditions. Combined with the fact that there is no size distinction in the larval stage between giant and wild type flies until they are fully grown, and also that the duration of the larval stage is longer in giant than in wild type, this decrease in phenotypie expression of the giant mutation may be interpreted as an indication of semistarvation.

The history of the study of the inheritance of size starts with GALTON's (1889) work on man, which led to his "law of ancestral inheritance."

This law of ancestral inheritance naturally leads to the conclusion that diverse types can be produced by selection. PEARSON (1895) and PEARSON and LEE (1903) restudied the inheritance of human stature by elaborate statistical methods and found that the coefficient of correlation between parent and offspring in stature, span, and forearm length, was, in their material, on the average, about 0.5. Similar values of correlation coefficients between parent and offspring were obtained by PEARSON and his collaborators in human eye-color and in coat color of horses, basset hounds, and greyhounds.

WARREN (1902) reported quite high correlation coefficients $(+.47 \text{ and } .44)$ between parent and offspring in the parthenogenetic forms, *Daphnia magna* and the aphis *Hyalopterus trirhodus,* respectively.

Since the rediscovery of the MENDELIAN theory of heredity, the "law of ancestral inheritance" has been brought under critical reexamination from the genetic point of view. This was first done by JOHANNSEN (1926) in his extensive work on weight and dimensions of beans. JOHANNSEN showed that a population, though its distribution may appear homogeneous, is not usually genotypically pure. Therefore the diverse types which appear after selective breeding from a population represent simply the isolation of different pure strains which existed from the beginning. When a population of beans was made genotypically pure selection was no longer effective.

This general result was confirmed by JENNINGS (1908) working on *Paramecium*. In *Paramecium caudatum* and *Paramecium aurelia* he found many diverse biotypes as to size which are transmitted through vegetative reproduction to the progeny. Selection of diverse size in a single clone (pure line) did not produce any diverse biotypes.

However, in later work by the same author (1916) on *DiHlugia corona,* by ROOT (1918) on *Centropyxis aculeata*, and by HEGNER (1919) on *Arcella dentata*, it was found that even in a single clone selection of size was effective in producing diverse biotypes, though their permanency is still doubtful (JENNINGS, 1929).

But in inheritance of size in higher organisms, whore a "pure line" production (in Jom~Ns~'s sense) is impossible, the situation is complicated and little is known in this field. The work of MAcDowELL (1914) on rabbits, PHILLIPS (1912) on ducks, CASTLE (1929, 1931) on rabbits, and GREEN (1931) on mice, may be cited. By crossbreeding 2 races or species where the difference in size is conspicuous these authors found that:

1. These interracial differences of size arc "inherited in blending form when crossed".

2. Linkage studies with known genes so far have not been successful.

The problem with which the present investigation is concerned is that of the correlation between parent and offspring in *Drosophila,* reared under carefully controlled environmental conditions. Starting with a homogeneous strain of flies, whose genetic behavior, variability, etc. are thoroughly known from long breeding experience in the laboratory, what degree of correlation between parent and offspring will be found relative to somatic characters, when the flies are reared under uniform, standard, and constant environmental conditions ? Will such correlations be changed, and if so in what way and to what degree, if the environmental conditions are altered ?

Material and Methods.

1. The material for this study was the normal wild type fruit fly, *Drosophila melanogaster.* The flies used came from Line 107 which originated from a single pair brother and sister mating in 1920, and has been inbred since in the laboratory of the Department of Biology of the School of Hygiene and Public Health of the Johns Hopkins University (PEARL and PARKER $[1922]$). The flies of this Line 107 have shown great constancy in their morphological and physiological characteristics. The population from which the matings were made for the present experiments consisted of nearly 2,000 flies which were collected by shaking from 40 pint bottles. These 40 pint bottles had been prepared previously in the following manner: 10 pairs of flies from the stock in each bottle were kept laying eggs for 4 days, at a temperature of 250 C. On the 8th day the imagoes started emerging. On the tenth day, by three successive shakings within intervals of 2 hours, nearly 2,000 flies were collected.

From these flies the matings were made according to the following scheme, in order to cover roughly the whole range of size in both males and females.

a) 15, large male \times large female

b) 15, large male \times small female

c) 15, medium male \times medium female

d) 15, small male \times large female

e) 15, small male \times small female

Twenty single pair matings were actually made in each set in order to make certain of having the desired number of matings. Each fly was less than 3 hours old when mated. Selection of the individuals for mating was carried out by naked eye examination only. There were difficulties in this, due mostly to the normally very small variation of *Drosophila in* size, as shown in Table 3, and also to the rapid judgment required for the selectibn. However, it was possible to cover fairly all parts of the range. It should be clearly understood that this was all that was desired in the plan of the investigation. The object of the work was not primatily to study the effects of selective breeding, but rather to examine the parent-offspring correlation in homogeneous material.

2. One-ounce bottles were prepared with 8 c.c. of synthetic food $(PERR, ALLEN and PENNIMAN [1926])$ on which yeast was grown. They were prepared a day and a half before being used in the experiments. Immediately after the mating was made the bottles were divided into three groups and put into three constant temperature compartments of a large Freas incubator, the temperatures being 28° C, 23° C, and 18° C.

