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COMPETITION AMONG IMMATURES AFFECTS THEIR ADULT FERTILITY: POPULATION DYNAMICS

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A great many organisms, including humans and flies, exhibit a life history phenomenon whereby the environmental conditions experienced by immatures can affect the adult phase of the life cycle. We are concerned with the consequences of this phenomenon for population dynamics. Some preliminary results have been reported (Prout 1984).

For population purposes the specific effects of interest are, first, the density of immatures resulting in their mutual competition for survival and, second, the lasting consequences of this competition on the fertility of these same individuals when they become adults. The type of population considered is one with discrete generations, so that the theory will consist of finite recurrence equations that incorporate this delay.

In part 1 we report some very limited data on certain life history attributes of *Drosophila melanogaster* in laboratory culture bottles. The data were collected in an attempt to explain the population behavior of the flies when they are kept on a discrete-generation regimen. Although this latter objective enjoyed only limited success, the important result is the family of recursion functions constructed to account for the effect on adult fertility of the density these adults experienced as larvae.

Part 2 documents the widespread occurrence of this biological phenomenon. The consequences for population dynamics are explored by a theoretical investigation of the recursion functions constructed in part 1 to accommodate the fly data. In part 2 we will also show that a number of designs for population experiments reported in the literature can lead to spurious conclusions because the experiments do not consider this delayed effect in the life cycle.

1. *DROSOPHILA* PROLOGUE

An experimental study was conducted of certain life history stages of *Drosophila melanogaster* in laboratory culture bottles. We undertook this investi-

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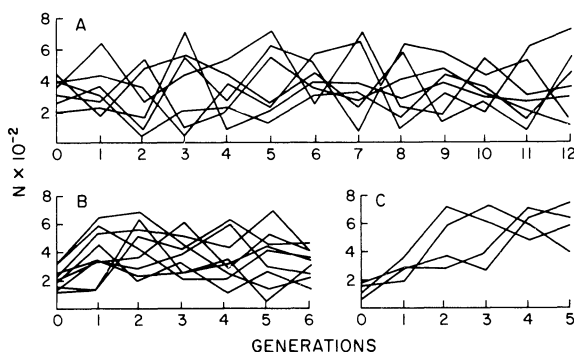


FIG. 1.—Three sets of populations exemplifying the variation in population size (N) produced by the regimen described in the text. Numbers of each set were maintained synchronously and during a different time interval from members of each other set. There are seven populations in set A, nine in set B, and five in set C.

gation because we have conducted a number of population genetic studies using discrete-generation bottle cultures, and although the genetic composition of the populations behaves reasonably well (see, e.g., Prout 1971; Foster et al. 1972), the total population size exhibits large and erratic variation.

Figure 1 shows three examples of population size data: seven populations maintained for 12 generations (A); nine populations maintained for 6 generations (B); and four populations maintained for 5 generations (C). (Four other, published examples can be found in Prout 1980, p. 18.) The consistently erratic behavior of this population regimen suggested that a study of the components of the life history might reveal that this laboratory regimen induces an underlying complex limit cycle, which enhances the stochastic variation.

The life cycle was divided into two parts, survival and fertility; survival was determined by counting adults produced by a known number of eggs, and fertility was determined by counting eggs produced by a known number of females.

MATERIALS AND METHODS

All experiments were performed under conditions as close as possible to those of the reference populations that motivated the study. A population in which adults had been emerging for 4 days was allowed to lay eggs in a standard $\frac{1}{2}$ -pint culture bottle for 24 h; the flies were then removed, counted, and discarded. This bottle was kept at 25° C for 14 days, during which time emergence, starting about day 10, was completed. This population, which we refer to as a “4-day-old population,” was then used to initiate a new round of 24-h egg laying to initiate the next generation. Thus, in the experiments to be described we attempted, whenever possible, to use flies from rather crowded (ca. 200–400) 4-day-old bottles. Although this procedure reproduced the population environment, it also generated large experimental errors, which resulted in a considerable sacrifice of statistical resolution.

In the egg-to-adult survival experiments, varying numbers of flies (from 4-day-old populations) were allowed to lay eggs for 24 h in "split bottles." These bottles were the same in every way as those used in the populations, except that they were cut into two parts about 2.5 cm from the bottom. After removal of the flies and the top half of the bottle, eggs were counted. The top was then replaced, secured by tape, and cultured at 25° C. The adults that emerged were counted. A wide range of egg numbers was obtained by simply varying the number of egg-laying adults among bottles. Fertility was usually determined by counting the number of eggs laid by 25 pairs ($N = 50$ flies) in split bottles for 24 h, which was the interval allowed for the females in the populations to lay eggs for the next generation. The only exception to this procedure was in the determination of the effects of adult density on fertility, when the number of flies was varied systematically. The stock used for all experiments has been under standard laboratory culture for over 10 yr and is designated "Desert Center." (This stock is available on request.)

Five experiments were performed to determine (1) the effects of egg density on egg-to-adult survival; (2) the effect of adult density on fertility; (3) the effect of egg density on the fertility of adults derived from the eggs; (4) the interaction between egg and adult densities and fertility; and (5) "maternal effects" of the fertility of female parents on egg-to-adult survival of offspring. The results of each of these experiments will be described in turn.

RESULTS

Egg Density and Egg-to-Adult Survival

The effects of egg density on survival are presented graphically in two ways. Figure 2A shows the number of adults, N , as a function of the number of eggs, n . Figure 3A shows the survival rate, $S(n)$, computed as $S(n) = N/n$. Figures 2B and 3B present the same data grouping the independent variable, egg numbers, into 200-egg intervals and placing the means of the dependent variables, N or $S(n)$, at the center of the interval.

In the section "Data Analysis and Conclusions," the results of fitting functions to the data of Figure 3A will be presented. It is sufficient to note here that there is a clear effect of egg density on survival. Biologically, this effect is, of course, due to competition among the larvae that hatch from the eggs. We also performed a separate, rather large-scale experiment on low egg densities ranging from 10 to 100 eggs per bottle. This experiment showed no trend over this region of low densities; the survival rate was approximately .85. The data from this latter experiment are not included in figures 2A and 3A. There is a "flat region" at very low densities, but it has essentially no effect on the global dynamics of the populations of figure 1.

Finally, figure 2 suggests that the population size in this regimen is not likely to exceed approximately 700 flies. This is in reasonable agreement with the data of figure 1. (The possibility of such a maximum will be discussed in some detail later.)

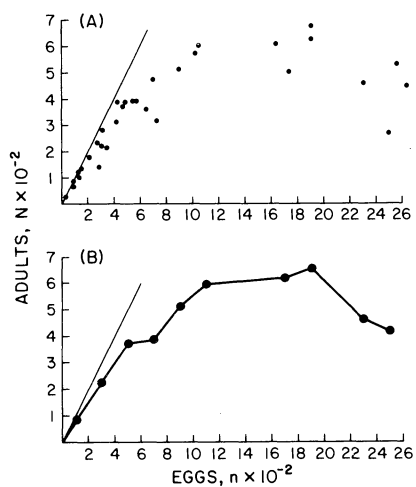


FIG. 2.—Adult population number, N , as a function of egg density, n : *A*, raw data; *B*, data grouped in 200-egg intervals. Mean number of adults, \bar{N} , placed at midpoint of the interval.

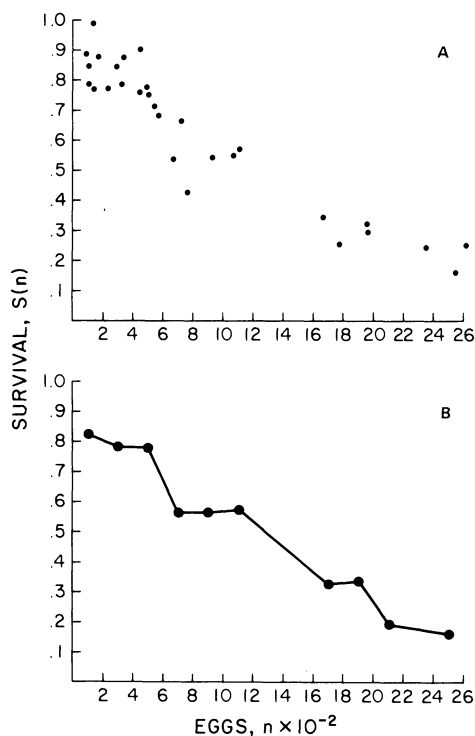


FIG. 3.—Egg-density data on fig. 2*A* converted to survival rate, $S(n) = N/n$: *A*, raw data; *B*, data grouped in 200-egg density intervals, as in fig. 2*B*.

Adult Density and Fertility

Figure 4 summarizes the experiments on the effects of adult density on their own fertility. The total eggs laid, n , is shown as a function of the number of flies, N . Sexes were counted separately, and equal numbers of females and males were introduced; thus, the number of females is $\frac{1}{2}N$. The three lines on the graph represent experiments done at different times; each point is the mean of five bottles. The principal conclusion is that there is no suggestion of nonlinearity; that is, the number of eggs laid per female is not affected by densities of up to 600 flies observed in the reference populations. Although adult crowding can affect egg laying, this particular regimen evidently holds adult numbers below what would result in such an adult crowding effect. Using linear regression for the three experiments we obtained fertility rates of 7.2, 6.0, and 5.6, with a combined estimate of 6.3 eggs (± 0.5 SE) per female. This value for 24-h fecundity was low because the females used came from crowded 4-day-old bottle populations.

Egg Density and Fertility

Fertility was determined for females that had emerged from bottles with initially different egg densities. Fertility is designated $F(n)$, representing the eggs per female as a function of the density of the population of eggs from which the females came. The measurement of $F(n)$ was done in the same way regardless of the egg density; namely, 25 pairs of flies were placed in a split bottle for 24 h, and the resulting eggs were counted. In this way we obtained fertilities of females from bottles with densities of 30–2530 eggs per bottle. The resulting data are presented in graphical form in figure 5, where the results in 5A are summarized in 5B using 200-egg intervals (as in figs. 2B, 3B).

The large errors in these data probably arise in part from the notorious variance in direct fertility measurements and in part from the fact that the females came, as usual, from crowded, 4-day-old cultures. Nevertheless, it is quite clear that egg density has a substantial effect on the resulting adult female fertility. This effect evidently results from the persisting effects of larval competition.

Interaction of Egg and Adult Densities and Fertility

In experiment 2, on the effects of adult density on fertility, the adults were pooled from 4-day-old moderately crowded bottles. The densities of the eggs from which the females came may affect their mutual sensitivity when laying eggs. That is, females only from low or high egg densities might show an adult density effect on fertility that was not evident in experiment 2.

We therefore conducted a limited experiment, designed to detect such an interaction. The experiment is limited in the sense that we tested fertility effects over a range with a maximum of only $N = 200$ (100 females); we accordingly have no information about such an effect at the substantially higher numbers the reference population does achieve. Nevertheless, we feel the results are of sufficient value to be included in this report.

Rather than count eggs to obtain a large number of flies raised at different egg densities, we set up culture bottles with different densities of female parents. Five

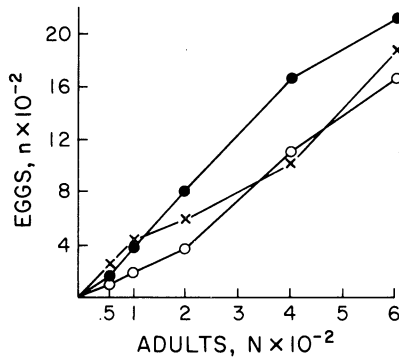


FIG. 4.—Total eggs laid, n , as a function of different fly densities, N . Half the flies were females. Each point is the mean of five bottles. Three different sets of experiments, done at different times from different source cultures, are shown.

