

POPULATION TRACKING OF FLUCTUATING ENVIRONMENTS  
AND NATURAL SELECTION FOR TRACKING ABILITY

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Environmental variation is often a very important aspect in the ecology of organisms, with most populations experiencing at least seasonal fluctuations in resource availability and thus in their carrying capacity (Annegers 1973; Emmel 1976, chap. 10; Fleming and Hooker 1975; Fretwell 1972). A recent body of literature has begun to explore the dynamics of populations experiencing a fluctuating carrying capacity (e.g., Levins 1969; May 1973, 1974, 1976, 1978; Goel and Richter-Dyn 1974; Roughgarden 1975). In this paper we clarify some aspects of the dynamics of the logistic model with a variable  $K$  and suggest implications for natural selection on the ability of organisms to follow or "track" fluctuations in  $K$ .

THE MODEL

Although often too simplistic, the logistic model governed by the equation

$$\dot{N} = rN(1 - N/K) \quad (1)$$

has been shown to describe population growth quite well in a broad range of species (see, e.g., Andrewartha and Birch 1954; Davidson 1938*a*, 1938*b*; Emmel 1976, p. 103; Istock 1977; Gause 1931, 1934; Crombie 1945; Pearl 1930; Lotka 1925; Odum 1971). It is only recently, however, that there have been attempts to explore the dynamics of the model with the carrying capacity  $K$  not constant but variable, so that it may represent environmental fluctuations, e.g., seasonality. Specifically, it is essentially shown in Levins (1969) that when equation (1) holds for a constant intrinsic rate of increase  $r$  and time-dependent carrying capacity  $K(\cdot)$ , assumed here to be a piecewise continuous positive function, the solution of equation (1) is (for any  $t > u$ )

$$\begin{aligned} [N(t)]^{-1} &= e^{-r(t-u)}[N(u)]^{-1} + \int_u^t re^{-r(t-v)}Q(v) dv \\ &= e^{-r(t-u)}[N(u)]^{-1} + \int_0^{t-u} re^{-rv}Q(t-v) dv, \end{aligned} \quad (2)$$

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where  $Q(t) = 1/K(t)$  is also positive and piecewise continuous. Thus, envisaging the present population  $N(t)$  as having arisen from the infinite past,

$$[N(t)]^{-1} = \int_{-\infty}^t Q(v) r e^{-r(t-v)} dv = \int_0^{\infty} r e^{-rv} Q(t - v) dv \tag{3}$$

provided  $e^{-ru}N(-u) \rightarrow 0$  as  $u \rightarrow \infty$ , which is a reasonable assumption. Observe that since  $\int_0^{\infty} r e^{-rv} dv = 1$ ,  $N(t)$  is the reciprocal of a weighted average of the reciprocal of the carrying capacity  $K(u)$  for  $u \leq t$ .

In several places, including Goel and Richter-Dyn (1974, sec. 4.2c), the function  $K$  or  $1/K$  incorporates a white noise term, which in solving equation (1) leads to the problem of the definition of a stochastic integral; Turelli (1977) gives a recent discussion of the problem and includes many references. Our formulation incorporates better-behaved functions of  $K$ , though it is likely that the main analytical results at equation (7) below hold without  $K$  necessarily being piecewise continuous.

ERGODIC PROPERTIES

An important parameter both in population and evolutionary theory is the average population size, which we define (assuming the limits exist) as

$$\bar{N} \equiv \langle N \rangle \equiv \lim_{t \rightarrow \infty} t^{-1} \int_0^t N(u) du.$$

Again assuming that the limits exist, we similarly define

$$\bar{K} \equiv \langle K \rangle = \lim_{t \rightarrow \infty} t^{-1} \int_0^t K(u) du, \quad \bar{Q} \equiv \langle K^{-1} \rangle = \lim_{t \rightarrow \infty} t^{-1} \int_0^t Q(u) du. \tag{4}$$

In ecological systems, there are two important nonconstant functions  $K$ : (a) those that are periodic (representing seasonality), say  $K = K_p$ , and (b) those that differ from such a periodic function by some zero mean ergodic random function (representing stochastic variation), say  $K = K_p + W$ . In the former case it follows that  $Q = Q_p = 1/K_p$  is also periodic, and it is a consequence of a consistency result in convergence of means that the limits at (4) will exist, and that also

$$\bar{K} = \lim_{t \rightarrow \infty} t^{-1} \int_{-t}^0 K(u) du, \quad \bar{Q} = \lim_{t \rightarrow \infty} t^{-1} \int_{-t}^0 Q(u) du. \tag{5}$$

