A Theoretical Study of Population Regulation in Tribolium Confusum

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A THEORETICAL STUDY OF POPULATION REGULATION IN *TRIBOLIUM CONFUSUM*

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Abstract. A deterministic mathematical model is constructed to describe the population growth in colonies of the grain beetle, *Tribolium confusum,* under laboratory conditions. It is shown how the eating of eggs by adults can account for the main features of the observed population growth, in particular the occurrence of a maximum in the adult numbers and the tendency then to reach a steady state.

Introduction

The aim of this paper is to construct a deterministic mathematical model describing the population growth in colonies of the grain beetle, *Tribolium confusum,* under laboratory conditions. The work is based on experiments reported by J. Le Gay Brereton (1962), in which the colonies are started with small populations, are self-contained so that there is no migration between them, and are provided with an unrestricted food supply. By substituting in the model the values estimated by Brereton of the various biological constants, theoretical graphs of the population growth are obtained which can be compared with those given by the actual experiments.

Certain hypotheses concerning the behavior of the insects have been put forward to account for features in the growth of the experimental populations. By constructing a mathematical model based on these hypotheses and then comparing the model with the experimental results, it can be tested whether such behavior would, in fact, affect the population growth in the required manner.

The *Tribolium* Model

Let

$N(t) =$ number of adults at time t,
$n_1(\tau_1, t) =$ number of eggs per unit age range of age τ_1, at time t,
$n_2(\tau_2, t) =$ number of larvae per unit age range of age τ_2, at time t,
$n_3(\tau_3, t) =$ number of pupae per unit age range of age τ_3, at time t,
$a_1, a_2, a_3 =$ the respective age spans of eggs, larvae, and pupae,
$b_1 =$ egg laying rate of an adult (the average for all adults),
$c =$ mortality rate of an adult,
$p_2 =$ probability of survival of the larvae,
$p_3 =$ probability of survival of the pupae.

(If necessary, the theory could be extended to include further stages, for example, immature adults.)

Then, since the rate of increase of adults is equal to the rate at which they are emerging from the pupae less the death rate,

$$(1) \qquad dN(t)/dt = n_3(a_3, t) - cN(t).$$

The rate at which eggs are entering the population is

$$(2) \qquad n_1(0, t) = b_1N(t).$$

Since a fraction p_3 of pupae survive the full age span a_3 and a fraction p_2 of larvae survive the time a_2,

$$\begin{aligned}(3) \quad n_3(a_3, t) &= p_3n_3(0, t-a_3) = p_3n_2(a_2, t-a_3)\\ &= p_3p_2n_2(0, t-a_3-a_2) = p_3p_2n_1(a_1, t-a_3-a_2).\end{aligned}$$

To obtain an equation in N only, it is necessary to have, in addition to these, a relation between $n_1(a_1, t)$ and $n_1(0, t)$. That is, the survival characteristics of the eggs must be determined. From various experiments, it has been concluded by Park (1933), Stanley (1942), Boyce (1946), Rich (1956), Brereton (1962), and others, that eggs are destroyed by adults.

Suppose that, in time τ_1, a fraction υ of the medium is explored and the eggs in it eaten. Then, of the eggs which were laid at the time $t - \tau_1$, only a fraction $1 - v$ will remain at time t. i.e.,

$$1-v = \frac{n_1(\tau_1, t)}{n_1(0, t - \tau_1)}. \tag{4}$$

Let k_o be the proportion of eggs destroyed by an adult per unit time, or, alternatively, the medium exploring rate. Then the additional fraction explored in time dt will depend on the amount so far unexplored $1 - v$, the number N, the rate of exploring per member k_o, and the time dt. So

