

INTERNAL REPORT 13

Computer Simulation of Animal Population Dynamics

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ABSTRACT

Two major objectives were accomplished.

1. A summary of the work done during 1970-71 on a single species intra-specific competition model was written.
2. A multispecies predator-prey model, incorporating the competition mechanism of the single-species model, was developed almost to completion.

The single species model is a computer program that describes the dynamics of a population of insects when food shortages form the only restraint upon population growth. This model deals with energy flow from food through the population's age classes, and simulated reproduction, development, and starvation, as influenced by these flows. Population fluctuations, average densities, and other properties generated by this model correspond closely with results observed in some of the experimental situations and show the need for revision of some model mechanisms in others.

The multispecies model currently simulated the Douglas-fir beetle's relation with two predators, the hairy woodpecker and a clerid beetle. This model incorporates the intraspecific competition mechanism mentioned above, a closely analogous interspecific competition mechanism, and the predation mechanisms. Its terminology and data requirements permit any food chain of any number of predaceous species to be investigated. Its design permits an investigator to study various hypotheses regarding the extent to which species omitted from the modeled food chain influence the population changes of the species included in the simulation.

The predator/prey model is now complete, but contains mechanical difficulties that have prevented its successful operation thus far. Robert Rydell, in conjunction with Scott Overton, Mary Ann Strand, and I, will attempt to remove these difficulties in the fall of 1971.

INTRODUCTION

Several workers (Watt 1961, 1968; Holling 1963) have summarized the benefits to be expected from simulation studies of insect populations. Types of models that have been developed, philosophies of model construction, and the advantages and disadvantages of the various simulation methods have similarly been summarized (Watt 1959, 1968). The purpose of this paper is to mention some aspects of modeling the author has found disturbing, and to present an example of a modeling technique that seems capable of providing penetrating explanations of population phenomena while avoiding some of these problems.

An inevitable consequence of any attempt to summarize a complex population interaction in one or a few model equations is what might be called the problem of the "obnoxious coefficient" and its corollary, "biologist rejection". Consider the Lotka-Volterra equations

$$\frac{dn_1}{dt} = rN_1 - \delta N_1 N_2 \quad (1)$$

$$\frac{dN_2}{dt} = \Theta N_1 N_2 - \beta N_2$$

where N_1 is the density of some prey species, N_2 that of a predaceous species, and r , δ , Θ , and β are coefficients that are seldom precisely defined. These equations are one conceptualization of the way in which the numbers of a predaceous organism of some species govern, and are governed by, those of a prey species in a very simple environment.

"Biologist rejection" is the phenomenon that causes most researchers to hesitate upon encountering $\frac{dN_1}{dt}$; calculus notation of this or any

other model is vaguely threatening to nonmathematicians and a barrier to communication. "Obnoxious coefficient" is a worse problem that baffles even well-meaning attempts by modeler and field man to overcome the communication gap. This is the tendency of such equations to contain coefficients that correspond to nothing measurable in nature.

If field data were required to test the validity of the above equations in a situation where they might apply--say, on an island containing cats, mice, and virtually no other animal species--"r" and " β " could be reasonably well defined as the average number of mice born per mouse present per day and the average fraction of the cat population dying per day. The dimensions of equations (1) suggest that δ is the average fraction of the mouse population captured per cat per day. Θ , however, is some number which, when multiplied by the numbers of existing cats and mice, yields the number of cats born per day. What quantity could a field worker conceivably examine to estimate Θ 's value for a test of equations (1)?

In this instance, Θ can be defined in a way that biologically speaking, makes sense. Dimensional analyses-- $\Theta = (\text{cats born/mouse eaten}) \cdot (\text{mice eaten/mouse present} \cdot \text{cat present} \cdot \text{day})$ --suggests that Θ is the product of two coefficients, one of which is δ in the first equation of set (1). The other is a conversion efficiency--the average number of cats born per mouse eaten--which, oversimplified as it may be, can at least be estimated from field or laboratory data.

A slight modification of the first equation by Leslie (1948) to

$$\frac{dN_1}{dt} = rN_1 - aN_1^2 - \delta N_1 N_2 \quad (2)$$

for reasons which, mathematically, force the equation to generate more realistic-appearing outputs, introduces a coefficient "a" that corresponds to nothing measureable in nature. Such coefficients, although they permit certain theoretical studies, automatically make a model virtually untestable.

A more widely cited equation containing coefficients that are impossible to define precisely is Watt's (1959) parasite-prey equation

$$N_A = PK (1 - e^{-aN_e P^{1-b}}) \quad (3)$$

In (3), P is the number of females of a parasitic insect species inhabiting an area at a certain time. N_0 is the number of prey individuals in the same area; N_A is the total number of prey individuals attacked by the parasites at the end of an interval short enough to preclude changes in the parasite population. K is maximum number of attacks each parasite is capable of making within that interval. Constants "a" and "b" are creations of the equation derivation process and correspond to no real natural quantities.

Constant "b" has been referred to as the "depression of efficiency induced by intra-attacker competition" (Watt 1961), "intraspecific competition pressure among predators or parasites" (Watt 1968), a "positive constant" (Watt 1959; Miller 1959), and in other vague terms. In practice, its value, and that of "a", can be estimated only by assuming that equation (3) correctly describes the relation between numbers of prey attacked and numbers of attackers and by fitting the equation to data such as that of Miller (1959). Numbers for "a" and "b" are thereby derived that automatically ensure that the data will be fitted by the equation. No independent test of the fit of equation (3) to parasite-prey data is possible, therefore.

An equation such as (3) forms an unstable foundation for the superstructure of modifications that must be added to increase the realism of its predictions. In addition to undefinable coefficients in the main equation, similar coefficients creep into the modifying equations (see Watt, 1961) to such an extent that the entire model quickly loses all credibility. Worse, it intimidates some researchers who are not mathematically inclined and hardens others attitudes toward modeling.

I believe that simple model formulations cannot explain (to the extent of predicting) most changes in animal population densities in nature. Population phenomena, such as pest outbreaks, result from interactions of so many biological and meteorological variables that any model that would encompass the mechanisms of a natural system must be designed to incorporate considerable complexity from its outset. Such a model has virtually no chance of success unless its complexity is the sum of elements and interactions between elements,

every one of which can be clearly and precisely defined in terms meaningful to nonmathematically oriented researchers. Models that lack this property cannot be amended or improved or tested by such workers to any meaningful extent.

OBJECTIVES

Our objective was to create a basis for a general model of animal species interactions within a natural ecosystem--a model that incorporates the above philosophy. The model so developed was designed to be communicable to biologists, to permit progressive incorporation of complexity in a rational manner, to use terms and concepts applicable to the life histories of almost any animal species, and, to simulate accurately the processes it models.

Any model that purports to explain features of a complex situation must be able to explain simpler situations that are subsets of the complex one. This model's mechanisms were tested initially, therefore, by using them to simulate an experiment conducted by A. J. Nicholson (1954, 1957) in which intra-specific competition among insects was the focus of study.

MATERIALS AND METHODS

Nicholson's Experiment

In the 1940's, Nicholson began several experiments, a central one of which can be characterized as follows. Cages were set up, each of which housed blowflies of the species Lucilia (now Phaenicia) caprina. Ample sugar, water, and protein were always provided for adult flies in the cages, but larval food was always provided at the rate of 50 gm meat per day, regardless of the size or need of the larval population. Adults were prevented from feeding upon the larval food supply. Cage temperatures and humidities were maintained at constant levels throughout the experiment. Adult flies were counted at frequent intervals over a period of 1 1/2 years, and other measures of population were made.

Nicholson observed that, when adult flies were abundant, the numbers of eggs laid, and larvae hatched, were sufficient to overwhelm the larval food supply, resulting in massive larval starvation and no survival to adulthood. As adult flies dwindled in numbers, oviposition decreased to a point that permitted survival and maturation of a few larvae. Subsequent oviposition led to increases in adult numbers and oviposition, which again resulted in larval starvation. Thus, numbers of adult flies fluctuated violently over the duration of the study, with an amplitude and period of oscillation that remained essentially unchanged throughout the entire experiment. Figure 1 shows results of this experiment observed by Nicholson (relevant part of his Figure 3, 1957).