In the latter case we have, by definition of ergodicity, that with probability one  $\lim_{t \rightarrow \infty} t^{-1} \int_0^t W(u) du = 0$ , and so the statements at (4) and (5) about  $\bar{K}$  will remain true. Provided that  $1/(K_p + W)$  is suitably regular in its behavior (for example, that it is with probability one uniformly bounded away from  $\infty$ ), the statements about  $Q$  will also be true, though in general we should have  $\langle K_p^{-1} \rangle$  different from  $\langle (K_p + W)^{-1} \rangle$ .

For any given  $K$  (or  $Q$ ), equation (3) shows that  $N$ , and hence also  $\bar{N}$ , is a function of the intrinsic rate of increase,  $r$ . Indeed, the behavior of  $N$  for large and

small  $r$  follows from equation (3) as

$$\lim_{r \rightarrow \infty} [N(t)]^{-1} = \lim_{h \downarrow 0} Q(t - h) \equiv Q(t - 0), \tag{5a}$$

$$\lim_{r \downarrow 0} [N(t)]^{-1} = \lim_{t \rightarrow \infty} t^{-1} \int_{-t}^0 Q(u) du = \bar{Q}, \tag{5b}$$

independent of  $t$ . (The proof of [5a] and [5b] simply uses the Abelian behavior of Laplace transforms, e.g., Widder [1941, p. 181].) Thus, writing  $\bar{N}(r)$  to emphasize the dependence on  $r$ ,

$$\bar{N}(0) \equiv \lim_{r \downarrow 0} \bar{N}(r) = 1/\bar{Q} = (\langle K^{-1} \rangle)^{-1}, \tag{6a}$$

$$\bar{N}(\infty) \equiv \lim_{r \rightarrow \infty} \bar{N}(r) = \bar{K} = \langle K \rangle. \tag{6b}$$

A more comprehensive statement which includes equation (6) and is proved in the Appendix is that

$$\bar{N}(0) = (\langle K^{-1} \rangle)^{-1} = 1/\bar{Q} = [\langle N^{-1}(r) \rangle]^{-1} \leq \bar{N}(r) \leq \bar{K} = \bar{N}(\infty), \tag{7}$$

from which we get support for the intuitively reasonable conjecture:

$$\bar{N}(r) \text{ increases with } r. \tag{8}$$

This relationship is illustrated in figure 1 for  $K(\cdot)$  varying in a manner described in equation (10) below. Jos van Kan and Peter Sonneveld have proved a stronger result from which the truth of the conjecture follows, but we have not seen details of it yet.

For the results at (7) to be true, it suffices that equation (3) be the solution of equation (1) and that the limits at equations (4) and (5) exist. In the case that  $K(\cdot)$  is the sum of a periodic term and a white noise error term, May (1974) uses the Ito stochastic integral and concludes that  $\bar{N} \equiv \langle N \rangle \leq \langle K \rangle \equiv \bar{K}$ , which is consistent with equation (7). Roughgarden (1975) questioned the relevance of this result on two grounds. First, for  $K$  differing from a constant by white noise, use of the Stratonovitch integral as in Feldman and Roughgarden (1975) leads to the conclusion that  $\bar{N} = \bar{K}$ , and second, using computer simulations, Roughgarden found no statistically significant difference between  $\bar{N}$  found from the stochastic logistic model and its value derived from a linear approximation to the model. Our results tend to refute Roughgarden's suggestions; also, the equality he obtained in the simulations can in part be attributed to the values of the parameters he used.

Equation 7 and the conjecture at equation (8) are exemplified in the Appendix, where we obtain explicit expressions for  $N(t)$  and  $\bar{N}(r)$  in the case that

$$[K(t)]^{-1} = Q(t) = Q_0 + Q_1 \cos 2\pi t \quad (\text{all } t), \tag{9}$$

for  $0 < Q_1 < Q_0$ . This form of  $K$  is easier to manipulate algebraically, e.g., as at equation (3), than taking

$$K(t) = K_0 + K_1 \cos 2\pi t \tag{10}$$

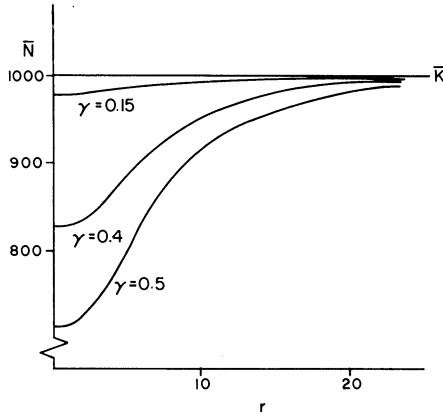


FIG. 1.—The function of  $\bar{N}$  on  $r$  for  $K(\cdot)$  varying in a sinusoid manner as defined at eq. (10). The function is plotted for  $\gamma = 0.15, 0.4, 0.5$  (see eq. [15]).