Table 1. Temperature - Centirade.

Intended constant tempera- ture	Observed mean	Maximum observed	Minimum observed	
280	$28.03^o + .02$	28.6°	27.5°	
230	$22.93^{\circ} + .02^{\circ}$	23.5°	22.0°	
180	$17.96^{\circ} + .02$	18.80	16.80	

The temperatures were checked from the recording thermometers three times .a day during the whole experiment. That they were fairly constant is shown in Table 1.

Bottles were changed every 8, 12, and 24 hours, for temperatures of 28° C., 23° C., and 180 C., respectively. New bott-

les were prepared in exactly the same way as the first ones. This plan of changing of bottles was based on previous experience, and was intended to ensure that there should not be in any bottle too great a density of population which would affect the size of the flies, and also to make possible the collection of the progeny flies at short intervals.

Under such a scheme each female of the 280 C., 230 C., and 180 C. groups was kept laying eggs for 6, 8, and 9 days, respectively. At the end of these periods the parents were removed from the last of the series of bottles and preserved in 70% alcohol for measurement.

Imagoes were collected after completing their emergence at the 9th, 13th and 22nd day, with a duration of emergence of roughly 1, 2, and 3 days respectively for 28° C., 230 C., and 180 C. groups.

They were then preserved in 70 % alcohol for measurement.

The numbers of the progeny flies produced in each bottle varied as shown in Table 2.

The production of progeny flies per bottle, in the stated times, was highest at 23° C. and lowest at 18° C. At 28° C. the production was

Fig. 1. Measurements of the wing (I), Front leg (IT) and middle leg (III). *AB* length of wing. CD breadth of wing. E and F length of femur.

intermediate between that at the other two temperatures. The differences in mean densities of population under which the progeny flies

Table 2. Number of propeny per bottle.

\mathbf{T} emperature	Mean number of offspring
28	$20.44 + .29$
23	$25.42 + .36$
18	$16.89 + .33$

developed were not, however, great enough sensibly to affect *per se* the size of the flies.

3. Four characters were measured. These were length and breadth of right wing and femur lengths of front and middle leg of the right side as shown in Figure 1.

The right wing and two right legs were detached from the body and were arranged in the position shown in Fig. 1. This was done with a dissecting needle under the binocular microscope. After putting on a few drops of 70% alcohol they were covered with a cover-glass and brought under the microscope for measuring.

Measurements were carried out with a Spencer microscope, with a $10 \times$ ocular and 4 mm. objective. They were read with the help of an eve piece micrometer, one unit of which corresponds to 1.055μ . All figures in the tables will be shown in ocular micrometer units unless they are particularly stated to be transformed into actual lengths in μ .

4. In both the 280 C. and 230 C. series of the progeny samples were 50 of each sex, while in the 180 C. series the samples were 40. The samples consisted of the first 50 or 40 progeny to emerge in each case.

Results of Experiments.

A. Variation.

1. Parents.

Biometric constants of the general population of Line 107 from which the parent pairs were taken are shown in Table 3. The frequency distributions for the males are presented in Fig. 2. Also the biometric constants for the parents in each temperature series are given in Table 4.

Table 3.

Biometric constants of the general population of Line 107, Drosophila melanogaster (in μ). $N = 50$.

Comparing the figures in Tables 3 and 4 it is seen that the parents in each temperature series are fair samples of the original general population of Line 107. So far as the means are concerned, none of the differences between general population and parent means is significant as compared with its probable error, A larger variability in the parental samples was to be expected as a result of the deliberate selection of

Fig. 2. Histograms showing the variation in 4 characters in the general population. Males.

extreme variants in excess of their proportionate frequency in the general population. This expected greater variation was actually observed