$$dv = (1 - v)Nk_o dt,$$

giving

$$1 - v = exp \left\{ - k_o \int_{t-\tau_1}^{t} Ndt \right\}. \tag{5}$$

From (4) and (5),

(6) $n_1(\tau_1, t)$

$$= n_1\,(0, t - \tau_1)\; exp \left\{ - k_o \int_{t-\tau_1}^{t} Ndt \right\}.$$

In particular,

(7) $n_1(a_1, t - a_3 - a_2)$

$$= n_1(0, t - a) exp \left\{ - k_o \int_{t-a}^{t+a_1-a} Ndt \right\},$$

where

$$a = a_1 + a_2 + a_3. \tag{8}$$

After using (7) and (2), (3) gives

(9) $n_3\,(a_3, t)$

$$= b_1p_2p_3N(t - a) exp \left\{ - k_o \int_{t-a}^{t+a_1-a} Ndt \right\}.$$

Put

$$b = b_1p_2p_3 \tag{10}$$

in (9); then by substituting in (1), the equation giving $N(t)$, the number of adults at time t, is obtained. It is

(11) $\left[\frac{dN}{dt} + cN\right]_t$

$$= \left[bNexp \left\{ - k_o \int_{t}^{t + a_1} Ndt \right\} \right]_{t - a}$$

where the subscript outside the square brackets denotes the time at which the expression inside the brackets is to be evaluated.

A feature of this equation, different from many cases of population growth, is that the population is allowed to reach a steady value, N_c. An expression for N_c is obtained by substituting the constant N_c in (11). The result is

$$N_c = \frac{1}{k_o a_1} log \frac{b}{c}. \tag{12}$$

The fact that such an N_c exists arises essentially from the nonlinear nature of the equation (11) in N, caused by the linking of egg survival with the adult numbers.

If the experiments proceed only for a time rather less than the natural life span of the adults (about 200 days), the simple mortality term $c\,N(t)$ is sufficiently accurate, since death will be due mainly to accidental causes. For longer experiments, a mortality term corresponding to natural as well as accidental causes must also be included. This would cause long term fluctuations to appear which would gradually diminish until a steady state with a population less than N_c is ultimately reached. The experiments of Park (1954) indicate this kind of behavior.

A result identical with (12) has been obtained by Neyman, Park, and Scott (1956) using a simplified but partly indeterministic model in which the unit of time is taken as one generation and there are only two stages, an inactive and an active. Their formula for the number of adults for which there is no expectation of an increase or decrease in succeeding generations is

$$\epsilon = \frac{1}{\mu\tau} log\ \bar{\nu}$$

where μ is a constant characterizing the "voracity," τ is the time taken for an egg to hatch, and $\bar{\nu}$ the average number of eggs laid by an adult, which in the present notation, is equal to b times the lifetime of the adult, or b/c as long as mortality is due only to accidental causes.

The equation (11) shows that the adult population at time t depends on its value in the interval $t - a$ to $t + a_1 - a$, and in general a solution can be found only by numerical methods. However, some simple cases will now be discussed.

Suppose N remains approximately constant and equal to X in the time interval $t = -a$ to 0. Then during the next generation, from $t = 0$ to $a - a_1$, the equation (11) for the population becomes

$$\frac{dN}{dt} + CN = bXe^{- k_oXa_1}.$$

The solution to this satisfying the condition that $N = X$ at $t = 0$ is

$$N = X \left\{ e^{-ct} + \frac{b}{c} e^{-k_oXa_1} \left(1 - e^{-ct}\right) \right\},$$

or, using (12),

(13) N

$$= X \left\{ e^{-ct} + \left(1 - e^{-ct}\right) e^{k_oXa_1(N_c - X)} \right\}.$$

Suppose $X < N_c$. Then, from (13), $N > X$. Similarly, if $X > N_c$, (13) shows that $N < X$. This agrees with a result of Neyman, Park, and Scott (1956) who show that, if a generation has an average number, say X', of adults and if $X' < N_c$, then the expected number in the next generation will be greater than X'. Also, if $X' > N_c$, the expected number in the next generation will be less than X'. However, the equation (13) which gives this result applies only to the case where the initial population has a steady value. A case will now be considered in which there is some variation in the population of the initial generation.