as in May (1976, 1978). The example also illustrates algebraically, as asserted and illustrated graphically elsewhere (e.g., see May 1973, 1974, 1976, 1978; Roughgarden 1975), that the magnitude of  $r$  determines the ability of the population to track variations in  $K$ , for we find (with eq. [9] holding) that

$$\begin{aligned}
 [N(t)]^{-1} &= Q_0 + Q_1 \left(1 + \frac{4\pi^2}{r^2}\right)^{-1/2} \cos 2\pi(t - \theta_r) \\
 &= [K(t)]^{-1} + Q_1 \left[ \left(1 + \frac{4\pi^2}{r^2}\right)^{-1/2} \cos 2\pi(t - \theta_r) - \cos 2\pi t \right] \quad (11)
 \end{aligned}$$

where the phase lag of  $N$  relative to  $K$  is the fraction  $\theta_r$  of a period  $0 < \theta_r < \frac{1}{4}$  for which  $\tan 2\pi\theta_r = 2\pi/r$ . For  $r$  small,  $\theta_r \approx \frac{1}{4}$  and  $[N(t)]^{-1}$  deviates from  $Q_0 = \langle K^{-1} \rangle$  by at most about  $rQ_1/2\pi$ ; while for large  $r$ ,

$$[N(t)]^{-1} = \left[ [K(t)]^{-1} + \left(\frac{2\pi Q_1}{r}\right) \sin 2\pi t + O(r^{-2}) \right]. \quad (12)$$

The long-term average  $\bar{N}(r)$  averages out these first order effects in the sense that

$$\bar{N}(r) = \langle [K^{-1}] \rangle^{-1} \left(1 + \frac{r^2 Q_1^2}{8\pi^2 Q_0^2}\right) + O(r^4) \quad \text{for } r \rightarrow 0, \quad (13)$$

$$\bar{N}(r) = \bar{K} \left[1 - \frac{2\pi^2 Q_1^2}{r^2(Q_0^2 - Q_1^2)}\right] + O(r^{-4}) \quad \text{for } r \rightarrow \infty. \quad (14)$$

Setting

$$\gamma^2 = \frac{\langle K^2 \rangle}{(\langle K \rangle)^2} - 1, \quad (15)$$

a pseudosquare of the coefficient of variation of  $K$  ( $C.V._K$ ), equations (11) and (12) can be expressed for small  $\gamma^2$  in the form (cf. eq. [A11])

$$\bar{N}(r) \approx \langle (K^{-1}) \rangle^{-1} \left( 1 + \frac{r^2 \gamma^2}{4\pi^2} \right) + O(r^4) \quad \text{for } r \text{ small,} \tag{16}$$

$$\bar{N}(r) \approx \bar{K} \left[ 1 - \frac{4\pi^2}{r^2(\gamma^{-2} - 1)} \right] + O(r^{-4}) \quad \text{for } r \text{ large.} \tag{17}$$

These results are similar to those quoted in May (1976, 1978) for  $K$  as given at equation (10). In figure 2 we illustrate the strong dependence of  $\bar{N}$  on  $\gamma$  for numerical approximations of equation (3) where  $K(\cdot)$  is described by equation (10). The magnitude of deviation in  $\bar{N}$  from  $\bar{K}$  for large  $\gamma$  emphasizes the invalidity of Roughgarden's (1975) assertion that  $\bar{N}$  and  $\bar{K}$  are equal.

In figure 3 we attempt to offer an intuitive understanding to the mechanisms producing the results described above. Consider  $N$  responding to a fluctuating  $K$ . When  $N \ll K$ , it will be growing at a rate considerably less than the rate of decrease when  $N \gg K$ . This is attributable to the concavity of  $\dot{N}$  as a function of  $N$ .