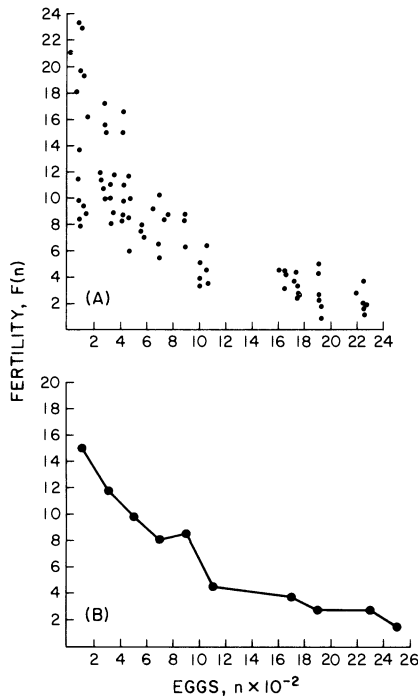


FIG. 5.—Eggs per female, $F(n)$, during 24-h intervals, as a function of the initial egg density in the cultures from which the females emerged: A, raw data; B, data grouped in 200-egg intervals. All fertilities were determined under standard conditions of 25 pairs per bottle for 24 h.

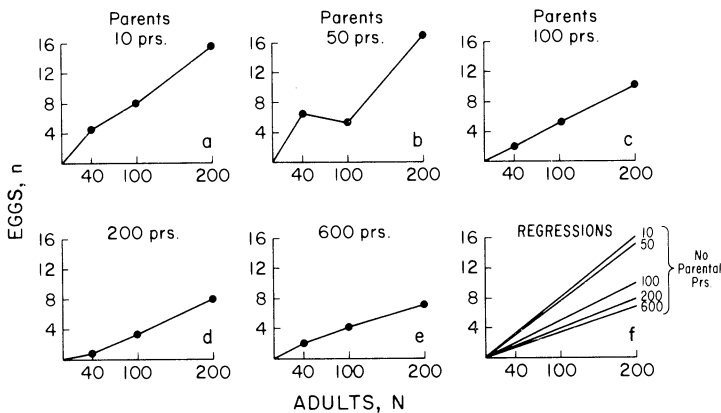


FIG. 6.—Each graph (except *f*) gives total eggs laid, n , in 24 h as a function of the density of flies, N , per bottle. Half the flies were females. Also given is the number of pairs of parents (\varnothing , σ) that produced the cultures from which the N egg-laying flies were taken. Graphs *a–e* show different levels of parental crowding. *f*, Linear regression lines of n on N obtained from *a–e*. Amount of parental crowding is indicated for each regression line. Each point on each graph is the mean of three bottles except in *b* where two bottles for each adult density were used.

sets of cultures were used, which had 10, 50, 100, 200, and 600 pairs of parental flies. The daughter flies from these different maternal densities were then used for this limited test of adult density (of daughters) on fertility. The results of this experiment are summarized graphically in figure 6. Each point on these graphs represents the mean of three replicate cultures, with the exception of *6b*, for which the points represent only two cultures each. There is no suggestion of nonlinearity of eggs produced, n , as a function of parental density up to at least $N = 200$. The linear regressions for all five experiments are shown together in figure 6*f*.

One additional reason for showing the results of this experiment is that it provides another data set showing the effects of egg density on fertility. Because the number of females is $\frac{1}{2}N$, the slopes of the regression lines in figure 6*f* are one-half the fertility, F , which is eggs per female. It can be seen in the figure that these slopes decrease with increased density of the parents that produced the flies whose fertility is being measured. This effect is summarized graphically in figure 7 with the coordinate of filial fertility as a function of maternal density. Using the findings in figure 4, which gave a value of 6.3 eggs per female, the data of figure 7 are in reasonable agreement with those in figure 5, which gives the fertility as a function of egg density.

We conclude that females emerging from uncrowded cultures or from very crowded cultures show no important effects of adult density on fertility at least up to densities of $N = 200$ flies. It is possible, of course, that the kind of interaction sought in these limited experiments could be manifested at higher adult densities.

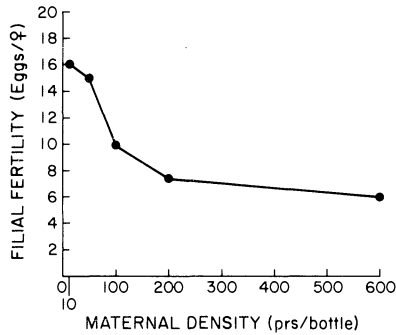


FIG. 7.—Data taken from fig. 6f. Filial fertility, $F(n)$, is twice the linear regression coefficient of the regression lines (no. females = $\frac{1}{2}N$ in f). Maternal density is as in fig. 6, the number of pairs (= females) per bottle that produced the daughters whose fertility is measured by $F(n)$.

Maternal Effects of Female Fertility on Offspring Survival

What are the limits of the persisting effects of larval crowding (proportional to egg density)? The effect persists to the adult stage for females. Does it continue into the next generation?

In order to answer this question, we performed two small-scale egg-to-adult survival experiments. In one we used eggs from females reared in crowded cultures, and in the other the egg-producing females came from uncrowded cultures. Specifically, the crowded females came from several bottles, having 2502–2633 eggs per bottle. The uncrowded females came from 40 bottles, with egg numbers ranging from 1 to 103.

Figure 8 gives the number of adults (N) as a function of the egg density, n , in two cases: *PC*, parents crowded; and *PU*, parents uncrowded.

A quadratic function of the form $N = An + Bn^2$ was fitted by least squares to both data sets. The resulting estimates of the constants A and B , shown on the graphs, clearly indicate no statistical difference in the survival of adults from eggs laid by females who themselves were reared in crowded conditions compared with the survival of those from uncrowded conditions. There could well be some kind of effect on the quality of the eggs produced by the two types of females, but the effect on egg-to-adult survival is evidently not large.

We therefore conclude that the reference population constitutes a well-defined recursive system, in which each operation begins and ends with eggs.

DATA ANALYSIS AND CONCLUSIONS

In order to use these life history data to deduce the dynamics of this bottle-population regimen (fig. 1), the data must be incorporated into a recursion function whose properties can be examined and compared with the population data. Even though the population data include the adult census, it follows from the preceding results that it is first necessary to construct the recursion between the

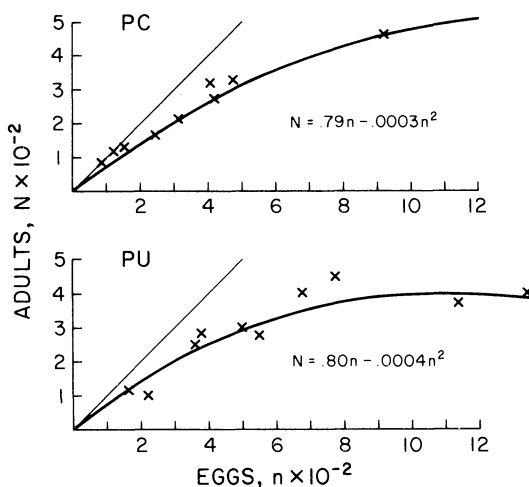


FIG. 8.—Adults, N , as a function of egg density, n , where the eggs were produced by females from crowded cultures, *PC*, and by females from uncrowded cultures, *PU*. *PC* females came from bottles initiated with egg densities of 2300–2500 eggs per bottle. *PU* females came from 40 bottles with egg densities of 1–103 eggs per bottle. Quadratic functions shown were fit to the data by least-squares regression.

numbers of eggs in succeeding generations, n_{t+1} and n_t . Furthermore, there are two intervening density-dependent processes, one affecting survival and one fertility, both dependent on the egg density, n_t . The recursion, therefore, should be of the following form:

$$n_{t+1} = F(n_t)^{1/2} S(n_t) n_t, \quad (1)$$

where $F(n_t)$, fertility, and $S(n_t)$, survival, are both decreasing functions of n_t . (The factor $1/2$ indicates that one-half of the survivors are females.) Three functions were fitted by nonlinear regression to the survival data (fig. 3A) and to the fertility data (fig. 5A). These functions are defined in table 1. The uppercase letters define maximum survival, S , or fertility, F , and lowercase letters are sensitivity parameters for survival, s , and fertility, f .

Table 2 shows the results of fitting the three functions to the two data sets. The parameter estimates with their standard errors are given. Also shown are the total variance of the dependent variable, the mean square error obtained from the residual sum of squares (normalized by dividing by the total variance), and the fraction of the total variance explained by the regression function.

In the case of survival, it is evident that the data will accommodate all three functions equally well. In the case of fertility, the linear function clearly provides a poorer fit than the two curvilinear functions. This is not surprising because, although the data of figure 5A are highly variable, there is a distinctly curvilinear aspect. In general, however, owing to the obviously large inherent errors in the two data sets and the general paucity of data, no statistical procedure will be capable of clearly discriminating between the functions used. More-extensive data

TABLE 1
SURVIVAL AND FERTILITY FUNCTIONS

FUNCTION	Survival*	Fertility**
Linear	$S - sn$	$F - fn$
Exponential	$S e^{-sn}$	$F e^{-fn}$
Hyperbolic	$S(1 + sn)^{-1}$	$F(1 + fn)^{-1}$

* S , maximum survival; s , sensitivity parameter for survival.
 ** F , maximum fertility; f , sensitivity parameter for fertility.

TABLE 2
RESULTS OF FITTING FUNCTIONS TO THE DATA

	SURVIVAL		
	Linear, L_S	Exponential, E_S	Hyperbolic, H_S
Maximum, S (\pm SE)*	.845 ($\pm 2.69 \times 10^{-2}$)	.898 ($\pm 3.72 \times 10^{-2}$)	.929 ($\pm 5.51 \times 10^{-2}$)
Sensitivity parameter, s (\pm SE)*	2.8×10^{-4} ($\pm 2.2 \times 10^{-5}$)	5.4×10^{-4} ($\pm 6.6 \times 10^{-5}$)	8.3×10^{-4} ($\pm 17.5 \times 10^{-5}$)
Sample size, N	31	31	31
Total variance, V	6.26×10^{-2}	6.26×10^{-2}	6.26×10^{-2}
Mean square error, MSE†	$.11 \times 10^{-2}$	$.17 \times 10^{-2}$	$.14 \times 10^{-2}$
MSE/ V	.018	.027	.022
Explained variance‡	.982	.973	.978
	FERTILITY		
	Linear, L_F	Exponential, E_F	Hyperbolic, H_F
Maximum, F (\pm SE)*	13.538 ($\pm .397$)	16.429 ($\pm .873$)	19.081 (± 1.448)
Sensitivity parameter, f (\pm SE)*	5.7×10^{-3} ($\pm 5.3 \times 10^{-4}$)	1.0×10^{-3} ($\pm 1.2 \times 10^{-4}$)	2.2×10^{-3} ($\pm 4.3 \times 10^{-4}$)
Sample size, N	75	75	75
Total variance, V	29.95	29.95	29.95
Mean square error, MSE†	11.84	9.44	9.42
MSE/ V	.395	.315	.315
Explained variance‡	.605	.685	.685

* Standard error.

† Obtained from residual sum of squares.

‡ Fraction of total variance explained by regression function.

TABLE 3

RECURSION FUNCTIONS RESULTING FROM COMBINING COMPONENT FUNCTIONS

SURVIVAL \times FERTILITY	Symbol	Function*
Linear \times linear	$L_S L_F$	$R - \frac{1}{2}(Sf + Fs)n + \frac{1}{2}sf n^2$
Exponential \times exponential	$E_S E_F$	$R e^{-(f+s)n}$
Hyperbolic \times hyperbolic	$H_S H_F$	$R[1 + (f + s)n + fsn^2]^{-1}$
Linear \times exponential	$L_S E_F$	$R e^{-fn} - \frac{1}{2}sFn e^{-fn}$
Linear \times hyperbolic	$L_S H_F$	$(R - \frac{1}{2}Fsn)(1 + fn)^{-1}$
Exponential \times hyperbolic	$E_S H_F$	$R(1 + fn)^{-1} e^{-sn}$

* $R = \frac{1}{2}FS$.

obtained under more rigorously controlled experimental conditions would be required for this.

