Theory of the dependence of population levels on environmental history for semelparous species with short reproductive seasons

(ecology/population dynamics/synchronous reproduction)

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ABSTRACT   A population that is strongly self-regulating through density-dependent effects is expected to be such that, if many generations have elapsed since its establishment, its present size should not be sensitive to its initial size but should instead be determined by the history of the variables that describe the influence of the environment on fecundity, mortality, and dispersal. Here we discuss the dependence of abundance on environmental history for a semelparous population in which reproduction is synchronous. It is assumed that at each instant t: (i) the rate of loss of members of age a by mortality and dispersal is given by a function ρ of t, a, and the present number $x = x(a,t)$ of such members; and (ii) the number $x(0,t)$ of members born in the population is given by a function F of t and the number of $x(a_f,t)$ at a specified age a_f of fecundity. It is further assumed that the functions ρ and F have the forms $\rho(x,a,t) = \pi_1(a,t)x + \pi_2(a,t)x^2$ and $F(x(a_f,t),t) = \nu_t x(a_f,t)$. For such a population, a change in the environment is significant only if it results in a change in ν_t, $\pi_1(a,t)$, or $\pi_2(a,t)$, and, hence, the history of the environment up to time t is described by giving ν_τ, $\pi_1(a,\tau)$, and $\pi_2(a,\tau)$ for each $\tau \leq t$ and all a in $[0,a_f]$. We show that the dependence of x on the history of the environment can be calculated explicitly and has certain properties of "fading memory"; i.e., environmental events that occurred in the remote past have less effect upon the present abundance than comparable events in the recent past.

The ecological literature contains many statements of the proposition that established populations are self-governing systems that have regulated their size in accord with their own properties and those of their environments (e.g., refs. 1–6). When a population that is strongly self-regulating through density-dependent factors has been in existence for many generations, its abundance should depend not upon initial data but rather upon the history, particularly the *recent* history, of the variables that describe the influence of the environment. This suggestion was recently (7) made precise and explored for a model in which the nonlinear functional giving the dependence of abundance upon environmental history can be calculated explicitly and shown to be of a type occurring in the "theory of fading memory"—a mathematical theory of the general behavior of systems for which the present influence of events that occurred in the remote past is much weaker than the influence of comparable events in the recent past (8–11).

The model of ref. 7 leads to a logistic equation with r and K functions of time whose values describe the influence of the environment. Such a model does not account for a possible effect of age structure—i.e., a dependence of overall rates of fecundity, mortality, and dispersal upon the distribution of ages. Here, however, we are concerned with populations for which age structure is important because we consider species for which reproduction occurs only once in an individual's life and then only at a precisely defined *age of fecundity* a_f (also called the "reproductive age"). Such is the case for annual plants and many species of animals, particularly in the class Insecta.

Using a theoretical framework developed in refs. 12–14, we here make the following assumptions:

(i) The net rate at which the population loses individuals of age a at time t through mortality and dispersal is given by a function ρ of t, a, and the number $x(a,t)$ of members of the population that have age a at time t; ρ is called the *loss function*.

(ii) The number $x(0,t)$ of individuals born in the population at time t is given by a function F of t and the number $x(a_f,t)$ of members at the age of reproduction; F is called the *fecundity function*.

If we use a unit of time such that $a_f = 1$, then assumptions (i) and (ii) are rendered mathematical by writing:

$$Dx(a,t) + \rho(x(a,t),a,t) = 0 \qquad [1]$$

and

$$x(0,t) = F(x(1,t),t), \qquad [2]$$

in which

$$Dx(a,t) = \frac{d}{dh} x(a + h, t + h)\Big|_{h=0} \qquad [3]$$

is the negative of the net rate at which the population loses, at time t (by the overall effects of death, immigration, and emigration), members that have age a at that time. For a detailed discussion of the relation of these equations to those used by Von Foerster (15), Gurtin and MacCamy (16), Hoppensteadt (17), and Griffel (18), see the article of Coleman (12).

Assumption (i), which yields Eq. 1, is equivalent to the assertion that the intraspecific interactions that influence mortality and dispersal occur only between individuals of equal age. For a semelparous population for which reproduction is seasonal, synchronous, and followed by parental mortality, the assertion holds well; in such a population the distribution of ages is narrow, and a member with age in $(0,1)$ [i.e., in $(0,a_f)$] can interact only with members of the same age, for individuals of other ages are not simultaneously present. Eqs. 1 and 2 do have solutions in which the distribution of ages is narrow at all times (this point is discussed in detail in ref. 14), and it is such solutions that interest us here.