Goel and Richter-Dyn (1974, sec. 4.2c) study the process  $N$  determined by  $Q(t) = Q_0 + \sigma w(t)$  where  $w(t)$  is a white noise process and the constant  $\sigma > 0$  is the standard deviation. Their approximations lead them to conclude that the distribution for the stationary stochastic process  $N_s$ , satisfying a suitably defined stochastic differential equation (related to eq. [1]), should have its mode at

$$\frac{Q_0}{2\sigma^2 r} \left[ \left( 1 + \frac{4\sigma^2 r}{Q_0^2} \right)^{1/2} - 1 \right] \approx Q_0^{-1} \left( 1 - \frac{\sigma^2 r}{Q_0^2} \right). \tag{18}$$

At first sight it seems strange that the mode of  $N_s$  should decrease with increasing  $r$ , yet (assuming  $\bar{N}(r)$  is finite) the mean increases. (In Goel and Richter-Dyn's approximations, the mean is infinite, but taking the distribution of  $N_s$  truncated at some large value, the truncated mean increases with  $r$ .)

The two properties are consistent in that the size of the mode behaves for small  $\sigma^2 r$  like  $(\sigma^2 r)^{-1/2} e^{-\sigma r/Q_0}$  which is decreasing, and the mode merely reflects a weighted average of those values of  $N_s$  that occur often and for which  $N_s$  changes relatively slowly. For example, the proportion of time  $t$  for which  $N(t)$  (as at eq. [11]) is below  $x$  equals

$$\begin{aligned} \pi^{-1} \arccos \left[ (x^{-1} - Q_0) \frac{(1 + 4\pi^2/r^2)^{1/2}}{Q_1} \right] \\ = \int_a^x (\pi y)^{-1} \left[ Q_1^2 y^2 \left( 1 + \frac{4\pi^2}{r^2} \right)^{-1} - (1 - Q_0 y^2) \right]^{-1/2} dy \end{aligned} \tag{19}$$

provided  $a \equiv [Q_0 + Q_1(1 + 4\pi^2/r^2)^{-1/2}]^{-1} \leq x \leq [Q_0 - Q_1(1 + 4\pi^2/r^2)^{-1/2}]^{-1} \equiv b$ . This relative frequency has a bimodal density with infinite peaks at the two end-points, the peak at the lower end being the fatter; this lower end point decreases with increasing  $r$ , and the peak becomes less fat.

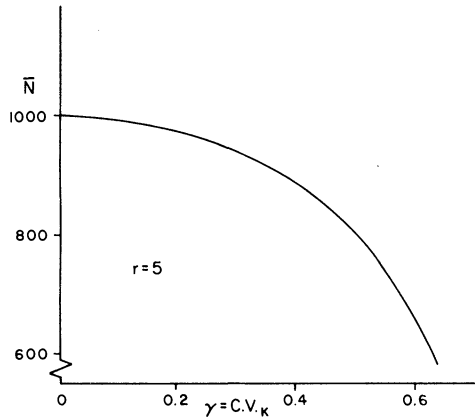


FIG. 2.—The relationship between mean population size,  $\bar{N}$ , and the magnitude of variation in  $K$ ,  $\gamma$ . Values were determined by numerical approximation of eq. (1) with the carrying capacity varying as described at eq. (10).

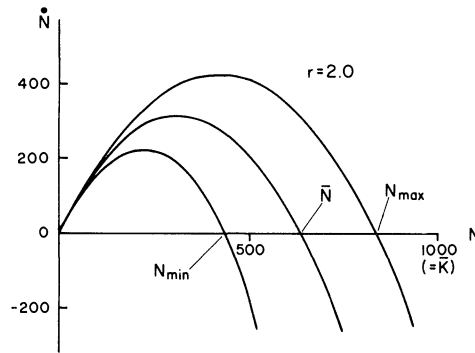


FIG. 3.—Curves of  $\dot{N} = rN(1 - N/K)$  as a function of  $N$  for  $K = N_{\min}$ ,  $\bar{N}$  and  $N_{\max}$  when  $r = 2$  and  $K(\cdot)$  fluctuates as at eq. (10) with  $K_0 = 1,000$ ,  $K_1 = 800$ , so that  $\gamma = 0.57$ .