Nevertheless, these life history data can be combined to provide some limited information concerning the dynamics of this population regimen, and, more important, in part 2 they will be used for numerical illustrations of a class of models with rather novel behavior that could have general implications. Indeed, this is the principal reason for presenting the data of this section.

We will therefore proceed to construct the egg-to-egg recursion function set forth in its most general form as equation (1). Since none of the functions in table 2 stand out as clear favorites, we will construct all nine recursion functions by forming the nine possible products of the three fertility and three survival functions of table 1. The resulting functions are shown in table 3. Only six of the nine are shown: the first three are products of components with the same functional forms; the second three are products with different functional forms. The second column defines a shorthand procedure for identifying the functions. Not shown are the three remaining products of the functions of different form: $E_S L_F$, $H_S L_F$, and $H_S E_F$. These are the same as their counterparts shown in the table except for the exchange of F for S and f for s . The functions are written in such a way as to show that in five of the six, the four component parameters collapse into three parameters. In the case of the product of two exponential components the result is also an exponential function, so that the four parameters collapse to two. R is the finite rate of increase when n is small and is defined as shown, $R = \frac{1}{2}FS$. For each of the nine product functions, the equilibrium egg numbers, k , can be calculated as well as the single eigenvalue associated with the equilibrium by

$$\left. \frac{dn_{t+1}}{dn_t} \right|_{n' = k} = \lambda.$$

Also, the equilibrium adult numbers, K , can be obtained by the relation

$$K = S(k)k.$$

The numerical results of these calculations and additional information are shown in table 4. To have some means of ranking the functions for a combined goodness of fit, the normalized mean square errors for the two components were summed;

TABLE 4
PARAMETER VALUES AND OTHER CHARACTERISTICS OF RECURSION FUNCTIONS

FUNCTION*	MSE†	RANK	$\lambda‡$	$k§$	$K^ $	$N(\max)^{\#}$	FOR CYCLES		
							Of Points	Minimum N^{++}	Maximum N^{++}
L_3E_F	.332	1.5	-1.14	1330	629	637	2	504	629
L_3H_F	.332	1.5	-.67	1435	636				
H_3E_F	.337	3.5	-.82	1282	577				
H_3H_F	.337	3.5	-.29	1387	599	(1119)**			
E_3E_F	.343	5.5	-.998	1278	572	607			
E_3H_F	.343	5.5	-.50	1371	587				
L_3L_F	.412	7	-1.86	1542	637	637	?		
E_3L_F	.417	8	-1.52	1498	599	607	8	335	607
H_3L_F	.423	9	-1.10	1486	538	(1119)**	4	432	699

* See table 3 for symbols.

† Mean square error as in table 2.

‡ λ is the eigenvalue.

§ k is the equilibrium number of eggs.

|| K is the equilibrium number of adults.

Altitude of hump.

** Limit of the $A(n)$ function, S/s .

†† Largest and smallest points in the cycle for adults.

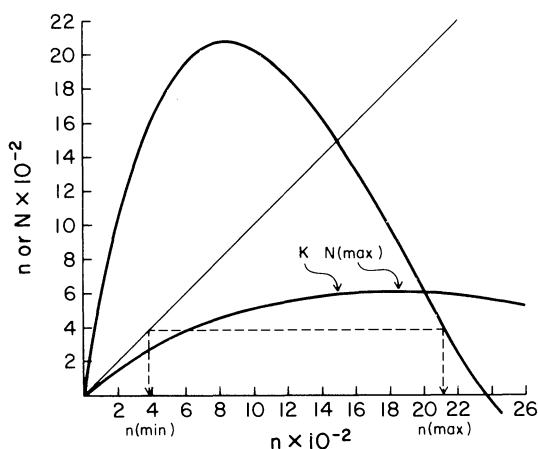


FIG. 9.—The upper curve is the $E_S L_F$ recursion function of $n_{t+1} = (F - fn_t)^{1/2} S \cdot \exp(-sn_t)n_{t+1}$. The lower curve gives the number of adults, N_t , from eggs, n_t , $N_t = S(n_t)n_t$ or $N_t = S \exp(-sn_t)n_t$. K and $N(\max)$ are the equilibrium and maximum points, respectively, for adults. Likewise, $n(\min)$ and $n(\max)$ are, respectively, the minimum and the maximum number of eggs possible. Dashed line shows the two successive iterations which give $n(\min)$ and $n(\max)$.

these values for the nine functions are ranked with the smallest combined error at the top and largest at the bottom.

As expected from the lack of clear discrimination among the fits of the component functions based on their mean square errors, the nine combined functions do not show impressive differences between those giving the best and worst fits. The fourth column gives the eigenvalue, λ ; the fifth, the equilibrium number of eggs, k ; and the sixth, the equilibrium adult numbers, K .

To explain the remaining calculations in the table and also to display some additional features common to all the functions, figure 9 shows a graphical representation of the recursion resulting from combining exponential survival, E_S , and linear fertility, L_F or $E_S \times L_F$. This has the resulting functional form of equation (4) in table 3 when this function is multiplied by n_t to obtain n_{t+1} . This recursion is the upper curve in the figure. The lower curve is the egg-to-adults function, $N = S(n)n$, which in this case is

$$N = nS \exp(-sn) . \quad (2)$$

In this case the adult numbers pass through a maximum, $N(\max)$. The linear survival function also produces a maximum for adult numbers ($N = Sn - sn^2$). The hyperbolic survival function does not produce a maximum, but as $n \rightarrow \infty$, $N \rightarrow S/s$, which sets an upper limit to adult numbers. The maximum (or limiting value in the H_S case) is also listed in the table.

The graphical representation in figure 9 shows that K is very close to $N(\max)$. This is also true for the five other cases in the table for which the linear or exponential survival functions were used. The figure shows two other features common to all nine functions that are not indicated in the table. First, if the

population is initiated with moderately low egg numbers, the system can never crash "naturally," even though the recursion itself can take negative values if the initial value is high enough ($n_t > \text{ca. } 2400$ in fig. 9). The minimum value of n , $n(\text{min})$, is shown. Four other functions have a linear component function such that negative values are possible, but in all cases $n(\text{min}) > 0$. This conforms to the reference populations where crashes never occurred.

The second feature of the graph to note is a minor one involving an apparent discrepancy with the data: the number of adults that survive from the $n(\text{max})$ eggs is greater than the number of eggs they produce, $n(\text{min})$. This might appear to be a discrepancy with the fertility data, in which even at the highest egg densities the number of eggs per female did not drop to fractional values. This discrepancy is only apparent because N in the figure is for total individuals, only half of which are females. This function and all the others accurately reflect, as they must, the fertility data from which they were derived. Finally, all recursion functions exhibit a single maximum similar to the one in figure 9.

Table 4 shows that all eigenvalues are negative, and for four of the nine, $\lambda < -1$. The number of points in the resulting cycles and the maximum and minimum values of adults are also shown.

Figure 10 shows a few generations of iteration of the $E_S L_F$ function whose recursion function is shown graphically in figure 9. This function has an eight-point limit cycle. Figure 10A for egg numbers shows two complete cycles. The dashed line is the equilibrium egg number, $k = 1442$. Figure 10B shows the corresponding adults, N . Because of the proximity of K to $N(\text{max})$, the points corresponding to high points for egg numbers are "truncated," so that the adults are either close to K or substantially below it.

The $L_S L_F$ function apparently produces chaos, or at least a complex limit cycle. In figure 11A, egg numbers were iterated for 20 generations; 11B shows the corresponding adult numbers. In this case the adults almost always remain below the equilibrium, K , because, as shown in table 4, $N(\text{max})$ and K are the same.

Discussion of additional aspects of these recursion functions is deferred to part 2, so that we can assess the extent to which the results of this life history study can explain the behavior of the experimental reference populations of figure 1.

Although all the eigenvalues were negative, only four of the functions give limit cycles. Clearly, more-extensive data are required for distinguishing between the models. Indeed, we cannot rule out at this point the possibility that all of the variation is due to stochastic variation around some stable equilibrium. What information we have, but have not presented, about the culture variance in fertility for a given number of females and about the variance of viability for a given number of eggs permits the possibility that all of the variation could be the result of stochastic effects. A very large study would be required to investigate this question, as well as to distinguish models. However, that the model-fitting procedure could have ruled out limit cycling but did not do so permits the conclusion that limit cycling is a possibility. The equilibrium population size, K , produced by the nine functions seems at first too high, since the actual populations range from about 100 to 800 with a median size of about 350 (depending on which set of populations is used, see fig. 1). Two of the survival functions place a

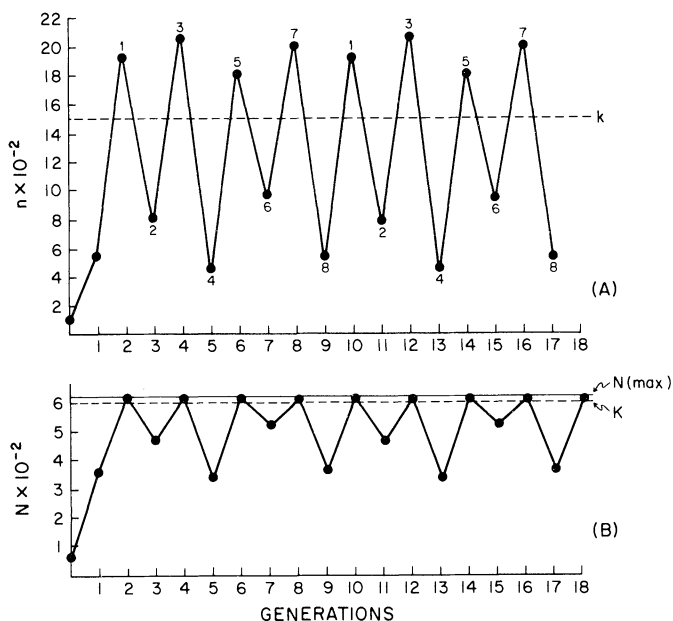


FIG. 10.—Iteration of $E_S L_F$ recursion shown in fig. 9 for two complete 8-point cycles. *A*, The 8 points are numbered; k , equilibrium eggs. *B*, Adult numbers from lower curve in fig. 9; K , equilibrium; $N(\max)$ adult maximum as shown in fig. 9.

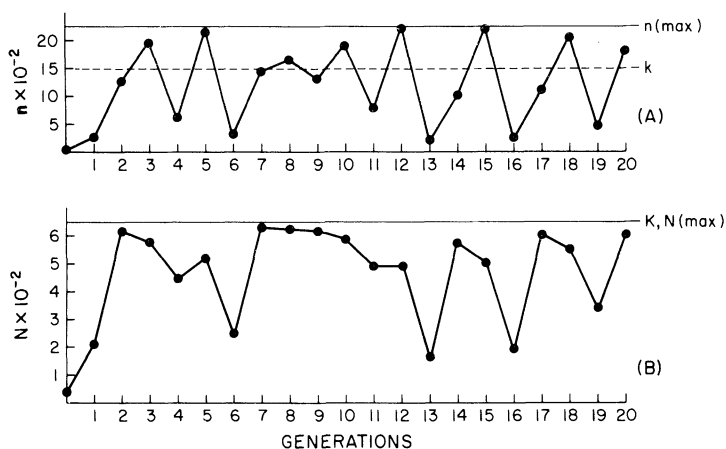


FIG. 11.—Iteration for 20 generations of the $L_S L_F$ function. *A*, Eggs; *B*, adults. $n(\max)$, k , $N(\max)$, K as defined in fig. 9.

maximum on adult numbers, and in the cases with limit cycling, the cycling points sometimes cover rather well the range of observed population numbers. Even the hyperbolic survival function dampens the upper ranges of population size, $N(\max) = 1123$. Such an upper limit on size would also tend to lower the purely stochastic effects with respect to a stable equilibrium of the magnitude we have obtained. It would appear then that the adult equilibrium estimates are compatible with the population data.

