QUANTITATIVE GENETICS OF FERTILITY
I. LIFETIME EGG PRODUCTION OF *DROSOPHILA*
MELANOGASTER—THEORETICAL[1]

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M ATED females of *Drosophila melanogaster* commence egg laying on the second or third day following emergence from the puparium (Figure 1). Oviposition rapidly reaches a maximum during days six to ten post eclosion, depending upon the strain, and subsequently declines geometrically at a constant rate, egg production ceasing just prior to the death of the female (ROBERTSON and SANG 1944; GOWEN and JOHNSON 1946; ROBERTSON 1957).

GOWEN and JOHNSON (1946) showed that lifetime egg production in Drosophila is a function of (1) the maximum daily production, (2) the age of the female at that maximum, (3) the rate of decline (senescence) from the maximum, (4) the duration of life of the female, and (5) the number of days on
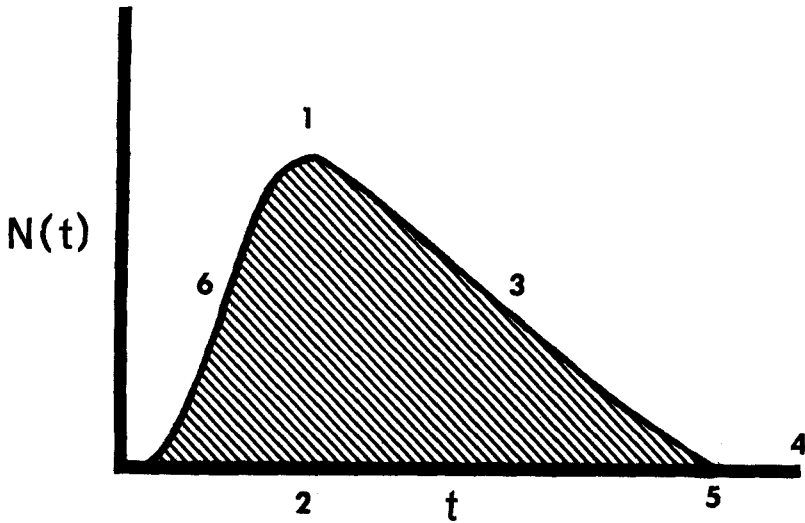

FIGURE 1.—Principal factors influencing the egg production of *Drosophila melanogaster*: (1) Maximum production, (2) Age of female at that maximum, (3) Decline from maximum, (4) Duration of life of female, (5) Number of days of egg laying, (6) Increase in production. $N(t)$ is the number of eggs laid on day t.

which the female laid eggs in her lifetime. The maximum daily production and the days the female laid eggs during her lifetime were found to be the most important factors influencing lifetime egg yield.

The decline in production of eggs during the period following the maximum output closely follows an exponential decay of the form: $N(t) = N(t_{max}) e^{-\alpha t}$, for $t > t_{max}$, where $N(t)$ is the daily egg production corresponding to a day t of egg laying and t_{max} is the time of maximum production. The rates of decay (α) for seven wild strains and a hybrid examined by GOWEN and JOHNSON (1946) were of the order 0.04 to 0.17 (4% per day to 17% per day). The maximum egg yields for these strains at age six days ranged from 19.8 to 107.6. NARAIN (1962) described the decline in egg production of *D. melanogaster* from Nai-Basti (India) by the model: $N(t) = 66.56 e^{-0.0269t}$.

This paper describes a model for characterizing the complete lifetime egg production profiles observed in Drosophila strains. The derivation of the model incorporates the knowledge of the factors influencing fecundity outlined above. The model is tested with some of our own data in the subsequent publication (McMILLAN *et al.* 1970).

<center>A TWO-FACTOR MODEL</center>

If the exponential decay rate (α) operates throughout an adult lifetime, then the egg production curve (Figure 1) may be factored into two components,

$$N(t) = F(t) e^{-\alpha t} \tag{1}$$

The observed shape of actual production curves suggests that egg production does not usually begin until some time t_0 several days post eclosion, and therefore

$$F(t) = 0 \text{ for } t < t_0.$$

From t_0 onwards, however, $F(t)$ appears to have the form displayed in Figure 2; that is, for $t \geqslant t_0$ the factor $F(t)$ is a concave, strictly increasing, bounded function of t. Thus, $N(t)$ appears to factor into two independent, counteracting components, one reflecting an increase in potential egg production rate towards its maximum level (M), while the other reflects a declining ability to utilize this potential.