NATURAL SELECTION FOR TRACKING ABILITY

MacArthur (1962, 1972, pp. 226–230) noted that the logistic model may be written as a simple model of density-dependent natural selection. The Malthusian parameter of fitness,  $m$ , is thus the function of population density

$$m = \dot{N}/N = r - (r/K)N. \tag{20}$$

MacArthur points out that, of genotypes with different values of  $r$  and  $K$ , the one possessing superior positive fitness may depend upon population density.

Our results for a periodic extension of MacArthur's model may be illustrated in a similar fashion by plotting  $\dot{N}/N$  as a function of  $N$  as at equation (20) with  $K$  replaced by  $\bar{N}(r)$ . We plot this function for three  $r$  values as the dashed lines in figure 4. Note that as  $r$  increases, positive fitness ( $m = \dot{N}/N$ ) is higher at all

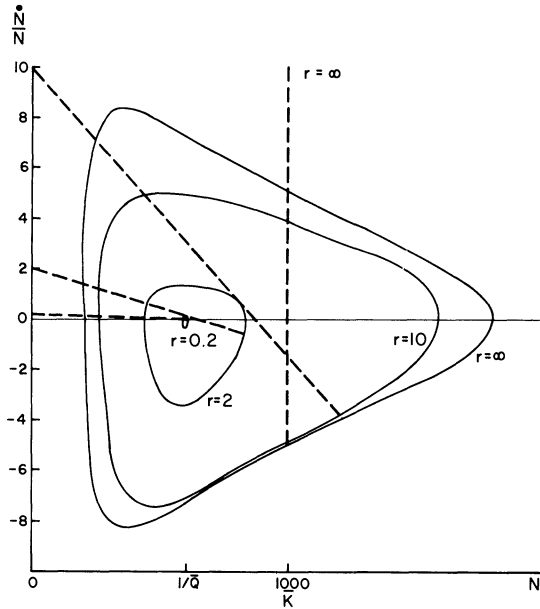


FIG. 4.—The per capita rate of increase,  $\dot{N}/N$ , as a function of  $N$  for  $r = 0.2, 2, 10, \infty$ . The heavy dashed lines illustrate the density-dependent fitness function for genotypes with different  $r$  values. Note that  $\bar{N}$  at equilibrium increases with  $r$ . The closed curves illustrate the dynamics of genotypes (populations) with respective  $r$  values, each tracking  $K(\cdot)$  varying as at eq. (10) with  $K_1 = 800$ ,  $\gamma = 0.57$  and  $\bar{K} = 1,000$ .

population densities. Thus, one would expect natural selection to favor forms with superior “responsiveness” or tracking ability regardless of population density. The advantages to high  $r$ , as reflected by high reproductive effort or short developmental periods, become greater with increasing C.V.<sub>K</sub> (=  $\gamma$ , eq. [15]).

In view of the large number of organisms with low  $r$ , the result that natural selection should always favor high  $r$  seems intuitively capricious. A mitigating aspect of the dynamics of our model is that the probability of extinction is highest for genotypes with high  $r$  because, although  $\bar{N}$  is higher for forms with high  $r$ ,  $N_{\min}$  decreases with increasing  $r$  as illustrated by the closed curves in figure 4. As Pielou (1977) and MacArthur and Wilson (1967) point out, the probability of extinction is highest for populations with the lowest actual population size.

This interpretation marches well with the conclusions of Murphy (1968). In essence, Murphy argued that severely fluctuating environments result in the extinction of genotypes with high reproductive effort (high  $r$ ), whereas genotypes which allocate a greater proportion of their limited resources to somatic functions may enjoy an enhanced probability of survival for future reproductive attempts. Similarly, our model suggests that genotypes with low tracking ability (low  $r$ ) have a lower probability of extinction during periods of low  $K$  than responsive genotypes with high  $r$ . As Schaffer (1974) showed with somewhat different rationale, selection against forms with high  $r$  becomes more intense with increased severity of environmental fluctuations.

## DISCUSSION

To assume that life histories, as reflected by  $r$  values, are shaped solely by tracking ability is, of course, naive. In reality many factors may control the optimum life history. For example, age specific expectations of fertility and survivorship (Taylor et al. 1974), predator pressures and trophic position (Wilbur et al. 1974) have influences which may prevail over tracking ability. Also, some life-history attributes associated with high  $r$  may affect other determinants of  $\bar{K}$  and thus  $\bar{N}$ ; e.g., high reproductive output may increase an organism's resource demands so that  $\bar{K}$  for an energy-limited organism is reduced.

