INFLUENCE OF PREIMAGINAL ENVIRONMENT ON FECUNDITY AND AGEING IN *DROSOPHILA MELANOGASTER* HYBRIDS—II. PREIMAGINAL TEMPERATURE

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INTRODUCTION

IN THE first paper in this series it was shown that the degree of larval crowding to which *Drosophila melanogaster* hybrids are submitted determines to a large extent the life-span of the imagos. The influence of preimaginal population density on other quantitative characters, i.e. size, duration of development and various traits related to fecundity, was described in the same paper; some apparently interesting relations between those traits and longevity were established (Lints and Lints, 1969). As a conclusion it was suggested that the observed life-spans supported, at least partially, the delayed maturity hypothesis proposed by Medvedev (1967).

It is well known that preimaginal temperature affects size and duration of development of *Drosophila* imagos in a different way from the preimaginal population density (Lints, 1965; Lints and Lints, 1969). It is also known that the temperature at which embryonic and postembryonic development of *Drosophila* take place affects the duration of subsequent life. This was first demonstrated by Alpatov and Pearl (1929), confirmed by Miller and Thomas (1958), Lints (1963, 1970) and more recently Burcombe and Hollingsworth (1970).

However nothing very clear is known about the possible influence of preimaginal temperature on fecundity and related traits, and nothing about relationships of the kind described in the first paper of this series, viz. between longevity and other quantitative traits (a review in Lints, 1971).

An experiment was therefore designed to look into those problems. The present paper gives the results of that investigation. A third paper in the same series will present some conclusions on the determinism of life-span arising from the comparison of the results of both experiments.

MATERIAL AND METHODS

In I_{174} generation of the *Gabarros* 4 inbred line of the *Gabarros* strain (Spain) and the I_{207} of the *Abeele* inbred line (Belgium) were reciprocally crossed in order to obtain the hybrids *Gabarros 4* ♀ × *Abeele* ♂ (GA) and *Abeele* ♀ × *Gabarros 4* ♂ (AG). Reports on the previous history of the *Abeele* and *Gabarros* strains from 1959 onwards have been

published elsewhere (Lints and Lints, 1965, 1968). From their emergence inbred virgin females and males were kept, at 25°C, in separate culture bottles, and well fed. The day before the beginning of the experiment the inbred female and male flies were brought together, according to the crossing scheme. They were at the same time transferred to a fresh medium and fed with a large amount of live yeast. After 24 hr the young flies, aged 3 to 10 days, were brought to lay, at 25°C, on an agar-agar gelled acetic medium, during a 4-hr period. The collected eggs were redistributed in standard culture tubes in lots of 30. The surface of the medium was of 5·5 cm² and the total weight of the food amounted to 10·0 ± 0·1 gr. The medium was the classical agar–agar sugar syrup cornmeal baker's yeast mixture. 20 replicates were made for each of the preimaginal environments chosen. Immediately after distribution of the eggs in the culture tubes, they were transferred to the incubation rooms, regulated to a tenth of a degree. Six different temperatures were used, viz. 31, 28, 25, 22, 19 and 16°C. At each temperature the number of emerged flies was recorded twice a day. Immediately after recording the hatched individuals were transferred at 25°C, where they stayed until death occurred.

Upon emergence all females were measured for thorax size, according to the method described by Robertson and Reeve (1952). Females of a modal size and a modal duration of development only were then retained for the subsequent measurements of life-span and egg-production. Tables 1 and 2 give for each of the temperatures used the modal

TABLE 1. IN DAYS, MODE, MEAN AND RANGE OF THE DURATION OF DEVELOPMENT FOR THE TOTALITY OF FEMALES HATCHED AT EACH OF THE PREIMAGINAL TEMPERATURES TESTED; IN ARBITRARY UNITS, WHERE 60 UNITS EQUAL 1 mm, MODE, MEAN AND RANGE OF THE SIZE FOR THE TOTALITY OF THE FEMALES HATCHED ON THE DAY OF MAXIMAL EMERGENCE; MEAN SIZE OF THE TOTALITY OF THE FEMALES HATCHED AT EACH OF THE PREIMAGINAL TEMPERATURES USED. Gabarros 4 ♀ × Abeele ♂ (GA) HYBRIDS

