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https://doi.org/10.5109/12575

出版情報：Bulletin of informatics and cybernetics. 36, pp.11-18, 2004-12. Research Association of Statistical Sciences
バージョン：
権利関係：

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Reprinted from the Bulletin of Informatics and Cybernetics
Research Association of Statistical Sciences, Vol.36

FUKUOKA, JAPAN
2004

Bulletin of Informatics and Cybernetics, Vol. 36, 2004

ERADICATING NOXIOUS HOSTS BY PARASITES

By

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Abstract

A population of i parasites is distributed at random among M hosts; any host carrying more than n parasites dies. We first find the expected numbers of hosts carrying $0, 1, \ldots, n$ parasites. Parasite-free hosts then produce offspring according to a birth-death process over a breeding season T, while the parasites also breed in a birth-death process, again killing any host carrying more than n of them at time T. We find the expected number of surviving hosts and the total expected number of surviving parasites after the breeding season. We illustrate the process by a simple example.

Key Words and Phrases: Host, Parasite, Random allocation, Birth-death process, Survival probability, Expected number of survivors.

1. Introduction

One of the problems which arises in animal and insect populations is their control by the introduction of predators or parasites. A simple prey-predator model of this kind was previously studied by Mertz and Davies (1968). In this paper, we consider a simplified model where i parasites are introduced among M previously parasite-free hosts; any host carrying more than n parasites dies. It is assumed that the initial distribution of parasites among hosts is a random allocation process, so that each parasite selects a host with probability $1/M$, independently of all other parasites. Once this distribution is complete, only the parasite-free hosts breed over a breeding season T.

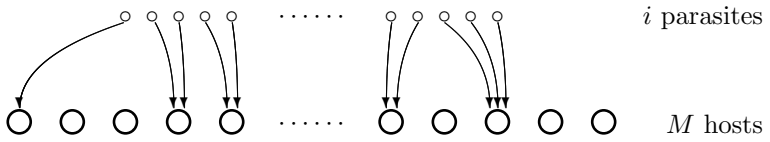

Figure 1: Random allocation of parasites among hosts

The parasites on the other surviving hosts also breed, killing their hosts and themselves if they exceed the number n at time T; some hosts with parasites survive, and the total

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number of their parasites also survives until the next breeding season, when the process is repeated. We begin with a random allocation model for the distribution of i parasites among M hosts (see Feller (1968), Chapter 4.2).

We need to find the probability distribution

$$p_{s_0 s_1 \ldots s_n}(i, M) = P\Big\{ s_j \text{ hosts with } j \text{ parasites}, j = 0, \ldots, n;\ M - \textstyle\sum_{j=0}^{n} s_j \text{ dead hosts} \\ \text{with } n+1 \text{ or more parasites} \ \Big|\ i \text{ parasites and } M \text{ hosts initially} \Big\} \tag{1}$$

This may be derived recursively by considering what happens if the number of parasites increases to $i+1$. In that case, we can readily see that

$$\begin{aligned} p_{s_0 s_1 \ldots s_n}(i+1, M) = {} & p_{s_0 s_1 \ldots s_n}(i, M) \left(1 - \textstyle\sum_{j=0}^{n} s_j / M\right) \\ & + p_{s_0+1, s_1-1, \ldots, s_n}(i, M)\,(s_0+1)/M + \cdots \\ & + p_{s_0 s_1 \ldots s_n + 1}(i, M)\,(s_n+1)/M, \end{aligned} \tag{2}$$

where the probability that the $(i+1)$th parasite falls on a host with $n+1$ or more parasites is

$$1 - \sum_{j=0}^{n} s_j / M,$$

while the probability that it falls on a host with $j = 0, 1, \ldots, n$ parasites, to increase the load from j to $(j+1)$ parasites is $(s_j+1)/M$. This model generalizes an earlier one described by Gani (1991) in which $n = 2$.