Many organisms have evolved mechanisms which enhance "tracking ability" irrespective of  $r$ . For example, many organisms are able to increase reproductive output when resources are abundant, but have low reproductive output when resources are scarce (Ballinger 1977; Lack 1968; Sadler 1969). If the probability of successfully rearing a large clutch or litter is positively correlated with resource availability, individuals that maximize reproductive output when availability is high will clearly possess higher reproductive success than nonresponsive forms. On the other hand, limiting reproductive output when resource availability is low may be an adaptation to minimize risks associated with reproduction such that survivorship is maximized, since the chances of successful reproduction are low anyway. Clearly, phenotypes which can successfully track fluctuations in the environment will possess a selective advantage. This sort of tracking, through environmentally responsive reproductive output, may well override the advantages of low variance in reproductive output demonstrated by Gillespie (1977) and Boyce (1977).

In this paper we have shown that nonlinearities in the logistic model may have implications of biological significance. The qualitative results presented here also apply to a wide range of population models, e.g., those presented by Pielou (1977, p. 35ff), where  $\bar{N}$  is a concave function of  $N$ . However, these results do not apply to the linear approximations formulated by Roughgarden (1975) and Nisbet et al. (1977). We contend that the linearization and oversimplification of population models as encouraged by Nisbet et al. (1977) should be avoided if at all possible, since inherent nonlinearities may offer valuable insight into biological mechanisms. This is especially significant when investigating the importance of sizable stochastic or periodic variations in model parameters.

## SUMMARY

The mathematics of stochastic nonlinear population models is notoriously intractable and has led some investigators to study linear approximations to make computations easier. However, nonlinear models may often better describe biological systems, and linearization may obscure dynamics of biological significance.

We clarify various aspects of the dynamics of the logistic population model with a fluctuating carrying capacity. Average population size decreases with an increasing magnitude of variation in  $K$ , but  $\bar{N}$  is always less than or equal to  $\bar{K}$ . This effect is mediated by the intrinsic rate of increase,  $r$ . In general,  $\bar{N}$  increases as  $r$



increases. This pattern should be general for models where  $\bar{N}$  is a concave function of  $N$ .

In environments where the magnitude of variation in  $K$  is not large, natural selection will favor genotypes which are best able to track fluctuations in  $K$ . However, when the fluctuations in  $K$  are large, natural selection may favor forms which are not highly responsive to fluctuations in  $K$ .

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APPENDIX

Integration of eq. (1) as it stands shows that

$$r^{-1} [N(t) - N(0)] = \int_0^t N(u) du - \int_0^t N^2(u)Q(u) du, \tag{A1}$$

so the existence of the limit  $\bar{N} = \langle N \rangle$  at eq. (4) implies the existence of  $\langle N^2Q \rangle$  with

$$\langle N^2Q \rangle \equiv \lim_{t \rightarrow \infty} t^{-1} \int_0^t N^2(u)Q(u) du = \bar{N}. \tag{A2}$$

Now

$$\begin{aligned} 0 &\leq \int_0^t [Q^{-1/2}(u) - N(u)Q^{1/2}(u)]^2 du \\ &= \int_0^t K(u) du - 2 \int_0^t N(u) du + \int_0^t N^2(u)Q(u) du; \end{aligned}$$

so, using eq. (A2),

$$\bar{N} \leq \bar{K} \text{ independent of } r. \tag{A3}$$

Integration of eq. (3) coupled with eqs. (4) and (5) shows that, when the limits exist,

$$\begin{aligned} \langle N^{-1} \rangle &\equiv \lim_{t \rightarrow \infty} t^{-1} \int_0^t du \int_0^\infty r e^{-rv} Q(t-v) dv \\ &= \bar{Q} \text{ independent of } r. \end{aligned} \tag{A4}$$

Since also

$$\begin{aligned} 1 &= \lim_{t \rightarrow \infty} \left( t^{-1} \int_0^t [N^{1/2}(u) \cdot N^{-1/2}(u)] du \right)^2 \\ &\leq \lim_{t \rightarrow \infty} \left[ t^{-1} \int_0^t N(u) du \cdot t^{-1} \int_0^t N^{-1}(u) du \right] \\ &= \bar{N} \langle N^{-1} \rangle, \end{aligned} \tag{A5}$$

the results at eqs. (A3), (A4), and (A5) yield equation (7).

