QUANTITATIVE GENETICS OF FERTILITY II. LIFETIME EGG PRODUCTION OF *DROSOPHILA MELANOGASTER*—EXPERIMENTAL

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EGG production in *Drosophila melanogaster* is an inherited trait (GILBERT 1961; KELLER and MITCHELL 1964; CHAPCO 1968). Unlike some quantitative characters such as numbers of sternopleural chaetae, egg production is not constant over time. Flies do not oviposit eggs at the same rate during the first 5 days post eclosion as they do during days 6–10 post eclosion. Hence, there are certain constraints upon fecundity measurement. The least ambiguous egg production measurement would involve egg counts over the whole lifetime of the animal. For *D. melanogaster*, in which productive lifetime can be as much as 30 days, obtaining lifetime egg productions can be prohibitively tedious.

Criteria for measurement of egg production over a period less than lifetime have varied among researchers. BONNIER (1961) used egg production during a sixteen hour period; CHAPCO (1968) examined the fecundity of females for days four, five and six post eclosion; NARAIN (1962) studied three-day egg laying at various intervals throughout the lifetime; days 4–8 were used by ROBERTSON (1957), while GOWEN (1952) measured egg production on days 5–9 post eclosion. All these workers used such intervals on the assumption that egg production during the study periods is highly correlated with lifetime production (GOWEN and JOHNSON 1946). Unfortunately, such correlations are not homogeneous between strains and hence comparisons between strains are sometimes invalid. The period chosen may include the increasing part of one strain and its peak, the decreasing part and peak for another strain or may not include the peak at all for a third strain. It seems apparent that if two strains are to be compared realistically, then the periods should not be arbitrarily chosen 4- or 5-day intervals but should involve the same relative portions of their respective egg production profiles, as for example the interval encompassing one or two days prior to and one or two days after their peak productions.

To provide a more consistent basis for comparisons of fecundity between strains of *D. melanogaster* we have suggested a new approach to the problem of measuring fecundity involving the following model (McMILLAN, FITZ-EARLE and ROBSON 1970):

$$N(t) = M (1 - e^{-\xi(t-t_0)})e^{-\alpha t}$$

where $N(t)$ is the daily egg production rate; M is the potential maximum daily egg production; t_0 is the initial day of egg laying; ξ is the rate of increase in oviposition; and α is the rate of decrease in oviposition.

To fit the model for any given strain, egg production on only six strategically chosen days during the lifetime are necessary. From these data the four parameters M, t_0, ξ, α may be estimated. Furthermore, egg production during any desired time interval—whether it be days 3 to 6 post eclosion or the entire lifetime —may be deduced by using relationships derived from the integration of the model over the appropriate limits. Likewise, differentiation of the model yields identities useful in predicting the maximum production and the time at which this occurs. All these variables are useful in genetic analyses of fertility.

LEWONTIN (1964) examined triangular reproductive functions, whose shape could be varied by using a few biologically meaningful parameters. He derived expressions for both daily and lifetime offspring productions in terms of parameters essentially similar to ours but with reference to offspring rather than egg production; namely, age of first offspring, the turnover point (day of maximum numbers), age of last offspring, and the total numbers of offspring.

This paper will be an application of the egg production model to strains of *Drosophila melanogaster* maintained in our laboratory.

MATERIALS AND METHODS

Strains: The *Drosophila melanogaster* strains used to test the egg production model were the two wild-type lines P1 I Oregon-R (designated as A) and M Oregon-R (designated as D) and a line carrying the X-chromosome body color mutant, yellow (y) (designated as Y) (SEIGER 1966). At the time of this study the strains had been maintained by single pair brother-sister matings each generation for 570 (A), 500 (D), and 210 (Y) generations, respectively.

Medium: Throughout the egg production determinations, the flies were maintained at 25°C in glass shell vials (23 × 85 mm) containing 5 ml of standard propionic acid medium (1000 ml water; 19 g agar; 54 g sucrose; 32 g brewer's yeast and 5 ml propionic acid). The surface of the medium was inoculated with a half ml drop of live yeast suspension.

Crosses examined: For these genetic studies 40 randomly selected pairs of the parent crosses (A × A, D × D, Y × Y), their intercrosses (A × D, D × A, A × Y, Y × A), and the F_1's (AD_{F_1}, DA_{F_1}) were all examined in the manner outlined below.

Egg production determinations: Males and females of age less than 12 hr were set up, one pair per vial and permitted to remain undisturbed for two days. On the 3rd each pair of flies was transferred to another vial containing fresh medium. Subsequently, transfers were repeated every day or every second day until all the females had died. The eggs deposited during a 24 hr period were counted and egg production was measured as the number of eggs laid per female per day.

Treatment of data: Only those females which laid fertile eggs (i.e., some of their daily productions subsequently hatched) for at least four consecutive days were included in the analysis with the exception of A × Y, which is an infertile cross. Thus, females which laid nonhatching eggs either because they or their mates were sterile or because there was no mating, were disregarded. Occasionally, productive females laid no eggs on one or more days during their lifetimes, especially at the beginning or end of the productive period. These zeros were included in the analysis up to the time of death of the female.