A useful way to handle these probabilities is through their probability generating function (pgf)

$$\phi_{iM}(u_0, u_1, \ldots, u_n) = \sum_{s_0 s_1 \ldots s_n} p_{s_0 s_1 \ldots s_n}(i, M)\, u_0^{s_0} u_1^{s_1} \cdots u_n^{s_n}, \\ 0 < u_j \le 1,\ j = 0, 1, \ldots, n,$$

where $\phi_{0M}(u_0, \ldots, u_n) = u_0^M$, $\sum_{j=0}^{n} j s_j \le i$, and $\sum_{j=0}^{n} s_j \le M$. Multiplying (2) by $u_0^{s_0} u_1^{s_1} \cdots u_n^{s_n}$ and summing over all values of $s_0, s_1, \ldots, s_n$, we find that

$$\begin{aligned} \phi_{i+1,M}(u_0, \ldots, u_n) = {} & \phi_{iM}(u_0, \ldots, u_n) \\ & + \frac{1}{M} \left[(u_1 - u_0) \frac{\partial \phi_{iM}}{\partial u_0} + (u_2 - u_1) \frac{\partial \phi_{iM}}{\partial u_1} \right. \\ & \qquad \left. + \cdots + (1 - u_n) \frac{\partial \phi_{iM}}{\partial u_n} \right]. \end{aligned} \tag{3}$$

The difference-differential equation (3) may be used to construct the first few pgfs for $n \ge 3$, namely

$$\begin{aligned} \phi_{0M}(u_0, \ldots, u_n) = {} & u_0^M \\ \phi_{1M}(u_0, \ldots, u_n) = {} & u_1 u_0^{M-1} \\ \phi_{2M}(u_0, \ldots, u_n) = {} & \frac{1}{M} u_0^{M-1} u_2 + \left(1 - \frac{1}{M}\right) u_0^{M-2} u_1^2 \\ \phi_{3M}(u_0, \ldots, u_n) = {} & \frac{1}{M} u_0^{M-1} u_3 + \frac{3}{M} \left(1 - \frac{1}{M}\right) u_0^{M-2} u_1 u_2 \\ & + \left(1 - \frac{1}{M}\right) \left(1 - \frac{2}{M}\right) u_0^{M-3} u_1^3, \end{aligned} \tag{4}$$

or to derive the expected numbers of hosts carrying $j = 0, 1, \ldots, n$ parasites, as we shall see in Section 2. For larger values of i, the pgf $\phi_{iM}(u_0, \ldots, u_n)$ becomes cumbersome; it is fairly straightforward, however, to derive the expectations of the numbers of hosts $Y_j(i)$, carrying $j = 0, 1, \ldots, n$ parasites, however large n may be.

2. Expected number of hosts carrying j parasites

We can readily derive $E(Y_j(i))$, $j = 0, 1, \ldots, n$, by differentiating (3) with respect to u_j to obtain for each $j = 0, 1, \ldots, n-1$,

$$\begin{aligned}\frac{\partial \phi_{i+1M}}{\partial u_j} = \frac{\partial \phi_{iM}}{\partial u_j} + M^{-1}\Bigg[& (u_1 - u_0)\frac{\partial^2 \phi_{iM}}{\partial u_0 \partial u_j} + \cdots + \frac{\partial \phi_{iM}}{\partial u_{j-1}} \\ & + (u_j - u_{j-1})\frac{\partial^2 \phi_{iM}}{\partial u_{j-1}\partial u_j} - \frac{\partial \phi_{iM}}{\partial u_j} \\ & + (u_{j+1} - u_j)\frac{\partial^2 \phi_{iM}}{\partial u_j^2} + \cdots + (1 - u_n)\frac{\partial^2 \phi_{iM}}{\partial u_n \partial u_j} \\ & + \frac{\partial \phi_{iM}}{\partial u_{j-1}} - \frac{\partial \phi_{iM}}{\partial u_j}\Bigg].\end{aligned} \tag{5}$$

For $j = n$, the formula holds with $u_{n+1} = 1$. Setting all $u_j = 1$, we find that

$$\begin{aligned}E(Y_0(i+1)) &= \left(1 - \frac{1}{M}\right) E(Y_0(i)) \\ E(Y_j(i+1)) &= \frac{1}{M}\, E(Y_{j-1}(i)) + \left(1 - \frac{1}{M}\right) E(Y_j(i)), \quad j = 1, \ldots, n.\end{aligned} \tag{6}$$