Let N be approximately equal to X in the interval $t = -a$ to $a_1 - a$, but equal to Y at $t = 0$ Then, by (13), the rate of change of the population at $t = 0$ is

$$\frac{dN}{dt} = -cY + bXe^{-k_oXa_1}$$

or, using (12),

$$(14)\qquad \frac{dN}{dt} = c\left\{ Xe^{k_oa_1(N_c - X)} - Y \right\}.$$

This equation can be used to give a good numerical approximation to the solution of (11).

When $X < N_c$, dN/dt is positive only when $Y < Xe^{k_oa_1(N_c - X)}$ Hence it would be a simple matter to construct a population growth curve for which the average in one generation is X but in the succeeding generation is less than X. Similarly, for the case where $X > N_c$, the succeeding population could be greater than X. These conclusions will be confirmed later when the numerical solution of (11) for an actual population is discussed.

Egg Population

Substituting from the equation (2) in (6),

$$(15)\quad n_1(\tau_1, t) = b_1N(t - \tau_1)exp\left\{ -k_o\int_{t-\tau_1}^{t} Ndt \right\}.$$

With the equation (11) solved for $N(t)$, this gives the age distribution of the egg population at any instant.

When the adult population reaches the steady state N_c, the age distribution of the egg population becomes steady, being given by

$$(16)\qquad n_{1c}(\tau_1) = b_1N_ce^{-k_oN_c\tau_1}.$$

The number of eggs present at time t is

$$(17)\qquad N_1(t) = \int_0^{a_1} n_1(\tau_1, t)d\tau_1.$$

Substituting from (15), and integrating by parts, this reduces to

$$(18)\quad N_1(t) = \frac{b_1}{k_o}\left[1 - exp\left\{ -k_o\int_{t-a_1}^{t} Ndt \right\} \right].$$

As the adult population tends to its steady state, the total egg population rapidly approaches a constant value which can be determined from (16) or (18), and (12),

$$(19)\qquad N_{1c} = \frac{b_1}{k_o}\left(1 - \frac{c}{b}\right).$$

An experiment which proves conclusively that the eggs are subject to severe losses consists in removing them from the destructive environment and recording the number hatching each day after removal. In the experiments by Brereton (1962) the adult population is kept at a steady value and all immature forms except eggs are removed. If the experiment begins at $t = 0$, then

$$N(t) = \begin{cases} 0 \; for \; t < 0, \\ X, \; a \; constant \; for \; t > 0. \end{cases}$$

The equations appropriate to this experiment are (2) and (6). When conditions become steady (after time $t = a_1$ for (6)) these give, respectively,

$$n_1(0, t) = b_1X,$$

$$n_1(\tau_1, t) = n_1(0, t - \tau_1)e^{-k_oX\tau_1}.$$

Hence

$$(20)\qquad n_1(\tau_1, t) = b_1Xe^{-k_oX\tau_1},$$

and the total egg population is

$$(21)\; X_1 = \int_0^{a_1} n_1(\tau_1, t)\,d\tau_1 = \frac{b_1}{k_o}\left(1 - e^{-k_oXa_1}\right).$$

Equation (19) is the special case of (21) in which $X = N_c$

The number $n_1(\tau_1)$ hatching during the day from $a_1 - \tau_1$ to $a_1 - \tau_1 + 1$ after removal from the influence of adults is the number whose ages lie between τ_1 and $\tau_1 - 1$; i.e., from (20),

$$(22)\; n_1(\tau_1) = \int_{\tau_1 - 1}^{\tau_1} n_1(\tau_1, t)dt = \frac{b_1}{k_o}e^{-k_oX\tau_1}(e^{k_oX} - 1).$$

For the simplified model at present under investigation, these same results would hold even if the other immature forms were not removed, provided X were maintained constant.

Populations of the Intermediate Forms

So far, the only properties of the larvae and pupae which have been required are the age spans and the final survival rates. If a more detailed investigation of these populations is required, functions specifying the survival rates to any age must be introduced. Let

$q_2(\tau_2)$ = probability of survival of the larvae to age τ_2,
$q_3(\tau_3)$ = probability of survival of the pupae to age τ_3.