Tempera-ture	Duration of development ♀♀			Size ♀♀ Day of maximal emergence			Mean size ♀♀ (totality)
	Mode	Mean	Range	Mode	Mean	Range	
31°C	8	7·58 ± 0·04	7–11	60	58·51 ± 0·18	51–62	58·89 ± 0·10
28°C	8	7·82 ± 0·03	7–10	60	59·50 ± 0·15	54–63	59·82 ± 0·13
25°C	9	9·20 ± 0·04	8–12	62	61·81 ± 0·10	57–65	61·49 ± 0·09
22°C	12	12·97 ± 0·07	11–17	64	63·61 ± 0·09	61–66	62·30 ± 0·12
19°C	18	19·03 ± 0·10	17–25	65	64·53 ± 0·17	60–66	63·02 ± 0·14
16°C	27	27·05 ± 0·13	23–37	66	65·12 ± 0·15	62–67	64·38 ± 0·10

TABLE 2. AS IN TABLE 1 FOR Abeele ♀ × Gabarros 4 ♂ (AG) HYBRIDS

Tempera-ture	Duration of development ♀♀			Size ♀♀ Day of maximal emergence			Mean size ♀♀ (totality)
	Mode	Mean	Range	Mode	Mean	Range	
31°C	8	7·83 ± 0·07	7–11	59	56·80 ± 0·31	51–61	57·76 ± 0·27
28°C	8	7·65 ± 0·05	7–10	60	59·29 ± 0·24	54–64	60·20 ± 0·18
25°C	9	9·34 ± 0·05	8–13	61	61·46 ± 0·16	56–65	60·96 ± 0·16
22°C	12	12·51 ± 0·08	11–17	63	62·96 ± 0·12	60–66	62·33 ± 0·15
19°C	18	18·71 ± 0·13	17–25	65	63·91 ± 0·45	60–66	62·97 ± 0·19
16°C	25	27·02 ± 0·18	23–34	66	64·97 ± 0·20	62–67	63·62 ± 0·18

TABLE 3. FECUNDITY, RELATED TRAITS AND LONGEVITY OF THE Gabarros 4 ♀ × Abeele ♂ (GA) HYBRIDS RAISED AT DIFFERENT PREIMAGINAL TEMPERATURES

	Total fecundity	Mean daily egg-prod.	Maxim. daily egg-prod.	Day of max. egg-prod.	Final non laying period	Longevity
31°C	903 ± 214	17·84 ± 4·24	46·30 ± 10·26	8·30 ± 1·75	8·10 ± 2·64	34·75 ± 6·03
28°C	1371 ± 241	23·10 ± 4·30	64·40 ± 10·12	7·50 ± 1·37	7·30 ± 1·76	48·30 ± 5·53
25°C	1864 ± 120	39·20 ± 2·36	99·90 ± 1·94	5·70 ± 0·66	4·60 ± 1·41	53·90 ± 2·82
22°C	1637 ± 121	35·65 ± 1·88	92·80 ± 2·63	11·60 ± 1·35	1·00 ± 0·49	53·90 ± 2·94
19°C	1715 ± 252	29·03 ± 3·04	91·00 ± 10·47	5·50 ± 0·57	3·90 ± 1·38	59·40 ± 4·08
16°C	1573 ± 119	33·98 ± 2·11	85·60 ± 2·53	8·40 ± 0·43	3·80 ± 1·33	55·30 ± 3·59