This set of equations can be solved to yield

$$E(Y_j(i)) = M\left[\binom{i}{j} \frac{(1 - 1/M)^{i-j}}{M^j}\right], \quad j = 0, 1, \ldots, n, \tag{7}$$

a formula already derived in Johnson and Kotz (1977), p.114 by different methods in the context of an urn model. Note that when $j \le i$, so that $Y_j(i) = 0$ for $j > i$, these expectations will add up to M if $i \le n$, but if $n < i$, then there will be an expected number

$$D(i) = M\left[1 - \sum_{j=0}^{n} \binom{i}{j} \frac{(1 - 1/M)^{i-j}}{M^j}\right] \tag{8}$$

of dead hosts. We can readily verify the equation (7); since $E(Y_0(0)) = M$, we see from (6) that $E(Y_0(i)) = M(1 - 1/M)^i$, the result given in (7). For $j > 0$, on substituting (7) in equation (6), we obtain

$$E(Y_j(i+1)) = M\left[\binom{i+1}{j} (1 - 1/M)^{i+1-j}/M^j\right].$$

Asymptotic results follow when both i and M are very large, and $i = cM$, where c is a positive constant, while n remains fixed and relatively small. We find that

$$\begin{aligned} E(Y_0(i)) &= Me^{-c}, \\ E(Y_j(i)) &= Mc^j e^{-c}/j!, \quad j = 1, 2, \ldots, n, \end{aligned} \tag{9}$$

with the expected number of dead hosts when $i > n$ being

$$D(i) = M\left[1 - \sum_{j=0}^{n} c^j e^{-c}/j!\right].$$

3. Expected number of surviving hosts after breeding

Once the i parasites have spread among the M hosts, we know that the expected number of surviving hosts is

$$M - D(i) = M\left[\sum_{j=0}^{n} \binom{i}{j} \frac{(1-1/M)^{i-j}}{M^j}\right], \tag{10}$$

of which $M[1-1/M]^i$ are without parasites. Asymptotically, these numbers tend to

$$M\left[e^{-c}\sum_{j=0}^{n}\frac{c^j}{j!}\right], \quad Me^{-c}, \tag{11}$$

respectively. What we now require is to follow these surviving hosts through a breeding season of length T. The survivors will consist of parasite-free hosts which breed, and of hosts carrying $1, 2, \ldots, n$ parasites which do not breed, but for which the number of parasites breeding on them will remain no larger than the death threshold n by the end of the breeding season.

Let us first consider the parasite-free hosts, and assume that they breed according to a birth-death process with birth and death rates $a > 0$ and $b > 0$ respectively, with $a > b$. Then the expected number of survivors after the breeding season will be

$$M[1-1/M]^i e^{(a-b)T}; \tag{12}$$

when $i = cM$, both large, this tends to $Me^{-c+(a-b)T}$. We now consider the hosts carrying $1, 2, \ldots, n$ parasites, where these parasites also breed according to a birth-death process with birth and death rates $\lambda > 0$ and $\mu > 0$ respectively, and $\lambda > \mu$.

The pgf of such a process starting with $1 \le j \le n$ parasites is given in Bartlett (1966), Chapter 3 as

$$f_j(u) = \left[\frac{\mu\left(1-e^{(\lambda-\mu)T}\right) - \left(\lambda - \mu e^{(\lambda-\mu)T}\right)u}{\mu - \lambda e^{(\lambda-\mu)T} - \lambda\left(1-e^{(\lambda-\mu)T}\right)u}\right]^j, \quad 0 < u \le 1. \tag{13}$$