Calculation of the parameters: For sufficiently large t, $N(t) \simeq M e^{-\alpha t}$ and therefore $\log_e N(t) \simeq \log_e M - \alpha t$. Thus, α and M were estimated by using log-linear regression of mean daily egg production, $N(t)$, against days, t. In practice the first value of t was about one or two days after the time of maximum egg production (see APPENDIX). Letting $F(t) = M(1 - e^{-\xi(t-t_0)}) = N(t) e^{\hat{\alpha} t}$, then $\log_e \{(\hat{M} - \hat{F}(t))/\hat{M}\} = - \xi(t - t_0)$ for $F(t) < M$, from which estimates of t_0 and ξ were obtained by a regression analysis. Again this necessitated using values

of t one or two days prior to the time of maximum production. With estimates of the four parameters $(\hat{\alpha}, \hat{\xi}, \hat{t_0}, \hat{M})$, daily egg production curves were fitted and the various predictions from the model were calculated (see McMILLAN *et al.* 1970).

RESULTS

The predicted daily egg production values $\hat{N}(t)$ (APPENDIX) were used to draw the curves for each cross in Figure 1. The observed daily egg production values $(N(t))$ are also shown for comparison.

I. *Comparison of the parameters*: Table 1 gives the parameters α, ξ, t_0 and M corresponding to the profiles of each of the crosses examined in the study (Figure 1).

Crosses A × A (1) and D × D (2) are similar in their increasing (ξ) and decreasing (α) rates of egg production and in the limiting values (M) of their increasing functions, but differ in their initial day of egg production (t_0). Cross A × A has initial day of egg production (t_0) 1.0, whereas cross D × D has t_0 value 2.4.

When the A female is crossed with a D male (3), her ξ value is reduced from

TABLE 1

Estimates of the parameters in the egg production model
$$N(t) = M(1 - e^{-\xi(t-t_0)})\, e^{-\alpha t}$$

| Cross	α	M	ξ	λ	t_0	Days used for increase	Days used for decrease
A × A	0.12	130.7	0.49	0.61	1.0	1.5, 4	7, 8, 11, 14
Y × Y	0.05	88.4	0.74	0.79	2.3	3, 4	7, 8, 9, 10, 13, 14, 15, 16, 17, 18
D × D	0.12	139.6	0.42	0.54	2.4	4, 5	7, 8, 11, 14
A × Y	0.04	51.9	0.33	0.37	3.5	4, 6	17, 18, 19, 22, 23, 24, 25
Y × A	0.07	84.7	0.70	0.77	1.2	1.5, 3	7, 8, 11, 16, 17, 18
A × D	0.06	116.1	0.37	0.43	2.3	3, 4	12, 15, 17
D × A	0.11	145.9	0.46	0.57	2.3	3, 4	9, 12, 15
ADF$_1$	0.06	89.3	0.94	1.00	0.3	1, 2	5, 6, 7, 8, 9, 10, 11, 12, 13
DAF$_1$	0.06	105.7	0.75	0.81	0.0	1, 2	5, 6, 7, 8, 9, 10, 11, 12, 13, 14

$\alpha =$ rate of decrease in egg laying
$M =$ potential maximum egg production rate (the limiting value of $F(t)$)
$\xi =$ rate of increase in egg laying
$\lambda =$ egg developmental rate
$t_0 =$ initial day of egg laying.

