Non-continuous interaction between hosts and parasites. By V. A. BAILEY, M.A., D.Phil. (Oxon), Associate Professor of Physics, University of Sydney. (Communicated by Professor P. A. M. DIRAC.)

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In a recent publication* the problem of determining the abundance of two interacting species of animals was investigated, and the fundamental equations were established.

A special form of this problem, with concurrent life-cycles and non-continuous interaction between the two species, was also discussed, and certain interesting properties of the interaction were mentioned which had been originally discovered by Dr A. J. Nicholson by arithmetical and graphical methods alone.

It is proposed here to derive some of these properties from the fundamental equations and to compare some numerical deductions with the results obtained by Dr Nicholson.

The fundamental equations of the non-continuous problem are as follows:

$$h_{n+1} = F h_n e^{-a p_n}, \tag{1}$$

$$p_{n+1} = F h_n - h_{n+1}, \tag{2}$$

where p_n, h_n are the densities at the nth generation of the parasites and hosts respectively, a is the "area of discovery" of a parasite, i.e. the gross area effectively traversed by a parasite during its life-time, and F is the "power of increase" of the hosts, i.e. the factor† by which a generation would exceed the previous one were no parasites present.

From these equations the following are easily derived:

$$h_{n+1} = p_{n+1}/(e^{a p_n} - 1), \tag{3}$$

$$p_{n+2} = p_{n+1} F (1 - e^{-a p_{n+1}})/(e^{a p_n} - 1), \tag{4}$$

$$h_{n+2} = h_{n+1} F e^{a(h_{n+1} - F h_n)}. \tag{5}$$

It will first be shown that neither p_n nor h_n can tend monotonically to any limit.

If a monotonic limit of p_n exists, it must, by (4), be the steady density $p = a^{-1} \log F$.

Supposing then that monotonic approach has begun before the rth generation, we may write, for $n > r$,

$$p_n = p + P_n,$$

where P_n, P_{n+1}, etc. are relatively small.

* V. A. Bailey, *Quarterly Journal of Mathematics*, 2 (1931), 68.

† The symbol F replaces the symbol E previously used.

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Substituting for p_n, p_{n+1}, and p_{n+2} in (4), expanding the exponential terms and retaining only linear terms*, we obtain

$$P_{n+2} - 2bP_{n+1} + c^2 P_n = 0, \tag{6}$$

where $b = \frac{1}{2}\{1 + L(F)\}, \quad c = \sqrt{L(F^{-1})},$

and $L(F) = (\log F)/(F-1).$

This is an equation in finite-differences which may be written, with u_n replacing P_n, in the form

$$(E^2 - 2bE + c^2)\, u_n = 0. \tag{7}$$

The general primitive of this is

$$u_n = A_1 \alpha_1^n + A_2 \alpha_2^n,$$

where A_1, A_2 are arbitrary constants and α_1, α_2 are the roots of

$$\alpha^2 - 2b\alpha + c^2 = 0.$$

From the inequalities $L(F) < 1 < L(F^{-1})$ (since $F > 1$) it follows that $b < 1$ and $c^2 > 1$, so that we may put

$$b = c\cos\phi,$$

where ϕ is real, and where, without loss of generality, we have taken

$$c = +\sqrt{L(F^{-1})}.$$

We thus find the roots α_1, α_2 to be given by $ce^{\pm i\phi}$.

The general primitive of (7) is then

$$u_n = Ac^n \sin(\phi n + \gamma), \tag{8}$$

where $c = +\sqrt{L(F^{-1})}, \qquad \phi = \cos^{-1}\left(\dfrac{1 + L(F)}{2\sqrt{L(F^{-1})}}\right),$

and A, γ are arbitrary, but necessarily real, constants.

We thus find that the behaviour of u_n, i.e. of small P_n, is oscillatory, and so the value p cannot be monotonically attained by p_n.

The behaviour of h_n may be investigated in a similar way. Thus equation (5) shows that no value other than the steady value $h = a^{-1}L(F)$ can be a monotonic limit. Also the behaviour of h_n in the neighbourhood of h depends on the following approximate form to which (5) then reduces:

$$H_{n+2} - 2bH_{n+1} + c^2 H_n = 0.$$

* This is justified by the fact that by taking P_n, P_{n+1}, etc. as small as we please their squares, cubes, mutual products, etc. can be made as relatively unimportant as we please.

