THE APPROACH TO EQUILIBRIUM AND THE STEADY-STATE PROBABILITY DISTRIBUTION OF ADULT NUMBERS IN *TRIBOLIUM BREVICORNIS*

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In an effort to improve upon deterministic ecological theory, there has been interest in stochastic models of population growth (e.g., Bartlett 1960; Pielou 1969, 1977; May 1973, 1974; Ludwig 1974; Keiding 1975). This approach is more realistic in that one obtains a probability distribution for population size rather than a single deterministic equilibrium value. One method of incorporating stochasticity into a deterministic model is to assume random fluctuations in one or more of the biological parameters of the model. Costantino and Desharnais (1981) used this stochastic differential equation formulation to derive a gamma steady-state probability distribution for adult numbers in laboratory populations of flour beetles belonging to the genus *Tribolium*. They examined 13 observed frequency distributions of adult numbers for *T. castaneum* Herbst and *T. confusum* Duval and found that the data supported the gamma steady-state hypothesis.

Our perspective here is to characterize population growth as a stochastic birth-death process involving the rates of pupal production, adult mortality, and adult inhibition of the immature life stages. Our objectives are to describe (1) the approach of adult numbers to equilibrium, and (2) the steady-state probability distribution of adult numbers. We begin by presenting the deterministic population dynamic model, followed by the stochastic birth-death model and then apply this theoretical construct to data on *T. brevicornis*.

TRIBOLIUM POPULATION MODEL

Deterministic Model

Crombie (1946, p. 99) characterized the rate of population growth in *Tribolium* as "determined almost entirely by the rates of oviposition and of development on the one hand, and by the rates of cannibalism on the other. . . . The eating of eggs and pupae probably takes place after random encounters between feeding stages (adults and larvae) and prey stages (eggs and pupae). The relationship between

the stages would then be analogous to a second order chemical reaction." With this statement, Crombie (1946) wrote the differential equation

$$dX/dt = -XCA. \tag{1}$$

The change in the number of eggs or pupae (recruits) is a function of the cannibalism rate of adults (C), the number of adults (A), and the number of eggs or pupae produced (X). We can integrate (1) to obtain the number of eggs or pupae at time t in the presence of A adults as

$$X = X_0 \exp(-CAt). \tag{2}$$

Statement (2) is central to several mathematical models of population growth in *Tribolium* including Neyman et al. (1956), Rich (1956), Bartlett (1957), Mertz and Davies (1968), Lloyd (1968), Park et al. (1970), Desharnais and Costantino (1980), and Costantino and Desharnais (1981).

   We shall direct our attention to a Ricker-type model (Ricker 1954) that attempts to explain the changes in the size of the adult beetle population based on the association between the number of adults and the number of the progeny produced by these adults. The density-dependent regulation stated in equation (2) is an important aspect of this kind of model. To begin, we let C be the probability that a single adult prevents a potential recruit from entering the adult population in some small time interval (t, $t + \Delta t$). Assuming that the adult beetles act independently, the proportion of potential recruits that become adults during (t, $t + \Delta t$) will be $(1 - C)^A \doteq \exp(-CA)$ for small C. Defining X as the rate at which potential recruits are produced per adult and D as the adult mortality rate, we can describe the change in adult numbers during (t, $t + \Delta t$) as

$$A(t + \Delta t) - A(t) = \Delta t \, A(t) \, X \, e^{-CA(t)} - \Delta t \, A(t) \, D. \tag{3}$$

Dividing through by Δt and taking the limit as Δt goes to zero we have

$$dA(t)/dt = A(t) \, X \, e^{-CA(t)} - A(t) \, D \tag{4}$$

as our model. The rate of recruitment, $R(A) = X A e^{-CA}$, and the rate of mortality, $M(A) = D A$, are plotted as functions of adult number in figure 1. This model has also been discussed, for example, in fisheries biology by Ricker (1954, 1975) and in general population studies by Moran (1950), May (1974b), Smith (1974), Hoppensteadt (1975), Hunt (1980), Fisher et al. (1979), and Cull (1981).