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	Characters	Mean	Standard deviation	Coefficient of variation
28° C.	$N\!=\!28$			
8	Wing length \ldots \ldots	$1603.00 + 3.00$	$24.50 + 2.12$	$1.47 + .13$
	Wing breadth \mathbf{r} , and \mathbf{r} , and \mathbf{r}	$892.48 + 2.17$	$16.99 + 1.53$	$1.90 + .17$
	Femur length of front leg.	$540.42 + 1.23$	$9.61 + .87$	$1.78 + .16$
	Femur length of middle leg	$625.38 + 1.08$	$8.51 + .77$	$1.36 + .12$
¥.	Wing length \ldots	$1818.49 + 6.40$	$50.22 + 4.53$	$2.76 + .16$
	Wing breadth \ldots .	$978.00 + 2.81$	$22.08 + 1.99$	$2.26 + .20$
	Femur length of front leg.	$560.95 + 1.97$	$15.42\!\pm\!1.39$	$2.75 + .25$
	Femur length of middle leg	$-656.27 + 2.41$	$18.91 + 1.70$	$2.88 + .26$
23 ⁰ C.	$N = 25$			
යි	Wing length \ldots	1598.29 ± 3.29	$24.36 + 2.32$	$1.52 + .15$
	Wing breadth \ldots	$891.43 + 2.41$	$17.88 + 1.71$	$2.01 + .19$
	Femur length of front leg.	541.46 ± 1.63	$12.09 + 1.15$	$2.23 + .21$
	Femur length of middle leg	$627.53 + 1.61$	$11.95 + 1.14$	$1.90 + .18$
ç	Wing length \ldots \ldots	$1814.13 + 5.30$	$39.26 + 3.74$	$2.16 + .21$
	Wing breadth \ldots	$976.58 + 3.12$	$23.10\!\pm\!2.20$	$2.36 + .23$
	Femur length of front leg.	$560.23 + 1.87$	$13.88 + 1.32$	$2.48 + .24$
	Femur length of middle leg	$656.65 + 2.31$	$17.11 + 1.63$	$2.61 + .25$
18 ^o C.	$N=24$			
3	Wing length \ldots	$1607.33 + 2.91$	$21.17 + 2.06$	$1.32 + .13$
	Wing breadth \mathbf{r} . The set of t	$895.75 + 2.13$	$15.50 + 1.51$	$1.73 + 0.17$
	Femur length of front leg.	$543.69 + 1.15$	$8.33 + .81$	$1.53 + .15$
	Femur length of middle leg	$625.88 + 1.23$	$8.96 + .87$	$1.43 + .14$
¥	Wing length \ldots \ldots	$1810.83 + 5.74$	$41.72 + 4.06$	$2.30 + .22$
	Wing breadth \ldots	$974.42 + 2.38$	$17.31 + 1.69$	$1.78 + .17$
	Femur length of front leg.	$561.17 + 1.77$	$12.83 + 1.25$	$2.28 + .22$
	Femur length of middle leg	$658.40 + 2.06$	$14.97 + 1.46$	$2.27 + .22$

Table 4. Biometric constants of parents (in μ).

in the case of females but it was not distinct in the ease of males, a result presumably due to the difficulties previously mentioned connected with picking out the flies for mating.

Comparison of the 3 parentalgroups for the different temperatures shows no significant differences, one from another, in the means and variations.

In the general population (Line 107) Table 3 shows that: a) the coefficients of variation of the 4 measurements are of the same order of magnitude, b) females are somewhat more variable both absolutely and relatively than males in every one of the measurements, though most of the sex differences are not statistically significant, taken separately.

2. Progeny.

Variation constants for the progeny flies are shown in Table 5. The frequency distributions, showing the variation in each of the 4 characters, for male progeny flies reared in each of the three different temperatures, are shown in the form of frequency polygons in Figs. $3-6$ inclusive. The females show essentially the same relations but considerations of space forbid giving the diagrams for them.

	Characters	Mean	Standard deviation	Coefficient of variation
28 ⁰ C.				
ර	Wing length \ldots \ldots	$1488.98 + .45$	$24.89\pm.32$	$1.67\pm.02$
	Wing breadth \ldots	$821.36 + .25$	$13.78 + .18$	$1.68\!\pm\!.02$
	Femur length of front leg.	$533.84 + 13$	$7.47 + .10$	$1.40 + .02$
	Femur length of middle leg	$611.02\pm.17$	$9.61 + .12$	$1.57 + .02$
Ω	Wing length \ldots \ldots	$1714.98 + .58$	$32.25 + .41$	$1.88{\pm}.02$
	Wing breadth \ldots	$919.24 + .30$	$16.73 + .21$	$1.82 + .02$
	Femur length of front leg.	$557.57 + .20$	$10.99\!\pm\! .14$	$1.97 + .03$
	Femur length of middle leg	647.01 \pm .19	$10.62 + .14$	$1.64 + .02$
23 ^o C.				
යි	$\text{Wing length} \quad \ldots \quad \ldots \quad \ldots$	$1652.73 + .46$	$24.36 {\pm} .33$	$1.47 + .02$
	Wing breadth \ldots	$905.16 + .27$	$14.31 + .19$	$1.58 + .02$
	Femur length of front leg.	$547.82 + .16$	$8.27 + .11$	$1.51\!\pm\!.02$
	Femur length of middle leg	$632.70 + .16$	$8.58\!\pm\!.12$	$1.36\!\pm\! .02$
¥	Wing length \ldots	$1885.21 + .46$	$24.25\!\pm\! .33$	$1.29 + .02$
	Wing breadth \ldots .	$997.23 + .30$	$15.95\pm.22$	$1.60 + .02$
	Femur length of front leg.	$580.37 + .20$	$10.32\!\pm\! .14$	$1.78\pm.02$
	Femur length of middle leg	$676.28 + .26$	$13.41 + .18$	$1.99 + .03$
18 ^o C.				
්	$\text{Wing length} \quad \ldots \quad \ldots$	$1811.92 + .49$	$22.35\!\pm\!.20$	$1.23 + .02$
	Wing breadth \ldots .	$975.01 + .33$	$14.94\pm.25$	$1.53 + .02$
	Femur length of front leg.	$556.66 + .23$	$10.35\!\pm\! .32$	$1.86 + .03$
	Femur length of middle leg	$649.74 + .24$	$10.83\pm.27$	$1.67 + .03$
¥	Wing length \ldots	$2010.02 + .54$	$24.65\!\pm\!.20$	$1.23 + .02$
	Wing breadth \ldots	$1051.93 + .26$	$11.83\!\pm\! .18$	$1.13+0.2$
	Femur length of front leg.	$591.02 + .23$	$10.76{\pm}.30$	$1.82 + .03$
	Femur length of middle leg	$698.73 + .29$	$13.18 + .31$	$1.89 + .03$

Table 5. Biometric constants of progeny (in μ).