In refs. 12 and 13 it was assumed that $\rho(x,a,t)$ and $F(x,a,t)$ are independent of t, and in ref. 14 it was assumed that $\rho(x,a,t)$ and $F(x,a,t)$ are periodic in t with integral period. No such assumptions of temporal constancy or periodicity are made here, but, for simplicity, we assume that the dependence of $\rho(x,a,t)$ on x has only a linear and a quadratic term, i.e.,

$$\rho(x,a,t) = \pi_1(a,t)x + \pi_2(a,t)x^2, \qquad [4]$$

and that $F(x,t)$ is linear in x, i.e.,

$$F(x,t) = \nu_t x. \qquad [5]$$

We assume that for each integer n, the functions $\hat{\pi}_{n,1}$ and $\hat{\pi}_{n,2}$, defined by

$$\hat{\pi}_{n,1}(a) = \pi_1(a,n + a), \quad \hat{\pi}_{n,2}(a) = \pi_2(a,n + a), \qquad [6]$$

are continuous and that $\hat{\pi}_{n,2}$ is not negative on [0,1]. We further assume that ν_t is (strictly) positive whenever t is an integer. (For species with synchronous, seasonal, reproduction, ν_t will be zero unless t is an integer.) The discussion below will show that for each n, the functions $\hat{\pi}_{n,1}$ and $\hat{\pi}_{n,2}$ determine the influence of the environment on the survival of the population during the nth generation and ν_n is a measure of fecundity of the $(n-1)$th generation.

Let $\mathcal{C}_n$ be the set of all individuals of the given species born at time $t = n$ in either the observed population $\mathcal{P}$ or in other populations from which they can be attracted into $\mathcal{P}$. Arguments given in refs. 13 and 14 can be applied here to show that Eqs. 1, 3, and 4 yield the following formula for the number $x(a, n + a)$ of members of $\mathcal{C}_n$ that are present in $\mathcal{P}$ at time $t = n + a$ as a function of their age a and the number $x(0, n)$ of members of $\mathcal{C}_n$ born in $\mathcal{P}$:

$$x(a, n + a) = \frac{x(0, n)\lambda_n(a)}{1 + x(0, n)\gamma_n(a)}, \qquad [7]$$

here

$$\lambda_n(a) = \exp\left(-\int_0^a \hat{\pi}_{n,1}(\tau)d\tau\right) > 0 \qquad [8]$$

and

$$\gamma_n(a) = \int_0^a \lambda_n(\tau)\hat{\pi}_{n,2}(\tau)d\tau \geq 0. \qquad [9]$$

Let x_n be the number of adults of the nth generation $\mathcal{C}_n$ that are present in the population $\mathcal{P}$; these individuals have age $a = a_f = 1$ at time $t = n + 1$; i.e., $x_n = x(1, n + 1)$. Because Eqs. 2 and 5 yield $x(0, n) = F(x(1, n), n) = F(x_{n-1}, n) = \nu_n x_{n-1}$, we have, by Eq. 7,

$$x(a, n + a) = \frac{x_{n-1}\nu_n\lambda_n(a)}{1 + x_{n-1}\nu_n\gamma_n(a)}. \qquad [10]$$

In the special case of $a = 1$, this last relation reduces to

$$x_n = \frac{\alpha_n x_{n-1}}{1 + \beta_n x_{n-1}}, \qquad [11]$$

with

$$\alpha_n = \lambda_n(1)\nu_n > 0, \qquad \beta_n = \gamma_n(1)\nu_n \geq 0. \qquad [12]$$

Let m and n be two integers with $n > m$. By successive applications of Eq. 11 one can express the number x_n of adults present in $\mathcal{P}$ in the nth generation as a function of the number x_m adults in $\mathcal{P}$ in the mth generation:

$$x_n = H^{n,m}(x_m). \qquad [13]$$

An elementary calculation shows that here $H^{n,m}$ has the form

$$H^{n,m}(x) = \frac{A_{n,m}x}{1 + A_{n,m}C_{n,m}x} \qquad [14]$$

in which

$$A_{n,m} = \prod_{k=m+1}^{n} \alpha_k = \prod_{j=0}^{n-m-1} \alpha_{n-j} > 0 \qquad [15]$$

and

$$C_{n,m} = \sum_{j=0}^{n-m-1} \frac{\beta_{n-j}}{\alpha_n\alpha_{n-1}\cdots\alpha_{n-j}} \geq 0. \qquad [16]$$

We consider first the case in which m is fixed, x_m is known, and one is interested in the behavior of the population as n increases without bound.