   When the rate of recruitment is equal to the rate of mortality, a single nontrivial equilibrium exists at $A^* = \log(X/D)/C$. If the partial derivative $\lambda = \partial(dA/dt)/\partial A$ evaluated at $A = A^*$ is negative, then small disturbances in adult numbers from A^* dissipate with time and the population returns to its equilibrium number. In our case, $\lambda = D \log(D/X)$ and if $X > D$ then $\lambda < 0$ and the equilibrium is locally stable. The amount of time it takes for a perturbation to decay is generally described by $\tau = 1/|\lambda|$ called the "time constant" of the stable equilibrium. The entity τ is the amount of time required for a perturbation to decay to 37% (e^{-1}) of its original value. This time is independent of the magnitude of the perturbation.
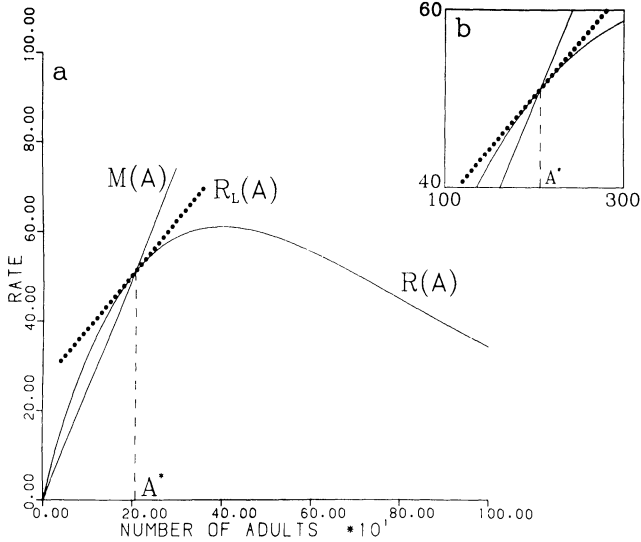
FIG. 1.—A model for the number of adults based on equation (4). The rate of recruitment is $R(A) = X A \exp(-CA)$ and the mortality rate is $M(A) = A D$. The parameter values were obtained from data on *Tribolium brevicornis*: $X = 0.413, D = 0.247$, and $C = 0.002485$. $R_L(A)$ is a linear approximation of $R(A)$ in the vicinity of $A^* = 207$. The small inserted figure in the upper right shows that $R_L(A)$ is a good approximation for these data in the neighborhood of A^*.

Birth-Death Process

We shall now move from the deterministic model of equation (4) and consider changes in adult numbers as a stochastic "birth-death" process. By choosing an infinitesimal time interval Δt, we can let $R(A) \Delta t$ and $M(A) \Delta t$ represent, respectively, the probabilities that a single recruitment and a single mortality will occur during $(t, t + \Delta t)$ when A adults are present at time t. Furthermore, we can assume that the probabilities of two or more recruitments and/or mortalities are negligible. Under these assumptions, the probability of finding A adults at time $t + \Delta t$ is

$$P_A(t + \Delta t) = P_A(t) [1 - R(A) \Delta t - M(A) \Delta t]$$
$$+ P_{A-1}(t) R(A - 1) \Delta t + P_{A+1}(t) M(A + 1) \Delta t. \tag{5}$$

Bringing $P_A(t)$ to the left-hand side, dividing by Δt and taking the limit as Δt goes to zero gives

$$dP_A(t)/dt = -[R(A) + M(A)] P_A(t) + R(A - 1) P_{A-1}(t)$$
$$+ M(A + 1) P_{A+1}(t) \tag{6}$$

for $A = 0, 1, 2, \ldots$. This system of equations is known as the Chapman-Kolmogorov differential equations and their derivation appears in many texts in various degrees of sophistication (e.g., Bhat 1972; Karlin and Taylor 1975).