Fig. 3. Frequency polygons showing the effect upon wing length of rearing *Drosophila* from groups of parents of substantially the same mean wing lengths (cf. Table 4) in 3 different temperatures, all other conditions being as nearly as possible the same. denotes male flies reared at 23 ~ C. -- -- -- denotes male flies reared at 28 o C. - denotes male flies reared at 18°C. Owing to an inadvertant error in draughting the abscissal figures are each 100 microns too small.

Fig. 5. Same as Fig. 3, but for femur length of front leg.

Figs. 3--6 inclusive briug out in the clearest manner the marked effect of temperature upon bodily size in *Drosophila.* **In these experiments** parents sensibly identical on the average in all of the 3 groups in respect of bodily size, and themselves all grown under the same environ. mental conditions including temperature, produced offspring under 3 different temperature conditions $(28^{\circ}, 23^{\circ}, \text{ and } 18^{\circ} \text{ C}.)$. These offspring

developed through egg, larval, and pupal stages into imagoes under their respective temperatures. The 3 sets of imagoes so differed from each other in respect of wing dimensions that their frequency distributions (Figs. 3 and 4) scarcely overlap at all. The differentiation in respect of femur lengths is not quite so great as for wing dimensions, but still it is so large as to leave no doubt about its existence.

Generally speaking, variation in the characters of *Drosophila* here dealt with is of a low order of magnitude. It will be worth while to compare these figures with some characters of man, as the parentoffspring correlations concerning size which are to be discussed have practically their only comparable counterpart in human characters such as stature and span. For this purpose human measurements, that is, male stature in man (PEARSON [1902]) and maximum length of right femur in English males (PEARSON and BELL [1919]), are compared with the

wing length and femur length of the middle leg of *Drosophila* males (280 C.). The coefficients of variation are shown in Table 6.

The coefficients of variation in these 2 human characters are roughly 3 times as large as those for the *Drosophila* characters. This

Fig. 7. Variation of *Drosophila* characters compared with those of man.

comparison is more effectively visualized when we plot the original frequency distributions on relative scales (Fig. 7), as has been proposed $b\bar{v}$ PEARL (1927). As abscissa is plotted the measurements in percentage of the mean of each character, and as ordinate is plotted the frequency per 1% of the mean. Thus all the frequency polygons have the same area. The diagram shows clearly how much more these characters of man vary than those of *Drosophila*. It should be added that these human characters are among the least variable of human measurements, as can be seen from the summarized table in PEARL (1930) .

The relative size of the sexes is shown by the ratio of male measurements to female in Table 7.

1. In all 3 temperature series the females have larger dimensions than the males. This has been recognized by many workers, such as LUTZ (1913), ALPATOV (1930), EIGENBRODT (1930), for wing size, and LUTZ (1913) and ALPATOV (1930) for femur length and also for other characters.

2. The degree of sexual dimorphism is greater in wing measurements than in femur measurements.

Characters	28 °C	23° C	18°C			
Wing length \ldots , \ldots Wing breadth \ldots , Femur length of front leg Femur length of middle leg	$86.73\% + .04$ $89.37\% + .04$ $95.78\% + .04$ $94.47\% + .04$	$87.68\% + .03$ $90.79\% + .04$ $94.42\% + .04$ $93.60\% + .04$	$90.15\% + .04$ $92.70\% + .04$ $94.22\% + .06$ $93.02\% \pm .06$			

Table 7. Ratio of male measurements to female.

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3. The degree of sexual dimorphism in wing dimensions is greater at higher temperatures than at lower. This has been noted by several workers for various characters, as by ALPATOV (1930) for wing length and breadth, and by EIGENBRODT (1930) for wing length and breadth, thorax length and head breadth. But in the present data this generalization does not apply to femur length in the 1st and 2nd legs. In the

Fig. 8. Relation between temperature and wing length, wing breadth, and femur lengths of front and middle legs of *Drosophila*.

present case it appears that sexual dimorphism in femur length is not much affected by temperature.

4. The small probable errors shown in Table 7 are due to the fact that they have been calculated on the basis of total numbers of progeny. But a check made by taking each bottle separately leads to no different conclusions.

5. A comparison of the variability of each measurement for the two sexes as expressed by the coefficient of variation (Table 5) shows the **same** tendencies as have been seen in the general population. In general,

Sex and temperature difference classes	Difference wing length	Ratio to 23° C	
Male $\left\{\text{Difference } 28-23^{\circ} \text{ C. } \ldots \text{ . } \ldots \right\}$	$163.75 + .64$ $159.19 + .67$ $170.23 + .73$ $124.81 + .71$	9.91 9.63 9.03 6.62	

Table 8. Effect of

females vary slightly more than males. But this is distinctly clear only at higher temperatures. In the 180 C. series no distinct difference is shown.