The following theorem follows forthwith from Eqs. 10 and 13-16: *If, as* n $\rightarrow \infty$, *either* $A_{n,m} \rightarrow 0$ *or* $C_{n,m} \rightarrow \infty$ *(or both), then the population is endangered in the sense that, no matter how large its "initial" adult membership* x_m,

$$\lim_{\substack{n \to \infty \\ 0 \leq a \leq 1}} \sup \; x(a, n + a) = 0. \qquad [17]$$

Let us suppose now that none of numbers $C_{n,m}$ is zero and, as n increases, $C_{n,m}$ remains bounded away from zero and infinity—i.e., that

$$\inf_n C_{n,m} > 0 \quad \text{and} \quad \sup_n C_{n,m} < \infty. \qquad [18]$$

Eq. 14 then yields, for $x \geq 0$,

$$\frac{1}{C_{n,m}} - H^{n,m}(x) = \frac{1}{[1 + A_{n,m}C_{n,m}x]C_{n,m}} > 0, \qquad [19]$$

and from this relation we may read off our main result: *If, as* n $\rightarrow \infty$, $A_{n,m} \rightarrow \infty$, *then, for each positive value* x_m *of the "initial" adult population* x(1, m + 1),

$$\lim_{n \to \infty} \left[\frac{1}{C_{n,m}} - H^{n,m}(x_m)\right] = 0. \qquad [20]$$

In view of Eq. 13, this theorem tells us that if, as n increases, $A_{n,m} \rightarrow \infty$, then the number $x_n = x(1, n + 1)$ of adults present in $\mathcal{P}$ during the nth generation $\mathcal{C}_n$ will be, for large enough n, very close to $C_{n,m}^{-1}$, i.e.,

$$\lim_{n \to \infty} [x(1, n + 1) - C_{n,m}^{-1}] = 0, \qquad [21]$$

and for each age a in $[0, 1]$ we shall have, by Eq. 10,

$$\lim_{n \to \infty} [x(a, n + a) - X_{n,m}(a)] = 0, \qquad [22]$$

in which the limiting "abundance function" or "age-distribution function," $X_{n,m}$, has the form

$$X_{n,m}(a) = \frac{\nu_n\lambda_n(a)}{C_{n-1,m} + \nu_n\gamma_n(a)}, \qquad [23]$$

with λ_n and γ_n as in Eqs. 8 and 9. We note that the limiting abundance function $X_{n,m}$ is completely independent of the initial number of members of the population $\mathcal{P}$ and their age distribution. In fact, $X_{n,m}$ is determined when one specifies the functions $\hat{\pi}_{n,1}$ and $\hat{\pi}_{n,2}$, which measure the influence of the environment on the population during the nth generation, and the ratio $\nu_n/C_{n-1,m}$, which is, from the point of view of the nth generation, a property of the past history of the environment.

Eqs. 20 and 21, which assert that, for each integer m and each $x_m > 0$, the numbers $x_{m+k} = H^{m+k,m}(x_m)$ approach $C_{m+k,m}^{-1}$ as k increases without bound, is illustrated in Fig. 1, where there are graphs of x_{m+k} against k for three values of x_m. For these calculations, as well as those shown in Figs. 2 and 3, we used a single randomly generated list of the pairs (α_n, β_n), with α_n drawn from the uniform distribution on the interval $(0, 4)$ and β_n from the uniform distribution on $(0, 10^{-2})$. The numbers x_{m+k}, for $k = 1,2,\ldots, 15$, were obtained by successive iterations of Eq. 11, with the initial value of x_{n-1} taken to be $x_m = 1$, 100, and 200.