Approach to equilibrium.—We will use equation (6) to derive the mean and variance of adult numbers as functions of time. We begin by using a linear approximation $R_L(A)$, for recruitment in the vicinity of A^* (fig. 1),

$$R_L(A) = R(A^*) + (A - A^*) \cdot [\partial R(A)/\partial A]_{A=A*}. \tag{7}$$

To find the change in the mean of adult numbers, $\bar{A}(t)$, we multiply both sides of equation (6) by A and sum the equations for $A = 0$ to $A = \infty$. This gives

$$d\bar{A}(t)/dt = G [A^* - \bar{A}(t)] \tag{8}$$

where

$$G = [\partial M(A)/\partial A - \partial R(A)/\partial A]_{A=A*} = D \log(X/D). \tag{9}$$

Notice that (8) is an approximation of (4). Multiplying both sides of equation (6) by $[A - \bar{A}(t)]^2$ and summing gives

$$dV(t)/dt = -2GV(t) + R_L[\bar{A}(t)] + M[\bar{A}(t)]. \tag{10}$$

The differential equations (8) and (10) are identical to the results obtained by MacArthur and Wilson (1967, pp. 33–41) for the number of species colonizing an island.

Solving for the mean number of adults we have

$$\bar{A}(t) = A^* (1 - e^{-Gt}) \tag{11}$$

and as $t \to \infty$, $\bar{A}(t) \to A^* = \log(X/D)/C$. Furthermore, we can compute the time required to reach 95% of the equilibrium value A^* by setting $\bar{A}(t)/A^* = 0.95$ so that

$$t_{0.95} = 2.9957/G. \tag{12}$$

Solving for the variance of adult numbers we have

$$V(t) = (1/C) (1 - 2e^{-Gt} + e^{-2Gt}) + \bar{A}(t)e^{-Gt} \tag{13}$$

and as $t \to \infty$ the variance at equilibrium is

$$V^* = 1/C. \tag{14}$$

Steady-state probability distribution.—The numbers of adults will, asymptotically, assume a constant mean and variance. Given this fact, it is reasonable to postulate the existence of a stationary distribution of adult numbers. If we assume $dP_A/dt = 0$ for all values of A, then from equation (6) we have

$$P_A = P_0 \prod_{J=1}^{A} R(J - 1)/M(J). \tag{15}$$

To convert the deterministic model (4) into a probabilistic one, we redefine recruitment as $R(A) = X (A + 1) e^{-CA}$. With this slight but important modification, $A = 0$ does not act as an "absorbing state." If an absorbing state did exist the probability of extinction is unity and no steady-state distribution is realized (Bhat 1972). We shall return to this item in the next section. Now, using equation (15) we have the following equilibrium probability distribution for adult numbers:

$$P_A = K (X/D)^A \exp[(-C/2) A (A - 1)]. \tag{16}$$

K, which equals P_0, is the normalization constant which makes the total probability equal unity. It can be shown (Appendix A) that the mean and variance for this distribution are

$$\bar{A} = A^* + 1/2 + K/C \doteq A^* + 1/2 \tag{17}$$

and

$$V = (1/C)(1 - K\bar{A}) \doteq 1/C. \tag{18}$$

In most cases K will be very small and the approximations will hold. Although different assumptions were made concerning the recruitment function, these results agree well with those of the previous section. If the density function (16) is expressed in terms of the approximate mean (17) and variance (18), then

$$P_A = (2\pi V)^{-1/2} \exp[-(A - \bar{A})^2/2V]. \tag{19}$$

The density (19) is the familiar normal distribution which yields the estimate

$$K = [\exp(-\bar{A}^2/2V)]/(2\pi V)^{1/2} \tag{20}$$

for that constant in equations (16), (17), and (18).