TABLE 4. AS IN TABLE 3 FOR Abeele ♀ × Gabarros 4 ♂ (AG) HYBRIDS

	Total fecundity	Mean daily egg-prod.	Maxim. daily egg-prod.	Day of max. egg-prod.	Final non laying period	Longevity
31°C	792 ± 126	16·31 ± 2·61	58·80 ± 7·32	8·80 ±1·64	10·80 ± 3·09	43·70 ± 4·36
28°C	1299 ± 229	23·56 ± 3·32	68·60 ± 8·90	8·60 ± 2·26	10·80 ± 3·38	51·50 ± 4·35
25°C	2238 ± 49	35·50 ± 2·02	95·70 ± 2·08	7·80 ± 1·32	12·70 ± 3·59	58·35 ± 2·98
22°C	1980 ± 152	32·35 ± 1·58	95·50 ± 2·74	7·40 ± 0·90	12·40 ± 2·03	61·00 ± 3·65
19°C	1879 ± 151	33·94 ± 1·13	103·50 ± 2·17	7·00 ± 1·29	3·50 ± 1·15	57·65 ± 3·30
16°C	2072 ± 80	31·27 ± 1·21	87·50 ± 2·90	11·40 ± 2·06	7·60 ± 1·72	66·70 ± 1·81

duration of development and the modal and mean size of the flies hatched on the day of maximal emergence; Tables 1 and 2 also present mean and range for duration of development and size of all the females hatched at every temperature considered.

For both hybrids and every temperature considered, 10 females—120 in the whole—were placed, separately with a male, in a vial daily renewed. The daily egg-production of each of those females was recorded until death occurred. When a male died before his companion female he was replaced, in so far as it was possible, by an individual of the same age. A second series of 120 females, designed to measure life-span only, was handled exactly in the same way, except that the daily egg-production was not counted.

For both reciprocal hybrids and for every preimaginal treatment, the following means will be considered: size, duration of development, total fecundity, daily egg-production, maximum number of eggs laid in a 24-hr period, imaginal age at which the maximal egg-production occurs, number of days of the final period without egg-production, and longevity.

RESULTS

Though some of the present evidence appears to be without great significance, tables and figures are presented exactly in the same way as in the previous paper in the same series (Lints and Lints, 1969,) to facilitate comparison—in that paper we studied the effects of preimaginal population density. When referring to it, it will be called the "density" experiment, whilst the present study will be called the "temperature" experiment.

Tables 3 and 4 give, for both reciprocal hybrids, the means of different traits related to fecundity; these data are obtained from the measurements made daily on ten females of each genotype from emergence until death. Tables 3 and 4 also give the longevity at 25°C of the hybrids raised at different preimaginal temperatures, each figure being the mean of 20 females. Table 5 gives the value and significance of the coefficient of correlation calculated between preimaginal temperature and duration of development, size, longevity, fecundity and related traits.

TABLE 5. CORRELATION COEFFICIENTS AND SIGNIFICANCE OF THE CORRELATIONS BETWEEN PRE-IMAGINAL TEMPERATURE AND DURATION OF DEVELOPMENT, SIZE, FECUNDITY AND RELATED TRAITS AND LONGEVITY FOR HYBRIDS OF *Drosophila melanogaster* RAISED AT A CONSTANT PREIMAGINAL POPULATION DENSITY AND VARIOUS PREIMAGINAL TEMPERATURES

	GA (d.f.: 5)	AG (d.f.: 5)	GA + AG (d.f.: 11)
Duration of development	− 0·931†	− 0·922†	− 0·926‡
Size	− 0·993‡	− 0·969‡	− 0·976‡
Mean daily egg-production	− 0·626	− 0·742*	− 0·679†
Maxim. daily egg-production	− 0·758*	− 0·703	− 0·719†
Day of maxim. egg-production	− 0·719	− 0·264	− 0·111
Final non-laying period	0·729	0·582	0·482
Longevity	− 0·830*	− 0·912†	− 0·823‡

* 0·01 < P < 0·05.
† 0·001 < P < 0·01.
‡ P < 0·001.

The main results are as follows

1. *Imaginal size and duration of development.* It is known that for a given preimaginal population density, decreasing the preimaginal temperature increases size and prolongs the duration of development. The present experiment simply confirms previous evidence (Tables 1 and 2). The increase in size amounts to about 10 per cent between 31° and 16°C. The duration of development is almost quadrupled when the developmental temperatures fall from 31° to 16°C—from 7.8 ± 0.07 to 27.0 ± 0.18 days for AG hybrids and from 7.6 ± 0.04 to 27.1 ± 0.13 days for GA hybrids—whilst the range is considerably enlarged—from 3.5 days of emergence at 31°C to almost 14 days at 16°C. The relation between size and duration of development, which is positive in the present experiment, was negative in the "density" experiment.