In particular,

$$(23)\qquad q_2(a_2) = p_2,$$

and

$$(24)\qquad q_3(a_3) = p_3.$$

The age distributions can be written, respectively,

$$n_2(\tau_2, t) = n_2(0, t - \tau_2).\ q_2(\tau_2),$$
$$n_3(\tau_3, t) = n_3(0, t - \tau_3).\ q_3(\tau_3),$$

or, by (3) and (15),

$$(25)\qquad n_2(\tau_2, t) = b_1 q_2(\tau_2) N(t - \tau_2 - a_1) \times exp \left\{ - k_o \int_{t - \tau_2 - a_1}^{t - \tau_2} Ndt \right\},$$

$$(26)\qquad n_3(\tau_3, t) = b_1 p_2 q_3(\tau_3).\ N(t - \tau_3 - a_2 - a_1) \times exp \left\{ - k_o \int_{t - \tau_3 - a_2 - a_1}^{t - \tau_3 - a_2} Ndt \right\}.$$

The total numbers of larvae and pupae are then, respectively,

$$(27)\qquad N_2\ (t) = \int_0^{a_2} n_2(\tau_2, t)\ d\tau_2,$$

$$(28)\qquad N_3\ (t) = \int_0^{a_3} n_3(\tau_3, t)\ d\tau_3.$$

When the adult population reaches its steady state, the age distributions of the larvae and pupae are, from (25) and (26), using (10) and (12),

$$(29)\qquad n_{2c}(\tau_2) = cN_c q_2(\tau_2)/p_2 p_3,$$

$$(30)\qquad n_{3c}(\tau_3) = cN_c q_3(\tau_3)/p_3.$$

The total numbers are given by integration, as before.

With the assumption that there are no losses during changes from one form to the next, and that the probability of loss per unit time remains constant for a given form,

$$(31)\qquad q_2(\tau_2) = p_2{}^{\tau_2/a_2},$$

$$(32)\qquad q_3(\tau_3) = p_3{}^{\tau_3/a_3}.$$

For this case the total numbers in the steady state can be calculated readily. They are

$$(33)\qquad N_{2c} = ca_2 N_c (p_2 - 1)/p_3 p_2\ log\ p_2,$$

$$(34)\qquad N_{3c} = ca_3 N_3 (p_3 - 1)/p_3\ log\ p_3.$$

Occasionally in experimental work, the numbers up to a certain age are required. For example, the number of "small larvae" are counted in some experiments. The corresponding formulae are found by integrating (25) and (26) over the required range.

The number of new adults entering the adult population in unit time is sometimes counted. The expression for this at the time t is simply the right hand side of (11), i.e., the birth term

$$(35)\qquad \left[bNexp \left\{ - k_o \int_t^{t + a_1} Ndt \right\} \right]_{t - a}$$

The number entering during a finite period of time is given by integrating this over the appropriate range.

Comparison with Experiment

Several mathematical models describing the population growth of *Tribolium* have already been devised. For example, there is the simplified indeterministic model of Neyman, Park, and Scott (1956) already mentioned. An elaborate model in which very many details are taken into consideration is due to Stanley (1933). An advantage of the present model is its continuity on the time scale, so that it is not necessarily linked to the generation as a time unit. Although the equation (11) in $N(t)$ depends on values of N during the previous generation in a way which makes analytical solution extremely complicated, it has a form for which approximate numerical solution is quite simple and straightforward.

If Δt is the time unit, then from (11), the approximate change in N during this time is

$$(36)\qquad \Delta N = - c[N]_t\ \Delta t \left[+ bN\ exp \left\{ - k \int_t^{t + a_1} Ndt \right\} \right]_{t - a} \Delta t.$$

Hence ΔN can be found if the constants are given and N is known at the time t and during the interval $t - a$ to $t + a_1 - a$. The approximate value of N at the time $t + \Delta t$ is then known. The change in N during the next interval of time Δt can then be found if, in addition, N is known at the time $t + \Delta t + a_1 - a$. With this process, the whole history of the population can be traced if it is given during an initial time interval of length a. After we have found $N(t)$, the population growth of the immature forms can be determined.