After constructing the theoretical egg-to-egg recursion functions, as illustrated in figure 9, the adult-to-adult recursion function was constructed for comparison with the pattern of empirical one-generation transitions derived from the experimental populations. This graph produced a scattergram with no discernible pattern. We will show in the next section, however, that for six of the nine functions the theoretical adult-to-adult recursion is not defined.

The principal conclusion here is that the limited data of this *in vitro* life history study resulted in a set of theoretical models, most of which were in reasonable agreement with *in vivo* behavior of the running populations. This establishes the main purpose of presenting the data of this section: the parametric values of these functions were provided by the flies and, as such, are biologically reasonable; we therefore feel confident in using any one of this family of recursion functions for numerical illustrations of the theoretical considerations to follow.

2. THEORY AND APPLICATIONS

In this part we examine some of the theoretical properties of the recursion functions devised to accommodate the fly data of part 1. We then discuss how these theoretical findings might be relevant to the interpretation of several experimental studies that have been published by others.

It is important to point out that we are addressing a rather widespread phenomenon. This delayed effect on fertility arising from competition before maturity may be influencing the population dynamics of a great many organisms. Following the first studies on *Drosophila*, the effect of larval density or larval nutrition on adults has been reported on many occasions. Probably the first were the experiments of Alpatov (1930) and Pearl (1932), with subsequent documentation by Robertson and Sang (1944), Robertson (1957), Barker and Podger (1970), Caligari (1980), and Marks (1982). Most studied the effects of larval crowding on adult body size, but it has been shown on several occasions (Chiang and Hodson 1950; Robertson 1957) that fertility is proportional to body size when body size varies for this reason. In species other than *Drosophila*, the effect seems widespread (Marlatt 1907; Uhlenhuth 1919; Citus 1935; Ryan 1941; Bates 1949; Istock 1966; Southwood 1966; Azam and Anderson 1969; Engelmann 1970; Brown and Chippendale 1973; Wilbur and Collins 1973; Otto 1974; Lloyd and White 1976; Wilbur 1977; Howard 1978; Pritchard 1978; Steinwascher 1978; Sweeney and Vannote 1978; Vannote 1978; Anderson and Cummins 1979; Dunlap-Pianka et al. 1979; Ward and Cummins 1979; Caligari 1980; Harshman 1982; Marks 1982).

These citations, together with those for *Drosophila*, cover 15 species of insects spanning four orders, and one species of anuran as well. In addition, it is common

knowledge among entomologists that in order to rear healthy, fecund females, optimum larval conditions are required. Moreover, adult body size in *Drosophila* (Atkinson 1979) and in house flies (J. Kaeding, pers. comm.) has been used to assess the degree of larval crowding in natural populations. Finally, even in humans there is some evidence of a negative correlation between female cohort size and birth rate (Easterlin 1961, 1968). (Sociologists might protest against invoking here the same causes that apply to insects.)

Equation (1) is the most general formulation incorporating this delayed effect into population dynamics. This equation is repeated here, incorporating the factor $\frac{1}{2}$ into the fertility component.

$$n_{t+1} = F(n_t) S(n_t) n_t. \quad (3)$$

This formulation embodies three more assumptions. The first is the assumption of discrete generations. This can be arranged in laboratory populations, but discrete generations occur in many natural life histories, especially in species of univoltine insects, fish, and even birds. The second assumption is that adults enjoy a superabundance of resources for their own survival and for egg laying. This proved to be the case for the laboratory populations studied here, but other regimens of laboratory *Drosophila* population, such as the serial-transfer method (Buzzati-Traverso 1955), may well allow adult numbers in bottles, vials, or other containers to become great enough that competition occurs, in which case the fertility function is more complex, viz., $F(N, n)$. There are many natural life histories, perhaps including that of *Drosophila*, in which resources appear to be limiting for immatures only. The third additional assumption embodied in equation (3) is that there is no environmentally induced maternal effect. The extent to which this lack of maternal effect occurs is not known, even for *Drosophila*. Maternal effects do exist (as discussed, for instance, for *Hyla*; Kaplan 1980; Travis 1981); the maternal environment affects egg size, which in turn affects the time to metamorphosis. In plants, maternal effects are the rule rather than the exception.

Equation (3), therefore, makes four major assumptions (and many minor ones). The number of natural and artificial populations that satisfy all four assumptions is probably not overwhelming, but we would like to believe that there are enough to render their theoretical properties worthy of investigation.

DYNAMICS OF ADULT CENSUS: THEORY

We now examine in some detail the effect of the egg-to-egg recursion, natural for this system, on the adult-to-adult recursive relationship, N_{t+1}, N_t . This is because most experiments and observations report adult census data, as was the case in the fly study of part 1.

This system produces two distinct kinds of adult recursive relationships, which depend on the form of the egg-to-adult function, $N = S(n)n$, stated more succinctly hereafter as $N = A(n)$. The first type occurs when $A(n)$ is an increasing function of n ; the second type occurs when $A(n)$ passes through a maximum as n increases, $A'(\bar{n}) = 0$.

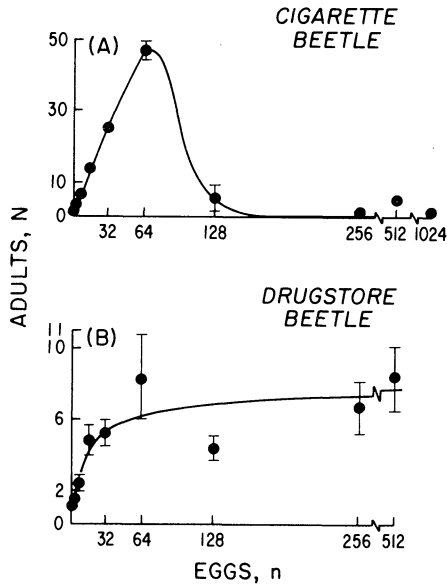


FIG. 12.—Adults, N , from eggs, n : A, cigarette beetle, *Lasioderma serricorne*; B, drugstore beetle, *Stegobium paniceum*. The fitted function is $N = n(1 + an)^{-b}$. Modified from Bellows (1981). Common names from Sutherland (1978).

We use the data in figure 12 taken from Bellows (1981) as living examples: the drugstore beetle (*Stegobium paniceum*) indicates no maximum in the $N = A(n)$ function; the cigarette beetle (*Lasioderma serricorne*) clearly shows that there is a maximum. (The fly data of fig. 2 suggest a maximum, but because of the large errors this cannot be ascertained with certainty; the existence of a maximum in the case of the cigarette beetle is unambiguous.)

The two types of adult recursion arise from the fact that in order to construct the recursion, it is first necessary to multiply the N_t adults by their fertility, viz., $F(n_t)N_t$, and in order to obtain $F_t(n_t)$, it is necessary to know n_t , the number of eggs from which the adults arose.

We will refer to cases like that of the drugstore beetle, for which $A(n)$ is an increasing function, as “smooth.” Here, the number of eggs can be calculated, in principle, because the function is invertible; but in the cigarette case, hereafter referred to as “humped,” the number of eggs producing a given number of adults is literally ambiguous.

Consider first the case of the smooth adult function. Examples are provided by three of the nine functions used in fitting the data of part 1. These are the three functions that employed the hyperbolic function for egg-to-adult survival. The hyperbolic function is smooth because it is an increasing function of n , and it is invertible as follows.

$$\text{Hyperbolic } A(n): N = Sn(1 + sn)^{-1} \quad (4)$$

$$\text{Inverse: } n = N(S - sN)^{-1} \quad (5)$$

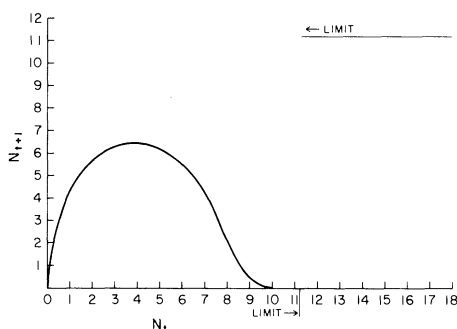


FIG. 13.—Adult-to-adult (N_{t+1}, N_t) recursion function derived from the $H_S E_F$ recursion function for eggs (n_{t+1}, n_t). The (N_{t+1}, N_t) function is eq. 6. LIMIT \rightarrow indicates the discontinuity at $N = 1123$.

The right side of equation (5) can now be substituted into $F(n)$, and the general equation (3) moved a “half”-generation forward to give a recursion function in N :

$$\text{if } n_{t+1} = F(n_t)N_t \quad (6a)$$

$$\text{and } N_{t+1} = S(n_{t+1})n_{t+1}. \quad (6b)$$

Then using, for example, the exponential function for $F(n)$ (see table 1) and equation (4) above for equation (6b), the result is

$$N_{t+1} = \frac{SFN_t \exp [-fN_t(S - sN_t)^{-1}]}{1 + sFN_t \exp [-fN_t(S - sN_t)^{-1}]} \quad (6c)$$

Using parameters provided by the experiment, this function (shown in fig. 13) produces a discontinuity of the “jump” type. When equation (5) is used together with the other two fertility functions, the hyperbolic type of discontinuity results. In all three cases, however, this is not really pathological because no matter how large the number of adults and the number of eggs, the number of progeny surviving to adulthood cannot exceed \tilde{S}/s ($= 1123$, in this case), which is the limit of equation (4) as $n \rightarrow \infty$. Thus, the next generation ($t + 1$) after very large N_t will always yield $N_{t+1} < S/s$ ($= 1123$); the population will be in the well-behaved region of figure 13 thereafter.

The production of a discontinuity is not a general property of the smooth $A(n)$ function, since some data sets might better fit an $A(n)$ function that increases without a limit, although such a situation might seem dubious on biological grounds.

It is important to consider now the humped $A(n)$ survival functions in order to demonstrate the two kinds of adult-to-adult recursive relationships. With the humped $A(n)$ function, an adult-to-adult recursion function is not defined because the fertility, $F(n_t)$, of the N_t adults cannot be determined since the number of eggs, n_t , that produce a given number of adults is ambiguous. A formal demonstration of this fact is straightforward. A given number of adults, \tilde{N}_t , can result from two different egg numbers, n_{1t} or n_{2t} , which are on either side of the maximum. This

means there could be two different fertilities $F(n)$, producing two different numbers of eggs in $t + 1$, as follows:

$$n_{1,t+1} = F(n_{1t})\tilde{N}_t \quad (7a)$$

$$n_{2,t+1} = F(n_{2t})\tilde{N}_t. \quad (7b)$$

This, in turn, means that \tilde{N}_t adults could give rise to two different numbers of adults in generation $t + 1$:

$$N_{1,t+1} = S(n_{1,t+1})n_{1,t+1} \quad (8a)$$

$$N_{2,t+1} = S(n_{2,t+1})n_{2,t+1}. \quad (8b)$$

Thus, in the humped case there is evidently a one-to-two mapping between the number of adults in one generation and the next.

The formal properties of this mapping have not been studied, but the numerical results of fitting the functions to the fly data of part 1 can be used to display some of the geometrical behavior of this one-to-two mapping. A graph can be constructed by successive iterations for “1½” generations, starting each time with a different initial n_t as follows:

$$\text{Adults of generation } t: \quad N_t = S(n_t)n_t \quad (9a)$$

$$\text{Adults of generation } t + 1: \quad N_{t+1} = S[F(n_t)N_t]F(n_t)N_t. \quad (9b)$$

Four numerical examples are shown in figure 14. The stability of each system is indicated by the eigenvalue, λ , as recorded in table 4. In one case the survival function is exponential, and in the other three it is linear, so that in all four the $A(n)$ function has a hump. In each case the graph was produced by performing the 1½-generation iteration using equations 9, beginning with small values of n_t and then repeating the process with systematically increasing increments of the initial n_t . The arrows indicate the path of the (N_t, N_{t+1}) point with increasing initial n_t .