How does temperature affect the means ? In Table 8 are shown the differences of means among different temperature series and the ratios of these differences to the 230 C. measurements. These are also plotted in Fig. 8.

As is generally recognized and confirmed by ALPATOV (193) , EIGEN- $BRODT$ (1930) and HERSH and WARD (1932), the size dimensions in *Drosophila* decrease with increasing temperature.

EIGENBRODT (1930) found that wing length and breadth are linear functions of temperature, whereas HERSH and WARD (1932) suggested an exponential relation. It is the opinion of the writer that it is not clear in the present data whether this change in wing size is a linear or an exponential function. So far as the present range of temperature is concerned, the absolute changes as well as their ratio to the 23° C. measurements show even larger differences at 28° C.--23° C. than at 18° C.--23° C. This difference in slope is more marked in femur length. Thus if we apply the exponential formula, it will take the form $k - e^{rx}$ rather than e^{rx} as suggested by HERSH and WARD.

There are too few observed points for one to draw any certain conclusion as to the functional form of the dependence of size on temperature.

In connection with this point the data should be examined from the viewpoint of density of population in each bottle. If the number of flies in each bottle in these experiments had any effect on the size, it would be expected that the flies would be much smaller in size in the 230 C. groups, where the density was highest. But no such result was found.

It is clear from Tables 5 to 7 inclusive that the effect of temperature is more striking for wing length and breadth than for femur length. This fact, taken in connection with the stability of sexual dimorphism in femur length, leads to the conclusion that femur size is much more stable in relation to changes of temperature than wing size.

The effect of temperature on variability is summarized in Table 9.

In the wing measurements there is a general tendency towards, a decrease in variability as temperature decreases, but this is not the case

temperature on means.

Difference wing breadth	Ratio to 23° C %	Difference femur length of front leg	Ratio to 23° C \mathbf{O}/\mathbf{E}	Difference femur length of middle leg	Ratio to 23° C $\mathbf{O}/$
$83.80 + .37$	9.26	$13.93 + .21$	$2.55\,$	$21.68 + .23$	3.43
$69.85 + .43$	7.72	$8.84 + .28$	1.61	$17.04 + .29$	2.69
$77.99 + .42$	7.82	$22.80 + .28$	3.93	$29.29 + .31$	4.33
$54.70 + .40$	5.48	$10.65 + .30$	1.84	$22.45 + .39$	3.32

in femur length, where the observations are so irregular that no trend is apparent.

Table 9. Effect of temperature on variability.

Difference in coefficient of variation between	Wing length	Wing breadth	Femur length of front leg	Femur length of middle leg
$28 - 23$ ⁰ C. Male $23-18^{\circ}$ C. $28 - 23^{\circ}$ C. Female $23 - 18^{\circ}$ C.	$.20\% + .03$ $.24\% + .03$ $.58\% + .03$ $.06\% + .03$	$.08\% + .03$ $0.05\% + 0.03$ $.22\% + .03$ $.47\% + .03$	$-.11\% + .03$ $-.35\%+.04$ $.20\% + .04$ $-.05\%+.04$	$.21\% \pm .03$ $-.31\%+.04$ $-.35\%+.04$ $.10\% + .04$

Data on the sex ratios of the progeny flies are shown in Table 10. The sex ratio of total flies was $48.86 \zeta : 51.15 \zeta$. This is very near to the figures published by WARREN (1918), and BRIDGES and MORGAN

Series		Male	Female	Total
28° C.	Numbers Ratio	3,371 49.17	3.485 50,33	6.856 100.0
23° C.	Numbers Ratio	3.527 48,33	3,770	7.297
18 ⁰ C.	Numbers	1,842	51.67 1,893	100,0 3.735
Total	Ratio Numbers Ratio	49.32 8,740 48.86	50.68 9,148 51,14	100,0 17,888 $_{100,0}$

Table 10. Sex rations at different temperatures.

(1923), 95 δ : 100 φ , that is 48.78 δ : 51.22 φ . The 3 temperature series show, on their face, some significant differences in sex-ratios, as compared with the probable errors which are very small.

B. Correlation between parents (assortative mating).

In Table 11 there are shown the coefficients of correlation (assortative mating) between the several pairs of parents.

Some of the figures, particularly those of the $23⁰$ C. and 18⁰ C. series, show fairly high coefficients of correlation, though their significance is doubtful as compared with the probable errors. In general, however,

Table 11. Coefficients of correlation between pairs of parents (assortative mating).

the values are highly irregular, as would be expected, since any observed "assortative mating" can have no biological cause, but is simply the result of the manner in which the selected matings were artificially made. But careful examination of the detailed correlation tables shows that the higher values of the coefficients are due simply to a few extreme cases. For example in wing length at 18° C., r = .312, but this is reduced to $r = .018$ simply by dropping 2 extreme cases where the male parents belong to the 1490-1499 group and the females belong to the 1620--1629 group. The same type of situation is seen in nearly every table. The effects of these artificial "assortative mating" correlations, on the correlations between parent and offspring, will be considered later.