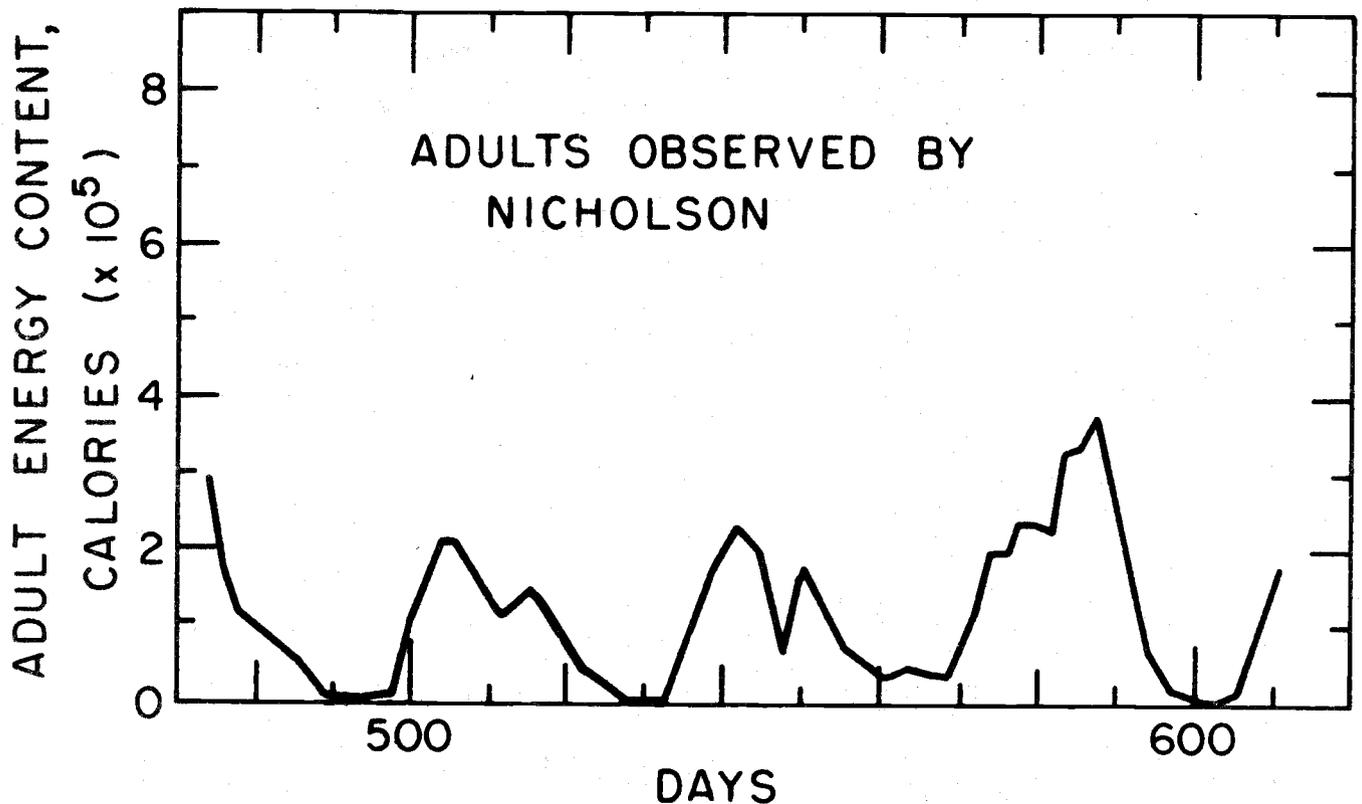


Figure 1. Changes in adult population observed by Nicholson. Larval ration was 50 grams of meat per day; adult food was unlimited. Data were converted to calories for comparison with simulation results.

This central study was one of intraspecific competition among the larvae in an environmentally simple single-species situation. Variations of this experiment were also conducted by Nicholson, in which daily larval food rations were varied in size, and in which adult food rations were restricted.

Simulation of Nicholson's Experiment

A Fortran IV program ("FLYLIFE") was written to direct a CDC 3600 computer to simulate the flow of energy from food through consumers in a system such as Nicholson's. No single equation can characterize the central mechanism of this model; rather, its action combines the effects of numerous subprocesses to generate resultant population growths and declines. The dominant principle in the model is the precise identification of the pathway followed by every unit of energy introduced into the cage under all of the conditions that could occur there and the consequent effect of such flows upon the flies.

The model subdivides the fly population into developmental classes (similar to age classes), each of whose individuals are assumed to be genetically and physiologically homogeneous. Each class is considered to feed, grow, develop toward maturity, reproduce, and starve, as occasion arises, in strict accordance with limitations dictated by the species' physiological properties. Total population growth and decline, therefore, is calculated as a result of processes occurring on a physiological level.

The FLYLIFE model consists of a series of submodels, each of which simulated one set of processes in the caged population. The submodels are linked in the order shown in Figure 2.

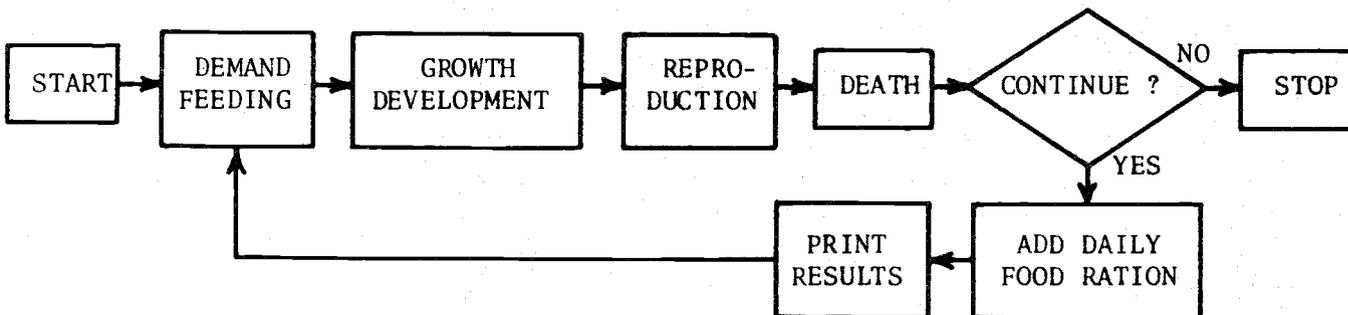


Figure 2. General structure of FLYLIFE model.

Data required to begin a simulation consists of 1) numbers describing certain physiological properties of the flies, and (2) numbers describing the characteristics of the population initially introduced into the cage. Given this information, the computer then proceeds through the simulation in the order shown in Figure 2, calculating the changes in each developmental class that result from feeding, respiration, maturation, reproduction, and death, where appropriate. If starvation has not exterminated the entire population, it then repeats these calculations, using as its starting population the changed population resulting from the previous calculations. Each passage through the submodels simulates one half-day's population changes.

The FLYLIFE program instructs the computer to store the information with which it works in a table such as that shown in Figure 3.

DEVELOPMENTAL CLASS	1	2	3	99	100	
A(J) (calories)			11023.0			Class energy content, total
BA(J) (calories)			0.0			Class energy content in adult biomass
N(J) (individuals)			155			Number of individuals in class
L(J) (half-days)			22			Age of class in half-days
DEV(J) (%)			0.96			% development completed by
DEF(J) (calories)			292.7			Class "hunger"

Figure 3. Storage of data used in FLYLIFE calculations. Numerals illustrate data for one developmental class.

Each vertical column contains numbers that describe one developmental class (usually equivalent to an age class) of flies. Each class is defined, therefore, by six different variables, and up to 100 classes can be accommodated.

Easily definable class variables are $N(J)$, the number of individual insects in class J , and $L(J)$, the age of the class in half-days. $A(J)$ is the number of calories currently stored as biomass in all individuals of class J , or the number of calories that would be measured if the entire class were incinerated in a bomb calorimeter. Other variables, and assumptions upon which the model is based, are defined in the following.

Development

Each individual fly is assumed to begin life as an egg, with 0% of its larval development completed, and to progress toward 100% completion (that is, emergence from its pupa) at a rate governed by temperature. Under the constant-temperature conditions maintained by Nicholson, larval lifetimes were 23 half-days; thus, each larval class was considered to complete $1/23 = 0.0435 = 4.35\%$ of its development toward adulthood per half-day.

This developmental progress can be visualized by imagining a line of length 1.0 units (100%; Figure 4a). At any moment, the fraction of larval development completed by a class can be represented by a point x on the line that advances at the rate of 0.0435 units per half-day. Two "mileposts" in larval development--hatching, and pupation--are represented by points H and P on the line; as point x passes these mileposts, the energy demand and behavior of the class is modified appropriately. The quantity $DEV(J)$ in the central data matrix (Figure 3) is the position of the point x for class J in Figure 4a, or, in other words, the fraction of larval development completed by the class.

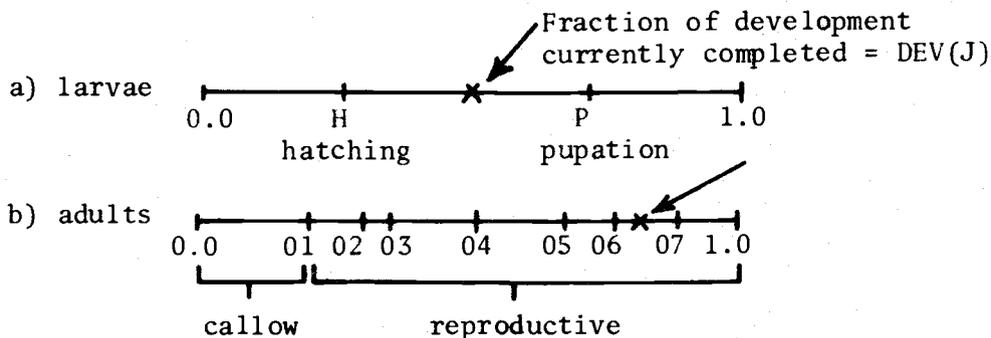


Figure 4. Visualization of FLYLIFE development submodel.

A similar development scheme is used for adult flies (Figure 4b). An adult is assumed to emerge from a pupa with 0% of its adult development completed, and to proceed toward 100% completion (that is, death of old age) at a rate governed by temperature. Under Nicholson's conditions, and with a maximum adult lifespan observed by him of 48 half-days, development of adults was simply advanced by $1/48 = 0.0208 = 2.08\%$ per half-day.

D1 is that fraction of adult development which must be completed before the adult fly is capable of reproduction; the other D's are subdivisions of the lifespan that are based upon the species' change in fecundity with age.

This development scheme distinguishes class progression toward maturity from the passage of time. In this simulation, time and development both proceed by constant increments, because the experiment was conducted under constant temperature. With variable temperature, the increments would not necessarily be constant.