2. Including the data collected for the highest preimaginal developmental temperatures used (Tables 3 and 4) the *mean total egg-production* equals 1517 ± 88 eggs for the GA hybrids and 1710 ± 88 eggs for the AG hybrids. Those data may be compared with the corresponding figures of the "density" experiment, viz. 2146 ± 44 eggs for the GA hybrids and 2236 ± 33 for the AG hybrids. That comparison is however not entirely justified, because of the very different environmental conditions used. A better comparison may be made between the data collected in the set of environmental conditions which is common to both the "density" and the "temperature" experiments, viz. a preimaginal population density of 30 eggs per vial at the preimaginal temperature of 25°C. For GA and AG respectively the figures are, in the "density" experiment of 2606 ± 150 and 2631 ± 73 and in the "temperature" experiment of 1864 ± 126 and 2238 ± 49 eggs. An analysis of variance shows that both those differences are significant $(F_{14}{}^{1}\text{GA} = 13.64: 0.001 < P < 0.01; F_{14}{}^{1}\text{AG} = 20.24: P < 0.001)$. An interval of 15 generations between the parental inbred strains may explain that difference. Another statistical test furthermore shows that the decrease in total egg-production affects all the flies in the same way. Indeed a Tukey-test applied to the data shows that the mean total egg-production of $\text{GA}_{31°}$ and $\text{GA}_{28°C}$ differ significantly from the fecundity of the other GA hybrids; the same test furthermore yields a z value of 2.67 for $\text{AG}_{31°C}$, the critical value of the normal distribution curve at the 0.05 level being equal to 1.96; for both GA and AG hybrids the other data do not differ significantly from each other. Thus in the present experiment, just as in the "density" experiment, fecundity appears as a relatively stable character; more precisely, with increasing preimaginal envionmental temperature the mean total fecundity is, at 25°C, a constant for flies developed at temperatures ranging from 16° to 25° or 28°C.

3. At 25°C, the *mean daily egg-production*, i.e. the total egg-production divided by the number of days of life, diminishes with the increase in preimaginal temperature (Tables 3 and 4). The correlation coefficient between temperature and mean daily egg-production is negative and significant for the AG hybrids and for both hybrids considered simultaneously; it is negative but not significant for the GA hybrids where indeed a maximum in daily egg-production occurs for flies developed at 25°C which is, by *Drosophila melanogaster*, the temperature generally considered as optimal for development. The relationship between mean daily egg-production and other measured traits—more precisely size and duration of development—will be considered and discussed later, in relation with the comparison between the "density" and the "temperature" experiment (Lints and Lints, 1971).

4. The *mean maximum number of eggs laid in a 24-hr period* is negatively correlated with the preimaginal temperature (Tables 3, 4 and 5). This means that the maximum number of eggs laid in a 24-hr period is, just as in the "density" experiment, positively correlated with the imaginal size ($r = 0.617$; $n = 12$; $0.01 < P < 0.05$); however the relationship between the variations of those two factors was much closer in the "density" experiment ($r = 0.979$; $n = 16$; $P < 0.001$); an optimum, due to the developmental temperature, is again, in the present experiment, more than plausible.

5. There is, contrarily to what was observed in the "density" experiment, no clear trend in the variations of the *day where the maximal egg-production is attained*, nor in the variations of the final non-laying period.

6. At 25°C, the *mean longevity of female flies* developed at various preimaginal temperatures increases with the decrease in those developmental temperatures (Tables 3 and 4). The coefficients of correlation between those two factors are all negative and significant, at least at the 5 per cent level (Table 5). For instance the longevity of the AG hybrids passes from 43.70 ± 4.36 days for the flies developed at 31°C to 66.70 ± 1.81 days for flies developed at 16°C, which is an increase of more than 50 per cent. That increase—expressed as a percentage—is even larger for the GA hybrids. The longevity of flies developed at 31 and 16°C was 34.7 ± 6.03 and 55.3 ± 3.59 days, respectively.