C. Parent-offspring correlations.

The coefficients of correlation between parents and progeny are exhibited in Table 12.

There are 2 ways in which probable errors in Table 12 may be computed, depending on whether the parental or progeny N is used. In PEARSON's (1903) study of inheritance of human stature and also in WARREN's (1902) study of inheritance in parthenogenetic *Daphnia* the total number of offspring was used as N for the calculation of the probable errors, but the difference between the number of parents and of

progeny was small enough in those cases so that this was not a serious disturbing factor. In the present material the situation is different, owing to the following facts:

1. Small number of parent individuals.

2. Great difference between numbers of parents and numbers of progeny.

3. Small values of the coefficients of correlation.

Thus if we take the progeny Nweshall have probable errors of theorder of $.018$ to $.022$, while if we take the parental N we have from .126 to .135.

At present, in order to err, if I do err, on the safe side, I am inclined to take the number of parents. It is to be understood, however, that this is essentially a matter of psy-

Fig. 9. Frequency polygons showing the distributions of the values of the coefficients of parentoffspring correlation in Table 12. $- - -$ denotes progeny flies produced and reared at 280 C. denotes progeny flies produced and reared at 23° C. \cdots denotes progeny flies produced and reared at 18' C.

chology. There is no established mathematical proof that the probable errors calculated on the parental numbers are any better, if indeed as good, indices as would be the probable errors calculated on the progeny numbers, of the unknown variance of bivariate samples of the order of magnitude here dealt with. No one has yet investigated the error distributions of bivariate samples where one variate is many times more numerous than the other.

The actual distributions of the correlation coefficients of Table 12 are shown graphically in Fig. 9, for the 3 temperature series separately.

From the standpoint adopted none of the coefficients of correlation are certainly significant in comparison with the stated probable errors. A common sense view of the data clearly indicates, however, that there is an orderly change in the value of the parent-offspring correlation with a change in temperature. It is repugnant to the intelligence to suppose that this observed orderliness in the coefficients is a purely chance result.

First of all, comparison of the figures at different temperatures shows that their magnitude varies with the change of temperature. The average values are shown graphically in Fig. 10. We see that in general the correlation becomes larger as the temperature decreases. The averages run from .020 at 28° C. through .051 at 23° C. to .245 at 18° C. The difference between the 28° C. and 23° C. series is not

Fig. 10. Mean values of the parent-offspring corre- terest in connection with the lation coefficients in Table 12, showing the effect

conclusive when compared for each character but the differences between the 280 C. and 180 C. series and between the regular and marked.

There is another interesting observation in the comparison of the correlations for wing measurements and femur measurements. In **all** the temperature series the coefficients for femur length are generally higher than those for wing length and *7emperature* **breadth.** This point is of ineffect of temperature on the mean measurements of wing

and femur. It has already been pointed out, that these wing dimensions react to the temperature differences more strongly than do the femur dimensions. Thus the percentage change in both wing dimensions was on the average more than 3 times that of the femur lengths.

Let us consider more carefully what has happened under different temperatures. It has been seen first that all dimensions measured increase significantly as temperature decreases, from 28° C. through $23⁰$ C. to $18⁰$ C., and at the same time the coefficients of correlation between parents and offspring become larger; second, that wing dimensions and femur dimensions respond to the temperature change to a significantly different degree; that is, wing dimensions were changed 3 times more than femur dimensions. Such coincidence of phenomena leads to the idea that the expression of parent-offspring correlation may be connected with differential growth forces. Possibly where growth proceeds more slowly and is more complete, the parent-offspring correlation may be more intense.

The average coefficient of correlation in the 18⁰ C. series was .245, which is approximately half the value of the parental correlations summarized by PEARSON (1903). (See Table 13.) These figures are what PEARSON thought to be the most reliable, and led him to the general

conclusion that "for most practical purposes we may assume parental heredity for all species (here cited) and all characters to be approximately represented by a correlation of .5." He further gave the frequency distribution for every coefficient of correlation he was aware of, which covered plants, insects and animals, and showed that this frequency distribution had a mean of .453 \pm .007, the standard deviation being .071.

But this is essentially only an empirical conclusion based on a rather small number of cases. Furthermore we must remember that these values were obtained under uncontrolled conditions. So far as I am aware there are no more available data concerning the inheritance of dimensions in animals. Such cases, however, as JOHANNSEN's bean experiment, or HANSEN'S experiments on the number of tentacles of *Hydra grisea,* show much smaller values of parental correlations, $.35 \pm .01$, and $.230$ $± .011$ respectively (figures cited from PEARSON, 1910). And at this point let us remember that the parental correlation of dimensions in *Drosophila* is small, ranging from nearly zero to .25, depending on the temperature conditions.

Let us now see what will be the correlation between parent and offspring if we eliminate the effect of the correlation between parents (assortative mating), by using the method of partial correlation.