Development, as simulated in this model, was assumed to be uninfluenced by the nutrition of the individuals.

Reproduction

Adults were assumed to be incapable of oviposition until fraction D1 of their development was completed. After this, their oviposition was calculated from data similar to that shown in Figure 5.

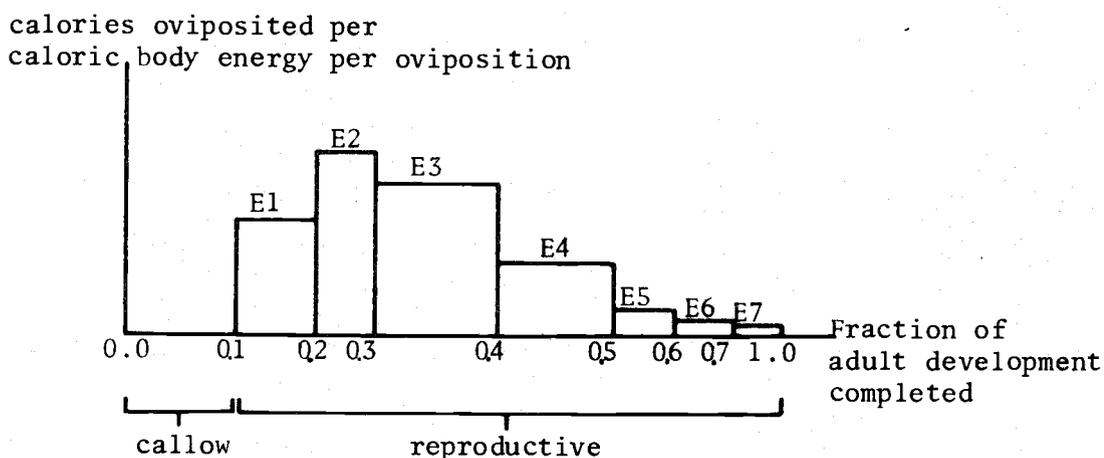


Figure 5. Age-specific fecundity relation used to determine potential principles.

Quantities D subdivide the adult lifespan into different reproductive periods. Each E variable is the number of calories oviposited in the form of eggs per calorie of adult female body energy (measured immediately after oviposition) per oviposition during the corresponding developmental interval. Thus, all female adult flies whose developments are between D_i and D_{i+1} % of completion are assumed to be capable of ovipositing an observable quantity E_i calories of eggs per calorie of body energy each time they oviposit, given sufficient food. Intervals defined by the D's correspond to natural changes with aging in the capacity of adult females to lay eggs.

Quantity BA(J) in the main data table (Figure 3) is the adult body energy of class J used in this calculation. BA(J) is zero until each class J reaches development D1. At this time, BA(J) is set equal to A(J), the stored energy content of the class and thereafter remains unchanged until the death of the class. Thenceforth, A(J) for adults is the sum of BA(J) plus any additional energy stored

in the class in the form of developing eggs. Upon oviposition, class energy content is reduced from $A(J)$ back to $BA(J)$, and the former difference becomes the stored energy content of the new batch of eggs. This energy content is divided by the calorie content of a single egg to determine the number of individuals present in the new batch.

Oviposition by females was assumed to occur every half-day, in conditions where adult food supply was not restricted. When a half-day's events resulted in a new batch of eggs, values of the variables $A(J)$ through $DEF(J)$ (Figure 3) describing the new eggs were stored in a separate column in the main data table, and were kept isolated from the values in other columns throughout the entire lifetime of the class. Thus, each developmental class J resulted from a single half-day's eggs.

Demand and Feeding

Three major processes dealt with in the demand and feeding subroutines are the energy acquisition and demand of each developmental class, and starvation.

Energy acquisition. Each class capable of feeding is assigned, at the beginning of each half-day, an energy demand in calories that is a function of the class calorie content $A(J)$ and of its starvation history. The total demand of all classes is then compared with the supply of energy available in the form of food. If the supply exceeds the demand, then the entire demand is assumed to be satisfied and the food supply is diminished by subtracting the demanded calories. In this instance, each developmental class then has added to its stored energy content $A(J)$ the calories demanded and eaten by that class; the calories respired during that half-day are subtracted.

When the calorie demand exceeds the food calorie supply, the entire supply is assumed to be consumed. In this event, each feeding class is assumed to acquire an amount of the devoured supply proportional to its contribution to the total energy demand. This amount of energy is added to the class, and the amount of energy respired during that half-day is subtracted.

Energy acquisition in the two examples is shown by Figure 6.

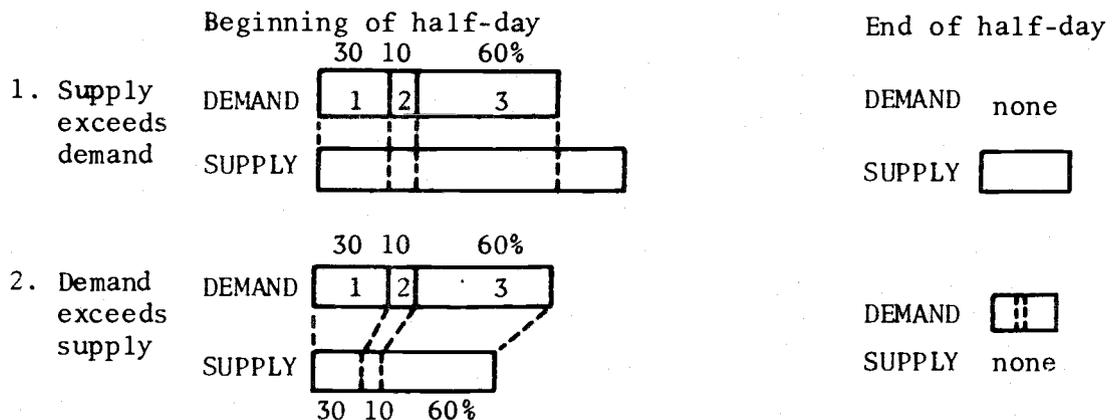


Figure 6. Visualization of two examples of FLYLIFE feeding submodel principles.

Suppose that, during a particular half-day, three developmental classes of larvae exist that require food, and that the sum of their demands in calories is a number represented by the length of the DEMAND bar in example 1. By the end of the half-day's feeding, the food supply has been diminished by the amount demanded, all demands have been satisfied, and the energy content of each class has been increased by the amount demanded and decreased by the amount respired. If, however, demand exceeds supply (example 2), then by the end of the half-day the entire supply is assumed to have been devoured. Each class is assumed to have obtained a share of the consumed supply equal to its fraction of the total demand. The stored energy content of each class is increased by the amount consumed and decreased by the energy respired during that half-day; class demand remains partially unsatisfied.

These simple assumptions define the entire mechanism of competition in this simulation and form the foundation upon which the whole simulation is based.

Starvation. To simulate starvation of a class, some measure of the "hunger" of the class must be retained. Quantity DEF(J) in Figure 3--energy "deficient"--is this measure, and is defined as follows:

Let $A(J)$ be the calorie content of a class of larvae that has experienced food shortages. Let A_N be the calorie content of a class of larvae hatched at the same time as class J, and consisting of the same number of individuals, but which has never experienced food shortages. DEF(J) is defined by $A_N = A(J) + DEF(J)$. In words, it is the difference between the energy that a larval class has actually managed to accumulate within a given time and that which it could have accumulated had the class been adequately fed during that time. A_N is referred to as the "normal counterpart" of class J.

For larvae and callow adults, the ratio $A(J)/A(J) + DEF(J)$ gives the fraction of normal stature that class J has achieved at any given time. If this fraction falls below a critical level, the class is assumed to have starved to death. For mature adults, $BA(J)$, the body energy present in a class at the beginning of its reproductive period, serves as the standard against which $A(J)$, the current total energy of the class, is compared. If, under food deprivation conditions, ratio $A(J)/BA(J)$ declines below a critical threshold, the adult class is considered to have starved to death.

Demand. A respiration rate R and a potential feeding rate F are used in the demand calculations, and in determining whether class hunger, $DEF(J)$, grows or dwindles within any given half-day. R , in calories respired/calorie body energy \cdot half-day, was estimated by the author (from data for comparable insects, Spector 1956) to be a constant 7.72×10^{-3} cal/cal \cdot half-day for both larvae and adults under the constant temperature conditions of Nicholson's experiment.

F is the rate, in calories consumed/calorie body energy \cdot half-day, at which a larva or adult can ingest food energy, given an adequate food supply. For larvae and callow adults, the constant values $F = 0.922$ and $F = 0.022$ cal/cal \cdot half-day were used, respectively, under all conditions, to calculate class demands. For each well-fed class of reproductive adults ($DEF(J) = 0.0$), a value of F was calculated that caused the class to demand exactly the energy needed to balance respiration and to acquire the excess it ultimately oviposited as eggs during that half-day. Under hunger conditions, ($DEF(J) > 0.0$) the value of F for callow adults was used for each hungry adult class.

Well-fed classes ($DEF(J) = 0.0$). The demand of each class of well-fed larvae and callow adults during a particular half-day was assumed to be proportional to the class energy content $A(J)$ at the beginning of the half-day. For such classes,

$$\text{Half-day demand} = A(J) \times F \text{ calories.} \quad (4)$$

The half-day's energy utilization, via respiration, of such classes was also assumed to be proportional to class energy content at the beginning of the half-day;

$$\text{Half-day respiration} = - A(J) \times R \text{ calories.} \quad (5)$$

With abundant food, where the food calorie supply exceeds the total demand of all classes, the class demand is also the amount of energy consumed by the class. The net energy gain per half-day is

$$A(J) \times (F-R) \text{ calories} \quad (6)$$

under these conditions.