1 A X A
2 D X D
3 A X D
4 D X A
5 D A F₁
6 Y X Y
7 A X Y
8 Y X A
9 A D F₁
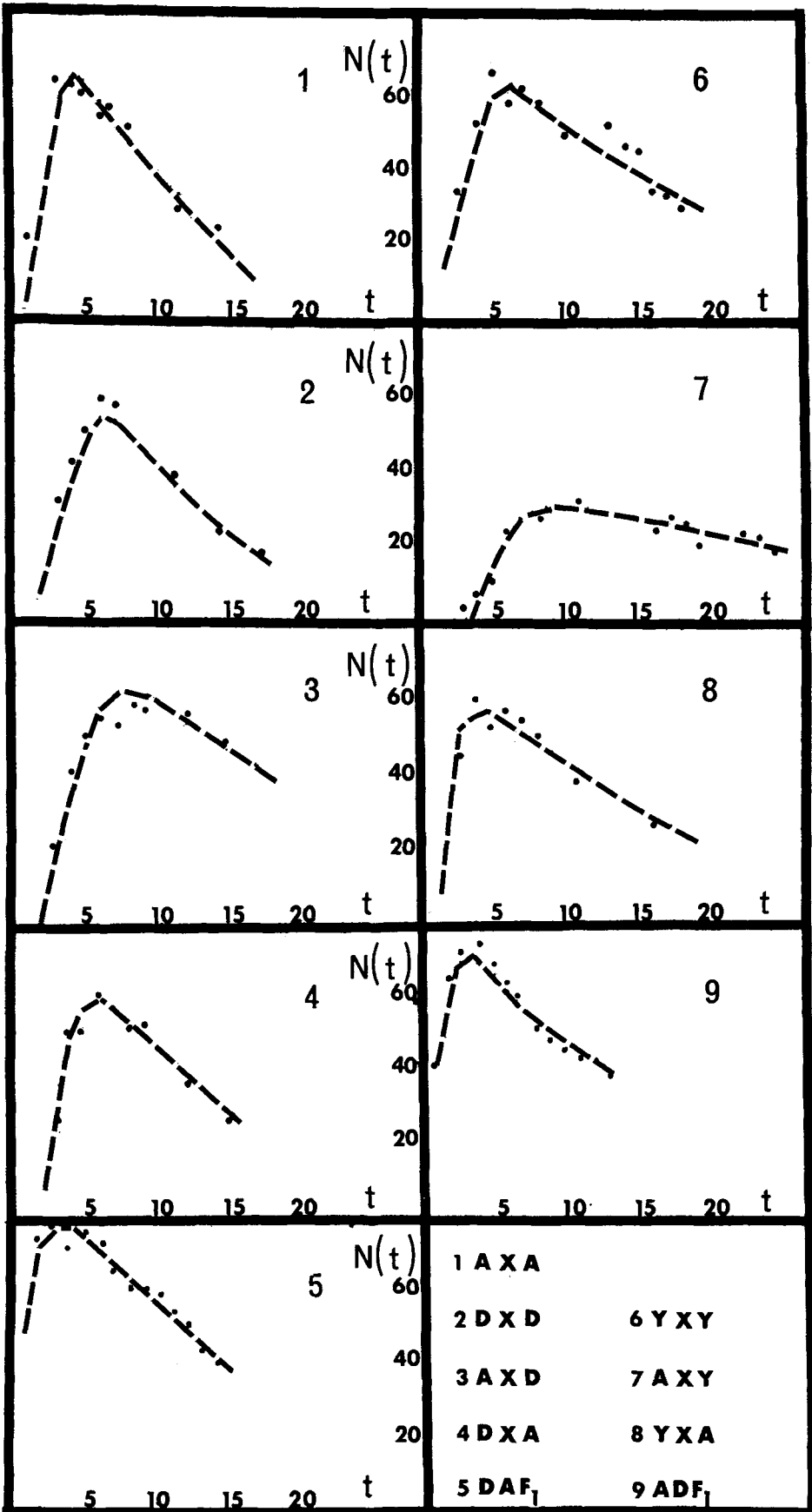
0.49 to 0.37 and her α value is halved from 0.12 to 0.06. Also, the M is reduced from 130.7 to 116.1 and t_0 is increased from 1.0 to 2.3. On the other hand, a D female crossed with an A male (4) is very similar for all four parameters to the D female crossed with a D male.

Crosses A $\times$ A (1) and Y $\times$ Y (6) are very different with respect to each parameter. The A female has a higher α and M and a lower ξ and t_0 than the Y female.

When the A female is now crossed with a Y male (7), her ξ value is reduced from 0.49 to 0.33 and the α shows a large reduction (0.12 to 0.04). Her M value drops from 130.7 to 51.9 and t_0 is increased from 1.0 to 3.5. These results are consistent with the fact that A $\times$ Y is an infertile cross (BASTOCK 1956; BARKER 1962) and is essentailly equivalent to the egg production of a virgin female. The Y female, when crossed with an A male (8) shows a slight increase in α and a slight decrease in M, ξ, and t_0, when compared to Y $\times$ Y matings.

Both F_1 crosses, (A $\times$ D)F_1 and (D $\times$ A)F_1 (5 and 9, respectively), show hybrid vigor with respect to all four parameters. In the hybrids, α, M and t_0 are all lower than the midparental value, and the ξ's are larger. Indeed, the α's are half those of the parents, the ξ's are approximately double and egg laying starts almost at eclosion whereas delays of 1–2 days occur in the parents. Therefore, the F_1 females start egg production sooner, have larger rates of increasing egg production, lower limiting egg laying rates and slower declines in egg production rate than either parental cross.

II. *Derivations from the model: (a) Total egg production over specified time intervals.* Table 2 lists the total number of eggs laid per female during various periods for each of the crosses. These values are calculated from expressions derived by integrating the egg production model over specified intervals (Mc-MILLAN *et al.* 1970).

TABLE 2

Derivations from the egg production model

Cross	Egg production for four-day periods $T(3,6)$	$T(t_1, t_2)$	t_1, t_2	Potential lifetime egg production $T(t_0, \infty)$
A $\times$ A	230	230	3, 6	772
Y $\times$ Y	164	205	5, 8	1360
D $\times$ D	143	212	5, 8	678
A $\times$ Y	30	112	9, 12	892
Y $\times$ A	184	198	4, 7	1022
A $\times$ D	144	246	7, 10	1445
D $\times$ A	165	236	5, 8	785
ADF$_1$	234	224	2, 5	1374
DAF$_1$	278	265	2, 5	1550

Production for four-day periods; $T(3,6)$ arbitrarily chosen. $T(t_1, t_2)$ chosen to include day of peak production; total potential lifetime egg production, $T(t_0, \infty)$.