EXPERIMENTAL OBSERVATIONS AND DISCUSSION

In this study, we wrote the probability $P_A(t + \Delta t)$ of finding A adults at time $t + \Delta t$ (eq. 5) and then obtained the mean number of adult beetles at time t, the variance in this number, and finally the steady-state probability distribution of adult numbers. We shall now consider some experimental data as a means of discussing this model.

Four cultures of the flour beetle *Tribolium brevicornis* were maintained with overlapping generations for 72 wk. Each culture was initiated with 20 young adults and kept in a one-half pint bottle with 20 g of standard media (percentage composition: 95% wheat flour and 5% dried brewer's yeast) and held in an unlighted incubator at $33 \pm 1°$ C and $60 \pm 5\%$ relative humidity. All life stages (except eggs) were counted every 2 wk and following the census the animals were placed in fresh media. The observed number of adults are presented in figure 2. Since each culture was started with adults only, time was rescaled so as to omit the initial 4 wk when pupae were unavailable for recruitment; consequently, $t = 1$ corresponds to week 6 and one time unit equals 2 wk.

The values of A^* and G of equation (11) were estimated using a general method for fitting nonlinear regression which is described in Appendix B. Least-squares estimates and approximate standard errors of $\hat{A}^* = 207.0 \pm 4.2$ and $\hat{G} = 0.127 \pm 0.009$ were obtained from a regression on the means of adult numbers. The regression equation

$$\hat{A}(t) = 207[1 - \exp(-0.127t)]$$

is a good fit ($R^2 = 0.86$) to the observed numbers of adult beetles (fig. 2).

An estimate of the variance in the vicinity of the equilibrium, $\hat{V}^* = 402.48$, was computed from the adult data for $t \geq 24$ ($n = 44$ observations) because at this time
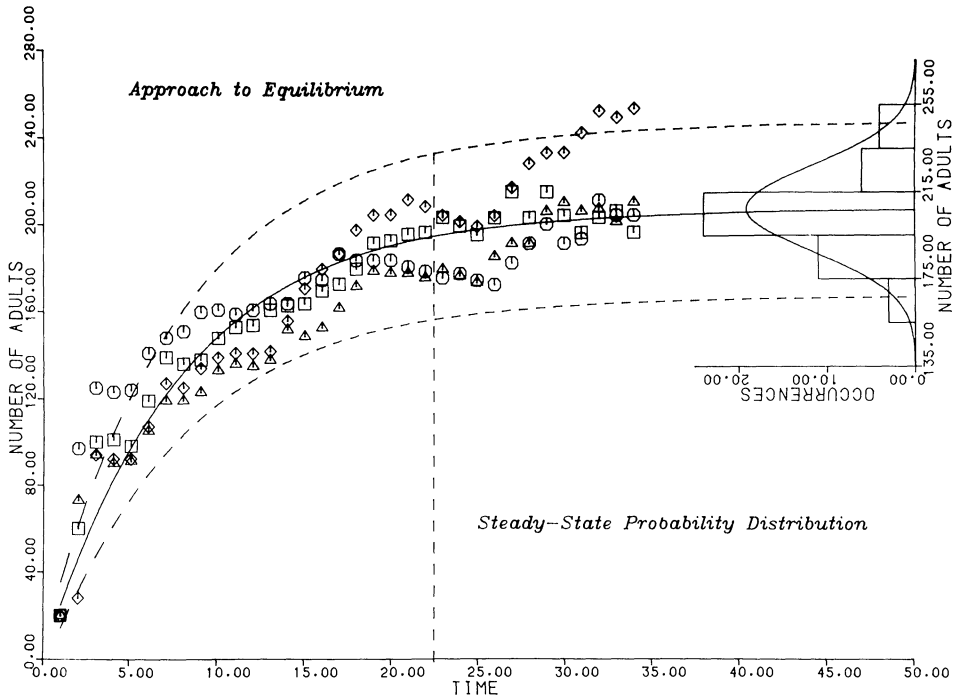
Fɪɢ. 2.—Observed number of adults for four cultures of *Tribolium brevicornis*. The solid curve is the mean number of adults, $\bar{A}(t)$, and the dashed lines are $\bar{A}(t) \pm 2[V(t)]^{1/2}$. The vertical dashed line at $t = 23$ corresponds to $\bar{A}(t) = 0.95A^*$. The observed frequency data (histogram) and theoretical (smooth curve) steady-state probability distributions appear in the upper right of the figure.