This demand assumption causes a class to gain energy at a geometrically increasing rate when food is abundant. A larva of energy content A_0 at the time of hatching will contain energy

$$A_1 = A_0 + A_0(F-R) = A_0(1+F-R) \quad (7)$$

at the end of the first half-day's feeding. At the end of the second, third, and n th half-days, its energy content will be given by

$$\begin{aligned} A_2 &= A_1(1+F-R) = A_0(1+F-R)^2 \\ A_3 &= A_2(1+F-R) = A_0(1+F-R)^3 \end{aligned} \quad (8)$$

$$\text{and } A_n = A_0(1+F-R)^n,$$

respectively. The latter equation is the basis for the estimate of the value of F for larvae, cited above. R was estimated from data for other insects. Using $A_0 = 0.118$ calories and $A_n = 78.3$ calories (estimated energy contents of a larva at hatching and pupation, respectively) and $n = 10$ half-days (time elapsed between hatching and pupation, Nicholson 1957), the last equation of set (8) may be solved for F for larvae. An analogous procedure produces the value of F used for callow adults.

For reproductive adult classes, $A(J)$ represents the total class energy, which, with abundant food, includes that present in the form of adult biomass, $BA(J)$, plus any excess in the form of developing eggs. For normal females in developmental stage $D_i \leq DEV(J) < D_{i+1}$, E_i calories of eggs can be oviposited per calorie of adult biomass per oviposition (Figure 5). The total quantity of calories oviposited per class of body energy $BA(J)$ is therefore $1/2 BA(J)E_i$, assuming that half the class consists of females. The energy needed to acquire this amount plus that required to offset respiration in one half-day is $1/2 BA(J)E_i + A(J)R$ calories. The demand of a well-fed reproductive class at the beginning of a half-day was assumed to be proportional to $BA(J)$ and was assumed to equal the required energy gain;

$$\text{half-day demand} = BA(J)F = 1/2 BA(J)E_i + A(J)R \text{ calories.} \quad (9)$$

This equation was solved for the value of F used for each reproductive class upon each half-day of food abundance conditions.

Hunger conditions ($DEF(J) > 0.0$). The demand of any class for which $DEF(J) > 0.0$ was assumed to be given by

$$\text{Half-day demand} = (A(J) + SRC \times DEF(J))F + SRC \times DEF(J) \text{ calories,} \quad (10)$$

an equation that incorporates the effect of hunger upon the class appetite. $A(J)$, $DEF(J)$, F , and R are as defined above. Starvation recovery coefficient, SRC , is the fraction of recovery to normal stature that a hungry class is capable of making in one half-day's feeding, given sufficient food.

SRC is a species property assumed obtainable from laboratory studies of most animal species. For the purpose of this simulation, it was approximated by the function defined by Figure 7.

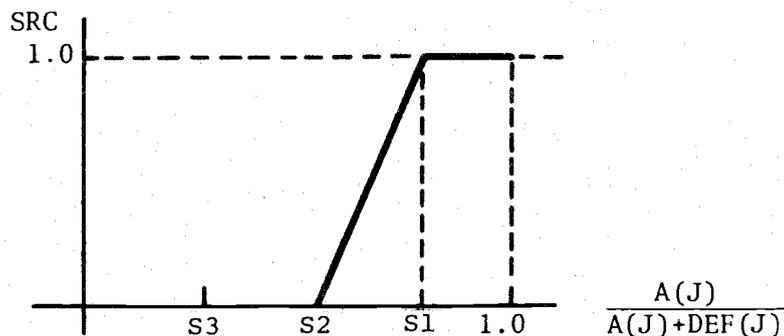


Figure 7. Function used to define starvation recovery coefficient.

Ratio $A(J)/(A(J)+DEF(J))$ (call it r for brevity) is the fraction of normal stature achieved by class J after having experienced food shortages during its lifetime. $S3$ is the fraction below which r must fall to result in death by starvation. $S1$ is the fraction above which r must remain to permit the class to make a complete recovery to normal stature within one half-day's feeding, given sufficient food. $S2$ is the ratio r below which the class is still capable of feeding and growing, but from which it is incapable of reducing the difference between its stature and normal stature, even given abundant food. SRC was set equal to 1.0 for $r \geq S1$, 0.0 for $S3 < r < S2$, and an intermediate value $((r-S2)/(S1-S2))$ for $S2 < r < S1$.

The demand function (10) is derived from the definitions of SRC and DEF(J). This equation builds the following biologically realistic features into the model.

- 1) The demand of a "hungry" class ($S2 < r < 1.0$) is greater than that of a well-fed class ($DEF(J)=0.0$) of the same stature $A(J)$.
- 2) As hunger increases, the demand of a class rises above, then diminishes below that of its normal counterpart (simulating first an increase in appetite, then increasing weakness because of hunger).
- 3) As the degree of hunger diminishes ($r \rightarrow 1.0$ as $DEF(J) \rightarrow 0.0$), the demand of a hungry class approaches and ultimately becomes the same as that of a well-fed class of the same stature.
- 4) A class that is only slightly hungry ($S1 \leq r < 1.0$) can recover to normal stature within one feeding, given sufficient food.
- 5) A hungry class ($S2 < r < S1$) can gradually recover toward normal stature, given sufficient food and time to feed before pupation.
- 6) Severely starved classes ($S3 < r \leq S2$) can survive, given sufficient food, and mature as stunted adults.

In a series of simulations of conditions in which adults, as well as larvae, were limited to a restricted food ration, starved adults ($DEF(J) > 0.0$) were assumed not to oviposit. Their demand was calculated from equation (10) using values of $S1$, $S2$, and $S3$ defined for adults, and the value of F for callow adults.

Summary of demand and feeding submodel mechanisms.

1) SRC is calculated for each class, using values $A(J)$, $DEF(J)$, $S1$, $S2$, and $S3$.

2) F is calculated for each well-fed reproductive class.

3) The demand of each class is calculated, with equation 4, 9, or 10, where appropriate.

4) Total larval demand is compared with the food supply. The food supply is reduced, either to zero (if supply \leq demand) or by the amount demanded (if supply $>$ demand).

5) An amount of energy $E = \frac{\text{class demand}}{\text{total demand}} * (\text{food harvested})$ is added to each class value $A(J)$; a respired quantity of energy is subtracted from $A(J)+E$.

6) The growth of the normal counterpart of each larval and adult class is calculated (from $A_{N2} = A_{N1} (1 + F - R)$).

7) The new energy content $A(J)$ is compared with the new normal counterpart energy content A_{N2} , and a new $DEF(J)$ value $DEF(J) =$

$A_{N2} - A(J)$ is calculated.

8) For reproductive adult classes, $DEF(J)$ is set equal to zero if $A(J) \geq BA(J)$, or $BA(J) - A(J)$ if $A(J) < BA(J)$.

Death

Flies in the model could die either by outliving their physiological life span ($DEV(J) \geq 1.0$, adults) or by failing to acquire enough energy, by feeding, to prevent $A(J)/(A(J)+DEF(J))$ from slipping below level S3. Classes meeting either criterion were reduced to zero individuals with zero stored energy content. Whether cannibalism was permitted in Nicholson's experiments is not clear. If so, deceased classes could be considered as additions to the supply of food available to those still living. In this simulation, dead insects were assumed to have been removed from the cage before they were eaten.

Input Data and Parameters

Table 1 summarizes the data required by the computer for one simulation. Values arbitrarily estimated by the author are indicated by *; + indicates values estimated or taken from the source cited. These values are not altered during the course of any given simulation, but were sometimes changed between simulations to investigate the effect of the change.

In most model studies, one class of newly laid eggs was used to begin the simulation, with the following properties:

A)1 = 25.0 calories; BA(1) = 0.0 (undefined for eggs); LIFE(1) = 0 half-days; N(1) = 211 individuals; DEF(1) = 0.0 calories deficient; DEV(1) = 0.0% developed. No food was assumed to be present at this time.

Simulations

Simulations were run in which the daily food ration of the larvae, the larval coefficients S1, S2, and S3, the age structure of the initial population, and the adult oviposition schedule (variables E) were varied. In another series, the adult food ration was restricted, as was the larval ration. Each simulation was continued either until the population within the cage had become extinct, or until a pattern of population fluctuations appeared that seemed likely to persist. In the latter instance, populations that survived through 250 simulated days were considered persistent.

The running time for a 250-day simulation was about 110 seconds; about 60-70 of the 100 available class storage spaces (Figure 3) were in use at the height of each simulation.

RESULTS

Series A. Input parameters as in Table I

Figure 8 shows the stored energy contents of the adults, pupae, larvae, eggs, and larval food supply generated by the model as functions of days after initiation of the simulated experiment. After an enormous transient surge in the cage population, made possible by the food buildup in the early weeks, the adult population settles into a cyclic steady-state pattern of outbreaks and declines.