The $E_S E_F$ graph forms a simple loop that passes through the equilibrium, K , and then retreats toward the limit $(0,0)$. Three cases are not shown: $E_S L_F$, $E_S H_F$, and $L_S E_F$. All three form loops similar to the $E_S E_F$ case except that the $E_S L_F$ and $L_S E_F$ retreats become negative. The $L_S H_F$ graph crosses the 45° line at K ; in addition, it crosses the diagonal again at $(250, 250)$. In the lower left $L_S L_F$ graph what appears to be a cusp is a tight loop just tangent to the 45° line at K . We computed the lower right $L_S L_F$ simply to provide a better display of looping; this case crosses the 45° line three times and the most extreme right-hand point is at K . To compute this case, different $L_S L_F$ parameter values were used. (See the legend; these parameters are within 1 SE of the point estimates given in table 2.)

Figure 15 is a graph of the parent-offspring transitions taken from the first 10 generations of continued iteration of the $L_S L_F$ case shown in figure 11B. The points sketch the left $L_S L_F$ graph of figure 14, as they must. But, of course, a naive observer would hardly be expected to recognize the figure 14 graph from the figure 15 sketch of it. We have more to say on this.

We call these graphs produced by the humped- $A(n)$ case “foldback” figures for geometrical reasons that will become apparent shortly. Although we have made

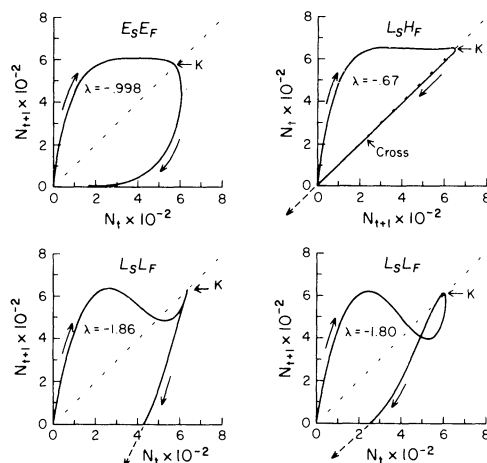


FIG. 14.—Examples of the one-to-two graphing of (N_t, N_{t+1}) for cases where the egg-to-adult function, $A(n)$, is humped. Functions are shown on the graphs and the method for making the computations is explained in the text (eqs. 9a, 9b). Arrows indicate the path of (N_t, N_{t+1}) with increasing initial n_t . λ is the eigenvalue associated with k calculated from the egg-to-egg recursion function. K is the adult equilibrium. The parameters are from table 2 for all but the lower right graph. Parameters for the lower right: $S = .859$, $s = .3 \times 10^{-3}$, $F = 13.4$, $f = 5.3 \times 10^{-3}$. Slope of the tangent at K is not necessarily equal to λ .

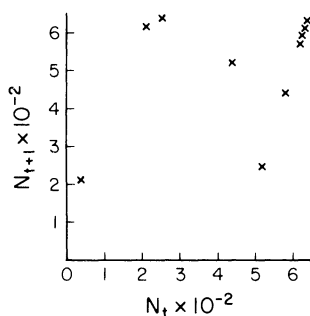


FIG. 15.—One generation's transitions, N_{t+1}, N_t , taken from the first 10 generations of iterations of the $L_S L_F$ function shown in fig. 11B.

no formal study of this system, we have devised a geometrical procedure that is useful in understanding how these foldback figures are generated. Figure 16 depicts a geometrical procedure for constructing the adult foldback figure. In figure 16A, the right side of the ordinate constitutes the space with n_{t+1}, n_t coordinates. The upper curve is the egg-to-egg recursion function as indicated. The lower curve in this same space is the $A(n)$ function; for this curve the ordinate is read as N_t adults. The space to the left of the line has the adult coordinates N_{t+1}, N_t , with N_t increasing to the left. The $1\frac{1}{2}$ -generation recursion of equations

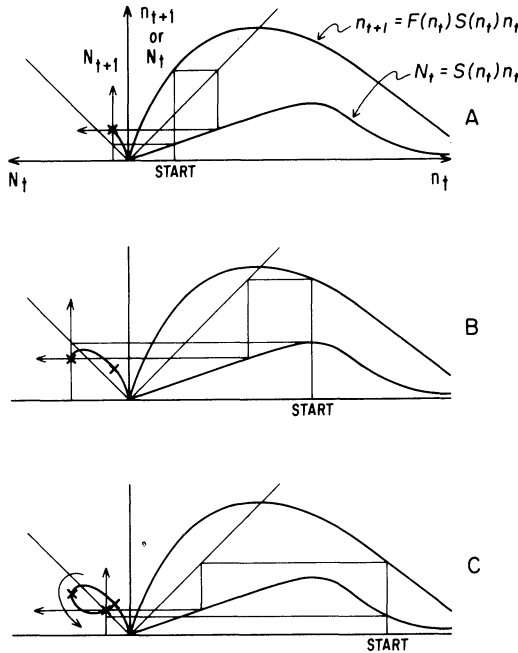


FIG. 16.—Geometrical representation of the $1\frac{1}{2}$ -generation iteration procedure, eqs. 9, for constructing the one-to-two mapping or foldback figures, illustrated in fig. 14. The space to the right of the ordinate has coordinates as indicated by the two functions. The left space has coordinates as indicated with N_t increasing to the left. The iteration procedure shown in 16A,B,C is explained in the text.

(9) can now be constructed graphically. A single N_{t+1}, N_t point is shown in figure 16A. On the right a number of eggs, n_t (“start”) survive to adults, N_t . A horizontal line is drawn to the left into the N_{t+1}, N_t space to the equality line, then downward to obtain the N_t point on the abscissa. This line is also extended upward to intersect the value on the N_{t+1} ordinate. This value is obtained on the right side by iterating the eggs to n_{t+1} and letting them survive to N_{t+1} . The latter value is then extended to the left into the N_{t+1}, N_t space, where a point is obtained at the intersection with the N_t line from the abscissa. In figure 16B the point for 16A is recorded and a new one generated with the new start point, which is under the egg-to-adult maximum. Figure 16C contains the previous two points and a third point, with the n_t start even farther to the right, beyond the egg-to-adult maximum. Evidently, the left-most extension of the adult figure is obtained when the n_t start point on the right is under the egg-to-adult maximum; after that the N_t abscissa points move back to the right again, causing the adult figure to fold back on itself (hence, the term “foldback” figure).

A geometrical property of the humped case is worth noting. On the right of the ordinate in figure 16 the $A(n)$ maximum occurs at a point greater than that at which the egg-to-egg recursion is a maximum. It is easy to show that if the $A(n)$ function has a maximum, then the egg-to-egg recursion will also have one. If fertility is

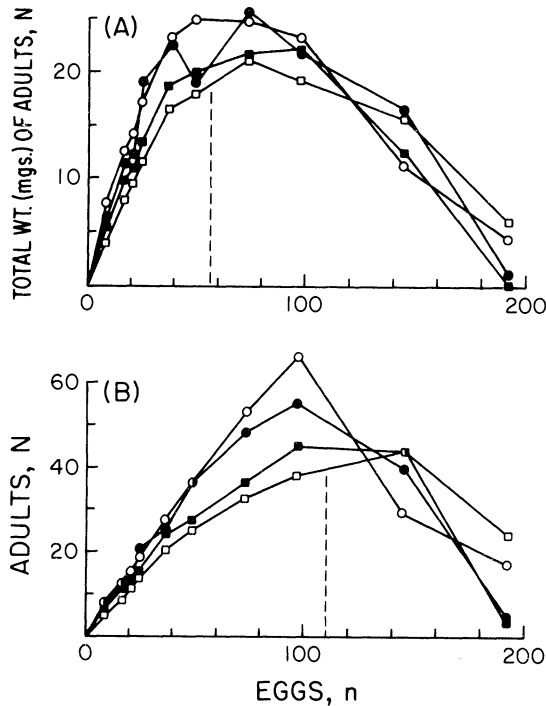


FIG. 17.—Four *Drosophila melanogaster* genotypes. Eggs, n , in 5-ml tubes. A, total weight of the N adults; B, number of adults, N , from eggs, n . Vertical lines, approximate location of maxima. Modified from Caligari (1980).

constant, the two maxima will occur at the same place; but if fertility is a decreasing function of n_t ($F'[n_t] < 0$), then the two maxima will have the $A(n)$ maximum displaced to the right. Figure 17 shows some data from experiments by Caligari (1980) on four *D. melanogaster* genotypes. These data constitute a live example that is equivalent to the system being discussed here. Figure 17B shows the number of adults from eggs, the $A(n)$ function. Figure 17A is the total weight of those adults. This is equivalent to the relationship being discussed for two reasons: biologically, fertility is directly proportional to body weight (see Chiang and Hodson 1950; Robertson 1957); mathematically, if body weight is a decreasing function of egg density, $w(n)$, then the total weight, W , is

$$W = w(n) S(n)n \quad \text{or} \quad W = w(n) A(n), \quad (11)$$

and the above function will have the same property of the right shift of the $A(n)$ maximum relative to the W maximum. (Mather and Caligari [1981] fit linear $s(n)$ and $w(n)$ functions to these data.) This property of the humped case concerning the relative positions of the maxima is, of course, a minor one compared to the important conclusion that the parent-offspring adult transitions take the form of a foldback figure.

This completes the theoretical description of the properties of this delay effect

within the life history as manifested in the census numbers of adults. The adult-to-adult recursion function is defined for an increasing egg-to-adult function; but when the egg-to-adult function has a hump, the one-to-two mapping of adult numbers between generations results in the foldback figures just described.

SOME APPLICATIONS AND CONCLUSIONS

The theoretical considerations just described clearly carry implications for experimental and observational studies of the dynamics of populations, especially when the data consist only of the numbers of adults.

As noted previously (Prout 1984), the *Drosophila* literature appears to be dichotomized. In one part are the numerous studies (cited in the beginning of part 2) of the delayed effect on adults of larval crowding. These investigators, however, did not incorporate their findings into a formal representation of population dynamics as was done in the investigation reported in part 1. In the other part of the dichotomy are a number of studies in which various kinds of data were used to construct formal dynamic theory, which do not incorporate the delay on fertility.

Most notable among these studies is an experimental design that entails constructing an experimental adult-to-adult recursion by counting different numbers of adults (N_1) and recording the number of adult offspring produced (N_{t+1}). We first discuss this type of experiment, then its two-species counterpart, and finally applications to other kinds of data.

The Experimental Recursion Method: One Species

Examples of the experimental procedure just described are the "monocultures" in the de Wit replacement-competition experiments of Ayala (1971), Ayala et al. (1973), and Tošić and Ayala (1981) and the strictly monoculture experiments of Hastings et al. (1981), Mueller and Ayala (1981), and Thomas et al. (1980). The latter two experiments specifically addressed the question of population stability by calculating the eigenvalue, λ , at equilibrium, K , from the experimental recursion data. Apparently, there are two variations of the experimental procedure entailed in counting flies for N_t : in one, individuals are taken directly from stock cultures; in the other, flies are taken from stock cultures and raised for one generation initiated at the particular size desired, and then N_t progeny are counted again for the experiment.

Our discussion above raises the question of the relationship between the empirical recursion obtained by such input-output experiments and the "natural" recursion governing the dynamics of the running population. It is not possible to obtain a definitive answer when the reference population is maintained by the serial-transfer method because this results in a more or less continuous, age-structured population, to which our discrete-generation theory does not strictly apply.