In Fig. 1 we see a case in which, although the "environment" fluctuates rapidly from generation to generation and, hence, the size of the population fluctuates rather wildly, the number x_{m+15} of adults in the population after 15 generations is not at all sensitive to the "initial" number x_m of adult members. In this example, fluctuations in environmental factors (which here are measured by the coefficients α_n and β_n) have a marked effect on population levels, but nonetheless the population is self-regulating in the sense that, after the passage of a few generations, present abundance is essentially independent of initial abundance. These calculations confirm a point made by Nicholson (5) in his debate with the abiotic school (see, e.g., ref. 19) of population regulation: The correlation of abundance with
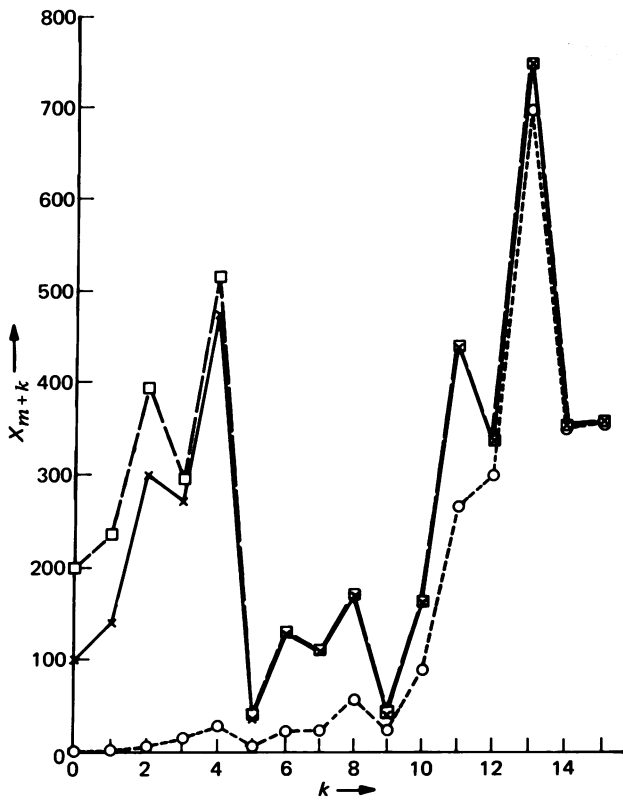
FIG. 1. Adult membership x_{m+k} in the $(m + k)$th generation plotted against k for a representative population in a randomly varying environment with α_{m+k} drawn from the uniform distribution on (0,4) and β_{m+k} from the uniform distribution on $(0,10^{-2})$. O---O, $x_m = 1$; ×——×, $x_m = 100$; ☐--☐, $x_m = 200$.
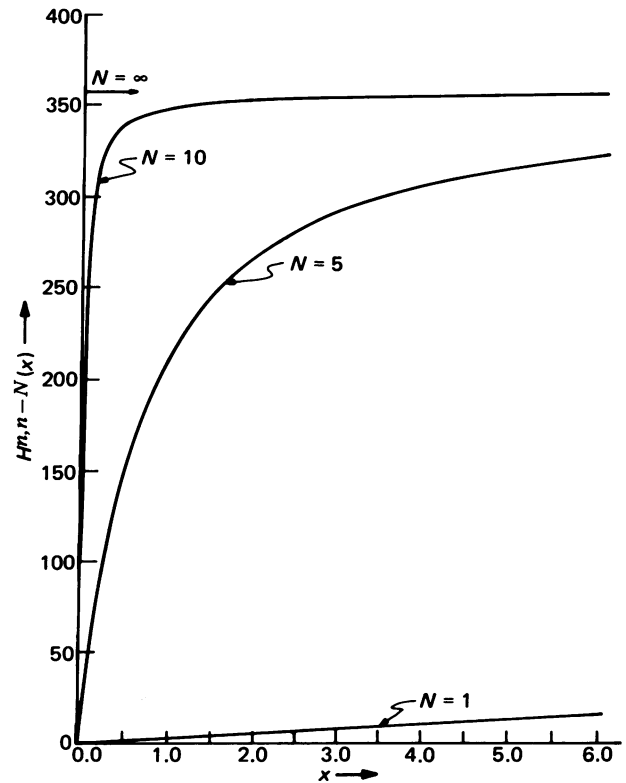

FIG. 2. Plot of $H^{n,n-N}(x)$ against x for $N = 1, 5$, and 10, calculated from Eqs. 14–16 by using coefficients $\alpha_{n-k}, \beta_{n-k}$ taken from the randomly generated list used for Fig. 1 with $n = m + 15$.

environmental factors does not imply the absence of self-regulation through density-dependent terms.