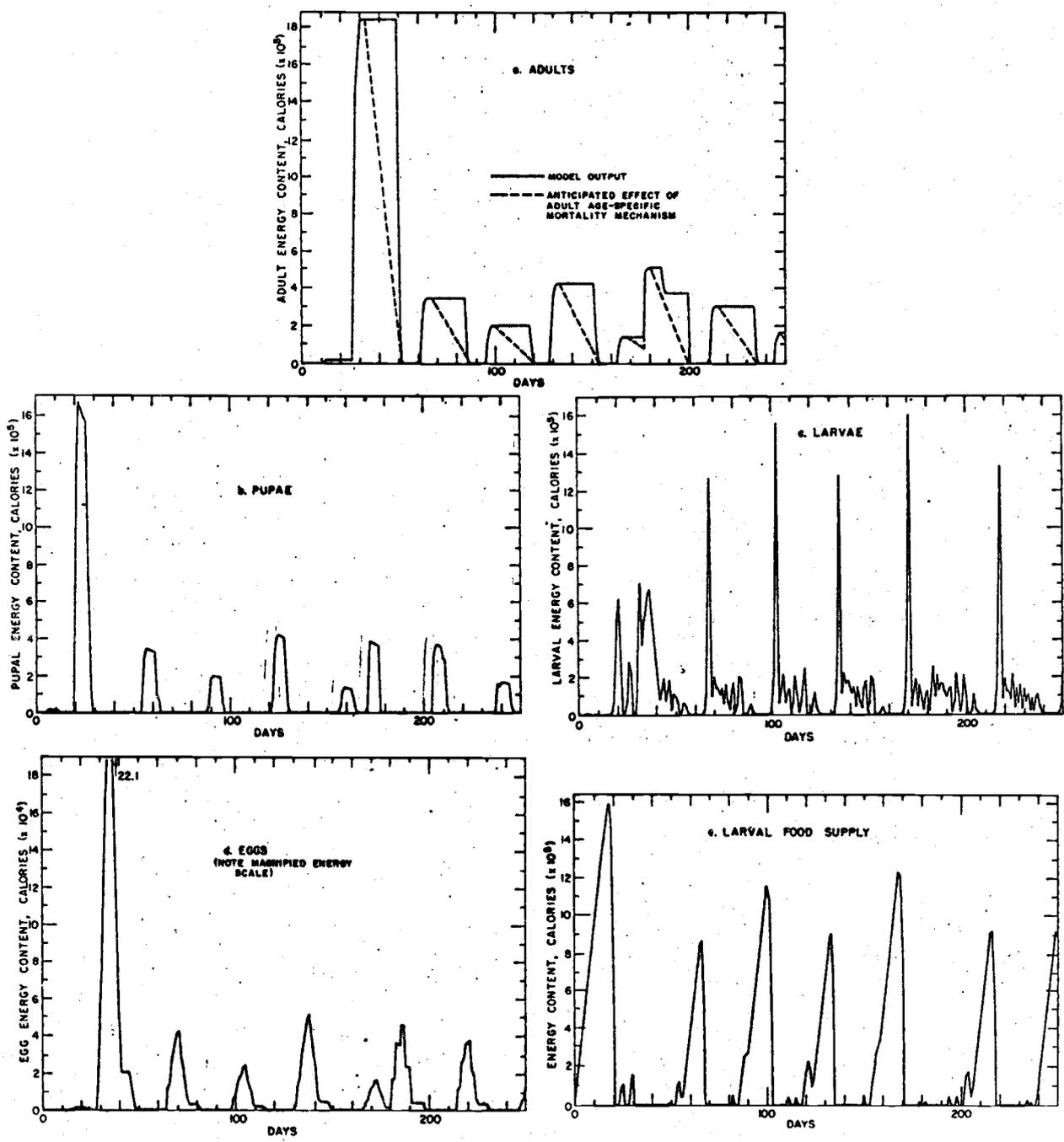


Figure 8. Relation of population energy contents to time. Simulation series a; input data as in Table 1.

Series B. Input parameters as in Table 1, except FOODL = 4.65×10^4 (25 gm meat/day)

Figure 9 shows the daily caloric content of adults calculated by the computer when the daily larval food ration is half that used in Series A. After the initial transient outbreak, the succeeding outbreaks reach about half the levels of those in Series A, with the timing of the outbreaks virtually unchanged.

Series C. Input parameters as in Table 1, except S1 and S2 were varied

Figures 10a, 11, and 12 show, respectively, the daily caloric contents of adults generated when larval resistance to starvation was progressively increased by lowering the values of S1 and S2. Figure 10b shows pupal energies from the simulation that produced Figure 10a.

Series D. Input parameters as in Table 1, plus adults restricted to daily food ration of 8.18×10^3 calories per day

Figures 13 and 14 show the effects of restricting the adult food ration as well as that of the larvae. In Figure 13, adult food restrictions began on day 125; in Figure 14, adult food was restricted from the first day.

DISCUSSION

Series A and B.

Adult data from Nicholson's (1957) central experiment (part of his Figure 3, converted to calorie units) is shown in Figure 1. The "fit" between the steady-state computer-generated curve in Figure 8a and that of Nicholson is close in both size and timing of the outbreaks. The most obvious discrepancy is in the shape of the outbreak curves; the computer outbreaks are flat-topped, but Nicholson's are not.

The explanation for this discrepancy probably lies in the fact that no age-specific mortality mechanism for adult flies was included in the model. Each adult was assumed to live 24 days, the physiological maximum for the species. Most of the square-topped outbreaks in the Figures result from the maturation of a single dominant class of individuals, all of which lived an identical length of time and then died of old age at the same moment. The adults observed by Nicholson, even under the food-abundance conditions of his experiment, began to die of unspecified causes 6 days after emergence from their pupae, and few lived as long as 24 days. Had an age-specific death rate been imposed upon the model population, the effect would probably have been to shave the trailing edges of the simulated outbreaks in the manner shown in Figure 8a, thus considerably improving the fit to Nicholson's data.

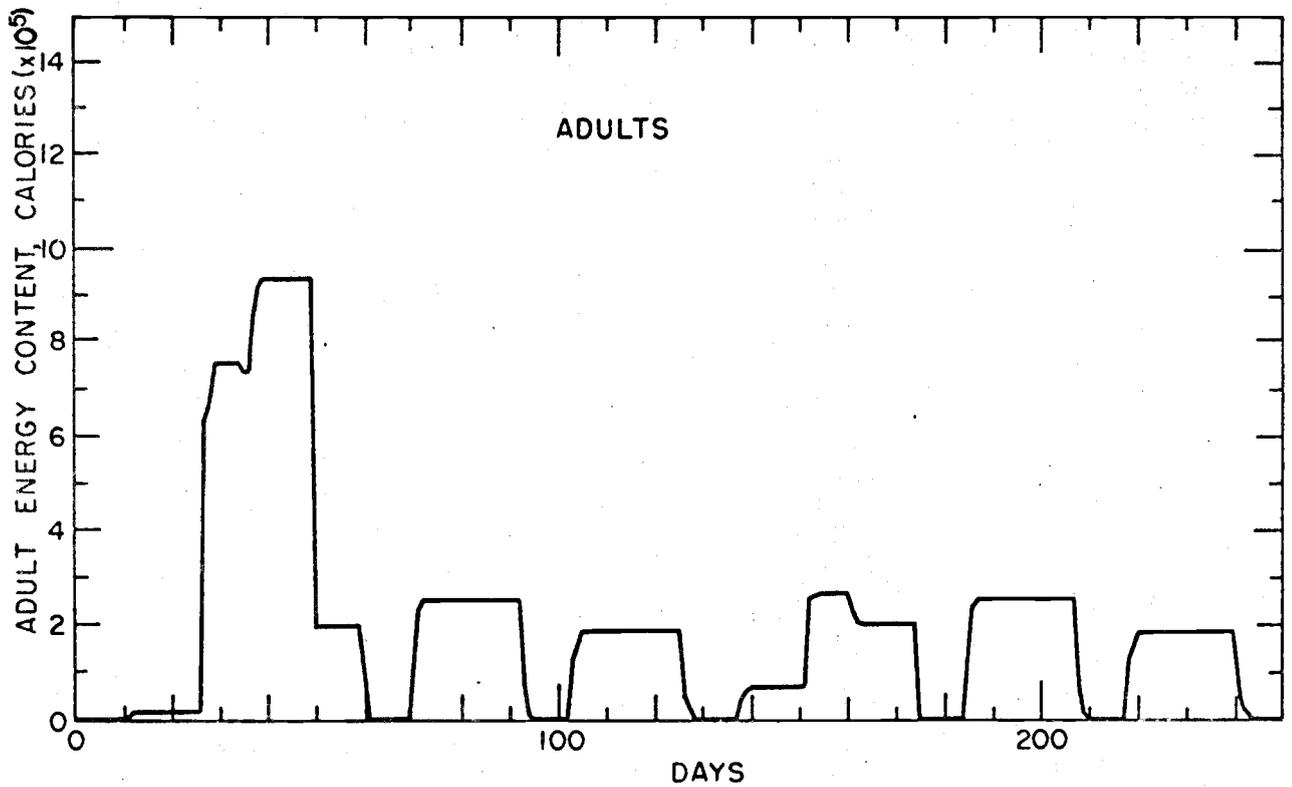


Figure 9. Relation of adult energy content to time. Simulation series b; input data as in Table 1, except larval food ration reduced by half.