First the partial correlations in which one of the parents is held constant were calculated, and are shown in Table 14.

The results show that the correlation coefficients have been considerably modified, particularly in the 180 C. series. Thus they are

Table 14. Coefficients of partial correlation between one parent and progeny, with other parent held constant.

still less certainly significant in comparison with their probable errors calculated in a manner to minimize any possible significance which they may have. But even so the general situation still remains the same as that shown in Table 12.

The effect of correlation between parents (assortative mating) may also be eliminated by directly removing a few cases from the parent tables so as to make the correlation between parents nearly equal to zero.. This was an easy process, owing to the fact that the high correlations between pairs of parents are due to only a few extreme cases, as has already been pointed out earlier, so that by eliminating such cases

Table 15.

Coefficient of correlation between pairs of parents, adjusted to zero by removing marginal pairs.

Tem- pera- ture ٠c	No. оf pairs	Wing length	No. οf pairs	Wing breadth	No. of pairs	Femur length of front leg	No. of pairs	Femur length of middle leg
28	28	$.015 + .127$	26	$.031 + .132$	26	$-001 + 132$	22	$.007 + .144$
23	21	$-.033 + .147$	22	$.067 + .143$	23	$.014 + .141$	23	$.055 + .140$
18	22	$.018 + .144$	24	$.021 + .138$	19	$.028 + .155$	20	$.048 + .150$

the correlation between pairs of parents will be reduced nearly to zero. Thus there are obtained the correlations between parents shown in Table 15. The coefficients of correlation between parent and offspring calculated after the inter-parent correlations have been reduced to zero in this way are shown in Table 16.

It is seen that while the resulting parent-offspring correlations in Table 16 have been slightly changed, they still show the same trend relative to temperature as did the original figures.

From these observations the conclusion is reached that the parental correlation in *Drosophila* of the wing and femur dimensions ranges from nearly zero to slightly more than .25 under the temperature conditions thus far studied, and their values change with the temperature; that is, with decrease of temperature, the correlations increase.

All these conclusions, however, are tentative owing to the higb probable errors that the writer preferred to use in the tables. But it must be remembered that these probable errors present the most unfavorable case possible, it is the writer's opinion that actually the parental correlations thus presented are far more reliable than would appear from the tables.

Discussion.

In this study an attempt has been made to find how the intensity of parent-offspring correlation, which has hitherto been studied chiefly in man and higher mammals, appears in normal *Drosophila,* where, so far as I am aware, the problem of size inheritance has never been attacked by biometric methods.

An attempt was also made to find whether or not the intensity of parent-offspring correlation will be different if the flies are raised under different temperature conditions.

While the results cannot be regarded as finally or completely conelusive, they do suggest several interesting points in regard to **these** questions.

First it has been seen that the parental correlation coefficients, as well as the regression coefficients, are far smaller than those found in man and other mammals by PEARSON. We have obtained correlation coefficients ranging from substantially zero to .25, as against .5 which PEARSON considers the representative value for man and other mammals. The conclusion as to this point is that the parent-offspring correlation relative to size in normal *Drosophila* is normally smaller than in man. But it must be noted that the *Drosophila* results here set forth come from a highly homogeneous strain, long inbred, while those for man come from a general population, genetically highly heterogeneous.

The results as to the intensity of parent-offspring correlation under different temperature conditions are of interest. There is shown a distinctly higher parental correlation $(+.245)$ at 18⁰ C., as compared with $+$.020 and $+$.051 at 28⁰ C. and 23⁰ C., respectively. Moreover the correlations run in orderly fashion suggesting that the intensity of parental correlation increases with decreasing temperature in the case of *Drosophila.*

Effects of temperature on phenotypic expression are of common occurrence and have been studied quite extensively. Even in *Drosa.* phila such characters as wing length of vestigial, facet number of bar mutation, or bodily dimensions in normal *Drosophila,* as has already been stated in the introduction and first part of the present study, are known to be modified by temperature. But so far as is known to the writer such effects as the modification of the intensity of parent-offspring correlation, with simultaneous modification of the bodily dimensions, have not hitherto been observed.

Let us analyse the case more carefully and thoroughly. 3 groups of parents, all arising from the same homogeneous strain (Line 107) which originated from a single brother \times sister pair of parents and has been inbred for more than 10 years, were put under three different temperatures, 280 C., 230 C., and 180 C. The means of the characters studied were substantially identical in each of the 3 groups of parents.

All progeny have developed on carefully prepared food and under fairly constant temperature conditions. As a result of the controlled differences in temperature, the progeny showed 2 remarkable differences in their development; that is, the rate of development and the final size they attained. Thus the progeny of the 28° C., 23° C., and 18° C. series completed their development (emergence) roughly on the 9th, 13th, and 22nd day respectively. At the same time lower temperature has resulted in distinctly larger size. In other words progeny flies under a lower temperature have grown much better (in the sense that they grew larger) than under higher temperature. This suggests that under such conditions as low temperature, where growth occurs slowly and more completely, it may be possible that parent-offspring correlation will appear in higher intensity and in a more exact way than at higher temperatures where growth proceeds more rapidly and with less integrated completeness.