It may be noted that the above argument leading to eq. (7) may be used in integrating  $NN^\alpha$  for any finite power  $\alpha$ , and since  $[N^{\alpha-1}K]^{1/2} - (N^{\alpha+1}Q)^{1/2}]^2 \geq 0$ , we can deduce that

$$(\langle N^{-\alpha} \rangle)^{-1} = (\langle N^{-\alpha+1}Q \rangle)^{-1} \leq \langle N^{\alpha+1}Q \rangle = \langle N^\alpha \rangle \leq \langle N^{\alpha-1}K \rangle, \tag{A6}$$

of which equation (7) is the special case  $\alpha = 1$ .

When  $K(\cdot)$  is periodic,  $N(\cdot)$  as defined at eq. (3) is also periodic with the same period, which without loss of generality may be taken as the unit of time.  $N(\cdot)$  may then be expressed in the form

$$[N(t)]^{-1} = \int_0^1 r(1 - e^{-r})^{-1} e^{-rv} Q(t - v) dv, \tag{A7}$$

which is the equation we used to compute  $N(t)$  via Simpson's rule for numerical integration. Similarly,

$$\bar{N}(r) = r^{-1}(1 - e^{-r}) \int_0^1 \left[ \int_0^1 e^{-rv} Q(t - v) dv \right]^{-1} dt. \tag{A8}$$

Differentiation twice with respect to  $r$  in (A8) leads eventually to the result that

$$\bar{N}(r) = \bar{N}(0) \left( 1 + r^2 \left\{ \int_0^1 dt \left[ \bar{N}(0) \int_0^1 u Q(t - u) du \right]^2 - \frac{1}{4} \right\} \right) + o(r^2), \tag{A9}$$

of which eq. (13) is a special case with a more detailed error term.

When  $K$  is as at eq. (9), straightforward computation or reference to tables of integrals shows that

$$\bar{K} = \int_0^1 (Q_0 + Q_1 \cos 2\pi t)^{-1} dt = \frac{1}{(Q_0^2 - Q_1^2)^{1/2}}, \tag{A10a}$$

$$\begin{aligned} \langle K^2 \rangle &= \int_0^1 (Q_0 + Q_1 \cos 2\pi t)^{-2} dt \\ &= 1/[(Q_0^2 - Q_1^2) \left( 1 - \frac{Q_1^2}{Q_0^2} \right)^{1/2}], \end{aligned} \tag{A10b}$$

so the standardized second moment measure of variability of  $K$  (loosely speaking the square of the coefficient of variation of  $K$ ) equals

$$\begin{aligned} \gamma^2 &\equiv \frac{\langle K^2 \rangle}{\bar{K}^2} - 1 = \left( 1 - \frac{Q_1^2}{Q_0^2} \right)^{-1/2} - 1 \\ &\approx \frac{Q_1^2}{2Q_0^2} \end{aligned} \tag{A11}$$

when  $Q_1^2/Q_0^2$  is small.

Substituting from eq. (9) into eq. (3) gives

$$\begin{aligned} [N(t)]^{-1} &= \int_0^\infty r e^{-rv} [Q_0 + Q_1 \cos 2\pi(t - v)] dv \\ &= Q_0 + rQ_1(r^2 + 4\pi^2)^{-1} (r \cos 2\pi t + 2\pi \sin 2\pi t), \end{aligned} \tag{A12}$$

which leads to eq. (11), and then by integration (cf. eq. [A10a]) to

$$\bar{N}(r) = Q_0^{-1} \left[ 1 - \left( \frac{Q_1}{Q_0} \right)^2 \left( 1 + \frac{4\pi^2}{r^2} \right)^{-1} \right]^{-1/2}. \tag{A13}$$

In figure 4 the closed curve shown as the asymptote of  $r(1 - N/K)$  versus  $N$  as  $r \rightarrow \infty$  can be shown to be

$$- \dot{Q}/Q = \dot{K}/K \text{ versus } K \tag{A14}$$

by straightforward analysis involving

$$\begin{aligned} 1/N(t) &= \int_0^{\infty} r e^{-ru} Q(t-u) du = \int_0^{\infty} e^{-rv} Q\left(t - \frac{v}{r}\right) dv \\ &= \int_0^{\infty} e^{-rv} \left[ Q(t) - \left(\frac{v}{r}\right) \dot{Q}(t) + \dots \right] dv \\ &= Q(t) - r^{-1} \dot{Q}(t) + O(r^{-2}). \end{aligned}$$

