Letter to the Editor

On Estimating Parasitic Fitness

Richard A. Fleming

Graduate student, Institute of Animal Resource Ecology, Department of Zoology, University of British Columbia, Vancouver, Canada, B6T 1W5. Present address: Department of Environmental Engineering, Hollister Hall, Cornell University, Ithaca, NY 14853.
The author thanks the National Research Council of Canada and the University of British Columbia for financial support, and John Barrett and Jim Groth for critical reviews.
Accepted for publication 4 March 1980.

MacKenzie (4, page 12, column 2, paragraph 6) makes the claim that if we know the apparent infection rates, r_S and r_R, of any two pathogenic strains, S and R, respectively, then the relative parasitic fitness of the less fit strain, say S, is

$$W = \exp(r_S - r_R) \tag{1}$$

I think this claim is incorrect. Since this error was overlooked in recent comments by Groth and Barrett (2) and Skylakakis (6) and repeated by MacKenzie (5), discussion is warranted.

The apparent infection rate, r, originally was defined by Vanderplank (7, pages 20 and 21) in the context of the logistic equation. This equation describes the rate of change of disease intensity with time as

$$dx/dt = rx(1-x), \qquad 0 \leqslant x \leqslant 1 \tag{2}$$

in which x is the intensity of disease at time t.

Integrating and rearranging Eq. 2 produces an expression for the apparent infection rate (cf 8, page 127):

$$r = \frac{1}{t}\left[\ln\frac{x(t)}{1-x(t)} - \ln\frac{x(0)}{1-x(0)}\right] \tag{3}$$

in which ln stands for the natural logarithm. Here the time-dependence of disease intensity is expressed explicitly: $x(t)$ being the disease intensity at time t and $x(0)$ being the initial ($t = 0$) disease intensity. Eq. 3 appears as the second equation on page 12 of MacKenzie's letter (4).

Since the definition of apparent infection rate, Eq. 3, is derived from the logistic growth model, Eq. 2, apparent infection rates are meaningful only when this model is used to describe disease progress.

In contrast, relative parasitic fitness, W, as defined by MacKenzie (4) on page 10 of his letter, is meaningful only when the exponential growth model is used to describe disease progress. With exponential growth the rate of change of disease intensity with time is:

$$dx/dt = mx \tag{4}$$

in which m is the exponential or Malthusian growth rate. It is equivalent to Vanderplank's (6, page 20) logarithmic growth rate.

Vanderplank (6) correctly points out that when x is small, Eq. 4 provides a good approximation to Eq. 2, and under these circumstances m provides a reasonable "estimate" of r. But we are not concerned with "estimates" here. Rather, judging the validity of Eq. 1 requires mathematical rigor and precise definitions. Hence, we will consistently distinguish between apparent infection rates, r, and exponential growth rates, m, even at small x, because these rates are defined in terms of models that differ in both the biological processes they represent and their resulting mathematical structures. The usefulness of this approach will become apparent.

Integrating and rearranging Eq. 4:

$$x(t) = x(0)\exp(mt).$$

Hence, if any two asexual pathogenic strains, S and R, are growing exponentially, the disease intensity due to each strain at time t, respectively, is

$$x_S(t) = x_S(0)\exp(m_S t), \quad \text{and} \quad x_R(t) = x_R(0)\exp(m_R t). \tag{5}$$

Therefore, the amount of strain S present at time t relative to the amount of strain R is

$$\frac{x_S(t)}{x_R(t)} = \frac{x_S(0)}{x_R(0)}\exp[(m_S - m_R)t]$$

This equation would be identical to Eq. 1 of Skylakakis (6) if he had not used the apparent infection rates r_S and r_R instead of the exponential growth rates m_S *and* m_R. If $q(t)$ is the fraction of disease intensity contributed by strain S at time t, and $1 - q(t)$ is the fraction due to strain R, then this equation can also be written

$$\frac{q(t)}{1-q(t)} = \frac{q(0)}{1-q(0)}W^t \tag{6}$$

in which $q(0)$ is the initial proportion of strain S and the relative parasitic fitness is

$$W = \exp(m_S - m_R). \tag{7}$$

Combining Eqs. 6 and 7, taking logarithms of both sides, and rearranging, results in:

$$m_D = \frac{1}{t}\left[\ln\frac{q(t)}{1-q(t)} - \ln\frac{q(0)}{1-q(0)}\right] \tag{8}$$

in which $m_D = m_S - m_R$. Eq. 8 corresponds to the first equation on page 12 of MacKenzie's (4) letter.