FIGURE 1.—Mean daily egg productions over lifetime of three inbred strains of *Drosophila melanogaster*, their intercrosses and F_1's. Observed values and derived curve from model.

The first time interval, days 3 to 6 inclusive, was an arbitrarily chosen 4-day period. An A female crossed to an A male laid 230 eggs during this period but only 144 eggs when crossed to a D male and 30 eggs when crossed with a Y male. However, both of the D and Y females, when mated with an A male, show an increase in egg production during this period compared to when they are mated with their brothers. Both F_1's show higher egg production over this period than the midparental value.

When the 4-day period was specifically selected to include the day of maximum egg laying, the A female had a lower total egg production with a Y male compared to her production with a A male, but a similar total with a D male. The D female again shows an increased total egg production over this period when she is mated with an A male, than when she is mated with her brother, while the Y female shows a slight decrease. It is to be noted that when egg production is estimated for a period which includes the maximum, it invariably exceeds 4-day production over an arbitrarily chosen interval. The two F_1's are exceptions to this result due to the skewed nature of the lifetime egg production profiles (Figure 1).

The last column in Table 2 lists the values for $T(t_0, \infty)$, the total number of eggs a female would lay if she lived indefinitely. An A female when mated with an A male has potential lifetime egg production of 772 but this value is increased to 892 when she is mated to a Y male, and further increased to 1445 when she is mated to a D male. $T(t_0, \infty)$ for a D female mated to a D male is 678, and this is increased to 785 with a A male. The Y $\times$ Y cross has a $T(t_0, \infty)$ of 1360 while Y $\times$ A is lower at 1022. The F_1's are both higher than either parental cross (1374 for AD_{F_1} and 1550 for DA_{F_1}).

III. *Derivations from the model: (b) Maximum egg production and time of this maximum.* In Table 3 is shown t_{max}, the time of maximum egg production rate, $N(t_{max})$, the maximum egg laying rate, and the ratio $N(t_{max})/T(t_0, \infty)$. An A female crossed with an A male takes 4.4 days to reach her maximum rate of egg production but is slower in reaching this maximum when mated to a D male (7.7 days) and with a Y male (10.0 days).

The D female takes 6.0 days, when crossed with her brother, to reach her maximum egg production rate. This value drops slightly to 5.9 days when she is crossed with an A male. Similarly the Y female takes 5.9 days when crossed with a Y male but reaches her maximum egg laying rate earlier, in 4.7 days, when mated to an A male.

Both F_1's reach their maximum rate of oviposition faster than either parental cross, t_{max} being 3.3 days for each.

$N(t_{max})$ for the A $\times$ A cross is 62.2 eggs per day. This value is unchanged at 62.9 eggs per day for the A $\times$ D cross and falls to 29.5 for the A $\times$ Y cross. The D $\times$ D mating has an $N(t_{max})$ of 53.0 eggs per day which increases to 59.8 per day for the D $\times$ A cross. By contrast, the Y female drops from 60.1 eggs per day for the Y $\times$ Y cross to 55.8 eggs per day for the Y $\times$ A mating.

Again the F_1 hybrids show vigor in having higher $N(t_{max})$ values than the midparental value. Indeed, the DA_{F_1} has a maximum egg production rate of 79 eggs per day only 3.3 days after eclosion.

$N(t_{\max})$ has been shown to be related to $T(t_0, \infty)$, the ratio being $\alpha / (1 + \xi/\alpha)^{\alpha/\xi}$. Hence $N(t_{\max})/T(t_0, \infty)$ provides and arithmetic check at the end of the calculations.

DISCUSSION

It has been established that egg production is an inherited characteristic of *Drosophila melanogaster* strains. The shape of the egg production profile as described by GOWEN and JOHNSON (1946) and later workers characteristically has a rise in production rate to a peak, followed by an exponential decline until oviposition ceases just before the female's death. This form of curve has gained general acceptance. The striking feature of the egg production curves which we have presented here (Figure 1) is that they are all adequately described by the model:

$$N(t) = M \,(1 - \mathrm{e}^{-\xi(t-t_0)})\, \mathrm{e}^{-\alpha t}.$$

Since egg production is an inherited trait and since it is reflected in the profile of the egg production curve, it follows that the parameters in the egg production model (M, t_0, ξ, α) are all genetic parameters. Consequently, the complex event of egg production may be factored into the four relatively simple observations of (1) increasing (ξ) and (2) decreasing (α) egg production rates, (3) the initial day of egg production (t_0), and (4) the potential maximum egg production rate (M).