In the present experiment the regression of longevity on duration of development equals $Y = 43.42 + 0.73X$. It was equal to $Y = 19.95 + 3.44X$ in the "density" experiment. Both regressions are significant and they differ significantly from each other.

DISCUSSION

The influence of preimaginal temperatures on various quantitative traits of *Drosophila melanogaster* hybrids was measured at 25°C. Those traits were measured during development (duration of development), or immediately after emergence (thoracic size) or during the entire imaginal life, which was spent in constant environmental conditions (fecundity and related traits, longevity). Clearly, most of those traits are affected to a considerable extent by the variations in preimaginal temperature; some vary directly with the variations in temperature, some others on the contrary present an optimum around 25°C, which is the optimum temperature for *Drosophila melanogaster*. The interrelations of those traits and their relationship with longevity will be discussed in the next paper in this series (Lints and Lints, following paper).

Life-span is negatively correlated with preimaginal temperature, and thus positively with size and negatively with duration of development. When those relations are compared with the "density" experiment (Lints and Lints, 1969), the only correlation whose sign is common in both experiments is the negative correlation between longevity and duration of development. Indeed the longest life-span is attained in the present experiment by the largest flies which have the longest duration of development; the longest life-span was, in the "density" experiment attained by the smallest flies which had also the longest duration of development. Apparently prolongation of the duration of development means prolongation of the duration of imaginal life. That was indeed supposed earlier (Lints, 1963) and stated recently (Lints, 1970, 1971). That point of view was also adopted by Burcombe and Hollingsworth (1970). In fact the highly significant difference between the regressions of longevity on duration of development for both
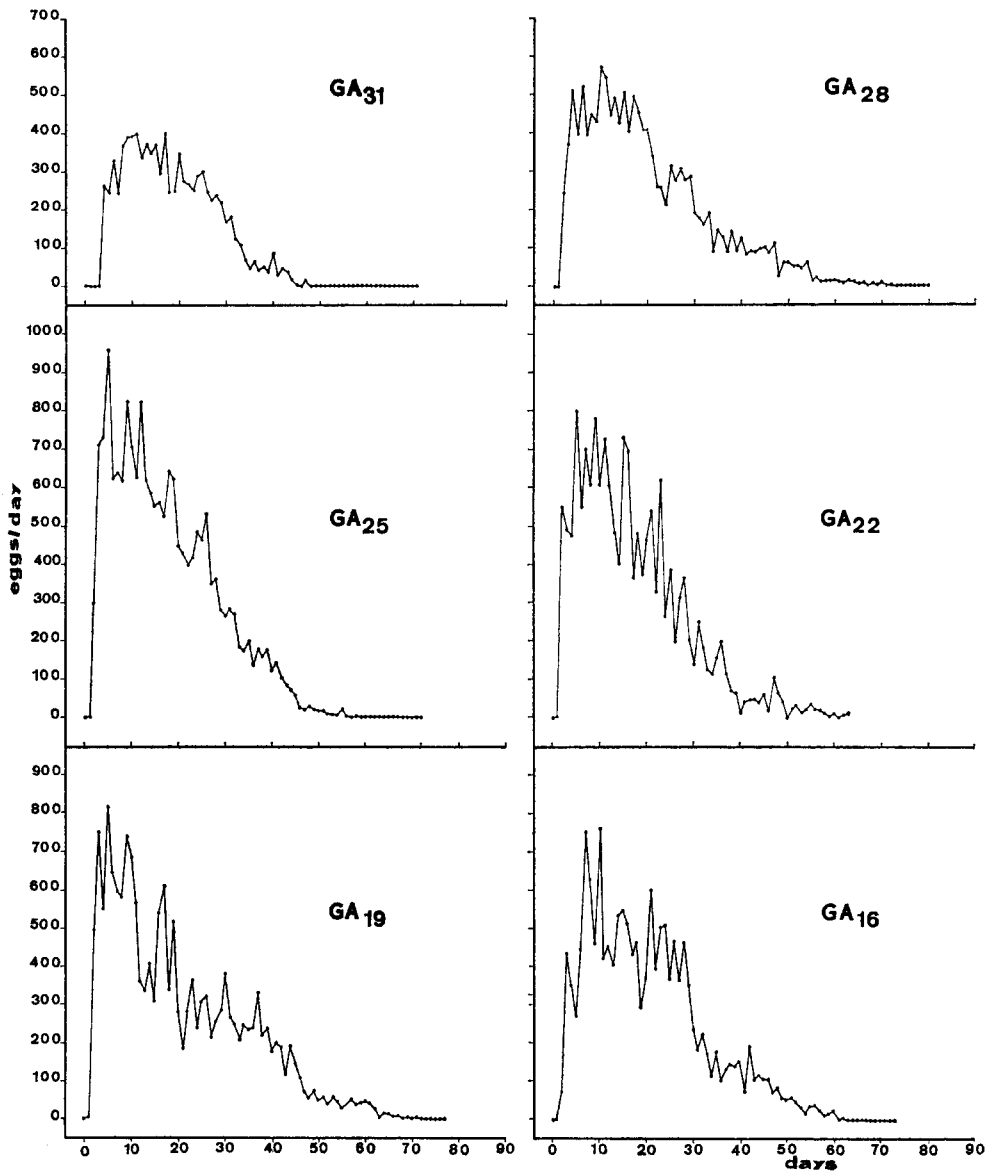
FIG. 1. Laying curves, at 25°C, of the Gabarros 4 ♀ × Abeele ♂ (GA) hybrids raised at a constant preimaginal population density and at six different preimaginal temperatures.
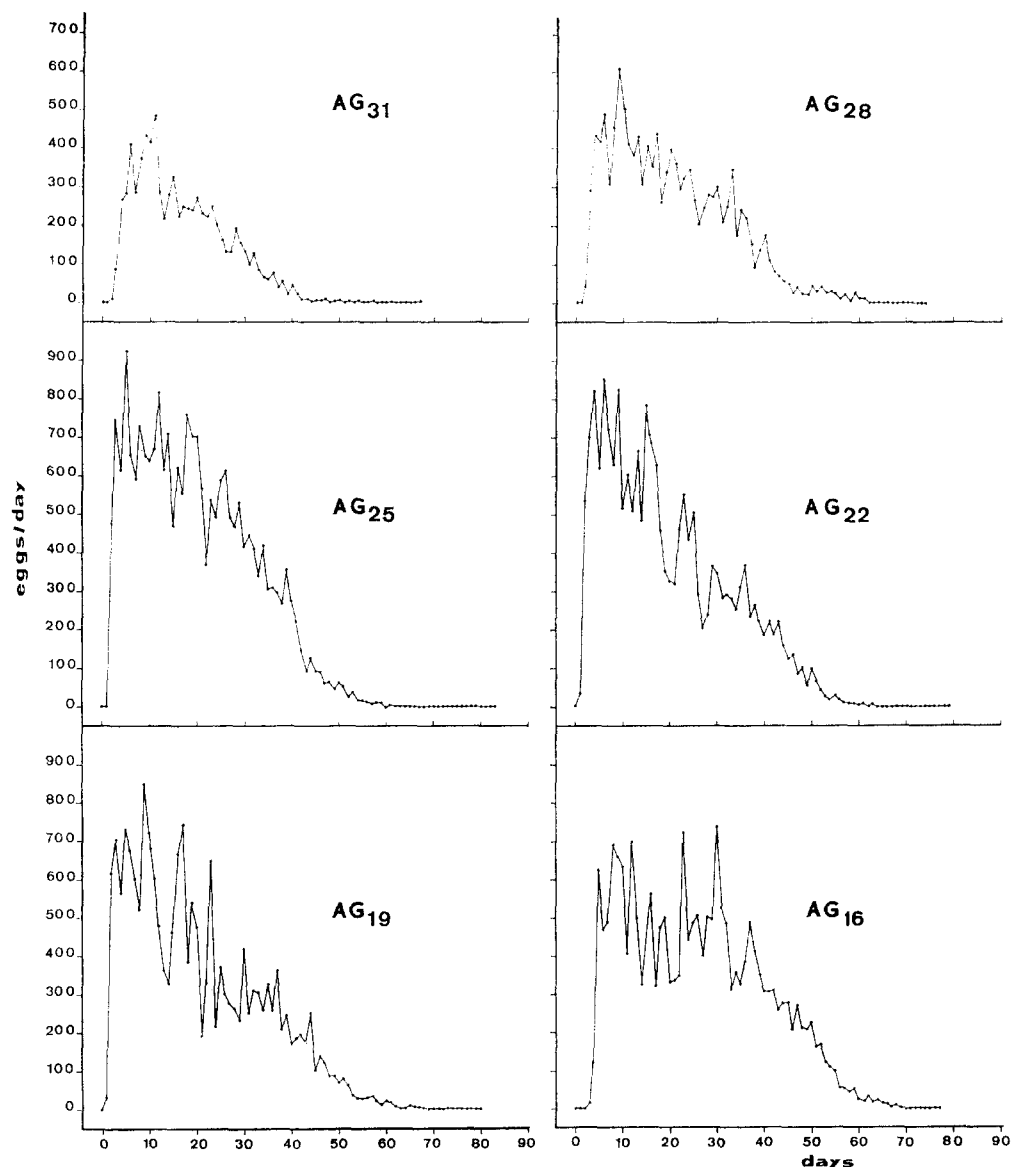
FIG. 2. As in Fig. 1, for the Abeele ♀ × Gabarros 4 ♂ (AG) hybrids.