Nevertheless, some useful insights can be gained by performing input-output gedanken experiments for the discrete-generation case. First, consider the case in which the natural recursion that actually governs the population has a smooth adult function, such that an adult-to-adult recursion function is defined (fig. 13).

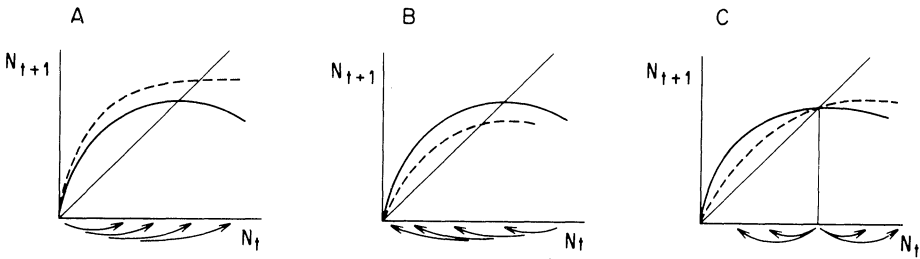


FIG. 18.—Three possible relationships between the true adult-to-adult recursion function and that produced by the experimental procedure, smooth $A(n)$ case. Solid lines in A, B, and C are the true adult-to-adult recursion functions in the running population for the case of a smooth $A(n)$ function. Dashed lines are the results of experimental recursions when the shelf fertility, $F(n)$, of the N_t adults and the true equilibrium fertility, $F(k)$, have the following relationships: A, $F(n) > F(k)$; B, $F(n) < F(k)$; C, $F(n) = F(k)$. Arrows indicate the kind of flies used for the count with reference to the true recursion (solid curve).

For the experimental procedure whereby the count for N_t is directly from the shelf, all of the adults over the various N_t will have the same fertility, the “shelf” fertility. Figure 18 illustrates the various ways in which the experimental recursion, the dashed line, could depart from the natural one, the solid line. In 18A, the shelf fertility is high, corresponding to low adult density, so that at higher N_t 's the fertility will be too high and the experimental recursion will be above the natural one (recall that the adult function, $A(n)$, is always increasing with the number of eggs, n). In 18B, the shelf fertility is low, with the opposite effect on the experimental recursion. In 18C, the shelf fertility is at equilibrium, $F(k)$; in this case, for $N < K$, fertility and N_{t+1} are too low, and for $N_t > K$, fertility and N_{t+1} are too high, suggesting that the correct equilibrium is obtained but that λ is too large.

For the cases in figures 18A and 18B this simple graphical procedure does not provide any information about the relation between the experimental and natural λ 's. In fact, when the maximum fertility, F , is used as a constant in place of the $F(k)$ functions in the nine functions emerging from the data in part 1, the exponential model shows no change in λ . Of the eight remaining functions, however, four λ 's increased and four decreased (as compared with table 4 values). This provides a numerical demonstration that no general statement can be made about the direction in which λ might be biased.

The case in figure 18C, however, is worthy of further consideration because it has been demonstrated by the authors cited above that this experimental procedure is successful in predicting the equilibrium K of the serial-transfer populations. One possible reason for this success (there are others; see below) is that the shelf fertility is reasonably close to the equilibrium fertility in the running populations. Both the populations and the stock cultures are rather dense, so that in both of them fertilities could be at a flat part of the $F(n)$ function and thus equal to each other.

Figure 19 is a numerical example of the case in figure 18C. The parameters for the $H_S E_F$ case were used. The adult-to-adult recursion for this case is equation (6) and shown graphically in figure 13. The discontinuity in figure 13 is not shown in

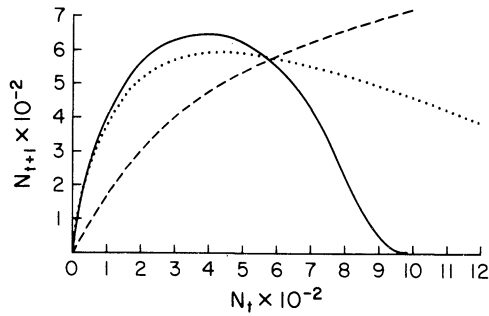


FIG. 19.—Numerical example of fig. 18C. Solid line, adult-to-adult recursion of the H_sE_F function as shown in fig. 13, but not showing discontinuity. Dashed line, experimental recursion when N_t are taken directly from the shelf. Dotted line, experimental recursion when cultured at N_t for one generation before counting. Dashed line has a maximum, which is not shown.

figure 19. The dashed line results from calculating what happens if the shelf fertility is $F(k)$ and the initial N_t is taken directly from the shelf. The natural $\lambda = -0.67$, and the slope of the experimental recursion at K is $\lambda_1 = +0.35$. This figure also provides an answer to an additional question: does the second experimental procedure of culturing at N_t one generation before counting remove the effects of the shelf fertility? (This calculation and the preceding one are represented formally as part of Appendix A, eqs. A4, A11.) The dotted line was calculated in accordance with this second procedure. The slope at K is $\lambda_2 = -0.01$. Thus, for this numerical case the shelf fertility does persist and still results in a substantial distortion of λ .

These numerical calculations can be generalized. Proof of the following expressions for λ are provided in Appendix A.

$$\text{Natural: } \lambda = 1 - kF(k)|S'(k)| - kS(k)|F'(k)| \quad (12)$$

$$\text{Experimental: Direct from shelf, } \lambda_1 = 1 - kF(k)|S'(k)| \quad (13)$$

$$\text{One generation at } N, \lambda_2 = \lambda + k^2|S'(k)F'(k)| \quad (14)$$

Equations (13) and (14), giving λ for the two experimental procedures, assume the shelf fertility to be $F(k)$. The natural, or true, λ (eq. 12) is expressed as a function of the equilibrium egg numbers, k . When the adult-to-adult recursion is defined (smooth case), the slope of the adult recursion at K is the same as that for eggs at k . For equations (13) and (14), representing the two experimental procedures, λ_1 and λ_2 are the slopes at equilibrium of the experimental recursions obtained using pairs of adults, N_{t+1} and N_t , but the right sides of equations (13) and (14) are written in terms of egg numbers, k , for comparison with the natural λ . The only assumptions are that $(f'[k], S'[k]) < 0$, as indicated. It can be seen that $\lambda_1 > \lambda$ and $\lambda_2 > \lambda$. It should be recalled that no such general statements can be made with arbitrary shelf fertility. One final point should be noted concerning the numerical example of figure 19: the natural recursion drops after K to approach the limit $N_{t+1} \rightarrow 0$ as $N_t \rightarrow S/s$ (see p. 539), but the experimental recursions do not

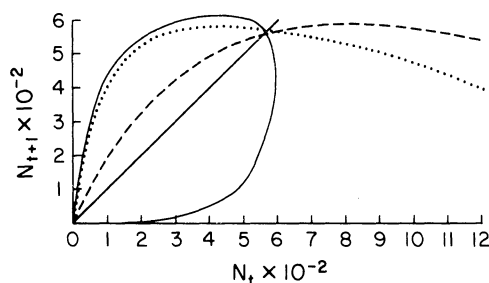


FIG. 20.—Same as in fig. 19, except the $E_S E_F$ function is used to produce the foldback figure shown in fig. 14.

do so. This will be explained presently in connection with humped adult function, $A(n)$, or the cigarette case, which we now open.

In the humped case, the adult-to-adult function is not defined but is replaced by a foldback figure. Figure 20 reproduces the $E_S E_F$ exponential-foldback case shown in figure 14 together with the calculated experimental recursion functions, using $F(k)$ shelf fertility. The reason for the lack of any peculiarities in the experimental recursion is the assumption in making the calculation that fertility is the same in females across the different N_t values obtained by the counting procedure. In this case the corresponding recursion function incorporates fertility as a simple constant, say, F . ($F[k]$ was actually used for fig. 20.) The survival function, $S(FN_t)$, used in figure 20 is exponential (with parameters from the flies), which gives a well-behaved gentle maximum shown by the dashed line in figure 20. This dashed line represents the data acquired by counting directly from the shelf. The second experimental procedure (dotted line) is not a simple exponential function (see eq. A11b); nevertheless, it also has a well-behaved maximum.

Another, less formal way of understanding the normal appearance of the experimental curves can be obtained by examining the geometrical construction of the $1\frac{1}{2}$ -generation recursion procedure in figure 18. The adult maximum sets the limit for the number of adults, which is why starting with eggs beyond the maximum results in retreating points on the left N_t abscissa, giving the foldback configuration. In the experimental situation, however, artificially high numbers of adults can be counted such that increasing N_t on the abscissa of figure 18 continues to proceed to the left and is associated with small N_{t+1} from the large number of eggs produced by the large N_t . Thus, the foldback figure is unfolded. This is also why in the case of the smooth adult function of figure 19 the experimental curve remains high, not being constrained by the maximum of $N(\max) \equiv S/s$ in that case.

It should be emphasized that equations (12)–(14) for natural and experimental slopes at K also apply to the foldback cases. The eigenvalue, λ , determined from the egg-to-egg recursion, establishes the true stability of the system, but λ_1 and λ_2 are the slopes at K of the experimentally produced N_{t+1}, N_t functions, because with constant fertility the slopes at k and K are the same. It is interesting that this

artificially produced function in the humped case reveals more about the underlying order in the system than does the natural foldback figure.

The discussion so far has emphasized the relation between the natural eigenvalue, λ , and the slope of the experimental function at K . This emphasis occurs, in part, because Thomas et al. (1980), who studied 23 *Drosophila* species, and Mueller and Ayala (1981) have offered their large eigenvalues as empirical evidence against the common occurrence of limit cycles or chaos. We see here that their determination of the eigenvalue could be biased upward. Hastings et al. (1981) were concerned with the shape of the early part of the experimental recursions, namely, its rapid rise to high values. The initial increase is the finite rate of increase, R , which is the eigenvalue as $N \rightarrow 0$. For the method of direct count off the shelf, $R = F(k)S$, assuming equilibrium shelf fertility. This is too small. For the method of one generation at N_i removed from the shelf, $R = \bar{F}\bar{S}$, which is correct (see figs. 19, 20). Thus, the delay effect has no apparent bearing on the problem addressed by Hastings et al.

Figures 19 and 20, then, simulate counting experiments on populations whose true egg-to-egg recursions are known, with parameters provided by the fly data of part 1. These simulated experiments resulted in biases, with curves not quite high enough at the start, too flat at K , and much too high beyond K , ultimately resulting in the complete obfuscation of the foldback configuration in the case of figure 20. For the experiments referred to above, it is not known whether all of these biases apply; this could be determined only by the appropriate experiments on the reference populations. However, the analytic results, equations (12)–(14), are quite general, at least for populations with discrete generations. They show that the experimental procedure results in a λ biased upward, so that the true λ might be small enough (negative) to produce limit cycling or even chaos. Equation (14) shows that the shelf history is not lost by culturing for one generation at N_i before the counting. Finally, if the shelf fertility is not equal to the equilibrium fertility in the reference population, $F(k)$, then nothing can be said about the direction of biases of the experimental curve, except that it is unlikely to reflect the true recursion. More likely, these latter, more general conclusions may apply to the conclusions of Thomas et al. (1980) and possibly also of Mueller and Ayala (1981), although the latter authors did take into account the age structure of their reference populations.

The Experimental Recursion Method: Two Species

The extension of the fertility-delay effect to two competitors introduces considerable complexity. We consider this case more for the purpose of introducing the problem than for supplying very much in the way of solutions.