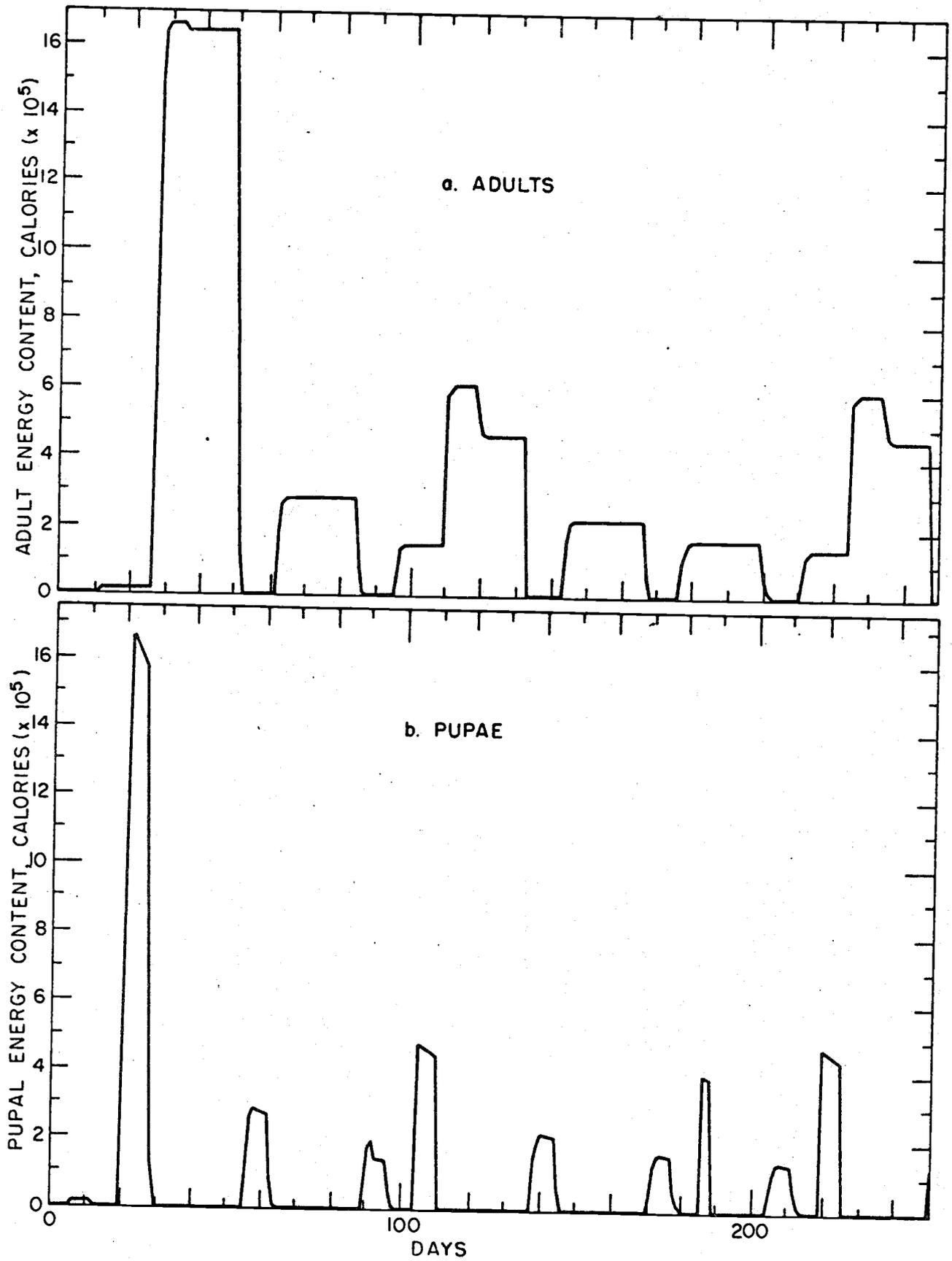


Figure 10. Relation of adult and pupal energy content to time. Simulation series c; input data as in Table 1, except $S_2 = 0.75$. Low larval resistance to starvation.

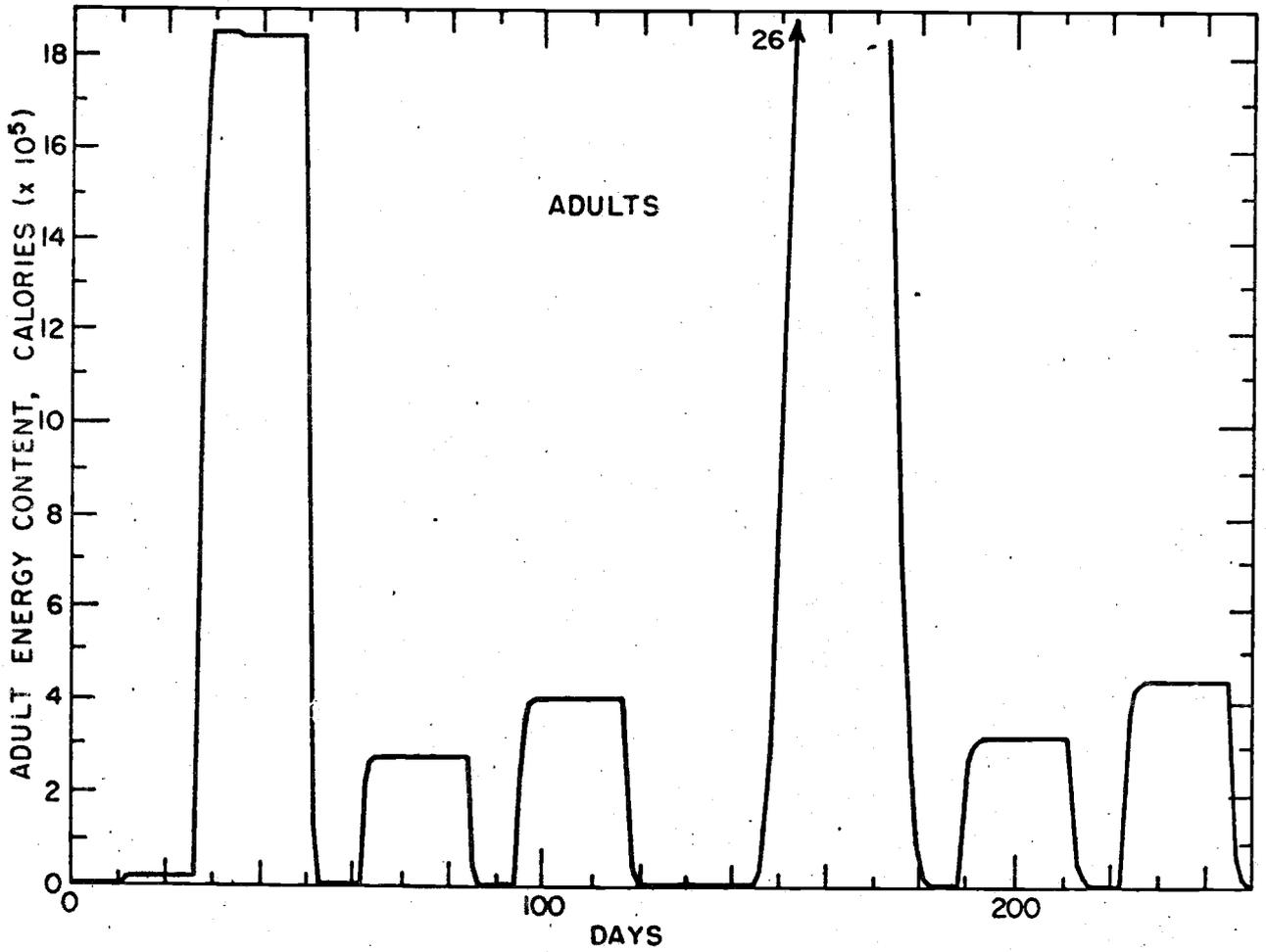


Figure 11. Relation of adult energy content to time. Simulation series c; input data as in Table 1, except $S_1 = 0.80$. Improved larval resistance to starvation.