The observed fact that $\log_e N(t)$ becomes a linear (decreasing) function of t for sufficiently large t implies that the factor $F(t)$ is then essentially constant; that is, $F(t)$ has essentially achieved its limiting value M, and

$$\log_e N(t) = \log_e F(t) - \alpha t$$
$$\doteq \log_e M - \alpha t \qquad \text{for large } t.$$

Log-linear regression analysis for large t therefore provides estimates $\hat{M}$ and $\hat{\alpha}$, and estimates of the factor $F(t)$ may then be calculated from equation (1) for all t simply by multiplying the observed $N(t)$ by $e^{\hat{\alpha}t}$.

<center>GROWTH MODEL</center>

Preliminary data analyses for several isogenic strains suggest that the function $F(t)$ is adequately described by the von BERTALANFFY (1934, 1938) growth model
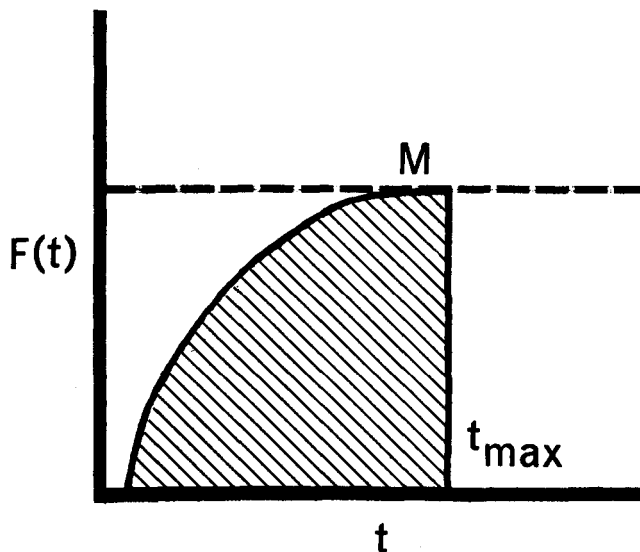
FIGURE 2.—Graph of the function $F(t)$ (see text). M is the potential maximum egg production.

$$F(t) = M(1 - \beta\, e^{-\xi t}) \text{ for } t \geqslant t_0,$$

or, since $F(t_0) = 0$ then $\beta = e^{\xi t_0}$ and

$$F(t) = M\ (1 - e^{-\xi(t-t_0)})\ \text{ for } t \geqslant t_0$$

and $F(t) = 0$ for $t < t_0$.

Therefore, taking logarithms,

$$\log_e \left(\frac{\hat{M} - \hat{F}(t)}{\hat{M}} \right) = -\ \xi(t-t_0) \text{ for } F(t) < M,$$

from which estimates of t_0 and ξ may be obtained by a regression analysis.

Thus, the complete model for characterizing daily egg production over lifetime

$$N(t) = M\ (1 - e^{-\xi(t-t_0)})\ e^{-at} \tag{2}$$

may be estimated by

$$\hat{N}(t) = \hat{M}\ (1 - e^{-\hat{\xi}(t-\hat{t}_0)})\ e^{-\hat{a}t}$$

in which the relevant parameters are (1) M, the potential maximum daily egg production; (2) t_0, the initial day of egg laying; (3) ξ, the rate of increase in egg laying; and (4) α, the rate of decrease in egg laying.

The model proposed here to describe daily egg production in *D. melanogaster* (equation (2)), implies that oviposition is under the influence of two components. Initially the rate of oviposition is increasing rapidly according to the component $M\ (1 - e^{-\xi(t-t_0)})$. This function may be thought of as describing the build-up of some factor, hormonal or otherwise, which governs either egg production in the ovaries or oviposition rate. However, the actual build-up does not tend asymptotically to M, the maximum potential output, and remain at this level, but is dampened by some other factor, probably an aging effect, which corresponds to the component of decrease, $e^{-\xi t}$. This second component is in effect throughout

the lifetime of the female and is the dominant term after the egg production has reached its maximum value.