Another way of specifying initial conditions would be by giving the numbers and ages of the various forms present at an initial instant. By tracing their growth using the formulae and methods of the previous sections, the changes in N during the subsequent time interval a can be determined, and the calculation then carried on as before.

To obtain the simplest and smoothest solution, the initial population would need to be as small as possible. The best experimental population for comparison with the theory therefore would be one starting from, say, three or four adults.

For the experiments described by Brereton (1962) the initial population was selected as follows: a colony which had reached a steady state at about 500 to 600 adults was taken, and 18 adults chosen from it, together with immature forms in proportion to their numbers in the steady state. A rather large initial population such as this produces oscillations in the population growth which tend to mask effects of more fundamental significance. Moreover, the larger the initial population, the more care is required in calculating $N(t)$ during the initial period of length a. However, in order to compare the theory with experiment, calculations were made for this case.

In the continuing experiments described by Brereton (1962), the colonies were grown in an environment containing 40 g of flour at a temperature of 29°C and a relative humidity of 75%. In these circumstances, the values he finds for the various constants are as given in the following paragraphs.

The time a_1 in the egg stage is about 5.5 days, the life span a_2 of the larvae is 16.5 days, and the life span a_3 of the pupae is 5.7 days. Hence, allowing time for adults to reach maturity, the length a of the generation in the theoretical model can be taken to be about 30 days.

From the similarity in the forms of the graphs of the intermediate stages, and also from statistical analysis, it is generally found that the probability p_2 of larvae becoming pupae and the probability $p_2 p_3$ of them finally becoming adults are independent of the density. Therefore, they can be assumed constant, as they were in the equations (31) and (32). It is found that $p_2 = 0.62$ and $p_2p_3 = 0.55$.

During the course of the experiment, there is no marked dependence of the death rate of adults on the density, but in the very early stages and toward the end at 190 days the losses are greater. Perhaps the vulnerability of newly emerged adults to accident would account for the initial increase whereas the final would be due to a number reaching their natural life span. In addition to these increases there are some random fluctuations. However, in constructing the theoretical curves, it is assumed that the death rate remains constant at its approximate mean, 2%, i.e., $c = 0.02$ adults per day.

There is a significant decrease in the number of eggs laid per adult with increase in the density of adults, owing probably to crowding and interference. In the continuing experiments the average number of fertile eggs laid per adult is about one, and so for the theoretical model it is assumed as a first approximation that $b_1 = 1$ egg per adult per day and remains constant.

In the continuing experiments each adult destroys about one egg per day. The egg population rapidly approaches the steady value of about 1,000 for the 40-g environment; hence the proportion of eggs destroyed per adult per day is taken in the theoretical model to be $k_o = 0.001$. The experiments show that when the density of adults is low the value of k_o is somewhat greater than this. This could be caused by the preference of adults for conditioned flour, i.e., flour which has already been explored, as described by Ghent (1963), and also by the tendency for the insects to cluster on the boundaries as noted by Neyman, Park, and Scott (1956). In each of these cases the effective size of the environment is reduced; hence the fraction of the effective egg-bearing medium explored by an adult in unit time would be increased.

Because of the wide variations in the egg-laying rate and egg-destroying rate, the numerical values chosen are somewhat arbitrary, being simple figures somewhere near the average of the experimental values, after allowing for adjustments due to fertility.

Making simplifications and approximations within the range of accuracy of the respective measurements, the values of the constants chosen in making the calculations are

$$
\begin{aligned}
a_1 &= 6 \text{ days} \\
a_2 &= 16 \text{ days} \\
a &= 30 \text{ days} \\
p_2 &= 0.62 \\
p_2\, p_3 &= 0.55 \\
c &= 0.02 \text{ adults per day} \\
b_1 &= 1 \text{ egg per adult per day} \\
b = b_1\, p_2\, p_3 &= 0.55 \\
k_o &= 0.001 \text{ of the total eggs per adult per day.}
\end{aligned}
$$