The physiological interpretation of these parameters is not immediately obvious; the following derivation of the model may be revealing in this respect. Consider egg production as a two-stage process, consisting of a primordial stage and a developed stage. Assume that the initial number of primordial egg cells
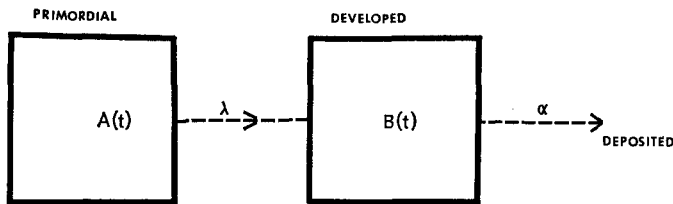
(A_0) is fixed at time t_0 when they begin to develop at a constant instantaneous rate, λ. Then the number of primordial egg cells remaining at time $t > t_0$ is $A(t) = A_0\, \mathrm{e}^{-\lambda(t-t_0)}$. Assume further that mature eggs are deposited at a constant instantaneous rate, α. If $B(t)$ is the number of mature eggs present in the female at time t, then $N(t) = \alpha\, B(t)$, where $N(t)$ is the rate of deposition of mature eggs. The rate of change in the number of mature eggs present in the female is the difference between their rate of development and their deposition rate. Therefore,

$$B'(t) = \lambda A(t) - \alpha B(t).$$

Solving this differential equation with initial conditions $A(t_0) = A_0$ and $B(t_0) = 0$, we have

$$N(t) = B(t) = \frac{\alpha \lambda}{(\lambda - \alpha)} A_0\, (1 - \mathrm{e}^{-\lambda(t-t_0)})\, \mathrm{e}^{-\alpha(t-t_0)}$$

or letting $\xi = \lambda - \alpha$ and $M = \dfrac{\alpha \lambda}{(\lambda - \alpha)} A_0 \, e^{\alpha t_0} = \dfrac{\alpha(\xi + \alpha)}{\xi} A_0 \, e^{\alpha t_0}$, then

$$N(t) = M \, (1 - e^{-\xi(t - t_0)}) \, e^{-\alpha t}.$$

From this derivation we see that α is the rate of oviposition of eggs while $\lambda = \xi + \alpha$ is the rate of egg development in the female. Further, $A_0 = \dfrac{M \, e^{-\alpha t_0}}{\alpha(1 + \alpha/\xi)}$ is the total number of germ cells which develop into mature eggs, assuming an infinite lifespan. A_0 also happens to be $T(t_0, \infty)$, the total potential lifetime egg production in this model which admits no egg losses.

The compartmental approach to model building is applicable to many areas of biology. HEINZ (1949), for example, considered muscle and blood as the two compartments in deriving this model to describe the passage of intramuscularly injected drugs from the muscle to the blood and thence their elimination from the blood.

Since A_0 is determined at t_0, it is independent of α and ξ. Therefore, the potential lifetime egg production $T(t_0, \infty)$ is fixed at t_0 and is independent of the parameters α and ξ.

Let the numbers of eggs actually laid by the female during her lifetime be $T(t_0, t_s)$ where t_s is the time of her death. Then $r(t_s) = T(t_0, t_s)/A_0$ is the proportion of the total potential egg production actually realized,

$$r(t_s) = 1 - \frac{1}{\lambda - \alpha} \{\lambda e^{-\alpha(t_s - t_0)} - \alpha e^{-\lambda(t_s - t_0)}\}$$

Letting $\rho(\lambda, \alpha) = \mathrm{E}\,\{r(t_s)\}$ denote the expected or average realized fraction of the potential lifetime production, then

$$\frac{\partial \rho}{\partial \lambda} = \frac{\alpha}{(\lambda - \alpha)^2} \, \mathrm{E} \, \{e^{-(\alpha - \lambda)(t_s - t_0)} - [1 - (\alpha - \lambda)]\} e^{-\lambda(t_s - t_0)} > 0$$

$$\frac{\partial \rho}{\partial \alpha} = \frac{\lambda}{(\lambda - \alpha)^2} \, \mathrm{E} \, \{e^{-(\lambda - \alpha)(t_s - t_0)} - [1 - (\lambda - \alpha)]\} e^{-\alpha(t_s - t_0)} > 0 .$$

Therefore, $\rho(\lambda, \alpha)$ is an increasing function of both α and λ. With no selection pressure other than adult mortality, α and λ would tend to increase indefinitely, since individuals with high α and λ would produce the greatest fraction of their potential before dying. However, environmental selection would determine values of these parameters to maximize fitness. This implies that strains of animals of the same species reared in the same environment would have a similar $\rho(\lambda, \alpha)$. Hence $r(t_s)$ is not a suitable basis for comparison of egg production between strains. Since $T(t_0, \infty)$ is independent of α and λ, it therefore becomes the logical basis of interstrain egg production comparisons.

From this argument it would seem reasonable to assume that A_0 should be constant for any particular female regardless of her mate, since A_0, which is independent of α and λ, is determined at t_0. However, our results indicate that A_0 is increased when the D female is mated to an A male and decreased when the Y female is crossed to an A male. This apparent male effect may be accounted for by amending the compartmental model to include "loss" factors from the two compartments:
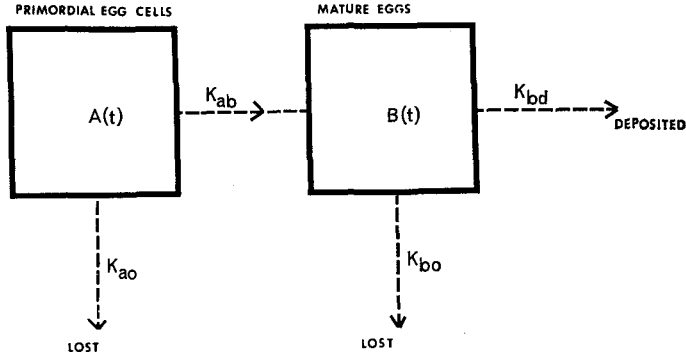
The equations to be solved are $A'(t) = -(k_{ao} + k_{ab})\, A(t)$