Writing

$$\begin{aligned} A(T) &= \left(1-e^{(\lambda-\mu)T}\right)/\left(\mu - \lambda e^{(\lambda-\mu)T}\right), \\ B(T) &= \left(\lambda - \mu e^{(\lambda-\mu)T}\right)/\left(\mu - \lambda e^{(\lambda-\mu)T}\right), \end{aligned}$$

we see that (13) can be expressed as

$$f_j(u) = [\mu\, A(T) - B(T)\, u]^j\, [1 - \lambda\, A(T)\, u]^{-j}.$$

When expanded, this leads to probabilities $p_{jk}(T)$ of j initial parasites generating k parasites by the end of the breeding season, having the form

$$p_{jk}(T) = (\lambda A)^k \sum_{r=0}^{\min(j,k)} (\mu A)^{j-r} (B/\lambda A)^r \binom{j}{r} \binom{j-k-1-r}{j-1}.$$

For a host to survive, together with its load of parasites, these must not exceed the number n; thus, the probability of survival of a host with an initial number j of parasites is

$$P_j(T) = \sum_{k=0}^{n} p_{jk}(T).$$

The expected number of parasite offspring on a host starting with j parasites will be

$$m_j(T) = \sum_{k=0}^{n} k p_{jk}(T).$$

It follows that the total expected number of surviving hosts will be

$$M_1 = M\,[1 - 1/M]^i\, e^{(a-b)T} + M \left(\sum_{j=1}^{n} \binom{i}{j} \frac{[1-1/M]^{i-j}}{M^j}\, P_j(T) \right), \tag{14}$$

while the expected number of parasites on surviving hosts will be

$$i_1 = M \left(\sum_{j=1}^{n} \binom{i}{j} \frac{[1-1/M]^{i-j}}{M^j}\, m_j(T) \right). \tag{15}$$

For $i = cM$, both large, these values tend asymptotically to

$$M_1 = M e^{-c} \left[e^{(a-b)T} + \sum_{j=1}^{n} P_j(T) \frac{c^j}{j!} \right], \tag{16}$$

and

$$i_1 = M e^{-c} \left[\sum_{j=1}^{n} m_j(T) \frac{c^j}{j!} \right]. \tag{17}$$

Assuming that these i_1 parasites distribute themselves at random over the M_1 hosts, the process then starts all over again.

4. A numerical example

In their recent paper, Herbert and Isham (2001) have concentrated on host–macro-parasite infection mechanisms; the present paper focuses rather on the eradication of noxious hosts. To illustrate our methods, let us suppose that entomologists are trying to eradicate a noxious host using a population of parasites. We take M to be 1000, and $i = 10M$, both very large so that $c = 10$, and the asymptotic approximations can be used. Let us take $n = 5$, so that all hosts carrying 6 or more parasites will die, and postulate that the host birth and death parameters are such that $a - b = 0.69315$, and the breeding season is $T = 1$, so that $e^{(a-b)T} = 2$. The parasite birth and death rates will be taken as $\lambda = 1.1$ and $\mu = 0.9$.

We find the pgf $f_1(u)$ of (13), when the host carries only 1 initial parasite to be

$$\begin{aligned} f_1(u) &= (0.44925 + 0.00167\,u)/(1 - 0.54908\,u) \\ &= 0.44925 + 0.24834\,u + 0.13636\,u^2 + 0.07487\,u^3 + 0.04111\,u^4 + 0.02257\,u^5 + \cdots \end{aligned}$$

so that $P_1(T) = 0.9725$, and $m_1(T) = 1.02296$.

The first 6 coefficients in increasing powers of u for the pgfs $f_2(u)$, $f_3(u)$, $f_4(u)$, $f_5(u)$, as well as the values of $P_j(T)$ and $m_j(T)$ are displayed in the Table below.

Table 1: Pgfs $f_j(u)$, probabilities $P_j(T)$ and expectations $m_j(T)$.