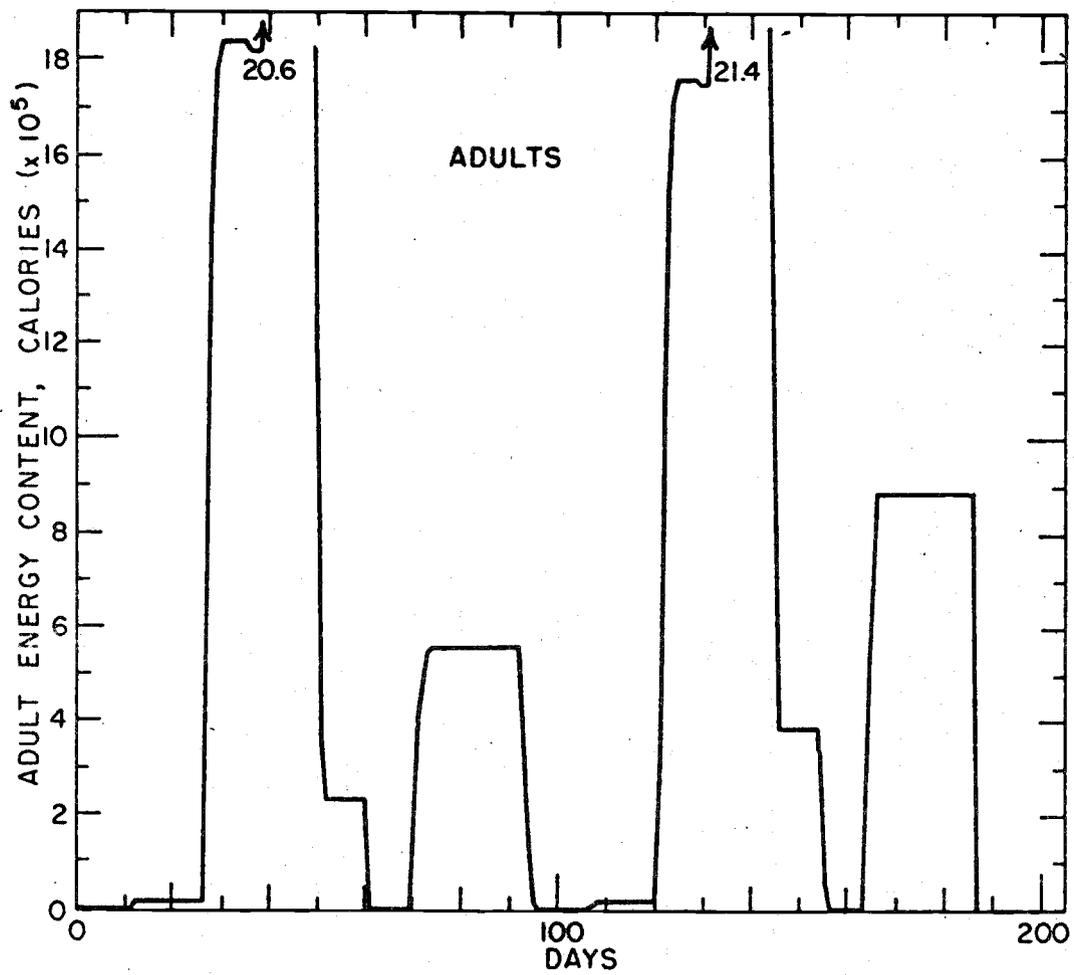


Figure 12. Relation of adult energy content to time. Simulation series c; input data as in Table 1, except $S_2 = 0.30$. High larval resistance to starvation.

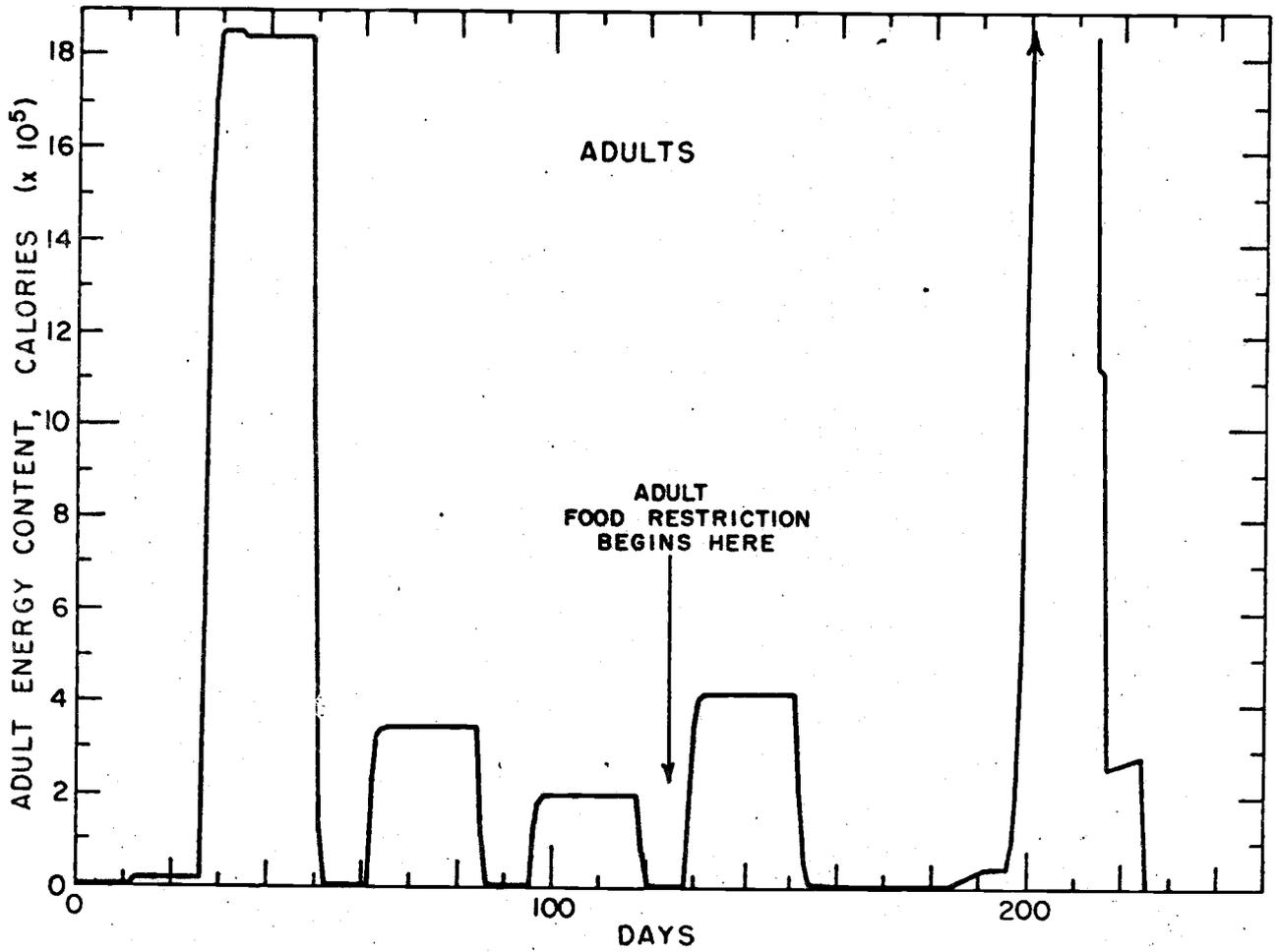


Figure 13. Relation of adult energy content to time. Simulation series d; input data as in Table 1, plus restriction of adult food supply.

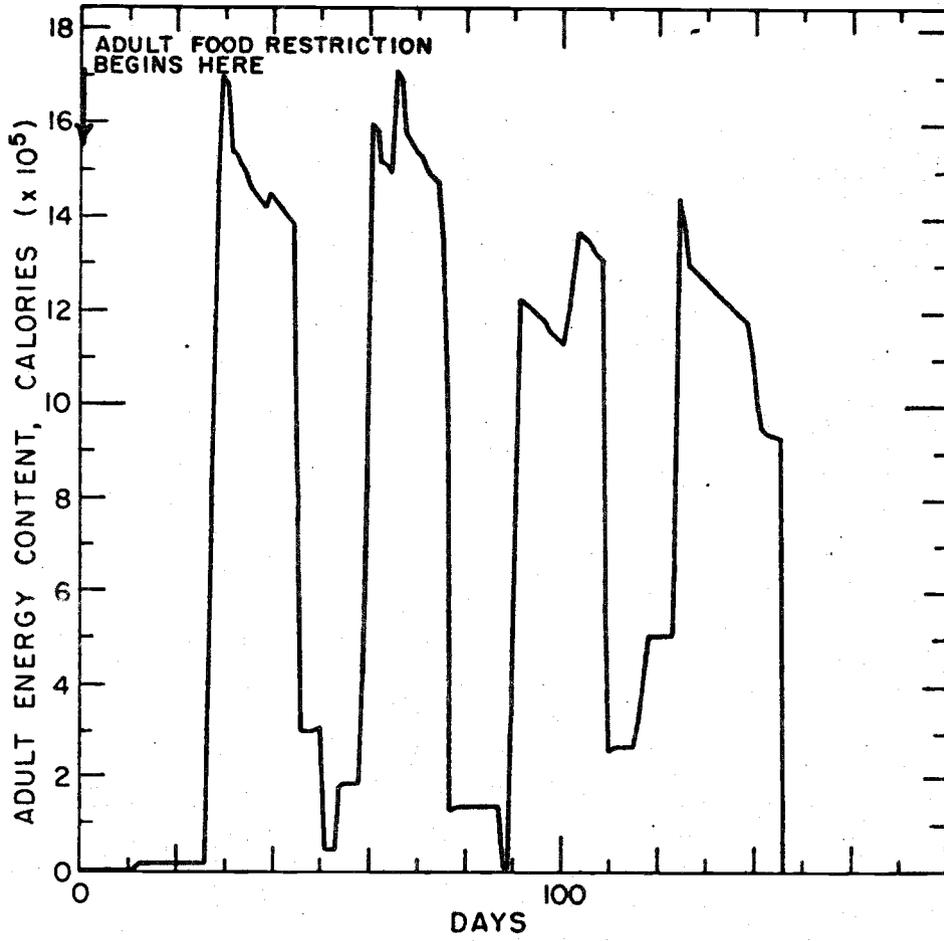


Figure 14. Relation of adult energy content to time. Simulation series d; input as in Table 1, plus restriction of adult food supply.

A comparison of Figures 8a, 8b, 8c, 8d and 8e (best done by tracing and superposition) shows the mechanism of population regulation in the model to be identical to that described by Nicholson. After the initial population outbreak in the early weeks, larval energy accumulation settles into a violently repetitive pattern. During each brief period when larvae are absent (about 4-5 day periods when only pupae are present) the 50-gm daily meat rations accumulate. When oviposition finally begins, this permits a spectacular buildup of larval energy. The food supply is exhausted, and a dramatic die-off of larvae occurs. Continued additions of meat permit some recovery by surviving classes, but repeated food depletion and starvation throttle larval growth until adult oviposition begins to dwindle. Eventually, larval numbers diminish to a level that the food supply can sustain, and a very few classes enter pupation just as the remaining adults die.

