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<https://doi.org/10.5109/13002>

出版情報 : 統計数理研究. 10 (3/4), pp.1-3, 1962-10. Research Association of Statistical
Sciences
バージョン :
権利関係 :

A SIMPLE POPULATION MODEL FOR PHAGE REPRODUCTION

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(Received June 5th, 1961)

In a recent paper on phage crosses, Hershey (1958) has raised a number of interesting problems in population and genetic processes. A very simplified model of phage reproduction may be imagined as follows: at time $t=0$ let n phage particles be released in a medium containing $N > n$ bacteria, and penetrate (infect) some bacteria, each with a probability $0 < p < 1$ of success. Only the bacteria free of phages reproduce in an ordinary birth-death process with constant parameters $\lambda > \mu > 0$; meanwhile in any infected bacterium, the number of phages may be considered to grow in a birth process with parameter α . When exactly r phages are produced, the bacterium dies, and releases these particles; they immediately infect more bacteria, and the process continues until all bacteria are killed. We are interested in the time of extinction T of the bacteria.

We adopt as our basic time unit τ the mean time taken by an infected bacterium to break open. In the phage birth process, the probability that an r -th phage is produced in the interval $t, t + \delta t$ is

$$P_{r-1}(t) (r-1) \alpha \delta t,$$

where $P_{r-1}(t) = e^{-\alpha t} (1 - e^{-\alpha t})^{r-2}$ is the probability that there are $r-1$ phages at time t . Thus the mean time τ for a bacterium to break open is

$$\tau = \int_0^\infty t e^{-\alpha t} (1 - e^{-\alpha t})^{r-2} (r-1) \alpha dt = \alpha^{-1} \sum_{j=1}^{r-1} (-1)^{j+1} \binom{r-1}{j} j^{-1}. \quad (1)$$

Starting with i phage-free bacteria, then after an interval of time τ , the average number of bacteria will be $i e^{\beta \tau}$ where $\beta = \lambda - \mu > 0$. Clearly the average numbers of infected and phage-free bacteria just after times $0, \tau, 2\tau, \dots$ will be:

Times	Infected bacteria	Phage-free bacteria
$0+$	np	$N - np$
$\tau+$	$np^2 r$	$(N - np) e^{\beta \tau} - np^2 r$
$2\tau+$	$np^3 r^2$	$(N - np) e^{2\beta \tau} - np^2 r e^{\beta \tau} - np^3 r^2$
$3\tau+$	$np^4 r^3$	$(N - np) e^{3\beta \tau} - np^2 r e^{2\beta \tau} - np^3 r^2 e^{\beta \tau} - np^4 r^3$
$\dots$	$\dots$	$\dots$

In general, just after time $j\tau$, there will be $np^{i+1}r^j$ infected bacteria, and

$$e^{j\beta\tau} \left\{ N - np \sum_{i=0}^j (pre^{-\beta\tau})^i \right\} = e^{j\beta\tau} \left\{ N - np \frac{(pre^{-\beta\tau})^{j+1} - 1}{pre^{-\beta\tau} - 1} \right\} \quad (2)$$

phage free bacteria.

For all the bacteria to die by time $T = (j+1)\tau$, ($j \geq 0$), we require that

$$e^{\beta\tau} \left\{ N - np \frac{(pre^{-\beta\tau})^{j+1} - 1}{pre^{-\beta\tau} - 1} \right\} > 0 \geq e^{(j+1)\beta\tau} \left\{ N - np \frac{(pre^{-\beta\tau})^{j+2} - 1}{pre^{-\beta\tau} - 1} \right\}$$

or, after taking logarithms and simplifying (if $pre^{-\beta\tau} > 1$), we find that

$$\frac{\log \left\{ 1 + \frac{N}{np} (pre^{-\beta\tau} - 1) \right\}}{\log pre^{-\beta\tau}} - 2 \leq j < \frac{\log \left\{ 1 + \frac{N}{np} (pre^{-\beta\tau} - 1) \right\}}{\log pre^{-\beta\tau}} - 1. \quad (3)$$

To gain some idea of the speed of the process, let us take $N=10^6$, $\tau=30$ (minutes), $\beta=.1$, $r=200$, $p=.7$; the following table gives values for T for different values of n .

n	$h=j+1$	$T=h\tau$
10^3	4	$T=120$
10^4	3	$T=90$
10^5	2	$T=60$
10^6	1	$T=30$
$10^k (k \geq 7)$	0	$T=0$

A far more interesting and complicated problem is the stochastic treatment of the present model. A second realistic problem arises if phage reproduction in an infected bacterium is treated as a birth-death process in which dead phages are in fact "mature", and can no longer reproduce; when the bacterium breaks open after the mature phages reach the number r , it is these only which are infective. Such a stochastic model would require the knowledge of the probabilities that r deaths have occurred in a birth-death process: this problem has not been fully solved. However, if the birth and death (maturation) parameters are η and r respectively ($\eta > r > 0$), the deterministic approximation will give for the number $N(t)$ of survivors at time t

$$N(t) = e^{(\eta-r)t},$$

and the time τ for r phages to have matured would then be given by

$$r = \int_0^\tau r e^{(\eta-r)t} dt,$$

whence

$$\tau = (\eta - r)^{-1} \log \{ 1 + (\eta - r) r r^{-1} \}. \quad (4)$$

With this value for τ , instead of the previous value (1), the remaining treatment remains unchanged for a deterministic model.

References

- HERSHEY, A. D. *The production of recombinants in phage crosses*. Cold Spring Harbor Symposia on Quantitative Biology, **23** (1958), 19-46.

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