## Abstract

Egg production in Drosophila typically begins 2 or 3 days after emergence of the adult female, and ~~increases its~~ daily production increases to a peak at 6 to 8 days then declines exponentially. The shape of this fecundity function is heritable, and in a study of its inheritance it became necessary to parameterize the function. A two-compartment model was devised which provided a satisfactory fit to observed egg production in a variety of strains. The model took the single form

Primordial Egg Cells

Mature Egg Cells
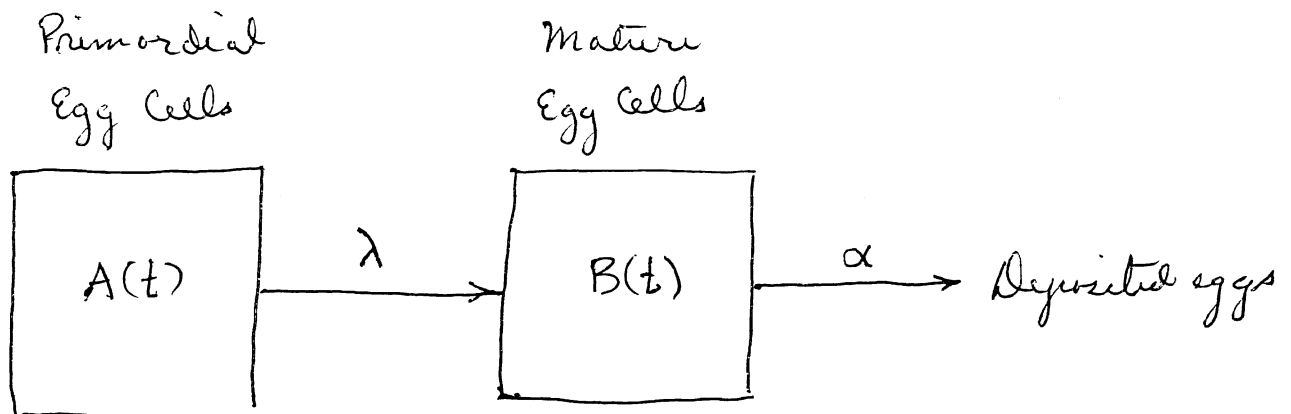
with initial conditions $A(t_o) = A_o$, $B(t_o) = 0$ and with the required egg deposition rate $N(t)$ being given by $\alpha B(t)$. Strains were then compared with respect to their values of the four parameters A_o, t_o, λ, α.

A GENERAL THEORY OF EGG PRODUCTION

by

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Introduction

Egg production in organisms which lay eggs continuously throughout their adult lifetimes, can generally be subdivided into two components. The first component is an increasing phase to a maximum egg production rate and the second component a decreasing phase from this maximum. For typical egg production profiles the simplest model involves a von Bertalanffy growth component and an exponential decay component. The overall profile is the resultant of these two components.

The Model

For simplicity, consider egg production as a two stage process. Mature eggs develop from 'primordial' egg cells and are then expelled from the ovary as 'developed' eggs. Assume that the initial number of primordial egg cells (A_o) is fixed at time t_o at which time they begin to develop at a constant instantaneous rate λ. Then the number of primordial egg cells remaining at time $t > t_o$ is

$$A(t) = A_o \, e^{-\lambda(t-t_o)}$$

Assume that mature eggs are deposited at a constant instantaneous rate α.

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If $B(t)$ is the number of mature eggs present in the female at time t, and $B(t_o) = 0$, 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 rate of deposition. Therefore,

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

Solving this equation with the initial conditions $A(t_o) = A_o$ and $B(t_o) = 0$, we have

$$B(t) = \frac{1}{e^{\alpha t}} \int e^{\alpha t} \lambda A(t) \, dt + \frac{C}{e^{\alpha t}}$$

where $C = $ constant and $A(t) = A_o e^{-\lambda(t - t_o)}$.

Hence

$$B(t) = \frac{e^{\lambda t_o}}{e^{\alpha t}} \int e^{\alpha t} \lambda A_o e^{-\lambda t} \, dt + \frac{C}{e^{\alpha t}}$$

$$= e^{-\alpha t} A_o e^{\lambda t_o} \int e^{-(\lambda - \alpha)t} \, dt + C e^{-\alpha t}$$

$$= e^{-\alpha t} A_o \frac{(-\lambda)}{(\lambda - \alpha)} e^{\lambda t_o} e^{-(\lambda - \alpha)t} + C e^{-\alpha t}.$$

But $B(t_o) = 0$ and since $e^{-\alpha t_o} \neq 0$,

$$C = \frac{\lambda A_o}{\lambda - \alpha} e^{\alpha t_o}.$$

So that

$$B(t) = e^{-\alpha t} \frac{\lambda A_o}{\lambda - \alpha} e^{\alpha t_o} \left\{ 1 - e^{-(\lambda - \alpha)(t - t_o)} \right\}.$$

