

## A Theoretical Model of the Winter Survival Dynamics of *Meloidogyne* spp. Eggs and Juveniles

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**Abstract:** A theoretical model of the winter survival dynamics of *Meloidogyne* spp. was developed by considering the roles of egg hatching and juvenile mortality and the initial populations of eggs and juveniles at the onset of winter. Two distinct patterns of juvenile dynamics appear which depend upon the numerical values of the model parameters. The model predicts whether eggs or juveniles are the major component of overwintering nematode populations at any time prior to planting. The model could be elaborated to include egg viability and differential mortality of eggs but at some cost in ease of mathematical analysis. A general procedure for fitting the proposed model to experimental or observational data is outlined.

**Key words:** root-knot nematodes, modeling, population dynamics.

Mathematical models serve many purposes in population ecology, including the explanation, prediction, optimization, and description of biological phenomena. Models vary according to their structural complexity and mathematical sophistication as well as to their applications. Models used as research tools serve largely as aids to calculation or as standards of comparison for experimental and observational data. For such applications it is desirable that essential features of the biological phenomenon be retained but in as simple a form as possible to allow for mathematical analysis (2). In this guise it is not important that models should incorporate every known influence of the physical or biological environment; rather, the calculations made with the model are used to make comparative statements about the environments in which the experiments were done or the observations made.

Starr and Jeger (7) reported data on the winter survival dynamics of populations of the plant-parasitic nematodes *Meloidogyne incognita* and *M. arenaria* at several sites in Texas. A qualitative model of the population dynamics emerged. The problem was to translate the qualitative model into quantitative relationships that could be used as a research tool in describing nematode population dynamics. Various models have been proposed to study nematode population dynamics since the review of Seinhorst (6). These include relatively complex models that simulate entire life

cycles of nematodes (3) and can be used to evaluate management decisions (4), models that determine dynamic action thresholds for management applications (1), and models that relate more limited aspects of epidemiology to environment. None of these models, however, was appropriate for our purposes. Accordingly, we present here a theoretical model of the winter survival dynamics of *Meloidogyne* spp. populations that can be used to explore the potential contribution of two different components of total population size (in the fall) to the population size at the beginning of the next growing season. The model has been used to analyze the specific data of Starr and Jeger (7).

### MATHEMATICAL ANALYSIS AND RESULTS

Suppose that, at harvest, a population of *Meloidogyne* sp. causing disease in an annual crop consists of adults, unhatched eggs ( $E$ ), and second-stage juveniles ( $J$ ). Second-stage juveniles will not develop further and adults of *Meloidogyne* spp. will not survive in the absence of a susceptible crop. Suppose that a time  $t = 0$  can be chosen such that no further eggs are laid, that eggs hatch at a constant rate proportional to egg population size, that all laid eggs are viable, and that there is no mortality of eggs. Then

$$dE/dt = -hE, \quad (1)$$

which is an equation for exponential decrease, with  $h$  the rate of hatching. Equation 1 is solved to give  $E$ , the egg population size at time  $t$  as

$$E = E_0 \exp(-ht) \quad (2)$$

where  $E_0$  is the fall egg population.

An equation for the population dynam-

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ics of second-stage juveniles can then be derived. Suppose that the rate of population change is given by the increases from hatch of eggs minus the losses due to mortality from whatever source, and that immigration and emigration are negligible or counter-balancing. Then

$$dJ/dt = hE - mJ, \quad (3)$$

which is an equation linked to equation 1 with  $m$  the constant rate of mortality. The solved form of  $E$  is known from equation 2 and can be substituted into equation 3. Upon rearrangement this gives

$$dJ/dt + mJ = hE_0 \exp(-ht), \quad (4)$$

which is a first-order nonhomogeneous linear differential equation with (for  $m \neq h$ ) the solution

$$J = (J_0 - A)\exp(-mt) + A \exp(-ht) \quad (5)$$

where  $J_0$  is the fall second-stage juvenile population, and  $A = hE_0/(m - h)$ .