Constructing experimental recursions with mixes of two species or genotypes has been done in the form of the de Wit (1960) replacement design. This has been done with *Drosophila* by the aforementioned authors. One of the dynamic aspects of special interest here is the detection of a stable joint equilibrium of the two species. By constructing one-generation recursions with different initial mixtures, Ayala et al. (1973) were notably successful in predicting the approximate stable equilibrium value actually observed in running populations of *Drosophila*. But the delayed effect on fertility under consideration here has been clearly demonstrated

experimentally by Caligari (1980; analysis in Mather and Caligari 1981) and also by Barker and Podger (1970) to occur in competition between two types (genotypes in the former and species in the latter). The crowding of larvae affects the size (and therefore the fecundity) of not only their own type but also that of the competitor. Indeed, in one instance Caligari showed that all of the larval competitive effect of one type on the other was expressed in adult body size, and not manifest at all in larval survival. The question then is how a set of experimental recursion experiments, which entail counting adult mixtures, can successfully identify the natural equilibrium that occurs in a running population. The analogous egg-to-egg recursion for two species is

$$n_{i,t+1} = F(n_{i,t}, n_{j,t}) S(n_{i,t}, n_{j,t}) n_{i,t} . \quad (15)$$

This formulation creates considerable complexity, and a general analysis will not be attempted here. One particular function, however, is quite tractable and does provide at least an example of how the experimental counting procedure could successfully predict equilibrium in a running population. This function is the exponential, which results from the product of two component exponential functions. These component functions are constructed as follows:

$$\text{Fertility: } F(n_{i,t}, n_{j,t}) = \exp [u_i - f_i (r_i/k_i) n_{i,t} - \phi_{ij} (r_i/k_i) \alpha_{ij} n_{j,t}] \quad (16)$$

and

$$\text{Survival: } S(n_{i,t}, n_{j,t}) = \exp [v_i - s_i (r_i/k_i) n_{i,t} - \sigma_{ij} (r_i/k_i) \alpha_{ij} n_{j,t}] , \quad (17)$$

where $i = 1, 2$ and $j = 2, 1$. When equations (16) and (17) are combined as in the general equation (15), their product results in the exponential form of the classic Lotka-Volterra equations, as follows:

$$n_{i,t+1} = n_{i,t} \exp [r_i - (r_i/k_i) n_{i,t} - (r_i/k_i) \alpha_{ij} n_{j,t}] . \quad (18)$$

This equation results from the following definitions of the parameters of equations (16) and (17):

$$r_i = u_i + v_i ,$$

where $u_i (> 0)$ gives the maximum fertility, e^{u_i} , and $v_i (< 0)$ gives the maximum survival, e^{v_i} ;

$$f_i + s_i = 1 \text{ } [(f_i, s_i) > 0] ,$$

where f_i and s_i are the proportions of the quantity r_i/k_i allocated to the fertility inhibition and to the survival inhibition, respectively, of type i by itself;

$$\phi_{ij} + \sigma_{ij} = 1 , \quad \text{and} \quad (\phi_{ij}, \sigma_{ij}) > 0 ,$$

where, ϕ_{ij} and σ_{ij} are the proportion of the quantity $(r_i/k_i) \alpha_{ij}$ allocated to the fertility inhibition and to the survival inhibition, respectively, of type i by type j .

At equilibrium,

$$1 - (\hat{n}/k_i) - \alpha_{ij}(\hat{n}/k_i) = 0 , \quad (19)$$

with the usual stability conditions

$$(k_1/\alpha_{12}) > k_2, (k_2/\alpha_{21}) > k_1. \quad (20)$$

Strictly speaking, these conditions only guarantee invasion from the boundaries $(k_1, 0$ and $0, k_2)$. Stability of the internal point (\hat{n}_i) requires additional conditions on the parameters.

We now suppose that pairs of adults (N_1, N_2) are counted directly from the shelf (Ayala 1971). The shelf fertilities of the two separate species are F_1 and F_2 ; the numbers of eggs laid will be $N_1 F_1$ and $N_2 F_2$. The survival component, equation (17), can now be used to obtain the offspring adults after a “ $1/2$ ” generation of survival competition. These offspring adults are denoted by \tilde{N}_1 and \tilde{N}_2 , or \tilde{N}_i :

$$\tilde{N}_i = N_i F_i \exp [v_i - s_i(r_i/k_i)N_i F_i - \sigma_{ij}\alpha_{ij}(r_i/k_i)N_j F_j]. \quad (21)$$

In this experimental procedure, “equilibrium” is defined by $\tilde{N}_1 = N_1 (= \hat{N}_1)$. Equilibrium, so defined, is obtained by solving the following equation for \hat{N}_i, \hat{N}_j :

$$\ln F_i + v_i - s_i(r_i/k_i)\hat{N}_i F_i - \sigma_{ij}\alpha_{ij}(r_i/k_i)\hat{N}_j F_j = 0. \quad (22)$$

With arbitrary F_i the above expression is not particularly informative. The shelf fertilities become much more circumscribed, however, if we assume that the single-species populations are cultured on the shelf in a manner similar to the conditions that they experience when in competition. This assumption is analogous to the one used earlier in the analysis of single-species populations. Taking this assumption literally, the two different shelf fertilities are those obtained at k_i , viz., $F_i(k_i)$. A calculation given in Appendix B shows that this assumption results in the following (eq. B3):

$$s_i r_i - (s_i r_i / k_i) \hat{N}_i F_i - \sigma_{ij} \alpha_{ij} (r_i / k_i) \hat{N}_j F_j = 0, \quad (23)$$

with the stability conditions

$$(s_1/\sigma_{12}) (k_1/\alpha_{12}) > k_2, (s_2/\sigma_{21}) (k_2/\alpha_{21}) > k_1. \quad (24)$$

“Stability” in this situation means obtaining experimentally the appropriate pattern of vectors in the N_1, N_2 space. These conditions provide considerable information about the problem at hand. If the actual running population comes to equilibrium, then conditions (20) are satisfied. And if these conditions are satisfied, then the conditions for the experimental, stable \hat{N}_1, \hat{N}_2 equilibrium, conditions (24), show that there will surely be an equilibrium somewhere if $\sigma_{ij} \leq s_i$. In words, a sufficient condition for an experimental equilibrium is that, in the survival component of the life history, there is more competition allocated to “self” than there is to the competitor, for both species. Because of the complementarity of these allocation coefficients, the opposite is true for the fertility component in the running population, viz., $\phi_{ij} \geq f_i$.

In Caligari’s (1980) experimental case, $\sigma_{12} \rightarrow 0$ and $\phi_{12} \rightarrow 1.00$, for one type. If this were true for the other type, σ_{21} and ϕ_{21} (not so in Caligari’s experiment), then an equilibrium in one-generation recursion experiments would be guaranteed. It is possible that future experiments directed toward this problem will show that often the two allocations are about equal, $\sigma_{ij} = s_j$ (and $\phi_{ij} = f_j$). (This does not mean that

the absolute magnitudes of the self effect, r_i/k_i , are equal to those of the competitor effect, $\alpha_{ij}r_j/k_i$, but only that they are allocated equally between the two components.) If, then, $\sigma_{ij} = s_i$, not only will a stable equilibrium be detected, but the equilibrium values, \hat{N}_1, \hat{N}_2 , will be precisely those of the running population. This latter result is by no means obvious; a demonstration of it is given in Appendix B.

Thus, there appears a reasonably large parameter space wherein the experimental recursion procedure approximates the behavior of the running population. It should be emphasized that this analysis of the two-species recursion experiment is strictly in terms of a simple exponential function. The robustness of these findings for other functions is unknown. It seems unlikely that other functions would show the experimental recursion finding the precise equilibrium, but the conditions for predicting an equilibrium somewhere might be a relationship analogous to that for the allocation parameters of the exponential, namely, that the self effects and the competitor effects are allocated about equally to the fertility and survival components, or in a way even more favorable to equilibrium.

This conjecture, then, suggests at least one reason why the experimental recursion method can successfully reveal the actual behavior of a running population. Furthermore, if each combination of N_1, N_2 is cultured for a generation of competition before being counted (as in Ayala et al. 1973), this can only improve the accuracy of the method, as was shown explicitly and more generally for the single-population system.

Before proceeding to other aspects of the fertility-delay phenomenon in single-species populations, we should emphasize once again that all of the above analysis of the experimental recursion method—for one species or two—cannot have the kind of precision implied. Because the serial-transfer reference population that accompanies some experiments are age-structured, the above discussion can apply to the “running population” only in a very approximate way, at best, and perhaps only metaphorically. It is possible that in these rather dense populations, direct competition among females dominates the variation in fertility, thus overriding the delay effect from larval crowding, but it would seem this requires experimental demonstration.

Other Applications and Conclusions

The work of Hassell et al. (1976) has been cited by Mueller and Ayala (1981), together with the work of Thomas et al. (1980), in support of the empirical generalization that limit cycling is uncommon in real populations. We suggest here that the two latter experiments may have resulted in overestimates of λ . The study by Hassell et al. consisted of incorporating life history data from 26 species of insects into a recursion function that was then analyzed for equilibrium stability, with the result that only one case, a laboratory population, showed a simple limit cycle; all the others indicated a stable equilibrium. These authors apparently used a constant value for fertility in all cases: “Estimates of λ [= R] . . . depend, in the first place, upon knowing *the* average maximum fecundity per adult” (1976, p. 474, emphasis ours). The details of the nature of competition in all life histories are not provided, but those that do appear indicate the existence of competition among immatures and the use of a constant for fertility. If this is the case for the

other species analyzed, then because of the widespread occurrence of the delayed effect in insects, the assumption of constant fertility seems questionable. Therefore, on the basis of the analysis by these authors and those by Mueller and Ayala and Thomas et al. the present empirical evidence bearing on the intrinsic nature of equilibrium stability is inconclusive.

These considerations might also apply to the monitoring of adult numbers in experimental and natural populations. Consider a population whose intrinsic recursive relationship is a foldback figure. If the population is following a complex limit cycle, even in the absence of stochastic effects, the temporal sequence will be difficult to interpret, and a graph of one-generation transitions will make no sense. In fact, May and Oster addressed the problems of how one might handle data produced by a population in a chaotic regime: "One might think that a simple way out of this dilemma if presented with a set of apparently unpatterned results would be to try and reconstruct a generating function [recursion] for the trajectory by plotting all adjacent pairs $[N_t, N_{t+1}]$ " (1976, pp. 585–586). Unfortunately, they continued, such a procedure is unlikely to be successful because the stochastic effects of a demographic nature, as well as those affecting parameter values, "fuzz out" the graph. But even with no stochastic effects, the foldback figure would surely obfuscate the order in the system (see fig. 15). This circumstance suggests the term "superchaos."

Even a population with an underlying stable equilibrium, but subject to perturbations of an episodic nature with a several-generation waiting time, does not reveal the truly simple order in a system that has a foldback pattern. In a literature review of monitoring data, Tanner (1966) analyzed N_t, N_{t+1} transitions in natural populations and found substantial evidence for density regulation among different populations of different species. How many more cases were there that conformed to the conditions being discussed here and that would have revealed density regulation had early immatures been monitored (n_t, n_{t+1}) instead of adults (N_t, N_{t+1})? Indeed, it would seem that the solution to this problem would be the regular monitoring of eggs or immatures. Although there are technical problems, efficient methods have been devised for monitoring immatures, particularly those of many agricultural arthropod pests.

A final aspect worth noting is the possible consequences of this delay effect within the life history when it occurs in age-structured populations. This could be the biological basis of a time delay resulting in limit cycling in such populations. Frauenthal (1975) showed that, in theory, limit cycles in human populations could result from the negative correlation between cohort size and fertility, which we mentioned earlier. This theory should apply to organisms which have smooth adult functions so that cohort size is an increasing function of the density of immatures and the latter has an inverse effect on fertility.