experiments may be considered as an indication that that point of view is too simple. More than one factor is probably involved in the regulatory mechanism of life-span by *Drosophila melanogaster*. The simultaneous consideration of the results of both the "density" and the "temperature" experiments is obviously necessary and will make the subject of the next paper in this series (Lints and Lints, following paper).

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Summary—Reciprocal hybrids of two highly inbred strains of *Drosophila melanogaster*, Gabarros 4 and Abeele, were cultured, at a preimaginal population density of 30 eggs per standard vial at the temperatures of 16, 19, 22, 25, 28 and 31°C. Afterwards for every preimaginal temperature considered and for the whole life, the daily egg-production of females of known size and duration of development was counted, at 25°C. Life-span was also recorded.

The mean total fecundity does not vary in function of the preimaginal temperature, exception made for the extreme 31°C. The mean daily egg-production, the size and the duration of development decrease with the increase in preimaginal temperature. Life-span at 25°C is prolonged when that temperature is decreased; life-span is thus positively correlated with size and duration of development. In a previous experiment, the life-span at 25°C of hybrids cultured at 25°C and at various preimaginal population densities was positively correlated with duration of development and negatively with size. The regressions longevity-duration of development observed in both experiments are of an identical sign; they differ however significantly. It is therefore concluded that longevity is not determined solely by preimaginal duration of development and that more of one developmental factor must be involved.

The next paper in the series will compare and discuss the results of both experiments.

Résumé—Chez *Drosophila melanogaster* des hybrides réciproques, issus du croisement de deux lignées hautement consanguines, Abeele et Gabarros 4, ont été élevés, à la densité préimaginale de 30 oeufs par milieu de culture standard, aux températures de 16, 19, 22, 25, 28 et 31°C. On a ensuite, à 25°C, la vie durant, pour chaque hybride et chaque température préimaginale considérés, dénombré la ponte journalière d'un certain nombre de femelles de tailles et de durées de développement connues. De même on en a mesuré la longévité.