If  $m = h$ , i.e., the mortality rate and hatching rate are equal, then the solution to equation 4 is

$$J = (J_0 + hE_0t)\exp(-mt). \quad (6)$$

The form of equation 5 is complex and depends upon the relative values of  $E_0$ ,  $J_0$ ,  $h$ , and  $m$  (each of which is specified as a positive constant). The number of eggs hatching decreases exponentially, but so long as  $hE > mJ$ , the juvenile population increases. When  $hE < mJ$ , the juvenile population decreases and approaches zero asymptotically. The point in time at which the juvenile population is at a maximum is obtained by setting equation 3 to zero, substituting in equation 2 and 5 (or 6) to give

$$hE_0\exp(-ht) = m[(J_0 - A)\exp(-mt) + A \exp(-ht)],$$

and solving for  $t$ . Following this procedure gives

$$t = \ln[(m/h)(1 - J_0/A)]/(m - h) \quad (7)$$

where  $m \neq h$ . If  $m = h$ , the value of  $t$  is given by

$$t = (1 - J_0/E_0)/h. \quad (8)$$

In the case of equation 7, the maximum occurs at a positive value of  $t$  if, and only if,  $hE_0 > mJ_0$ . This result applies irrespective of whether  $h < m$ , or  $h > m$ . In the case of equation 8, the equivalent condition is given by  $J_0 < E_0$ .

The total nematode population at any time  $t$  is given by the sum of equations 2 and 5 (or 6). The total population dynamics are given by

$$d(E + J)/dt = dE/dt + dJ/dt = -mJ, \quad (9)$$

which is negative for all values of  $t$ . The total population decreases monotonically from an initial size  $E_0 + J_0$  and asymptotically approaches zero. The question now arises as to whether the egg or juvenile population is the larger component of the total population during winter survival. This can be analyzed in several ways: the simplest is to look for values of  $t$  such that the two components are equal in size (i.e., with  $E = J$ ) and to examine parameter combinations on either side of the equality.

Setting equation 2 equal to equation 5 gives

$$(E_0 - A)\exp(-ht) = (J_0 - A)\exp(-mt). \quad (10)$$

Trivially, if  $E_0 = J_0$ , then the equality holds at  $t = 0$  and as  $t \rightarrow \infty$ . The existence of a nontrivial positive value of  $t$  such that  $E = J$  is dependent upon the relative values of  $h$  and  $m$ . In particular, if:

- (i)  $m < h$ , then a positive value of  $t$  exists only if  $J_0 < E_0$ ;
- (ii)  $h < m < 2h$ , then again we require  $J_0 < E_0$ ;
- (iii)  $m = 2h$ , and if  $J_0 = E_0$ , then  $J = E$  for all values of  $t$ ;
- (iv)  $2h < m$ , then a positive value of  $t$  exists only if  $J_0 > E_0$ .

Setting equation 2 equal to equation 6, in the case where  $m = h$ , gives

$$E_0 = J_0 + hE_0t \quad (11)$$

which when rearranged is identical to equation 8. Hence a positive value of  $t$  exists such that  $J = E$  only if  $J_0 < E_0$ . At this time  $J$  is also at a maximum.

Values for  $E$  and  $J$  generated over a 100-day period are shown in Figure 1A–D for differing parameter combinations. In each case the juvenile population commences at a lower level than the egg population. Both populations are scaled such that  $J_0 + E_0 = 1$ . Where  $h > m$  (Fig. 1A),  $hE_0$  is necessarily greater than  $mJ_0$ , and the number of juveniles increases to soon exceed the number of eggs and reaches a maximum value. The number of juveniles then decreases but always exceeds the number of eggs.