The regular pattern of pupal occurrence was broken in the Series A run at day 170, when a second class of larvae managed to survive and pupate. This leads to the step-shaped adult outbreak in Figure 8a, which, had it been corrected by including age-specific adult mortality, would closely resemble a double-topped outbreak of a type occasionally observed by Nicholson (as in Figure 1). Nicholson noted that these double-topped peaks in abundance were, indeed, the result of chance survival of larvae from batches of eggs spaced several days apart. Thus, this model seems to have, inherent in its structure, the capacity for including occasional events, as well as more regularly occurring ones.

The effect upon the computer-determined population of reducing the daily food ration by half is similar to, but not as marked, as that observed by Nicholson. The periodicity of the outbreaks is unchanged, but their amplitude is reduced by about one half.

Series C.

In this series, the ability of the larvae to resist starvation was improved by lowering the values of S1 and S2 between successive simulations. Low larval resistance to starvation ($S1 = 0.90$, $S2 = 0.75$) produces the result in Figure 10; increased resistance ($S1 = 0.90$ and $S2 = 0.50$; $S1 = 0.80$ and $S2 = 0.50$; $S1 = 0.90$ and $S2 = 0.30$) produced the results shown, respectively, in Figure 8a, 11, and 12. Such an experiment is biologically almost impossible to perform, as it would require an ability to alter aspects of the species' physiology; its outcome is instructive, however, to population dynamics enthusiasts.

The paradoxical result suggested by this series is that increasing the ability of each individual to recover from starvation increases the probability that starvation will exterminate the population as a whole. A detailed examination of the computer output suggests an explanation. Larvae with low starvation resistance ($S1 \approx 0.9$, $S2 \approx 0.5$) "die" quickly when confronted with food shortages, clearing the way for later food accumulations and feeding by new larvae in the reduced presence of older ones. Larvae with the ability to continue aggressive feeding, even when highly starved, persisted for longer periods in the simulation, depleting and wasting the limited food resource and forcing younger individuals into hunger earlier in their development. The net result was the extermination of all.

A run not reported here showed that, if larval starvation resistance is too low, extinction of the entire population will also occur. Thus, there appears to be a range of starvation recovery abilities within which populations of L. cuprina (and presumably other organisms) can persist in the caged condition. Whether this is a species property that is subject to natural selection is open to question. If so, organisms frequently subject to extreme crowding on a natural food supply might conceivably approach a limit in their ability to resist starvation imposed by population dynamic, rather than physiological, restrictions.

Figure 10b shows an unexpected and biologically realistic effect of the starvation simulation mechanism in the FLYLIFE model. The Figure shows the changes in pupal energy content that accompanied the adult changes (Figure 10a) in the low starvation-resistance condition. On day 185, some larvae entered pupation, but did not survive to adulthood. Respiration of these starved larvae, whose DEF values were high when they entered pupation, reduced their energy content A to such an extent that ratio $A/(A+DEF)$ declined below the fatal threshold S3, and they died.

Figure 11 is interesting because of the explosive outbreak of flies that occurs over days 146-180. Were this a natural situation, such an eruption of insects above the background level would almost certainly invite studies of the weather and other extrinsic factors in an effort to explain it. The events that made the outbreak possible, however, had their origins entirely in the physiological properties of the larvae. One might speculate that parallel situations may occur in nature, where outbreaks of insects might result from shifts in the physiological makeup of populations, even in the absence of any dramatic change in their environment. Such shifts could accompany increasing resistance to insecticides, mating with laboratory-reared strains of males, or other consequences of human manipulations.

Series D.

The shortcomings of the present model are partially revealed by this series. These runs attempted to simulate a variation of Nicholson's central experiment in which the adults, as well as the larvae, were restricted to a limited daily energy ration. Nicholson observed that a certain critical larval/adult daily food ratio destroys the periodicity of the adult population changes and raises the average density of their population. One series D run attempted the same condition by suddenly restricting the adult energy ration, beginning on day 125 (Figure 13). The curve generated is identical to that of Figure 8a until day 132, when flies emerging from the pupae (with most of their adult biomass already formed) were unable to find enough food to reach quite the same size as their counterparts in Series A. Thereafter, the regular pattern of change is broken, and extinction follows an enormous outbreak. Another run in which adult food limitation was begun on the first day of the simulation produced periodic outbreaks of enormous amplitude and ultimate extinction seen in Figure 14.

The extinction of the flies in the Series D simulations may not represent a model failure. Nicholson noted (1957) that adult and larval food rations not precisely in the ratio of 1 gm protein (energy unlimited):50 gm meat per day tended to increase the violence of the periodic oscillations of the adult population. Whether or not this resulted in extinction of his caged population, he does not say.

Other Series

Another experiment that is biologically impossible, but can be conducted via model studies, is an alteration of the reproductive schedule of the flies (the oviposition/age relation shown in Figure 5). In one series of runs, each fly was assumed to lay a normal quantity of eggs, but to produce them at a constant rate during its reproductive lifetime. The effect of such a change is to make the caged population extremely unstable and to cause its extinction after one or two spectacular outbreaks. The more the ovipositional effort is crowded into the early part of the adult's reproductive period (as in Figure 5), the more stable (i.e., like that of Figure 8a) its population becomes in the cage situation. This feature of the fly is surely subject to natural selection; whether crowding upon food sources replenished at a constant rate occurs frequently enough in its natural habitat to bring selective forces to bear upon it is questionable.

A few runs were conducted in which the population initially introduced to the cage was varied to include mixtures of eggs, larvae, pupae, and adults. After initial transient changes in such populations, they settled into routines of growth and decline similar to that in Figure 8a.

The Model

The probable reason for the failure of the model to duplicate Nicholson's results in the Series D runs, and probably its most significant shortcoming, is the assumption that the members of each developmental class are physiologically and otherwise homogeneous. We might expect (and, indeed, Nicholson observed) that some individuals, even in an overcrowded situation in which the food supply was grossly inadequate, might get more than their "share" of a limited supply either by first access to it, or by aggressive behavior. If true, the share of the supply acquired by each class might not be exactly proportional to its demand, and the share of the class's harvest would not be apportioned equally among its members. Little energy is required by an adult to survive and oviposit, and either chance or aggression might permit individuals to continue oviposition even in a general situation of starvation.

The class homogeneity assumption can be eliminated by assuming that the class value of $DEF(J)$ (Figure 3) represents the class mean and that individuals in the class are distributed about this mean in some (probably normal) manner. Deaths from starvation would then eliminate only that fraction of the class for which $DEF(J)/(A(J)+DEF(J)) < S_3$, rather than the entire class. Oviposition could occur if class members with $DEF = 0.0$ were present. Such a change would

require storage of a few more variables (for example, adult and larval standard deviation variables) and some appropriate changes in many of the model mechanisms.

The most interesting feature of the FLYLIFE model is the simplicity of the mechanism that simulated competition. Each organism and class is assumed to acquire a fraction of the limited food supply exactly equal to its fraction of the total demand. In certain situations, such as that, say, in which larger organisms whose demand constitutes 70% of the total, acquire more than 70% of the limited supply because of their aggressive behavior, such an assumption may be unrealistic. But the fact that the model generates data resembling Nicholson's suggests that, in the cage situation, this simple assumption is adequate to describe the outcome of all important competitive processes occurring in the cage. An interesting test of the validity of this assumption might be its use in a model of interspecific competition, where the competing classes are of different ages and species.

Other assumptions and mechanisms used in the model are all amenable to improvement in the direction of increased biological realism. The success of the current model in the limited situation to which it applies, however, suggests that the package as a whole is realistic enough to provide a close first approximation to most of the relevant processes that occurred in Nicholson's cages.

CONCLUSION

The model used here was developed as a collection of assumptions about how energy is subdivided and used by consuming factions of organisms, and about how their successes and failures combine to affect their development and survival. The population changes generated by the model represent the results of the interaction of numerous mechanisms, each of which parallels one process. The fact that the daily population trends fit those observed by Nicholson is not a preordained result of any curve-fitting techniques, but, rather, an indication that most or all of the relevant processes occurring in the cages must have been adequately described by the assumptions.

In its current form, FLYLIFE incorporates my philosophy in that it is complex, its complexity is of a form that permits expansion without loss of credibility, and its elements can be understood, amended, or rejected by biologists whose orientation is nonmathematical. This complexity immensely broadens the base from which a variety of interesting simulation experiments can be tried, and it increases the number of elements that can interact to produce unexpected but realistic irregularities in its output, such as the pupal deaths, double-peaked outbreaks, and initial transient outbreaks noted. As suggested here, not only questions of population dynamics, but those regarding evolution can be explored with a model whose foundation rests upon physiological properties of a species.

Were this a description of a population whose control was desired, an immense variety of strategies could be tested. Included in these are manipulations of larval and adult food supplies at strategic moments, "flooding" the population with different age structure mixes at various times in an effort to disrupt it, alteration of species physiological parameters by release of laboratory-grown males, and straightforward inducement of mortalities inflicted by agents such as insecticides. As FLYLIFE now stands, with its ability to simulate in seconds what took Nicholson years to observe, its ability to explore pathways that are biologically difficult or impossible to follow, and its ability to encompass most population parameters of current interest to ecologists, the model is probably a better tool for studies of the limited cage situation than would be an actual caged population.

The intent of the work described here was not merely to produce an elaborate computer model of a cage full of flies, but, rather, to examine the performance of assumptions regarding the partitioning of an energy supply by organisms in an environmentally simple situation. A model of a more complex natural system, incorporating such assumptions, may provide a more penetrating tool for analysis of such systems than any now existent. Whether or not the complexity of natural multispecies system will prove to be too formidable for an approach such as that employed here remains to be seen.