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The interpretation and misinterpretation of mortality rate measures

DOUGLAS SHEIL, DAVID F. R. P. BURSLEM and DENIS ALDER

Oxford Forestry Institute, Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK

Ecologists frequently measure and compare mortality rates and other count-dependent rates of change. The simplest measures employ mortality counts for predetermined populations over a defined census interval (e.g. Harper 1977; Putz & Milton 1983; Connell *et al.* 1984; Hubbell & Foster 1990; Turner 1990; Osunkoya *et al.* 1992). More complex formulations are required to allow comparison over varying time periods, because these measures require a knowledge or assumption of how probabilities of death change over time. In many ecological applications this probability is taken to be constant and can therefore be used to define a rate. In this paper we examine some potentially misleading discrepancies that occur in the recent ecological literature.

In its simplest form a constant mortality is modelled by exponential population decline:

$$\text{i.e. } dN/dt = -\lambda N \tag{1}$$

or, in the integrated form:

$$N_1 = N_0 e^{-\lambda t}, \tag{2}$$

where N_0 and N_1 are population counts at the beginning and end of the measurement interval, t, and λ is a constant. This model was apparently applied by Swaine & Hall (1983) and also by Lieberman *et al.* (1985) who explicitly stated that 'the annual mortality rate (λ) was calculated as the slope of the $\log_e$ survivorship vs. time'. This statement implies that their 'annual mortality', λ, is defined as:

$$\lambda = \log_e(N_0/N_1)/t \tag{3}$$

or

$$\lambda = (\log_e N_0 - \log_e N_1)/t. \tag{4}$$

This formulation was adopted by the 7th Aberdeen/Hull Symposium on the dynamics of tree populations in tropical forest (Swaine & Lieberman 1987; Lieberman & Lieberman 1987; Manokaran & Kochummen 1987; Swaine *et al.* 1987), and is now a standard method for the calculation of mortality rates (e.g. Kitajima & Augspurger 1989; Swaine 1989; Lieberman *et al.* 1990; Clark & Clark 1992; Condit *et al.* 1993; Milton *et al.* 1994).

Another algebraic formulation of constant mortality is provided by explicit use of mortality per year, m, as the defining rate variable:

$$N_1 = N_0(1 - m)^t, \tag{5}$$

where m is readily calculated in the form:

$$m = 1 - (N_1/N_0)^{1/t}, \tag{6}$$

or if counts of stems lost (i.e. $N_0 - N_1$) are more conveniently used:

$$m = 1 - [1 - (N_0 - N_1)/N_0]^{1/t}. \tag{7}$$

This was the approach implied by Primack *et al.* (1985) and is detailed by Alder (in press).

A problem can be seen to arise when the 'annual mortalities' of Lieberman *et al.* (1985) and Swaine & Lieberman (1987), i.e. eqn 4, are compared against m (eqn 6). The two measures are related independently of time, and their equivalence can be derived from eqns 3 and 5 as:

$$\lambda = -\log_e(1 - m) \tag{8}$$

and

$$m = 1 - e^{-\lambda}. \tag{9}$$

λ can be shown to be an instantaneous measure of decline per unit of population (see eqn 1) and should not be called or considered an 'annual mortality'. True annual mortality is defined correctly by eqns 6 and 7 above.

In reality the discrepancies are small except at high mortality rates, i.e. for low mortality rates the difference can be shown to be approximately $-m^2/2$ or $\lambda^2/2$ [by Taylor series expansion of $\log_e(1 + x)$]. For example, at 2% mortality the discrepancy is only 0.02%, while at 50% mortality the discrepancy rises to 19%. The difference between m and λ is shown in Fig. 1.

Clearly the problem becomes important when high mortality rates are encountered, e.g. in studies of seedling demography and following catastrophic events (Whitmore 1974; Kitajima & Augspurger 1989; Osunkoya *et al.* 1992). Indeed it can be shown that high rates measured over periods of less than one year may give rise to a λ (but not m) greater than 1, indicating the error in referring to λ as 'annual mortality'.

Given the current interest in widespread and general comparisons of data from different studies (e.g. Phillips & Gentry 1994) the correct interpretation and definition of units of mortality (and turnover) is essential. Although λ remains an adequate and consistent measure of mortality we advocate the use of the more tangible

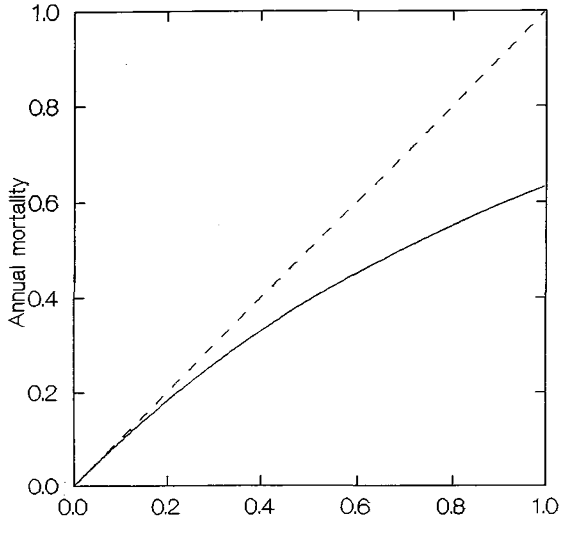

Fig. 1 The exponential mortality coefficient, λ, against true annual mortality, m (solid line). The 1:1 relationship is given for comparison (dashed line).

quantity provided by the true annual mortality estimate m (eqn 6). The λ measure should be referred to as the 'exponential mortality coefficient' and not as 'annual mortality'. We note that in many papers the method of mortality calculation is not stated explicitly, nor can it be checked or derived from the data presented (e.g. Primack & Lee 1991; Welden *et al.* 1991) or appears to be stated incorrectly (e.g. Korning & Balslev 1994). A statement that the annual mortality rate is derived according to the exponential model is not sufficient to distinguish λ from m, since both are consistent with this model.

Another measure of population decline is the half-life, i.e. the time that would be taken for a given population to lose 50% of all its individuals assuming, again, a constant probability of mortality. Half-lives can be calculated from both λ and m:

$$t_{0.5} = -\log_e 2/\log_e (1 - m) \tag{10}$$

and

$$t_{0.5} = \log_e 2/L. \tag{11}$$

Equation 11 is a clarification of that given by Swaine & Lieberman (1987).

We recommend m as a standard quantity for comparing annual mortality rates in plant ecology. The assumption of constant probability of mortality in itself requires critical evaluation (e.g. Mervart 1972) and is a suitable topic for future research.

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