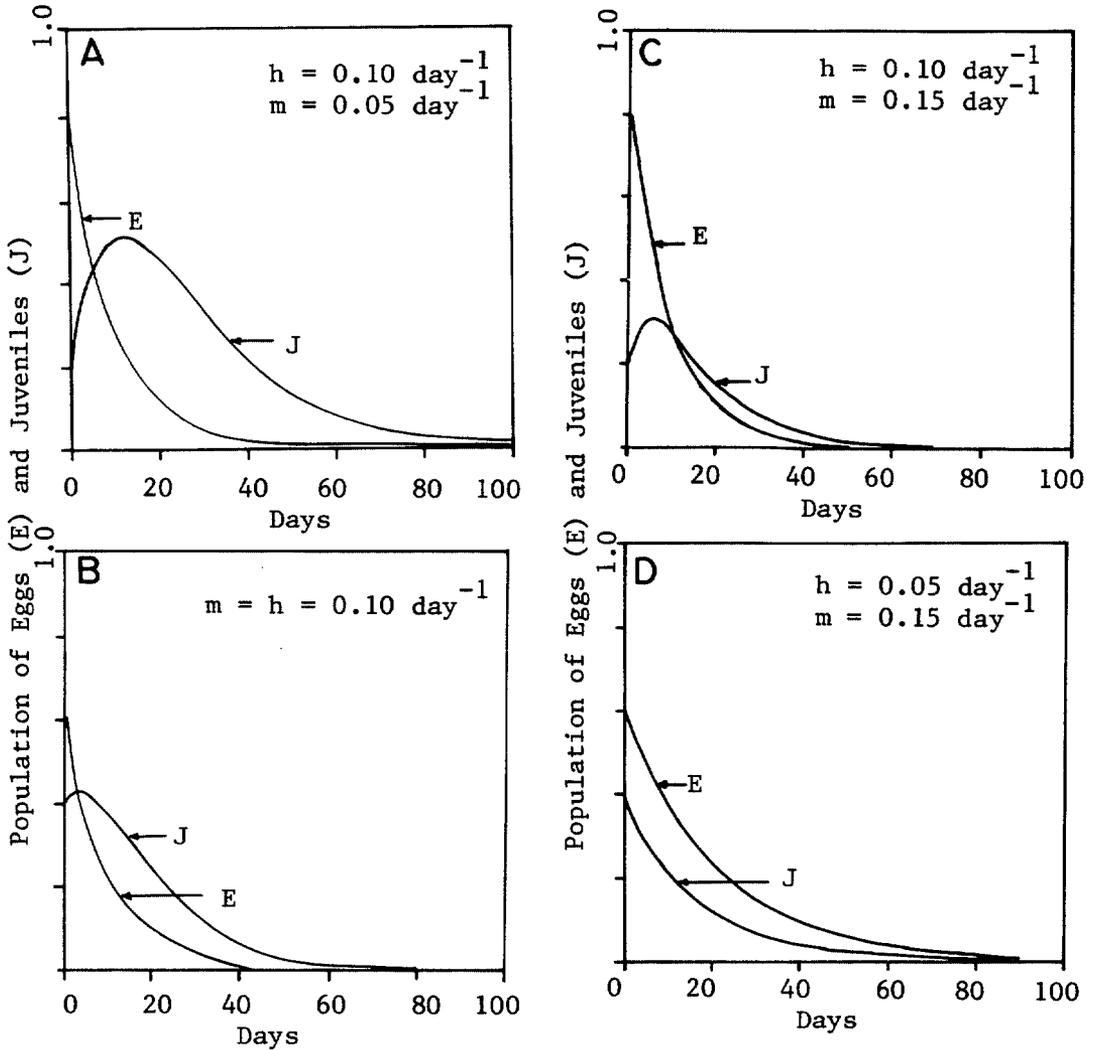


FIG. 1. Numbers of eggs ( $E$ ) and juveniles ( $J$ ), with  $J_0 + E_0 = 1$ , for parameter combinations: A)  $J_0 < E_0$  and  $h < m$ . B)  $J_0 < E_0$  and  $h = m$ . C)  $J_0 < E_0$  and  $h < m < 2h$ . D)  $J_0 < E_0$  and  $m > 2h$ . In A–C,  $hE_0 > mJ_0$  and the juvenile population increases initially; in D,  $hE_0 < mJ_0$  and the juvenile population decreases throughout.

Clearly, the later the maximum is reached, the more pronounced the survival of juveniles compared to eggs. Where  $h = m$  (Fig. 1B), the number of juveniles reaches a maximum at the same time that the two populations are of equal size. Where  $h < m < 2h$  but  $hE_0 > mJ_0$  (Fig. 1C), the number of juveniles increases and, in the example shown, reaches a maximum before exceeding the number of eggs. Finally, where  $hE_0 < mJ_0$ , the number of juveniles decreases from the start and in the example shown (Fig. 1D), never exceeds the number of eggs. Curves for parameter combinations in which  $J_0 > E_0$  (again,  $J_0 + E_0 = 1$ ) can also be generated. As given in

condition (iv) above, if  $m > 2h$  there will be a crossover point at which  $J = E$ . Otherwise  $J > E$  for all  $t$ .