Let us now take the point of view of the nth generation, and let n be held fixed while m varies over the integers less than n. If we assume, as we shall, that the functions $\hat{\pi}_{m,1}$ and $\hat{\pi}_{m,2}$ and the numbers ν_m have been specified for *all* values of m previous to n, that β_n and β_{n-1} are positive, and that

$$A_{n,m} \to \infty \quad \text{as} \quad m \to -\infty, \quad [24]$$

then we shall see that the population is either empty or may be regarded as having "existed forever," in which case its size is determined by the history of its environment. Indeed, it follows from Eq. 14 that if we define $H^n(x)$ to be

$$H^n(x) = \lim_{m \to -\infty} H^{n,m}(x), \quad [25]$$

then $H^n(x)$ exists for $x \geq 0$. Clearly, $H^n(0) = 0$. For $x > 0$, $H^n(x)$ is, by Eq. 19 and the relation 24, equal to the (finite) number C_n^{-1}, with

$$C_n^{-1} = \lim_{m \to -\infty} C_{n,m}^{-1}. \quad [26]$$

Thus, in view of Eq. 16, we have, for every $x > 0$,

$$H^n(x) = C_n^{-1} = \left[\sum_{j=0}^{\infty} \frac{\beta_{n-j}}{\alpha_n \alpha_{n-1} \cdots \alpha_{n-j}} \right]^{-1}. \quad [27]$$

In other words: *If the monotone increasing sequence* N $\longmapsto$ $C_{n,n-N}$ *has a finite limit* C_n *as* N $\to \infty$, *then for every* x $>$ 0, $H^n(x)$ *equals the positive number* C_n^{-1}.

If $C_{n,n-N} \to \infty$ as $N \to \infty$, then $H^n(x) = 0$ for all x; i.e., the population cannot have existed for all time and is in fact empty when $t = n$.

Of interest, of course, is the case in which C_n is finite; in that case Eqs. 13, 25, and 27 tell us that the number $x(1, n + 1)$ of adults present in $\mathcal{P}$ in the nth generation is either zero or the positive number

$$x_n = C_n^{-1}. \quad [28]$$

[When C_n is finite, x_n will be zero if and only if $x_m = 0$ for all $m < n$, which corresponds to taking the value of $H^n(x)$ at $x = 0$; if there is at least one $m < n$ with $x_m > 0$, then $x_n = H^n(x)$ for an $x > 0$, and Eq. 28 holds.] Moreover, if the population is not empty, substitution of Eq. 28 into Eq. 10 yields

$$x(a, n + a) = X_n^{\infty}(a), \quad [29]$$

in which X_n^{∞} is a canonical abundance function that is independent of initial data and is given by the formula

$$X_n^{\infty}(a) = \frac{\nu_n \lambda_n(a)}{C_{n-1} + \nu_n \gamma_n(a)}. \quad [30]$$

If we note that when C_{n-1} is finite, $C_{n-1,m}$ is approximately equal to C_{n-1} for large values of $(n - 1) - m$, and if we note further that Eqs. 22 and 23 describe a situation in which $n - m$ is large, then it becomes clear that Eqs. 22 and 23 are compatible with Eqs. 29 and 30.

The canonical abundance function X_n^{∞} gives the age distribution in a population that has "existed forever." For each a in [0, 1] there holds

$$\lim_{N \to \infty} X_{n,n-N}(a) = X_n^{\infty}(a); \quad [31]$$

i.e., $X_{n,n-N}(a)$ gives, for large N, an approximation to $X_n^{\infty}(a)$. This approximation is useful because $C_{n-1,m}$ in Eqs. 23 is given by a finite series, whereas C_{n-1} in Eq. 30 requires for its calculation the evaluation of an infinite series. Similarly, the functions $H^{n,n-N}$, with N again large but finite, give approximations to H^n.
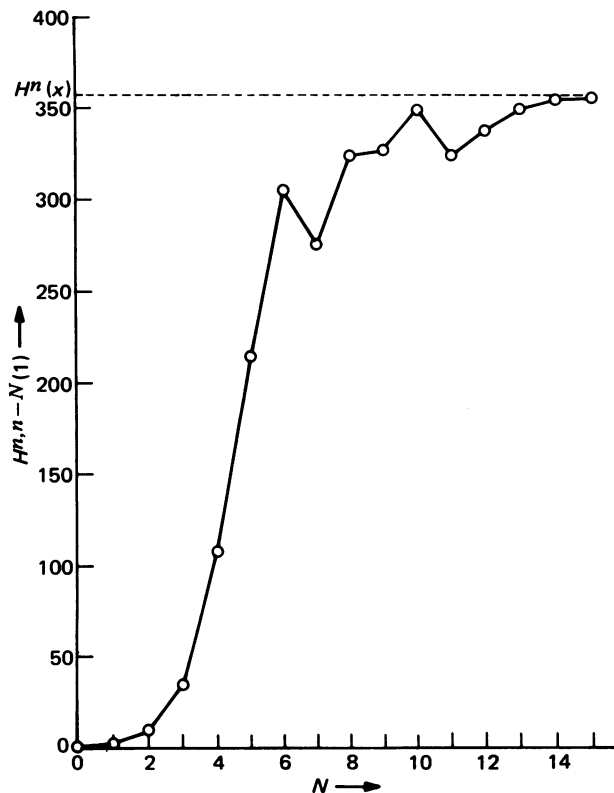
FIG. 3. $H^{n,n-N}(1)$ plotted against N with α_{n-k} and β_{n-k} as in Fig. 2.