$A(t)$ was within 95% of A^* (eq. 12, $t_{0.95} = 23.6$). Since the expected steady-state distribution is very nearly Gaussian (eq. 19), the quantity $[(n - 1)\hat{V}^*/V^*]$ follows a chi-square distribution with $(n - 1)$ degrees of freedom (Snedecor and Cochran 1967, pp. 73–76). Using this fact, we found the 95% confidence interval on the variance of adult numbers at the steady state to be $274.8 \leq V^* \leq 646.1$.

Crude estimates of the biological parameters C, D, and X can be obtained from $\hat{V}^*$, $\hat{A}^*$, and $\hat{G}$. To estimate C, the rate at which adults inhibit the recruitment of immatures, we made use of equation (14) to get $\hat{C} = 1/\hat{V}^* = 0.002485$. Similarly, the 95% confidence interval on the parameter C can be obtained by inverting the lower and upper bounds on V^* to obtain $0.0016 \leq C \leq 0.0036$. An estimate of the per capita adult mortality rate was obtained by rearranging (9) to read $\hat{D} = \hat{G}/(\hat{C}\hat{A}^*) = 0.247$ per time unit (2 wk). Finally, an estimate of the rate at which potential recruits are produced per adult per time unit was computed from the equation $\hat{X} = \hat{D} \exp(\hat{C}\hat{A}^*) = 0.413$.

The number of new adults, $R(A)$, is given by the product of the number of potential recruits produced per adult times the number of adults times a negative exponential function that describes the proportion of potential recruits that become adults. In these data, $R(A) = (0.413A)\exp(-0.002485A)$ which is sketched

in figure 1. To locate a maximum, $R(A)$ is differentiated with respect to A and equated to zero: $dR(A)/dA = X\exp(-CA)\,[1 - CA] = 0$. The value of A which makes $R(A)$ a maximum is $1/C$. Recall from (14) that the variance at equilibrium is $V^* = 1/C$; consequently, when the adult population size $A = V^*$, recruitment is a maximum. For these data on *T. brevicornis*, $\hat{A}^* = 207 < \hat{V}^* = 402$ and we conclude that $R(A)$ is not maximized.

The eigenvalue was computed using (9) to be $\hat{\lambda} = -G = -0.127$. Thus, A^* is locally stable and from inspection of figure 1 it is clear that the equilibrium is globally stable. The amount of time required for a perturbation to decay 37% of its original value is $\hat{\tau} = 1/|\lambda| = 7.87$ time units or 15.7 wk. Since we used a linear approximation for $\bar{A}(t)$ the time constant is also appropriate to predict the approach to equilibrium. In other words, it was expected to take $3\tau = 23.6$ time units or 47.1 wk for $\bar{A}(t)$ to reach within 5% of A^*. This statement is similar to equation (12).

The expected steady-state probability distribution of adult numbers was obtained using equation (16) with $\bar{A} = 207$ and $V^* = 402.48$ as

$$P(A) = (1.20 \times 10^{-25})\,(1.672)^A \exp[(-1.242 \times 10^{-3})\,A\,(A - 1)].$$

The hypothesis that the observed grouped frequency data (histogram in fig. 2) is distributed according to the density in (16) was accepted using a chi-square test for goodness-of-fit at the .05 level of probability with 2 degrees of freedom.