La fécondité moyenne totale ne varie guère en fonction de la température préimaginale, sinon à la température extrême de 31°C. La moyenne de ponte journalière diminue en fonction de l'accroissement de la température préimaginale; il en est de même pour la taille et pour la durée de développement. La longévité imaginale croit avec la diminution de cette température; cette longévité présente donc une

corrélation positive avec la taille et la durée de développement. Dans une expérience précédente, la longévité d'hybrides élevés à une température constante de 25°C et à des densités de population préimaginales très différentes, présentait une corrélation positive avec la durée de développement et négative avec la taille. Les pentes des régressions durée de développement-longévité, observées dans ces deux expériences, sont néanmoins très significativement différentes. Il en est conclu que le déterminisme de la longévité ne réside pas simplement dans la durée de développement préimaginale mais bien plutôt dans une interaction de différents facteurs liés au développement.

Un troisième article de la présente série étudiera par comparaison les résultats de ces deux expériences.

Zusammenfassung—Reziproke Hybride von zwei Inzuchtstämmen von *Drosophila melanogaster*, Gabarros 4 und Abeele, wurden mit einer präimaginalen Populations-dichte von 30 Eiern pro Standardglas bei Temperaturen von 16, 19, 22, 25, 28 und 31° gezogen. Für jede der Temperaturen im Präimaginalstadium und für das ganze Leben wurde die tägliche Eiproduktion von Weibchen bekannter Größe und Entwicklungsdauer gezählt, bei 25°. Die Lebensdauer wurde ebenfalls registriert. Die mittlere Gesamtfruchtbarkeit ändert sich als Funktion der Präimaginaltem-peratur nicht, außer bei dem Extrem von 31°. Die mittlere tägliche Eiproduktion, die Größe und Dauer der Entwicklungsphase nehmen mit der Präimaginaltempera-tur ab. Die Lebensdauer bei 25° ist erhöht für die niedrigeren Temperaturen; die Lebensdauer ist somit positiv mit der Größe und der Dauer der Entwicklungsphase korreliert. In einer früheren Untersuchung war die Lebensdauer bei 25° von bei dieser Temperatur gezogenen Hybriden, die jedoch bei verschiedenen präimaginalen Populationsdichten inkubiert waren, positiv korreliert mit der Dauer der Entwick-lungsphase, negativ mit der Größe. Die Regressionen Lebensdauer-Dauer der Entwicklungsphase beider Experimente haben gleiches Vorzeichen; sie unter-scheiden sich jedoch signifikant. Es wird daher geschlossen, daß die Lebensdauer nicht nur von der präimaginalen Entwicklungsdauer bestimmt ist, und daß mehr als ein Entwicklungsfaktor beteiligt sein muß.

Die in der Serie folgende Arbeit wird die Resultate beider Arbeiten vergleichen und diskutieren.

Резюме—Реципрокные гибриды двух сильно инбредных штаммов *Drosophila melanogaster, Gabarros* 4 и *Abeele*, культивировались при плотности популяции стадии предшествующей взрослой, равной 30 яйцам на каждую стандартную склянку при температурах 16, 19, 22, 25, 25, 28 и 31°Ц. После этого подсчитывалась для каждой из этих предимагинальных температур и для всего жизненного срока ежеденвная яйценоскость самок известного возраста и развития при 25°Ц. Регистрировалась также длительность жизни.

Средняя общая плодовитость не варьирует с предимагинальной температурой, за исключением крайней в 31°Ц. Средняя ежедневная яйценоскость, размер и длител-ьность развития снижаются с повышением предимагинальной температуры. Длител-ьность жизни при 25°Ц увеличивается при снижении температуры; следовательно жинзненный срок обнаруживает положительную корреляцию с размером и длител-ьностью развития. В предыдущем опыте длительность жизни при 25°Ц гибридов, которые культивировались при 25°Ц и при различных плотностях предимагинальных популяций, показывала положительную корреляцию с продолжительностью развития и отрицательную с размером. Регрессии между жизненных сроком и продолжитель-ьностью развития, которые наблюдались в обоих опытах, имеют одинаковый знак, но они значительно отличаются. Из этого делается вывод, что длительность жизни не зависит исключительно от продолжительности предимагинального развития, но также от других факторов, влияющих на ход развития.

В следующей статье этой серии проводится сравнение и обсуждение результатов обоих опытов.