MacKenzie (4,5) points out the similarity in structure of Eqs. 3 and 8 but seems to have overlooked the differences in their derivations. Eq. 3 applies to logistic models of disease progress while Eq. 8 applies to exponential models of disease progress. A comparison of Eqs. 2 and 4 illustrates the difference between logistic and exponential growth models, respectively. The logistic, Eq. 2, has an additional factor, $1-x$, which accounts for the limitations to exponential growth when host density is finite. Equation 1 relates the relative parasitic fitness, a parameter of exponential growth models, to the difference in apparent infection rates that are parameters of logistic growth models. Since it is strictly impossible for disease intensity to grow according to

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. § 1734 solely to indicate this fact.

0031-949X/81/07066502/$3.00/0

both exponential and logistic models at the same time, Eq. 1 is mathematically incorrect. It should be replaced by Eq. 7. At best, Eq. 1 can be regarded as an approximation to Eq. 7 when x is small.

Expressions for the exponential growth rates required in Eq. 7 can be found by integrating and rearranging Eq. 5:

$$m_S = \frac{1}{t}\left[\ln x_S(t) - \ln x_S(0)\right]$$

and (9)

$$m_R = \frac{1}{t}\left[\ln x_R(t) - \ln x_R(0)\right].$$

It follows from Eq. 9 that the logarithmic transformation, not the logit transformation as suggested by MacKenzie (4,5), should be used in determining relative parasitic fitness from disease intensity data. If the disease is increasing logistically neither Eq. 1 nor Eq. 7 is appropriate.

Therefore, I suggest that paragraph 6 on page 12, column 2, of MacKenzie's letter (4) be reworded:

Relative parasitic fitness (W) is mathematically linked to the rate of disease progress (m) of exponential growth models. It is not mathematically linked to apparent infection rates (r) which are meaningful parameters only for logistic disease progress models. If one knows the exponential growth rates (m) of two isolates and would like to derive an expression for the relative parasitic fitness (W) one needs only to subtract the larger m from the smaller m (less fit isolate). This difference would obviously be a negative decimal. When converted to W through Eq. 7 one would have, when measured without error, the relative parasitic fitness (W) of the less fit isolate (the more fit isolate would have, of course, $W = 1.0$).

Finally, as Fleming and Person (1) and Skylakakis (6) have stated and as I have indicated above, it is implicitly assumed in Eq. 7 that competitive or synergistic interactions between different units of inoculum on the common host are negligible. Hence, the measure of relative parasitic fitness proposed in Eq. 7 loses its meaning when diseases do not intensify exponentially. Skylakakis (6) and Jowett et al (3, page 118) have suggested a more complex model that allows for competition between two pathogenic races.

LITERATURE CITED

1. Fleming, R. A., and Person, C. O. 1978. Disease control through use of multilines: A theoretical contribution. Phytopathology 68:1230-1233.
2. Groth, J. V., and Barrett, J. A. 1980. Estimating parasitic fitness: A reply. Phytopathology 70:840-842.
3. Jowett, D., Browning, J. A., and Haning, B. C. 1974. Non-linear disease progress curves. Pages 115–136 in: J. Kranz, ed. Epidemics of Plant Diseases. Springer-Verlag, Berlin.
4. MacKenzie, D. R. 1978. Estimating parasitic fitness. Phytopathology 68:9-13, 1108 (erratum).
5. MacKenzie, D. R. 1980. The problem of variable pests. Pages 183–213 in: F. G. Maxwell and P. R. Jennings, eds. Breeding Plants Resistant to Insects. John Wiley & Sons, New York.
6. Skylakakis, G. 1980. Estimating parasitic fitness of plant pathogenic fungi: A theoretical contribution. Phytopathology 70:696-698.
7. Vanderplank, J. E. 1963. Plant Disease: Epidemics and Controls. Academic Press, New York. 349 pp.
8. Zadoks, J. C., and Schein, R. D. 1979. Epidemiology and Plant Disease Management. Oxford University Press, Oxford, England. 427 pp.