The total egg production of a female during her productive lifetime may be found by integrating the function $N(t)$ over the time interval (t_0, t_s), where $t_0 > 0$ is the time at which the female begins egg production and t_s is age at death,

$$T(t_0, t_s) = \int_{t_0}^{t_s} M\,(1 - e^{-\xi(t-t_0)})\,e^{-\alpha t}\,dt$$

$$= \frac{M\,e^{-\alpha t_0}}{\alpha\,(1 + \alpha/\xi)}\,\{1 - e^{-\alpha(t_s-t_0)}\,(1 + \frac{\alpha}{\xi}\,(1 - e^{-\xi(t_s-t_0)}))\}$$

This expression does not immediately suggest a close relationship between length of life, $t_s - t_0$, and lifetime production since the bracketed term rapidly approaches unity as $t_s - t_0$ becomes large,

$$T(t_0, \infty) = \frac{M\,e^{-\alpha t_0}}{\alpha\,(1 + \alpha/\xi)} \tag{3}$$

A close relationship with $t_s - t_0$ could exist when measured across genotypes, however, if the parameter varies between genotypes and, as seems likely, varies inversely with the expected length of life. Thus, the correlation between $t_s - t_0$ and $T(t_0, t_s)$ observed by GOWEN and JOHNSON (1946) may simply reflect the fact that $t_s - t_0$ is essentially proportional in expectation to $1/\alpha$ which, in turn, is essentially proportional to $T(t_0, \infty)$. They also correlated $T(t_0, t_s)$ with the production $T(t_1, t_2)$ during a specific time interval,

$$T(t_1, t_2) = T(t_0, \infty)\,\{1 + (\alpha/\xi)\,(1 - e^{-\xi(t_1-t_0)}) - e^{-\alpha(t_2-t_1)}\,[1 + (\alpha/\xi)\,(1 - e^{-\xi(t_2-t_0)})]\}.$$

ROBERTSON and SANG (1944) have stated that egg production does not begin until day 2 or day 3 post eclosion. This will be the case only if $t_0 > 0$. If $t_0 < 0$, then the interpretation of the curve is difficult since $N(t=0) > 0$, indicates that the female is producing eggs prior to day zero. However, if one thinks of egg production in the ovaries as opposed to the actual deposition of eggs, then it follows that $t_0 < 0$ indicates that the development of eggs in the ovaries has commenced prior to eclosion. Integration of the lifetime egg production in this case would extend over the interval $(0, t_s)$.

By differentiating equation (2),

$$N'(t) = M\,\{-\alpha + (\xi + \alpha)\,e^{-\xi(t-t_0)}\}\,e^{-\alpha t}$$

Therefore, maximum egg production occurs at

$$t_{max} = t_0 + (1/\xi)\,\log_e\,\{(\xi+\alpha)/\alpha\}$$

It follows that the maximum egg production reached is,

$$N(t_{max}) = \frac{M\,\xi\,\alpha^{\alpha/\xi}}{e^{\alpha t_0}(\xi + \alpha)^{(1+\alpha/\xi)}}$$

Therefore the relationship between the total lifetime egg production, $T(t_0, \infty)$, and the maximum egg production reached is, from equation (3),

$$T(t_0, \infty) = (1/\alpha)\,\{1 + \xi/\alpha\}^{\alpha/\xi}\,N(t_{max}).$$

SUMMARY

A model for characterizing the daily egg production of *Drosophila melanogaster* females over their lifetime was derived. The form of the egg production

curve may be expressed by $N(t) = M(1 - e^{-\xi(t-t_0)}) e^{-\alpha t}$, where $N(t)$ is the egg production on the tth day postclosion; t_0 is the initial day of egg laying; M is the potential maximum daily output of eggs; ξ is the rate of increase in egg laying; α is the rate of decay of egg production.—The model incorporates a component of growth in egg production, reflecting the possible hormonal influence upon fecundity. Also, there is a component of decrease in egg laying related to the progressive aging of the female.—Expressions were deduced from the model to predict: the maximum egg production during the lifetime, $N(t_{max})$, and the day on which this occurs, t_{max}; the total egg production, $T(t_1, t_2)$ over a given period (t_1, t_2); in particular, $T(t_0, t_s)$, the female's lifetime production; also, the relationships between $t_s - t_0$, $T(t_0, t_s)$ and $N(t_{max})$.

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