The following question now arises: Granted the relation 24, how large must N be (i.e., how many generations back in time must data and calculations be taken) in order that $H^{n,n-N}(x)$ be, for $x > 0$, a good approximation to $H^n(x)$? Calculations that bear on this question are shown in Figs. 2 and 3.

Fig. 2 contains graphs of $H^{n,n-N}(x)$ against x for $N = 1, 5,$ and 10, calculated from Eqs. 14–16 with the pairs $(\alpha_{n-j}, \beta_{n-j})$, with $j = 0,1,2, \ldots$, taken from the same randomly generated list used for the construction of Fig. 1. [In fact, this list contained 100 pairs (α_l, β_l), and whereas in Fig. 1 the fixed index m corresponds to $l = 85$, the fixed index n in Fig. 2 corresponds to $l = 100$.] The arrow labeled $N = \infty$ in Fig. 2 indicates the height of the function H^n which is constant on $(0, \infty)$ and whose value was obtained from Eq. 27 with 100 terms in the sum shown there. It is clear from Fig. 2 that, for population in a "random environment" such that α_{n-j} varies uniformly over $(0, 4)$ and β_{n-j} varies uniformly over $(0, 10^{-2})$, $H^{n,n-N}$ gives a useful approximation to H^n when N is as small as 10. Indeed, Eq. 27 here yields the value 358 for $H^n(x)$, the "present" adult membership of the population; if one were to assume that in the 9th, 10th, 11th, or 12th generation previous to the present generation the population contained only one adult member, the calculated adult membership of the population in the present generation would be, respectively, $H^{n,n-9}(1) = 327$, $H^{n,n-10}(1) = 350$, $H^{n,n-11}(1) = 324$, or $H^{n,n-12}(1) = 338$, and each of these numbers is close to the actual value $H^n(x) = 358$. The dependence of $H^{n,n-N}(1)$ on N is shown in more detail in Fig. 3.

The fact that $H^{n,n-N}(x)$, with N finite, gives a good approximation to $H^n(x)$, even for very small x, confirms the assertion that the dependence of abundance on environmental

history has, at least for the present model (as well as that discussed in ref. 7), a property of fading memory: One need know the environmental history only over a finite span of time, extending from the present back into the recent past, to obtain a good estimate of population size.

The number

$$K_n = (\alpha_n - 1)/\beta_n \qquad [32]$$

is the (unique) positive fixed point of the function $H^{n,n-1}$ that, by Eq. 13, takes x_{n-1} into x_n. K_n can be called the "carrying capacity of the environment of the nth generation." For the example of Figs. 2 and 3, $K_n = 359.9$; i.e., if the population had contained approximately 360 adult members at the end of the $(n - 1)$th generation, there would have been that number of adults produced in the nth generation. The actual number of adults present at the end of the nth generation, assuming the population existed forever in the changing environment under consideration, is $H^n(x)$ (for any $x > 0$), and this number here turned out to be 358. In general, in a fluctuating environment $H^n(x)$ will not be close to K_n for every n. However, changes in x_{n-1} here "correlate" with $K_n - x_{n-1}$ in the sense that, for each n, $x_n - x_{n-1}$ must have the same sign as $K_n - x_{n-1}$; i.e., in the course of one generation, say the nth, the population x_n of adults can show an increase only if the number x_{n-1} of adults present in the previous generation lies below the present carrying capacity.

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