Since $N(t) = \alpha B(t)$,

$$N(t) = e^{-\alpha t} \frac{\alpha \lambda A_o}{\lambda - \alpha} e^{\alpha t_o} \left\{ 1 - e^{-(\lambda - \alpha)(t - t_o)} \right\}.$$

or, letting $\xi = \lambda - \alpha$ and defining $M = \frac{\alpha \lambda}{\lambda - \alpha} A_o e^{\alpha t_o} = \frac{\alpha(\xi + \alpha)}{\xi} A_o e^{\alpha t_o}$

we obtain the model:

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

where M is the potential maximum daily egg production

t_o is the initial day of egg laying

ξ is the rate of increase in egg production

α is the rate of decrease in egg production

Derivations from the model

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_o, t_s), where $t_o > 0$ is the time at which the female begins egg production and t_s is age at death,

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

$$= \frac{M e^{-\alpha t_o}}{\alpha(1 + \alpha/\xi)} \left\{ 1 - e^{-\alpha(t_s - t_o)} \left[1 + \frac{\alpha}{\xi}(1 - e^{-\xi(t_s - t_o)}) \right] \right\}.$$

Letting $t_s \to \infty$, the bracketed term of this expression approaches unity and we obtain potential lifetime egg production,

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

Also, $T(t_o, \infty)$ may also be correlated with the production $T(t_1, t_2)$ during a specific time interval,

$$T(t_1, t_2) = T(t_o, \infty) \left\{ 1 + \frac{\alpha}{\xi}(1 - e^{-\xi(t_1-t_o)}) - e^{-\alpha(t_2-t_1)} \left[1 + \frac{\alpha}{\xi}(1 - e^{-\xi(t_2-t_o)}) \right] \right\}$$

By differentiating the equation for the egg production model,

$$N'(t) = M \left\{ -\alpha + (\xi + \alpha) e^{-\xi(t - t_o)} \right\} e^{-\alpha t}$$

Therefore, maximum egg production occurs at

$$t_{max} = t_0 + \frac{1}{\xi} \log_e \left\{ \frac{\xi + \alpha}{\alpha} \right\}$$

It follows that the maximum egg production reached is,

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

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

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

Interstrain egg production comparisons

Potential lifetime egg production, $T(t_0, \infty)$ has been expressed as

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

The constant M was defined as

$$M = \frac{\alpha(\xi + \alpha)}{\xi} A_0 e^{\alpha t_0}$$

Therefore

$$A_0 = \frac{M e^{-\alpha t_0}}{\alpha(1 + \alpha/\xi)} = T(t_0, \infty) .$$

Since A_0 is determined at t_0, it is independent of α and $\xi = -\alpha + \lambda$. 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 number of eggs actually laid by the female during her lifetime be $T(t_0, t_s)$ where t_s is the time of death of the female. Then $r(t_s) = T(t_0, t_s) / A_0$ is the proportion of the total potential egg production actually realised.

Hence

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

Now $E\left\{r(t_s)\right\} = \rho(\lambda, \alpha)$

$$\frac{\partial \rho}{\partial \lambda} = \frac{\alpha}{(\lambda-\alpha)^2} E\left\{e^{-(\alpha-\lambda)(t_s-t_o)} - \left[1 - (\alpha-\lambda)(t_s-t_o)\right]\right\} e^{-\lambda(t_s-t_o)} > 0$$

$$\frac{\partial \rho}{\partial \alpha} = \frac{\lambda}{(\lambda-\alpha)^2} E\left\{e^{-(\lambda-\alpha)(t_s-t_o)} - \left[1 - (\lambda-\alpha)(t_s-t_o)\right]\right\} e^{-\alpha(t_s-t_o)} > 0$$

Therefore $\rho(\lambda, \alpha)$ is an increasing function of both α and λ. With no selection pressure, α and λ would tend to increase indefinitely. However, environmental selection would determine intermediate values of these parameters to maximize fitness. This implies that strains of animals of the same species reared in the same environment would have similar $\rho(\alpha, \lambda)$. Hence $r(t_s)$ is not a suitable basis for comparison of egg production between such strains. Since $T(t_o, \infty)$ is independent of α and λ it therefore becomes the logical basis of interstrain egg production comparisons.