To obtain a steady-state probability distribution (16), it was necessary to modify recruitment as $R(A) = X\,(A + 1)\exp(-C\,A)$. Otherwise, if recruitment is defined as in equation (4), $R(0) = 0$ and from (15) it can be seen that no steady-state probability distribution exists. Furthermore, using a theorem from Karlin and Taylor (1975, p. 149), we can show that the probability of extinction always equals one. However, if initially there are A adults, the mean time to extinction, $\bar{T}_E(A)$, is

$$\bar{T}_E(A) = (1/D) \sum_{i=1}^{\infty} (X/D)^i\,(i + 1)^{-1}\exp[-(C/2)\,i\,(i + 1)]$$

$$+ (1/D) \sum_{r=1}^{A-1} \sum_{j=r+1}^{\infty} (j)^{-1}\,(X/D)^{j-r-1}\exp\{-(C/2)\,[j\,(j - 1) - r\,(r - 1)]\}.$$

(This expression was obtained using eq. 7.10 from p. 149 of Karlin and Taylor 1975.) Using our estimated values for X, D, and C and noting that each population of *T. brevicornis* was started with 20 adults, we have calculated the mean time to extinction to be 2.38×10^{23} time units which is 9.13×10^{21} years! Although extinction is certain, it is unlikely to be observed unless there are changes in the parameters of the system. Thus it is reasonable to assume the existence of a steady-state probability distribution.

The characterization of population growth as a Markov birth-death process appears to appropriate for *T. brevicornis*. This species differs from *T. castaneum* and *T. confusum* in that adults of this species delay the metamorphosis of large larvae into pupae, thus controlling recruitment into the adult population (Jillson and Costantino 1980). Consequently, a large pool of potential recruits (large larvae) is established and fluctuations in the number of potential recruits and dead

adults are small. This is in contrast to *T. castaneum* and *T. confusum* which control recruitment into the adult population by cannibalizing pupae. These cannibalizing species show large fluctuations in both X and D and are, perhaps, more appropriately studied using the stochastic differential equation formulation (Costantino and Desharnais 1981).

SUMMARY

The rate of population growth in adult numbers, A, for the flour beetle *Tribolium* was characterized by the mathematical model $dA/dt = X\,A\,\exp(-CA) - A\,D$ with the biological entities pupal productivity, X, adult inhibition of the immature life stages, C, and the death rate among the adults, D. A local stability analysis of the equilibrium $A^* = \log(X/D)/C$ revealed that the eigenvalue $\lambda = D\,\log(D/X)$ and A^* was stable if $X > D$. The time it takes for a perturbation to decay was evaluated using the time constant $\tau = 1/|\lambda|$.

The changes in adult numbers were then viewed as a stochastic birth-death process. The numbers of adults were found to asymptotically assume a constant mean value of $\bar{A}(t) = A^* = \log(X/D)/C$ and a constant variance of $V(t) = V^* = 1/C$. Equations were established for the approach of $\bar{A}(t)$ and $V(t)$ to their respective equilibrium values together with the steady-state probability distribution of adult numbers. Formulas to estimate A^*, X, D, C, and λ were obtained based on the adult population size data. Experimental observations on *T. brevicornis* showed a good correspondence to the theoretical construct.

APPENDIX A

Here we derive expressions for the expected mean and variance of adult numbers at the steady state. Consider the following continuous version of the equilibrium probability distribution (16):

$$P(A) = K\,(X/D)^A \exp[-(C/2)\,A\,(A-1)] \tag{A1}$$

for $A \geq 0$. Taking the derivative of (A1) with respect to A, we obtain the following:

$$dP(A)/dA = P(A)\,[\log(X/D) + (C/2) - (C\,A)]. \tag{A2}$$

Integrating (A2) with respect to A from zero to infinity we get

$$P(\infty) - P(0) = [\log(X/D) + (C/2)] \int_0^\infty P(A)\,dA - C \int_0^\infty A\,P(A)\,dA. \tag{A3}$$

Noting that $\lim_{A\to\infty} P(A) = 0$, $P(0) = K$, $\int_0^\infty P(A)\,dA = 1$, $\int_0^\infty A\,P(A)\,dA = E(A) = \bar{A}$, and $\log(X/D)/C = A^*$, we can rearrange (A3) to get expression (17) for the expected mean number of adults.