With the given initial conditions and the above values for the various constants, a graph of the approximate theoretical population was constructed using the equation (36). The result, together with the corresponding experimental curve, is shown in Fig. 1 by the curves A and A′ respectively. Although there are some differences these curves have important general features in common. In

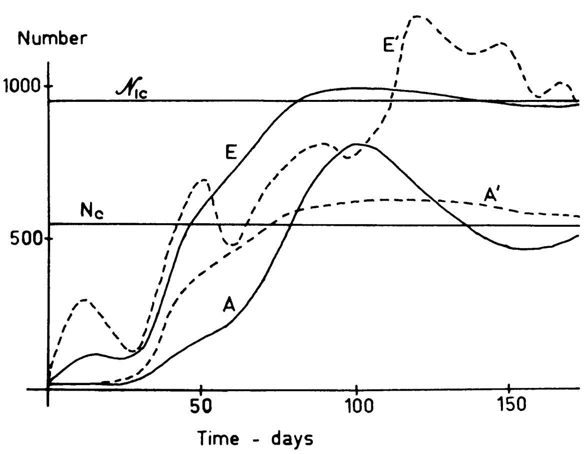

Fig. 1. A, theoretical number of adults. A′ experimental number of adults. E, theoretical number of eggs. E′, experimental number of eggs.

each, the population undergoes a gradual initial increase for about 30 days, then increases rapidly, overshooting the final equilibrium number, to reach the maximum after about 100 days. After some comparatively gentle fluctuations, the number then tends to its equilibrium value. By the equation (12) this is about 550, in close agreement with experiment.

Fig. 1 also shows the number of eggs at a given time (curve E), calculated from equation (18) using results already obtained in the determination of $N(t)$. This also is in general agreement with experimental results (curve E′). The final steady value calculated from equation (19) is about 960 and this, too, agrees fairly well with the experiments.

For the cases of larvae and pupae, calculation based on assumptions (31) and (32) were compared with experiment. In each case the theoretical populations showed oscillations of the required period. However, the times at which the strongest maxima occurred did not agree. Also, the steady state populations, given by (33) and (34) seem to be about twice the required number. Further experimental investigations would need to be carried out before these differences could be regarded as significant. In particular, the death rate c, on which (33) and (34) depend strongly, should be investigated more closely.

The calculations described above were made assuming that b_1, c, and k_o are constant. The experiments indicate that they are influenced to some extent by variable factors in the population system, and these variations would account for some of the differences between the theoretical and experimental results. Variations in b_1 c, and k_o can easily be incorporated in the numerical equation (36), but so far there is not sufficient information to describe these variations accurately. A tentative calculation was carried out taking into account the tendency for b_1 and k_o to decrease with increase in N, and a curve closer to the experimental curve A' was obtained. The discrepancy is reduced a little further if the destruction of eggs by larvae is considered. Again, more accurate information on the destruction of all inert forms by moving forms would be needed in order to incorporate these effects numerically in a mathematical formula.

Consider the result previously referred to, obtained by Neyman, Park, and Scott (1956) for their simplified model: If the average number X' of adults in a generation is less than N_c, then the expected number in the next generation will be greater than X', and if the average number X' is greater than N_c, the expected number in the next generation is less than X'. From the graphs it is apparent that this is in general true for both the theoretical and experimental curves. However, there are some small regions where this does not hold. For the theoretical curve, in the generation 72 to 100 days, $X'_1 = 650$. In the next generation 102 to 130 days, $X'_2 = 709$. Hence, $X'_1 > N_c$, but $X'_2 > X'_1$. It is apparent that the experimental curve behaves in the same way for this region. Again, for the theoretical curve, in the generation 128 to 156 days, $X'_1 = 549$, whereas in the next generation 158 to 186 days, $X'_2 = 510$. Hence $X'_1 < N_c$, but $X'_2 < X'_1$. The possibility that these cases can occur has already been noted in a previous section.