Summary.

In the first part of this paper the variation of wing length and breadth, and femur length of front and middle legs of normal *Drosophila melano. gaster* under different temperature conditions was described.

1. Sexual dimorphism in wing dimensions is far more striking than in femur length.

2. The effect of temperature on sexual dimorphism is also great in wing dimensions, and the higher the temperature the more striking the divergence. But in femur dimensions this is not the ease.

3. Temperature affects the means inversely. The higher the temperature, the smaller the dimension. But again the degree of change is nearly 3 times greater in wing dimensions than in femur length. There is no clear evidence that this change follows an exponential function of the form suggested by HERSH and WARD.

4. Variability of wing dimensions shows a tendency to increase as temperature rises, but the variability of femur length does not show any consistent change.

5. These facts lead us to the view that the femur is more stable than the wing, with respect to temperature, though it shows as high a variability (coefficient of variation) as wing dimensions.

6. No important differences are found in the sex ratios at different temperatures.

In the latter part of this paper correlation coefficients between parents and progeny under 3 different temperature conditions, in respect of 4 measured characters, were studied.

1. At 28° C. and 23° C. the correlation was very small, having mean values of $+$.020 and $+$.051 respectively, while at 18⁰ C. it was distinctly larger, being $+$.245. It was found that the correlations run in orderly fashion, that is, they become larger as the temperature becomes lower.

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2. On account of the ultra-conservative method chosen for the computation of the probable errors, none of the correlation coefficients calculated is certainly significant taken separately. However, the correlation coefficients are considered to be more reliable than the tables would indicate. The orderliness of the phenomena observed is impressive.

3. No conclusive explanation can be given at present for the orderly change in the parent-offspring correlations with temperature changes.

4. The parent.offspring correlation coefficients here observed for $Drosophila$ are far smaller than those found by PEARSON for parental inheritance in man and other mammals.

Zusammenfassung.

Im ersten Teil dieser Arbeit wird die Variation der Flügellänge und -breite und Femurlänge der vorderen und mittleren Beine normaler *Drosophila melanogaster* unter verschiedenen Temperaturzuständen beschriebem

1. Der geschlechtliche Dimorphismus ist in den Flügeldimensionen viel auffallender als in den Femurdimensionen,

2. Ebenso ist die Wirkung der Temperatut auf den geschlechtlichen Dimorphismus der Flügeldimensionen groß, und je höher die Temperatur ist, desto auffallender ist die Divergenz. Bei den Femurdimensioncn ist dies nicht der Fall.

3. Die Temperatur hat eine umgekehrte Wirkung auf die Mittelwerte. Je höher die Temperatur, desto kleiner ist die Dimension. Aber auch hier ist der Veränderungsgrad in den Flügeldimensionen beinahe dreimal größer als in der Femurlänge. Es ist nicht völlig bewiesen, daß diese Veränderung einer Exponentialfunktion folgt.

4. Die Variabilität der Flügeldimensionen zeigt eine Tendenz zur Zunahme bei Temperaturerhöhung, in der Variabilität der Femurlänge zeigt sich dagegen keine gesetzmäßige Veränderung.

5. Diese Tatsachen fiihren uns zu der Anschauung, dab der Femur gegenüber Temperatureinflüssen größere Stabilität besitzt als der Flügel, obwohl seine Länge eine ebenso große Variabilität (Variationskoeffizient) zeigt als die Dimensionen der Flügel.

6. Auf das Geschlechtsverhältnis hatten die verschiedenen Temperaturen keinen bemerkenswerten EinfluB.

Im zweiten Teil der Arbeit wurden die Korrelationskoeffizienten zwischen Eltern und Nachkommenschaft unter 3 verschiedenen Temperaturbedingungen untersucht, wobei wieder die vier obengenannten Merkmale zugrunde gelegt wurden.

1. Bei 280 C und 230 C war die Korrelation sehr klein, mit Mittelwerten von $+.020$ bzw. $+.051$, während sie bei 18° C deutlich größer war, nämlich $+245$. Es wurde beobachtet, daß die Korrelationen in

geregelter Weise verlaufen, insoferne sie sich bei abnehmender Temperatur vergrößern.

2. Wegen der hier gewählten übermäßig konservativen Methode für die Berechnung der mittleren Fehler ist keiner der berechneten Korrelationskoeffizienten, fiir sich betrachtet, bedeutsam. Gleichwohl werden die Korrelationskoeffizienten für zuverlässiger erachtet als Tabellen. Die Regelmäßigkeit des beobachteten Phänomens ist eindrucksvoll.

3. Die regelmäßige Veränderung in den Korrelationen zwischen Eltern und Nachkommenschaft bei Temperaturveränderungen kann gegenwärtig nicht entscheidend erklärt werden.

4. Die in dieser Arbeit an *Drosophila* beobachteten Korrelationen zwisehen Eltern und Naehkommensehaft sind viel kleiner als diejenigen, die PEARSON für Elternvererbung beim Menschen und bei anderen Säugetieren beobachtet hat.

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