#### LITERATURE CITED

- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.
- Annegers, J. F. 1973. Seasonal food shortages in West Africa. *Ecol. Food Nutr.* 2:251-257.
- Ballinger, R. E. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. *Ecology* 58:628-635.
- Boyce, M. S. 1977. Population growth with stochastic fluctuations in the life table. *Theor. Popul. Biol.* 12:366-373.
- Crombie, A. C. 1945. On competition between different species of graminivorous insects. *Proc. R. Soc. Lond., B. Biol. Sci.* 132:362-395.
- Davidson, J. 1938*a*. On the ecology of the growth of the sheep population in South Australia. *Trans. R. Soc. S. Aust.* 62:141-148.
- . 1938*b*. On the growth of the sheep population in Tasmania. *Trans. R. Soc. S. Aust.* 62:342-346.
- Emmel, T. C. 1976. *Population biology*. Harper & Row, New York.
- Feldman, M., and J. Roughgarden. 1975. A population's stationary distribution and chance of extinction in a stochastic environment with remarks on the theory of species packing. *Theor. Popul. Biol.* 7:197-207.
- Fleming, T. H., and R. S. Hooker. 1975. *Anolis cupreus*: the response of a lizard to tropical seasonality. *Ecology* 56:1243-1261.
- Fretwell, S. D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton, N.J.
- Gause, G. F. 1931. The influence of ecological factors on the size of populations. *Am. Nat.* 65:70-76.
- . 1934. *The struggle for existence*. Williams & Wilkins, Baltimore.
- Gillespie, J. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. *Am. Nat.* 111:1010-1014.
- Goel, N. S., and N. Richter-Dyn. 1974. *Stochastic models in biology*. Academic Press, New York.
- Istock, C. A. 1977. Logistic interaction of natural populations of two species of waterboatmen. *Am. Nat.* 111:279-287.
- Lack, D. 1968. *Ecological adaptations for breeding in birds*. Chapman & Hall, London.
- Levins, R. 1969. The effect of random variation of different types on population growth. *Proc. Natl. Acad. Sci. USA* 72:1061-1065.
- Lotka, A. J. 1925. *Elements of physical biology*. Williams & Wilkins, Baltimore.
- MacArthur, R. H. 1962. Some generalized theorems of natural selection. *Proc. Natl. Acad. Sci. USA* 48:1893-1897.
- . 1972. *Geographical ecology*. Harper & Row, New York.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- May, R. M. 1973. Stability in randomly fluctuating versus deterministic environments. *Am. Nat.* 107:621-650.
- . 1974. *Stability and complexity in model ecosystems*. 2d ed. Princeton University Press, Princeton, N.J.
- . 1976. Models for single populations. Pages 4-25 in R. M. May, ed. *Theoretical ecology*. Blackwell's, Oxford.

- . 1978. Mathematical aspects of the dynamics of animal populations. Pages 317–366 in S. A. Levin, ed. *Studies in mathematical biology. Part II.* Mathematical Association of America, Providence.
- Murphy, G. I. 1968. Patterns in life history and the environment. *Am. Nat.* 102:390–404.
- Nisbet, R. M., W. S. C. Gurney, and M. A. Pettipher. 1977. An evaluation of linear models of population fluctuations. *J. Theor. Biol.* 68:143–160.
- Odum, E. P. 1971. *Fundamentals of ecology.* 3d ed. Saunders, Philadelphia.
- Pearl, R. 1930. *The biology of population growth.* Knopf, New York.
- Pielou, E. C. 1977. *Mathematical ecology.* Wiley, New York.
- Roughgarden, J. 1975. A simple model for population dynamics in stochastic environments. *Am. Nat.* 109:713–736.
- Sadler, R. M. F. S. 1969. *The ecology of reproduction in wild and domestic mammals.* Methuen, London.
- Schaffer, W. M. 1974. Optimal reproductive effort in fluctuating environments. *Am. Nat.* 108:783–790.
- Taylor, H. M., R. S. Gourley, C. E. Lawrence, and R. S. Kaplan. 1974. Natural selection of life history attributes: an analytical approach. *Theor. Popul. Biol.* 5:104–122.
- Turelli, M. 1977. Random environments and the stochastic calculi. *Theor. Popul. Biol.* 12:140–178.
- Widder, D. V. 1941. *The Laplace transform.* Princeton University Press, Princeton, N.J.
- Wilbur, H. M., D. W. Tinkle, and J. P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. *Am. Nat.* 108:805–817.