and $B'(t) = k_{ab}\, A(t) - (k_{bo} + k_{bd})\, B(t)$,

where k_{ao} and k_{bo} are the rate of loss of primordial and developed egg cells, respectively, and the initial conditions are as before $A(t_0) = A_0$ and $B(t_0) = 0$. Solving the equations we obtain the model in the earlier form: $N(t) = M(1 - e^{-\xi(t-t_0)})\, e^{-at}$, where $\alpha = k_{bd} + k_{bo}$; $\lambda = k_{ab} + k_{ao}$; $\xi = \lambda - \alpha = (k_{ab} + k_{ao}) - (k_{bd} + k_{bo})$ and $M = \dfrac{k_{bd}\, k_{ab}\, A_0\, e^{(k_{bd} + k_{bo})t_0}}{(k_{ab} + k_{ao}) - (k_{bd} + k_{bo})}$. The potential lifetime egg production $T(t_0, \infty)$ now becomes $T(t_0, \infty) = \dfrac{k_{ab}}{(k_{ab} + k_{ao})}\ \dfrac{k_{bd}}{(k_{bd} + k_{bo})}\, A_0$.

Examination of the A × A and A × D matings illustrates how the male affects the potential lifetime egg production of the female. Assuming that the D male eliminates the losses (k_{ao} and k_{bo}) in the A × D mating, then since $\alpha = 0.06$ and $\lambda = 0.43$, $k_{bo} + k_{bd} = 0.0 + 0.06$ and $k_{ao} + k_{ab} = 0.0 + 0.43$. However, for the A × A mating which includes loss rates, since $\alpha = 0.12$ and $\lambda = 0.61$, $k_{bo} + k_{bd} = 0.06 + 0.06$ and $k_{ao} + k_{ab} = 0.03 + 0.58$. Thus, for the A × D mating $T(t_0, \infty) = A_0$ and for the A × A mating $T'(t_0, \infty) = 0.47\, A_0$. Hence $T'/T = 2.1$ and therefore in the absence of loss rates ($k_{ao} = 0.03$ and $k_{bo} = 0.06$), the potential lifetime egg production of A × D is approximately double that of A × A. This observation is consistent with the experimental results: $T(t_0, \infty)$ for A × D was 1445 and for A × A was 772. (The complete development of the compartmental model may be seen in FITZ-EARLE et al. 1969).

The disadvantage of this version of the model is that k_{ao} and k_{bo} cannot be determined by simply observing egg production rates; hence, values for A_0 using these loss factors cannot be obtained. The derivation is however theoretically more complete with the inclusion of the loss rates. In practice, only $T(t_0, \infty)$ can be calculated in terms of α, ξ, t_0 and M, and it is a biased estimate of A_0 due to the presence of unknown loss factors. KING (1957) estimated the time spent at each of 14 stages of egg development in *Drosophila melanogaster*. However, he did not measure loss rates in his work. Another unresolved question is whether A_0 is determined prior to t_0, in particular at the time of eclosion. KING states that all 14 stages are not evident at emergence, but the mature eggs only appear a day or two post eclosion.

The values of t_0, the initial day of egg production, indicate that t_0 is determined by the mate derived from the parental cross with the later initiation of egg laying. That is, an early maturing male or female must wait for his or her later maturing mate in the intercrosses. For example, A × A has a t_0 of 1.0 days while D × D has a t_0 of 2.4 days, but both A × D and D × A have t_0's of 2.3 days. Similarly, Y × Y has a t_0 of 2.2 days while A × Y has a t_0 of 3.5 days. The delay of the mating to time t_0 indicates that the development of the parent is limiting the initiation of egg production. Y × A deviates from this pattern with a t_0 of 1.2 days. Here the A male decreases the time the Y female takes to commence egg production as compared to when the Y female is mated to her brother. This discrepancy perhaps could be accounted for by considering the Y male to be a poor mate even in intrastrain matings. Hence Y × A is a superior cross with respect to t_0.

It is known that virgin flies are not as fecund as mated flies (WILSON, KING and LOWRY 1955). Our results confirm this and imply that mating does exert some influence on egg production, possibly as a trigger to stimulate oviposition. If such a mating stimulus is not supplied then oviposition is delayed. This is best demonstrated by comparing the t_0 of 3.5 for the cross A × Y, which is essentially equivalent to the production of an A virgin, with the t_0 of 1.0 for the A × A cross. Perhaps in the absence of the mating stimulus, oviposition does not commence until the ovary contains all of the mature eggs it can hold.

A comparison of the days of maximum egg production (t_{max}) for the various crosses (Table 3), shows that these values follow a similar pattern to the t_0's. However, no simple interpretation is possible for the maximum productions ($N(t_{max})$) over the matings.