The basic model can also be modified to incorporate additional suppositions concerning overwintering. For example, suppose that of the initial egg population only a proportion ( $p$ ) is viable and capable of hatching. The population size of nonviable eggs is then given by  $(1 - p)E_0$ , and

$$dE/dt = -h[E - (1 - p)E_0] \quad (12)$$

which is soluble as

$$E = E_0 \{1 - p[1 - \exp(-ht)]\}. \quad (13)$$

The difference between this equation and

equation 2 is that the egg population now approaches  $(1 - p)E_0$  rather than zero. As a further example, suppose that egg mortality occurs at a sufficiently high rate ( $l$ ) compared to hatching. Then

$$dE/dt = -(h + l)E \quad (14)$$

with the solution

$$E = E_0 \exp[-(h + l)t] \quad (15)$$

and describes a faster rate of egg depletion than equation 2, dependent upon the relative magnitude of mortality. Equation 13 or 15 may be used instead of equation 2 to obtain new formulations of equations 4–11. Differential mortality and viability of eggs can both be incorporated into the basic model of egg winter survival but at some increase in complexity.

#### APPLICATIONS

These equations can be used to obtain estimates of parameters related to winter survival of *Meloidogyne* spp. Interpretation of the numerical values obtained should of course make allowance for the appropriateness of the suppositions stated to the particular application. In some cases it may be wise to avoid descriptive labels, such as hatching or mortality rate, for the rate parameters.

Equation 2 can be fitted by a linear regression of  $\ln$  (egg population size) against time to give least squares estimates of  $h$  and  $E_0$ . There is no general means of linearizing equation 5, and alternative methods of estimation must be sought. Several statistical packages are available for maximum likelihood estimation of parameters (5), but may not generally be available; however, nonlinear curve fitting may be done using packages such as SPSS or SAS. The quantity and quality of data often do not merit the use of such sophisticated techniques. In many cases a simple graphical technique may suffice to obtain the parameter estimates, especially in preliminary studies and at a low level of replication or sampling intensity.

Equation 7 gives the time at which the juvenile population is at a maximum. If the data show such a trend, and if this time can be estimated with reasonable confidence, then an estimate of  $m$  can be made by inserting the known values of  $h$  (obtained by

linearization of equation 2) and the ratio of initial juvenile:egg populations into equation 7, and iterating until a convergent estimate of  $m$  is obtained. This was essentially the procedure used in our analysis of the winter population survival dynamics of *M. incognita* (7).

The model developed also allows a general analysis of the relative importance of the initial egg and juvenile populations in the fall and of hatching and mortality rates. If the juvenile population is smaller than the egg population in the fall, unless the mortality rate is much higher than the hatching rate the juvenile population will eventually exceed the egg population. The important consideration here is the magnitude of both rates and the length of time from harvest to planting. There is little published information on rates of egg hatching and second-stage juvenile mortality, largely because the means to calculate them, dynamically, have not been available. Hence few generalizations can be made. However, the model presented makes it feasible to take estimates of nematode egg and juvenile populations at harvest and to project likely population levels at planting once information on the rates of population changes over time becomes available.

#### LITERATURE CITED

1. Ferris, H. 1981. Dynamic action thresholds for diseases induced by nematodes. *Annual Review of Phytopathology* 19:427–436.
2. Jeger, M. J. 1985. Modelling the dynamics of pathogen populations. In M. S. Wolfe and C. E. Caten, eds. *Populations of plant pathogens: Their dynamics and genetics*. Oxford: Blackwell Scientific Publications (in press).
3. Jones, F. G. W., and R. A. Kempton. 1973. Population dynamics, population models and integrated control. Pp. 333–361 in J. F. Southey, ed. *Plant nematology*. London: HMSO.
4. Perry, J. N., and S. J. Clark. 1983. Use of population models to estimate the proportion of cyst-nematode eggs killed by fumigation. *Journal of Applied Ecology* 20:857–864.
5. Ross, G. J. S. 1980. *Maximum likelihood program manual*. Lawes Agricultural Trust, Rothamsted Experimental Station, Harpenden, UK.
6. Seinhorst, J. W. 1970. Dynamics of populations of plant parasitic nematodes. *Annual Review of Phytopathology* 8:131–156.
7. Starr, J. L., and M. J. Jeger. 1985. Dynamics of overwintering of eggs and juveniles of *Meloidogyne incognita* and *M. arenaria*. *Journal of Nematology* 17: 252–256.