Some experimental findings are suggestive: Taylor and Sokal (1976), working with house fly populations, analyzed the limit cycling using a time lag of 10 days, which is roughly equal to the time interval between egg and adult. Also, May (1973, pp. 100–102), analyzing with a finite recurrence equation the experimental blow fly populations of Nicholson (1957), used a time lag of 9 days and the egg-to-adult time of about 11 days. The blow fly, however, has a decidedly humped adult function (Nicholson 1954).

In conclusion, we reiterate that we do not claim to be dealing with a universal phenomenon. The number of species and populations meeting all of the assumptions enumerated earlier surely must be circumscribed. But the importance of this phenomenon within life history delay is common enough to be worthy of future research.

SUMMARY

In part 1 we present data from a life history analysis of a discrete-generation laboratory population of *Drosophila melanogaster*. Two related density-dependent processes govern the population dynamics. (1) The egg-to-adult survival rate is a decreasing function of egg density; $N = S(n)$, where N is adult density, n is egg density, and $S'(n) < 0$. (2) Because fertility depends on the egg (larval) density from which the females came, it is also a decreasing function of egg density; $F(n)$ is eggs per female, and $F'(n) < 0$. The recursion function must be written in terms of eggs; thus,

$$n_{t+1} = F(n_t)^{1/2} S(n_t) n_t. \quad (1)$$

Three different functions are fitted by least squares to the $F(n)$ data and to the $S(n)$ data. Combining these functions according to equation (1) gives several different recursion functions that fit the data about equally well. Some of these functions result in limit cycles; there is one case of chaos. This case yields predictions of adult numbers, N , falling within the experimentally observed range. In part 2 we document the widespread occurrence of this delay effect of competition among immatures on their subsequent fertility, justifying the study of some of the theoretical consequences of equation (1). For a common class of survival functions, the adult-to-adult recursion is not defined, but rather there is a one-to-two mapping of the number of adults from one generation to the next, with the result that experiments or observations dealing with adult numbers could appear stochastic, obscuring the true dynamic behavior of the population. In part 2 we also reexamine the conclusions of some published experiments and observations that did not consider this delay effect. In particular, the data adduced as empirical evidence against the common occurrence of limit cycles or chaos do not necessarily warrant that conclusion.

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APPENDIX A

ONE-SPECIES INPUT-OUTPUT EXPERIMENTS: THE SLOPE AT EQUILIBRIUM

Two methods have been employed to construct the experimental recursions. Method 1 entails counting out into bottles different numbers of adults, N , taken directly from the shelf, and then determining the number of offspring \bar{N} produced by these adults. Method 2

starts out the same as method 1 so we obtain, say, \hat{N} adults. From these \hat{N} we count another N adults, which produce \hat{N} adults.

The following provides the derivations of expressions (10)–(12), which relate the eigenvalues λ_1 and λ_2 from the two experimental procedures to the actual λ in the running population.

The basic relationships in the running population are as follows. The recursion function in terms of egg number is

$$n_{t+1} = F(n_t) S(n_t)n_t \quad (\text{A1})$$

at equilibrium, k ,

$$1 = F(k) S(k). \quad (\text{A2})$$

The eigenvalue is

$$(dn_{t+1}/dn_t) |_k = \lambda = 1 - kF(k) | S'(k) | - kS(k) | F'(k) |. \quad (\text{A3})$$

The absolute values of $S'(k)$ and $F'(k)$ are given so that their negative signs can show explicitly in equation (A3).

Experimental Method 1

Assume the shelf population has constant fertility, \bar{F} . Actually \bar{F} should be thought of as a mean taken over all cultures regardless of the number of adults, N , taken for the experiment.

For each N counted out,

$$\tilde{N} = S(\bar{F}N)\bar{F}N, \quad (\text{A4})$$

where \tilde{N} is the number of offspring produced, as explained above. The slope at N is

$$\tilde{N}' = \bar{F} S(\bar{F}N) - \bar{F}^2 N | S'(\bar{F}N) |. \quad (\text{A5})$$

“Equilibrium,” K_1 , is defined as

$$\tilde{N} = N = K_1.$$

(Here “equilibrium” simply means the number of adults occurring when the input and output are equal, and not a dynamic equilibrium achieved in a running population. The object of such experiments is to estimate the value of the dynamic equilibrium and its eigenvalue.)

At this equilibrium,

$$1 = S(\bar{F}K_1)\bar{F}. \quad (\text{A6})$$

The slope at equilibrium, λ_1 , is

$$\lambda = 1 - \bar{F}^2 K_1 | S'(\bar{F}K_1) |. \quad (\text{A7})$$

The number of eggs laid at any N is

$$n = \bar{F}N,$$

and at equilibrium, K_1 , the egg numbers are

$$k_1 = \bar{F}K_1. \quad (\text{A8})$$

Substituting equation (A8) into (A7),

$$\lambda_1 = 1 - \bar{F}k_1 | S'(k_1) |. \quad (\text{A9})$$

If the shelf population is at the same equilibrium as the running population, then $k_1 = k$ and $\bar{F} = F(k)$. Substituting into equation (A9) gives

$$\lambda_1 = 1 - kF(k) | S'(k) |. \quad (\text{A10})$$

Referring to equation (A3) we can see that $\lambda_1 > \lambda$.

Experimental Method 2

The steps in method 2 are as follows.

1. The number of eggs laid by the N adults counted from the shelf is $\tilde{N}F$.
2. These eggs produce \tilde{N} adults, whose fertility is $F(N\tilde{F})$.
3. N adults are counted out from the \tilde{N} , and these adults, too, have fertility $F(N\tilde{F})$. In the case of a foldback, the experimental N could be made to exceed the natural maximum by using replicate cultures.
4. The number of eggs laid by these N adults is $NF(N\tilde{F})$.
5. These eggs then survive to produce N adults, the output value used for the input, N , in the experiment. \tilde{N} is, therefore,

$$\tilde{N} = S[NF(N\tilde{F})] NF(N\tilde{F}) . \quad (\text{A11a})$$

Equation (A11a) can be more simply represented as follows:

$$\tilde{N} = S(N)F(N)N . \quad (\text{A11b})$$

At equilibrium,

$$1 = S(K_2)F(K_2) \quad (\text{A12})$$

and

$$\lambda_2 = 1 + K_2 S(K_2) F'(K_2) + S'(K_2) F(K_2) , \quad (\text{A13})$$

where $F'(K_2)$ and $S'(K_2)$ are derivatives with respect to N evaluated at K_2 . If, as discussed in the text, it is assumed that the shelf population and the running population are maintained in the same way, then taking this assumption literally means that both populations have the same equilibrium (K and k_1); and λ and λ_2 can be compared directly.

Assuming $\tilde{F} = F(k)$, then $K_2F(k) = k$; and using these, the following relationships can be derived:

$$\begin{aligned} F(K_2) &= F(k) \\ F'(K_2) &= F(k)F'(k) \\ S(K_2) &= S(k) \\ S'(K_2) &= S'(k)[F(k) + kF'(k)] . \end{aligned}$$

Substitution into equation (A13) yields

$$\lambda_2 = 1 - kS(k) | F'(k) | - kF(k) | S'(k) | + k^2 | S'(k)F'(k) | , \quad (\text{A14})$$

or, using equation (A13), $\lambda_2 = \lambda + k^2 | S'(k)F'(k) |$ so that $\lambda_2 > \lambda$.

APPENDIX B

TWO-SPECIES INPUT-OUTPUT EXPERIMENTS: JOINT EQUILIBRIUM

Competition between two species incorporating the fertility delay is formulated in the text using an exponential function. The observations considered here start with equation (22):

$$\ln F_i + v_i - s_i(r_i/k_i)\tilde{N}_iF_i - \sigma_{ij}\alpha_{ij}(r_i/k_i)\tilde{N}_jF_j = 0 . \quad (\text{B1})$$

The \tilde{N}_i are the numbers of adults taken from the shelf that give an equilibrium in the experimental recursion.

It is now assumed that the two species on the shelf have separately come to equilibria, k_i , under the same culture regimen as the population in which they compete. Under these circumstances, the shelf fertility, F_i , can be denoted by $F_i(k_i)$. Using the exponential

fertility function (16) with $\alpha_{ij} = 0$ (removing the competitor),

$$F_i(n_i) = \exp u_i - f_i(r_i/k_i)n_i.$$

When $n_i = k_i$,

$$F_i(k_i) = \exp u_i - f_i r_i. \quad (\text{B2})$$

Substituting (B2) for F_i in the first term of equation (B1) results in the first term becoming $u_i - f_i r_i + v_i$. Since $u_i + v_i = r_i$, this becomes $r_i(1 - f_i)$, which becomes $r_i s_i$ because $s_i = 1 - f_i$. Substituting into (B1) gives equation (23):

$$r_i s_i - (s_i r_i / k_i) \hat{N}_i F_i - \sigma_{ij} \alpha_{ij} (r_i / k_i) \hat{N}_j F_j = 0. \quad (\text{B3})$$

A straightforward boundary analysis gives the stability conditions (18) for these equilibria. The special case in which fertility and survival allocation are the same between the self effect and the competitor effect is specified by $\sigma_{ij} = s_i$ (for both species). Substituting s_i for σ_{ij} in equation (B3) results in the following:

$$1 - (\hat{N}_i F_i / k_i) - \alpha_{ij} (\hat{N}_j F_j / k_i) = 0. \quad (\text{B4})$$

The equilibrium equation for the running population is

$$1 - (\hat{n}_i / k_i) - (\alpha_{ij} \hat{n}_j / k_i) = 0 \quad (\text{B5a})$$

or

$$1 - (1/k_i)(\hat{n}_i + \alpha_{ij} \hat{n}_j) = 0. \quad (\text{B5b})$$

Since $\hat{N}_i F_i$ is the number of eggs laid by the species taken from the shelf, then, comparing equations (B4) and (B5), the experimental recursion will give an equilibrium when the eggs laid by the two species equal the equilibrium number of eggs, \hat{n}_i , in the equilibrium running population. This is not so reasonable as it may seem, because in the experimental system competition occurs only in the survival component. The equal allocation assumption produces this simple relationship. The equilibrium numbers of adults, \hat{N}_i , equal the equilibrium adult numbers in the running population, denoted by $\hat{N}_{i(\text{pop})}$. We already have the following relationship:

$$N_i F_i(k_i) = \hat{N}_{i(\text{pop})} F_i(\hat{n}_i, \hat{n}_j). \quad (\text{B6})$$

The left side of equation (B6) is the equilibrium egg number from the shelf, recalling that $F_i(k_i)$ was used for the shelf fertility, F_i (see eq. B2). The right side of equation (B6) is the equilibrium number of eggs in the population; the adults $\hat{N}_{i(\text{pop})}$ are multiplied by the equilibrium fertility $F_i(\hat{n}_i, \hat{n}_j)$ in the population. The two adult numbers are equal if the two fertilities are equal. The equilibrium population fertility is

$$F_i(\hat{n}_i, \hat{n}_j) = \exp [u_i - f_i(r_i/k_i)\hat{n}_i - \phi_{ij}\alpha_{ij}(r_i/k_i)\hat{n}_j]; \quad (\text{B7a})$$

if $\sigma_{ij} = s_i$, then $\phi_{ij} = f_i$. Substituting for ϕ_{ij} in the above gives

$$F_i(\hat{n}_i, \hat{n}_j) = \exp [u_i - f_i(r_i/k_i)(\hat{n}_i + \alpha_{ij}\hat{n}_j)]. \quad (\text{B7b})$$

From equation (B5b), $\hat{n}_i + \alpha_{ij}\hat{n}_j = k_i$ so that

$$F_i(\hat{n}_i, \hat{n}_j) = \exp (u_i - f_i r_i), \quad (\text{B8})$$

which is the same as $F_i(k_i)$ as given by equation (B2). The exponential function, at least, shows that with the equal allocation, the experimental recursion method will yield equilibrium adult members that would occur in a mixed population that was maintained in the same way as the separate shelf cultures of the two species. The robustness of this result is quite unknown.

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