When the effect of the male on the parameters ξ, α, and λ is examined it is seen that ξ, the difference between the development and deposition rates, is relatively unaffected by a change in mate. A × A has a ξ of 0.49 while A × Y and A × D are 0.33 and 0.37, respectively. D × D has a ξ of 0.42 as compared with 0.46 for

TABLE 3

Derivations from the lifetime egg production model

Cross	t_{max}	$N(t_{max})$	$\dfrac{N(t_{max})}{T(t_0, \infty)} = \dfrac{\alpha}{(1+\xi/\alpha)\,\alpha/\xi}$
A×A	4.4	62.2	0.086
Y×Y	5.9	60.1	0.044
D×D	6.0	53.0	0.078
A×Y	10.0	29.5	0.033
Y×A	4.7	55.8	0.055
A×D	7.7	62.9	0.044
D×A	5.9	59.8	0.076
AD_{F_1}	3.3	68.9	0.050
DA_{F_1}	3.3	79.0	0.051

Time to maximum egg production, t_{max}; maximum production, $N(t_{max})$; ratio of maximum egg production to total potential lifetime production.

D × A. Y × Y and Y × A are 0.74 and 0.70, respectively. On the other hand, α, the deposition rate, is very much influenced by a change of male. For instance, α for A × A is 0.12 while the α's for A × Y and A × D are 0.04 and 0.06, respectively. The question arises whether α is affected directly by the male or by changes resulting from a shift in t_0. A × A has a t_0 of 1.0 and an α of 0.12, while A × D has a t_0 of 2.3 and an α of 0.06. The late initiation of oviposition in the A × D cross allows the A female to accumulate more developed eggs and consequently her oviposition rate is not reduced as rapidly as when she is mated to an A male. A similar regulatory mechanism is apparent in the Y × Y and Y × A matings.

Table 2 illustrates the unreliability of using egg production over 4-day periods for interstrain comparisons. When production is compared over the arbitrary intervals days 3 to 6 inclusive, it might be deduced that A × A, Y × Y, and D × D are all different. However, when we select the 4-day period to include the day of peak production (a more reasonable criterion) the Y × Y and D × D crosses appear to be quite similar. In fact, when we examine the parameters from the model (Table 1), A × A and D × D are quite alike, the D × D profile simply undergoing a shift to the right. By contrast, the Y × Y is completely different from the other two matings. These observations are confirmed by examining $T(t_0,\infty)$, the potential lifetime production. $T(t_0,\infty)$ for Y × Y is almost double those of A × A and D × D; the latter two crosses have similar $T(t_0,\infty)$ values.

The two hybrids, (D × A)F_1 and (A × D)F_1 indicate something about the inheritance mechanism of the parameters α, ξ, t_0 and A_0. Both hybrids have ξ and A_0 values which are greater than the midparental values and they have α and t_0 values which are lower than the midparental values. Thus, chromosomal inheritance (relation to midparental values) with dominance (both hybrids same) is implied, rather than a cytoplasmic effect.

Some mention has been made of the effect of selection on the egg production parameters. ρ (λ, α) was found to be a strictly increasing function of α and λ (and therefore ξ) and thus would tend to increase indefinitely. However, it was concluded that in fact the environment would select values of these parameters to maximize fitness. If a species did have a large ξ and α, the majority of the eggs would be laid within a short space of time. This would put the species at a disadvantage because of subsequent larval competition and because a predator or some environmental setback could destroy a large proportion of the eggs and the parents would have few reserves to accommodate for the loss. To have a high ξ could be a selective advantage since it would enable a female to reach her maximum oviposition rate fairly early during the period when egg viability is at a maximum. Zygote viability declines rapidly following the maximum oviposition rate (McMILLAN, unpublished). A low α may be beneficial, since it would enable a female to maintain a high oviposition rate for an extended time period. Adopting these latter criteria of a high ξ with a low α, the F_1's clearly have superior fitness compared to either of the parents since they both have lower α's and higher ξ's than the parental types. Thus, it seems feasible from the F_1's a strain could be selected that is superior to either parent with respect to egg production.

SUMMARY

Parameters from the egg production model $N(t) = M(1 - e^{-\xi(t-t_0)})e^{-\alpha t}$ (McMILLAN *et al.* 1970), were calculated for three inbred strains of *Drosophila melanogaster*, their intercrosses, and hybrids. The following derivations from the model were obtained: maximum egg production rate, time of this maximum, total egg production over 4-day intervals and total potential lifetime egg production. This latter parameter, which in the absence of egg losses is also equivalent to the number of primordial egg cells at the time of initiation of egg laying, was suggested as the best genetic parameter for interstrain egg production comparisons. A feature of the model is that the parameters and derivations can be calculated without measuring daily egg productions throughout the entire lifetime of the females.——A compartmental derivation of the model was used to illustrate a possible physiological basis of Drosophila egg production from the primordial egg cell stage to the developed egg stage.——The evolutionary significance of the parameters in the egg production model was discussed.——Comparisons of the hybrid and parental crosses indicated that the parameters are chromosomally inherited.