In an experiment described by Brereton (1962) to demonstrate the destructive effect of the adult population on the eggs, populations of 2, 4, 8, and 16 adults per gram were placed in environments of 4 g of flour at 29°C and 75% R.H. The adult populations were kept constant, and intermediate immature forms were removed. It was found that the mean number of eggs in each population soon reached a constant value, about 93. The theoretical number is given by equation (21). Since the size of the environment is one tenth that in the continuing experiments the fraction of the medium explored at a given time will be ten times as great, and so $k_o = 0.01$. For the total populations $X =$ 8, 16, 32, 64, the equation (21) gives for the total numbers of eggs, $X_1 =$ 39, 62, 85, 98. The agreement with experiment is close for the denser populations, and would be fairly close also for the less dense populations if the increases in b_1 and k_o with decrease in the adult population were taken into account. By use of equation (22), the numbers of eggs hatching on successive days after their removal from the influence of the adult population can be calculated. For the higher populations, the calculated values in general agree with Brereton's experimental results, remembering that the deterministic model does not allow for variations in the hatching times of the eggs.

In conclusion, it can be stated that the model, based on the destruction of eggs by adults, can account for the main features of the observed behavior of *Tribolium* populations.

Extensions of the Model

The model described here is a simplified one. The data from the experiments on which it is based do not yet justify making it more elaborate. Further refinements could be introduced as more accurate knowledge of the various parameters and behavior of the insects becomes available, and some of these refinements have already been indicated in the previous section.

It is known that all moving forms destroy all inert forms, and it will now be shown how to incorporate these effects into the model. First, consider the destruction of eggs by larvae. Let k_2 be the proportion of eggs destroyed by a larva in unit time. The way in which the effect of egg eating by adults enters equation (11) indicates how this additional feature is to be introduced. The equation (11) must be replaced by

$$(37)\ \left[\frac{dN}{dt} + cN\right]_t$$

$$= \left[bN\,exp\left\{-\int_t^{t+a_1}(k_oN + k_2N_2)dt\right\}\right]_{t-a}.$$

In calculating the adult population from the equation (37), the population of the larvae also is required. The equation (25) must now be adjusted in the same way, giving

$$n_2(\tau_2, t) = b_1q_2(\tau_2)N(t - \tau_2 - a_1)$$

$$\times\ exp\left\{-\int_{t-\tau_2-a_1}^{t-\tau_2}(k_oN + k_2N_2)dt\right\}.$$

With this in (27) with the expression (31) for $q_2(\tau_2)$,

$$(38)\ \left[\ {}_2\right]_t = \int_0^{a_2} b_1p_2{}^{\tau_2/a_2}$$

$$\times\left[N\,exp\left\{-\int_t^{t+a_1}(k_oN+k_2n_2)\,dt\right\}\right]_{t-\tau_2-a_1} d\tau_2\ .$$

By means of the equations (37) and (38), the populations of the adults and larvae could be plotted simultaneously.

If pupae are destroyed by adults and larvae, a further similar exponential factor must be included in the righthand side of the equation (37). If l_o is the proportion of pupae destroyed by an adult, and l_2 the proportion destroyed by a larva, per unit time, this factor will be

$$\left[exp\left\{-\int_t^{t+a_3}(l_oN + l_2N_2)dt\right\}\right]_{t-a_3}.$$

This expression will tend to some extent to replace the p_3 which describes the loss of pupae in the simpler model.

The population of the larvae is still given by (38), since this process acts on a following stage, the pupae.

Corresponding adjustments must be made in treating the other components in the population.

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COLONIZATION OF THE ISLANDS OF THE GULF OF ST. LAWRENCE BY MAMMALS

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Terrestrial mammal colonization of the Gulf of St. Lawrence islands was recently studied by Cameron (1958) who postulates a sequence of temporary land bridges and a sequence of arrivals of various species on the adjacent mainland to account for their presence or absence on different islands. In so doing he violates the principle of parsimony. A simpler explanation would be that based on the probable behavior of different animals that find themselves aboard driftwood rafts.

For simplicity, assume that there were no land bridges and that all species arrive on the coast simultaneously. The species then can be divided into three groups with respect to island colonization: (1) those with bodies light enough to be easily carried on driftwood rafts (mice),