	1	u	u^2	u^3	u^4	u^5
$f_2(u)$	0.20183	0.22314	0.18420	0.13501	0.09272	0.06112
$f_3(u)$	0.09067	0.15037	0.16568	0.15193	0.12530	0.09641
$f_4(u)$	0.04073	0.09006	0.12413	0.13668	0.13159	0.11577
$f_5(u)$	0.01830	0.05058	0.05636	0.10775	0.11811	0.11871

$P_2(T) = 0.89802$	$m_2(T) = 1.67305$
$P_3(T) = 0.78036$	$m_3(T) = 1.92077$
$P_4(T) = 0.63896$	$m_4(T) = 1.85357$
$P_5(T) = 0.40093$	$m_5(T) = 1.55254$

From equations (16) and (17), we calculate $M_1 = 35.7$ and $i_1 = 111.19$, so that in this case the hosts DEFANGED.22 are nearly wiped out. Similar calculations for $c = 5$ instead of 10 lead to $M_1 = 413.91$ and $i_1 = 1042.66$; thus, if $n = 6$ parasites are required to kill their hosts, the value of c must be large enough for eradication to be effective. In this case $c = 10$ seems a sufficiently large value to be effective.

In some cases, for example when the breeding season is known to be N times as long for the host as for the parasite, it may prove convenient to consider an equivalent model in discrete time. This slightly different approach consists of discretizing the parasite

birth-death process, so that we can represent it as a random walk with probabilities

$$p = \frac{\lambda}{\lambda+\mu}, \quad q = \frac{\mu}{\lambda+\mu}$$

of birth and death respectively. If X_k is the number of parasites at the k-th step, the process will have the transition probability matrix

$X_{k+1} =$	0	1	2	3	4	5	6
$X_k = 0$	1	0	0	0	0	0	0
1	q	0	p	0	0	0	0
2	0	q	0	p	0	0	0
3	0	0	q	0	p	0	0
4	0	0	0	q	0	p	0
5	0	0	0	0	q	0	p
6	0	0	0	0	0	0	1

$$= \left[\begin{array}{c|c} P & Q \\ \hline 0 & 1 \end{array}\right]. \tag{18}$$

Here, 0 is the state where all parasites have died but the host remains alive, while 6 is the state where both host and parasites have died, since 6 is above the threshold $n = 5$.

We consider what happens after a breeding season of length T consisting of N steps, where we shall assume that N is known; we now specify that the number of parasites on a surviving host always remains at or below the threshold $n = 5$. Note that this is different from the previous assumption in the continuous time case, where the process ended with 5 or fewer parasites at time T, but was allowed to exceed this threshold at some time $t < T$.

For a host with an initial number $j = 1, 2, 3, 4, 5$, of parasites, the probability of survival of the host will be

$$P_j(N) = e'_j \, P^N E, \tag{19}$$

where $e'_j = [0, \ldots, 1, \ldots, 0]$ is a 1×6 row vector with a single 1 in the column corresponding to the j initial parasites, and $E' = [1, 1, 1, 1, 1, 1]$. The expected number of parasites on a surviving host with j initial parasites is

$$m_j(N) = e'_j \, P^N L, \tag{20}$$

where $L' = [0, 1, 2, 3, 4, 5]$.

For $\lambda = 1.1$, $\mu = 0.9$, p and q take the values 0.55 and 0.45 respectively. We adopt two arbitrary values $N = 8$ and $N = 16$ for the number of steps in the breeding season of length $T = 1$, and set $M = 1000$, and $c = 10$ as before. In these cases, we find that

$$M_1 = 1000 \left(e^{-c} \left[e^{(a-b)T} + \sum_{j=1}^{5} \frac{10^j}{j!} \, P_j(N) \right] \right), \tag{21}$$

while

$$i_1 = 1000 \left(e^{-c} \left[\sum_{j=1}^{5} \frac{10^j}{j!} \, m_j(N) \right] \right). \tag{22}$$

From these equations, we calculate for $N = 8$ and $N = 16$ respectively

$$\begin{aligned} M_1 &= 20.67 \text{ and } 4.81, \\ i_1 &= 60.62 \text{ and } 14.78. \end{aligned}$$

The first results (20.67 and 60.62) are respectively 58% and 55% of the values (35.7 and 111.19) obtained with the earlier continuous time model, and are roughly comparable to them. The second (4.81 and 14.78) are both 13% of (35.7 and 111.19). In the present more accurate procedure, the appropriate value of N which parallels the previous model lies close to 8.

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Received August 13, 2003
Revised June 11, 2004