The Interpretation and Misinterpretation of Mortality Rate Measures

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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:

$$\frac{dN}{dt} = -\lambda N$$

or, in the integrated form:

$$N_t = N_0e^{-\lambda t},$$

where $N_0$ and $N_t$ are population counts at the beginning and end of the measurement interval, $t$, and $\lambda$ 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 (\(X\)) was calculated as the slope of the log survivorship vs. time’.

This statement implies that their ‘annual mortality’, $X$, is defined as:

$$X = \frac{\log(N_0/N_1)}{t} \quad (3)$$

or

$$X = \frac{(\log(N_0) - \log(N_1))}{t}. \quad (4)$$

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 et al. 1992). Indeed it can be shown that high rates measured over periods of less than one year may give rise to a $X$ (but not $m$) greater than 1, indicating the error in referring to $\lambda$ 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 $\lambda$ remains an adequate and consistent measure of mortality we advocate the use of the more tangible
Mortality rate measures

Fig. 1 The exponential mortality coefficient, \( \lambda \), 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 \( \lambda \) 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 \( \lambda \) 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 \( \lambda \) and \( m \):

\[
t_{0.5} = -\log_2\log_e(1 - m)
\]

(10)

and

\[
t_{0.5} = \log_2/L
\]

(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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References


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