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This form is identical with that of (6), i.e. the behaviour of h_n near h is the same as that of p_n near p. We thus conclude that even the value h cannot be monotonically attained by h_n.

No longer restricting the magnitudes of p_n and h_n in any way, it will now be shown that p_n cannot perpetually exceed p.

If $p_n > p$ perpetually it follows from (1) that $h_{n+1} < h_n$, i.e. that h_n diminishes perpetually; and since monotonic approach is impossible, then ultimately h_n must become less than h and remain so.

From (1) and (2) we obtain

$$p_{n+1}/p_n = aFh_n/L(G^{-1}), \tag{9}$$

where $$G = Fh_n/h_{n+1}.$$

In the ultimate situation, as we have shown,

$$h_{n+1} < h_n < h,$$

and so, remembering that $L(G^{-1}) > L(F^{-1})$ when $G > F$, we deduce from (9) that

$$p_{n+1}/p_n < ahF/L(F^{-1}).$$

Since $$ah = L(F) = F^{-1}L(F^{-1}),$$

we therefore have $$p_{n+1} < p_n.$$

Thus p_n perpetually diminishes, and since monotonic approach is impossible, therefore p_n must ultimately become less than p, which is contrary to the initial assumption $p_n > p$.

Hence p_n *oscillates perpetually above and below the steady value* p.

The situation represented by

$$p_n > p, \quad p_n > p_{n+1}$$

will therefore perpetually recur.

From (3) we obtain

$$h_{n+1}/h = (p_{n+1}/p_n)\{L(G)/L(F)\},$$

where $G = e^{ap_n}$.

Since $p_n > p$, we have $G > F$,

i.e. $$L(G) < L(F),$$

and, since also $$p_{n+1}/p_n < 1,$$

therefore $$h_{n+1} < h.$$

The opposite situation

$$p_n < p, \quad p_n < p_{n+1}$$

will also perpetually recur, for which we similarly deduce that

$$h_{n+1} > h.$$

Hence h_n *oscillates perpetually above and below the steady value* h:

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It is easy, moreover, to show that when the parasite-density passes through its steady value the host-density attains a maximum or minimum value. Thus, when $p_{n-1} < p < p_n$, (1) requires that

$$h_{n-1} < h_n > h_{n+1};$$

i.e. h_n is a maximum. Thus the parasite oscillations lag behind the host-oscillations by about one-quarter of a period.

In order to examine the principal features of the oscillations of p_n and h_n when small we revert again to (8).

The period of such an oscillation is given by

$$T = 2\pi/\cos^{-1}\left(\frac{1 + L(F)}{2\cdot\sqrt{L(F^{-1})}}\right), \qquad (10)$$

the unit of time being the length of a generation. Since $c > 1$, the factor c^n increases with n and so with time. Hence the incremental factor I is equal to c^T, i.e.

$$I = \{L(F^{-1})\}^{\frac{1}{2}T}.$$

Thus the small oscillations ultimately become large ones.

Since $L(F)$ diminishes to zero and $L(F^{-1})$ increases indefinitely as F increases to infinity, it follows from (10) that T has the minimum value 4.

The remarkable result should be noted that the small oscillations of both species are identical in character, and that this character depends only on the value of the power of increase of the host; for example, the area of discovery has no influence on small oscillations.

Numerical values of T and I are shown in the following table:

F	2	4	∞
T	8·2	6·3	4
I	3·8	6·8	∞

Some two years earlier Dr Nicholson had given me some diagrams in which curves were drawn representing the results of his step-by-step computations *ab initio* of the densities which occur after the steady state has been slightly disturbed. In complete agreement with our present conclusions these curves show that the small oscillations are independent in character of the area of discovery a when the latter is changed from 3·5 to 10, and that with

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F equal to 2 and 4 the respective values of T are 8·3 and 6·1 and those of I are approximately 4 and 6.

In the typescript which accompanied these diagrams Dr Nicholson had also stated that as F becomes very large T tends to the minimum value 4.

In conclusion I desire to acknowledge the great value in elucidating this problem of some verbal reasoning given me by Dr Nicholson.

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