References

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McMillan, I., M.Fitz-Earle and L.Butler, 1969 Quantitative genetics of fertility. II Lifetime egg production in <u>Drosophila melanogaster</u> — Experimental. (Submitted for publication)

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Appendix : A modification of the model to include egg loss before deposition
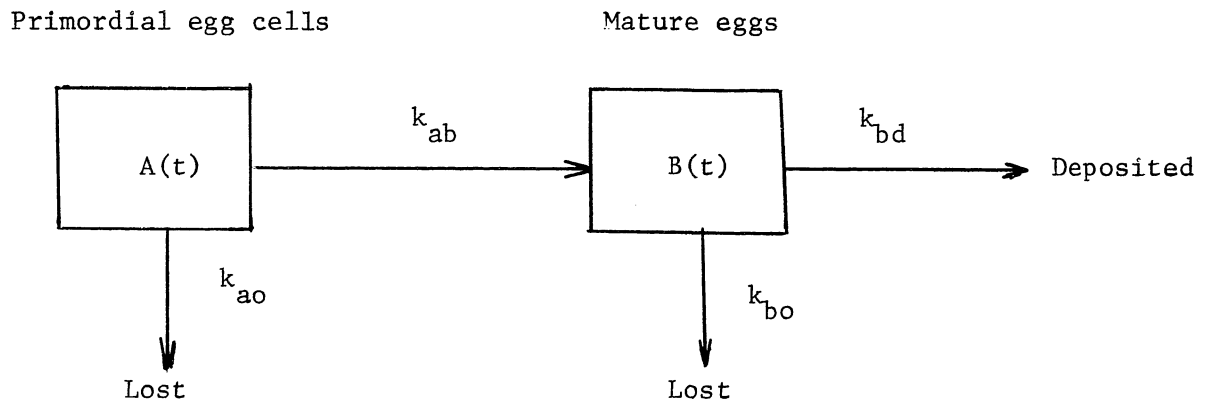
The egg production model as given earlier does not take into consideration loss of eggs either at the primordial stage or at the mature egg stage. In practice, such genetic wastage could exist through the atrophy and reabsorption of (1) the unfertilised developing eggs or (2) the fertilised eggs, through the effect of the male on zygote viability.

The first derivation of the model involved a two 'compartment' system: the primordial egg cells ($A(t)$) developing into mature eggs ($B(t)$) at an instantaneous rate k_{ab}, then being deposited from the ovary at an instantaneous rate k_{bd}. If we now include the loss rate from each compartment, k_{ao} and k_{bo} for the primordial and mature stages respectively, then with initial conditions $A(t_o) = A_o$ and $B(t_o) = 0$ as before,   the equations to be solved are

$$A'(t) = -(k_{ao} + k_{ab}) A(t)$$

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

The solutions are

$$A(t) = A_o e^{-(k_{ao} + k_{ab})(t - t_o)}$$

and $\quad B(t) = \dfrac{k_{ab} A_o}{(k_{ab}+k_{ao}) - (k_{bd}+k_{bo})} \left\{ e^{-(k_{bd} + k_{bo})(t - t_o)} - e^{-(k_{ao} + k_{ab})(t - t_o)} \right\}$

Thus, the rate of egg deposition is

$$N(t) = k_{bd} B(t) = \frac{k_{bd} k_{ab} A_o e^{(k_{bd} + k_{bo})t_o}}{(k_{ab} + k_{ao}) - (k_{bd} + k_{bo})} \left\{ 1 - e^{-[(k_{ab}+k_{ao})-(k_{bd}+k_{bo})](t-t_o)} \right\} e^{-(k_{bd}+k_{bo})t}$$

Letting $\quad k_{bd}k_{ab} = \beta$; $k_{ab} + k_{ao} = \lambda$; $k_{bd} + k_{bo} = \alpha$; then

$$\zeta = \lambda - \alpha = (k_{ab} + k_{ao}) - (k_{bd} + k_{bo}) \quad \text{and} \quad \frac{k_{bd} k_{ab} A_o e^{(k_{bd}+k_{bo})t_o}}{(k_{ab}+k_{ao}) - (k_{bd}+k_{bo})} = M.$$

Hence we obtain the model in the earlier form: $\quad N(t) = M(1 - e^{-\zeta (t-t_o)}) e^{-\alpha t}$.

It is to be noted that since two additional loss rates have now been introduced into the model, the k's cannot be estimated. Since A_o, the number of primordial egg cells at time t_o, is independent of all variables, it is the best egg production parameter for characterising a strain. Hence when females of a certain strain X are mated with a variety of males, it might be expected that A_o is characteristic to all females and therefore the values of A_o should be the same irrespective of the male. In practice, this is not the case and the discrepancies could be accounted for by the various egg losses which have been outlined above and included in the modified model. Now A_o can be readily obtained from the relationship $A_o = M e^{\alpha t_o}/\alpha (1 + \alpha/\zeta) = T(t_0, \infty)$. However, this does not use the loss factors included in the modified model and is therefore inaccurate. Unfortunately, it is impossible to obtain values for the k's and hence A_o cannot be estimated using

$$A_o = M e^{-(k_{bd} + k_{bo})t_o} \frac{[(k_{ab} + k_{ao}) - (k_{bd} + k_{bo})]}{k_{bd} k_{ab}} .$$