To obtain the variance, we multiply equation (A2) by A before integrating. This gives us

$$\int_{A=0}^\infty A\,dP(A) = [\log(X/D) + (C/2)] \int_0^\infty A\cdot P(A)\,dA - C \int_0^\infty A^2\,P(A)\,dA. \tag{A4}$$

Integrating the left-hand side of (A4) by parts we get

$$\int_{A=0}^\infty A\,dP(A) = [A\,P(A)]_{A=0}^\infty - \int_0^\infty P(A)\,dA = \lim_{A\to\infty} [A\,P(A)] - 1. \tag{A5}$$

Since $P(A)$ has a finite expectation, $E(A)$, we know that the limit in (A5) converges to zero. Substituting (A5) into (A4) and rearranging we have

$$\int_0^\infty A^2 P(A)dA = E(A^2) = (A^* + 1/2)\,\bar{A} + 1/C \tag{A6}$$

which can be used to compute the variance

$$V = E(A^2) - [E(A)]^2 = (1/C)(1 - K\,\bar{A}). \tag{A7}$$

APPENDIX B

Here we show how we obtained the least-squares estimates and the approximate standard errors for A^* and G of equation (11). We used the general method for fitting nonlinear regressions described in Snedecor and Cochran (1967, pp. 465–471). Let

$$f(A^*, G, t) = A^*[1 - \exp(-Gt)].$$

Our statistical model is

$$\bar{A}_t = f(A^*, G, t) + \epsilon_t \tag{B1}$$

where $\bar{A}_t$ is the mean number of adults observed at time t. The residual error terms, ϵ_t, are assumed to be independently identically distributed with a zero mean and variance σ^2. Although this standard statistical supposition is not consistent with equation (13), there is no trend in the variances of the observed data to justify an abandonment of this simplifying assumption.

In order to apply least squares regression we linearized our model. Let g be a first approximation to G. By Taylor's theorem

$$f(A^*, G, t) = f(A^*, g, t) + \sum_{k=1}^\infty (G - g)^k (1/k!)(\partial^k f/\partial G^k)_{G=g}. \tag{B2}$$

If g is a good approximation to G, we can drop the higher order terms of the series to get

$$\bar{A}_t \doteq A^*(1 - e^{-gt}) + A^*(G - g)(te^{-gt}) + \epsilon_t. \tag{B3}$$

Making the transformations $Y_t = 1 - \exp(-gt)$ and $Z_t = t \cdot \exp(-gt)$ we get the following linear statistical model with no intercept:

$$\bar{A}_t \doteq aY_t + bZ_t + \epsilon_t \tag{B4}$$

where $a = A^*$ and $b = A^*(G - g)$.

We performed a standard multiple regression on equation (B4) to obtain estimates for $\hat{A}^* = \hat{a}$ and $\hat{G} = g + \hat{b}/\hat{a}$. An estimate of the residual variance was given by $\hat{\sigma}^2 = \sum_{t=1}^n [\bar{A}_t - f(\hat{A}^*, \hat{G}, t)]^2/(n - 2)$, where n is the number of observations ($n = 34$). Since the accuracy of these results depends on the initial estimate g, we let $g = \hat{G}$ and repeatedly applied the procedure until $\hat{\sigma}^2$ converged to a minimum of 140.2. Our final regression gave us least-squares estimates of $\hat{A}^* = 207.0 \pm 4.2$ and $\hat{G} = 0.127 \pm 0.009$. The standard errors of these estimates were calculated in the usual way using $\hat{\sigma}^2$ and the inverse of the matrix of sums of squares and products of the transformed variables Y_t and Z_t. However, these results are only approximate, since $\hat{\sigma}^2$ is not an unbiased estimate of the residual variance when f is nonlinear.

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