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APPENDIX TABLE

Observed daily egg production N(t) *and their derived values from the model.*
The increasing function F(t)

Cross	Day	$N(t)$	$\hat{N}(t)$*	Number of females	$\hat{F}(t)$
A×A	1		—2.3		
	1.5	21.6		33	25.9
	2		38.6		
	3	63.7	56.3	33	91.3
	4	61.6	61.9	33	99.6
	5	59.9	61.4	33	109.2
	6	53.8	58.0	33	110.6
	7	55.5	53.4	33	128.4†
	8	50.8	48.4	33	
	11	31.5	34.7	31	
	14	24.4	24.3	25	
Y×Y	3	32.1	32.1	25	37.3
	4	51.8	51.8	25	63.2
	5	65.6	58.7	25	84.2
	6	58.0	60.0	25	78.2
	7	60.5	58.9	25	85.9
	8	57.2	56.7	25	85.3
	9	49.1	54.1	25	77.0
	10	49.3	51.5	25	81.3†
	13	51.4	44.0	23	
	14	45.7	41.7	22	
	15	44.4	39.5	20	
	16	35.1	37.4	19	
	17	35.2	35.5	19	
	18	29.2	33.6	19	
D×D	3	33.1	21.7	25	47.9
	4	41.1	42.3	25	67.2
	5	49.6	50.9	25	91.7
	6	59.4	53.0	25	124.2
	7	57.1	51.5	25	135.1†
	8	51.9	48.4	25	
	11	38.6	36.3	25	

Cross	Day	$N(t)$	$\hat{N}(t)$*	Number of females	$\hat{F}(t)$
	14	23.9	25.8	25	
	17	17.2	18.1	25	
A×Y	3	2.1	—8.6	35	2.4
	4	6.3	6.3	35	7.4
	5	16.1	16.1	35	13.3
	6	22.3	22.3	35	28.4
	7	26.0	26.1	35	34.4
	8	27.8	28.2	35	38.3
	11	32.4	29.3	35	50.3†
	16	23.3	25.3	35	
	17	27.5	24.3	35	
	18	24.6	23.3	35	
	19	20.1	22.4	35	
	22	23.2	21.5	35	
	23	22.8	20.7	33	
	24	20.1	19.9	30	
	25	12.6	19.1	30	
Y×A	1		—13.9		
	1.5	13.1		33	14.6
	2		30.7		
	3	45.7	48.9	33	56.4
	4	60.5	55.0	33	80.0
	5	52.8	55.6	33	74.9
	6	55.5	53.9	32	84.5†
	7	53.3	51.3	31	
	8	48.7	48.3	29	
	11	38.5	39.5	20	
	16	27.3	28.0	9	
	17	26.9	26.1	8	
	18	24.5	24.2	8	
A×D	3	21.2	21.2	35	25.4
	4	41.8	41.8	35	53.1
	5	50.1	53.6	35	67.6
	6	54.4	59.8	35	78.0
	7	52.4	62.5	35	79.8
	8	58.8	62.8	35	95.1
	9	55.4	61.7	35	95.1
	12	55.2	54.9	35	113.4†
	15	49.4	46.7	35	
	17	40.4	41.7	35	
D×A	3	26.9	26.9	24	37.4
	4	49.1	49.1	24	76.2
	5	50.3	58.0	24	87.2
	6	60.4	59.8	24	116.9
	7	57.4	57.9	24	124.0
	8	53.0	54.2	24	127.8
	9	53.0	49.8	24	142.6†
	12	36.2	36.7	24	
	15	26.8	26.3	24	
AD$_{F_1}$	1	40.7	40.8	39	43.2
	2	63.1	63.1	39	71.1†
	3	73.5	68.4	39	

Cross	Day	$N(t)$	$\hat{N}(t)$*	Number of females	$\hat{F}(t)$
	4	75.3	67.8	39	
	5	68.6	65.0	38	
	6	62.4	61.6	38	
	7	58.5	58.1	38	
	8	52.0	54.7	38	
	9	49.2	51.5	38	
	10	47.9	48.5	36	
	11	46.3	45.6	36	
	12	43.8	42.9	36	
	13	41.1	40.4	36	
DA_{F_1}	1	54.8	54.8	35	58.2
	2	73.5	73.5	35	82.9
	3	78.0	78.8	35	93.4
	4	71.4	78.3	35	90.7
	5	75.6	75.4	34	102.0
	6	73.2	71.6	34	104.9†
	7	65.4	67.6	34	
	8	61.9	63.6	33	
	9	61.7	59.8	32	
	10	60.1	56.2	32	
	11	55.1	52.6	32	
	12	50.4	49.5	32	
	13	44.3	46.5	32	
	14	42.3	43.6	32	

* Estimated from the egg production model $\hat{N}(t) = \hat{M}(1 - e^{-\hat{\xi}(t-\hat{t}_0)})e^{-\hat{\alpha}t}$ and $\hat{F}(t) = N(t) e^{\hat{\alpha}t}$.

† The function $\hat{F}(t)$ is essentially equal to its asymptotic value $\hat{M}$ subsequent to this day.