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SHORT COMMUNICATION

Mortality rate estimation when inter-census intervals vary

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The probability of death during a unit time period, or mortality rate, is an essential demographic parameter characterizing population turnover. There are several problems in estimating mortality of tree populations from censuses of marked trees in permanent plots (Sheil 1995). Besides these problems, a practical problem exists that is common with large-sized plots; namely, variable return intervals among trees between censuses. It usually takes a long time for establishment of large plots, as well as remeasurement. The duration of a single census takes a long time, and the return interval for each tree in each species population therefore becomes variable. Therefore, we cannot apply, for example, such a conventional estimation of instantaneous mortality rate λ (y^{-1}) between the two sequential censuses (e.g. Sheil *et al*. 1995):

$$\lambda = [\ \ln N - \ln N_s] \ / \ T, \qquad (1)$$

where N is the number of alive trees at the first census, N_s is the number surviving until the second census, and T (y) is the duration between the two censuses, because T is not fixed.

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Mortality rate is a population-level probability estimate, and the maximum likelihood method is applicable to its estimation using all records of census interval for each tree. Let us assume that time t is continuous, and the instantaneous mortality λ is constant throughout census intervals in a population or particular size-class of the population. Then, the probability of death during the period Δt is $\lambda\Delta t$. By time integration, the probability for a tree i to remain alive during interval T_i is $\exp(-\lambda T_i)$ and that for a tree j to die during interval T_j is $[1 - \exp(-\lambda T_j)]$. The likelihood function $L(\lambda)$ at the level of a population is defined as the product of the probabilities of the alternative fates of each tree,

$$L(\lambda) = \prod_{i=1}^{N_d} \exp(-\lambda T_i) \prod_{j=1}^{N_d} [1-\exp(-\lambda T_j)]$$

where N_s and N_d $(= N - N_s)$ are numbers of surviving and dead trees during the two censuses with variable intervals. The maximum likelihood estimate (ML estimate) of mortality corresponds to the value of λ that maximizes $L(\lambda)$. Equation (2) is differentiable, so that the ML estimate is equivalent to the solution of $d[\ln L(\lambda)]/d\lambda = 0$, or

$$-\sum_{i=1}^{N_s} T_i + \sum_{j=1}^{N_d} \frac{T_j \exp(-\lambda T_j)}{1-\exp(-\lambda T_j)} = 0.$$

Equation (3) is an implicit function of λ, and is readily solved by iterative methods. A sample code in Perl to solve Equation (3) is available at URL http://hosho.ees.hokudai.ac.jp/~kubo/kkpa/. When every recensus for all individuals both surviving and dying trees are with equal T (i.e. $T_i = T_j = T$), equation (3) collapses to equation (1), a conventional estimate of mortality.

To estimate mortality for duration-variable census of a 50-ha plot on Barro Colorado Island, Panama, Condit *et al.* (1995) employ equation (1) substituting the arithmetic average of census intervals of either surviving tree T_i's or dead tree T_j's for T. They show, using a simple simulation with uniform-distributed census interval, that the error by using equation (1) with average-duration tends towards underestimation, and that the error can usually be small enough to be ignored. Their simulation assumes that the distribution of T_i is equivalent to that of T_j, an assumption that can be violated for smaller-sized populations.

We compared ML and 'average-duration' (AD) estimates using the 50-ha plot data of Pasoh forest, Peninsula Malaysia (Manokaran *et al.* 1990). We calculated mortality during the first (1987) and the second (1990-) censuses of each species at each trunk diameter class (using 2-cm octave classes, e.g. 1–2, 2–4, 4–8, 8–16, . . . cm). The number of size-class populations was 1950 (with > 10 individuals) from 612 species. The average duration between the first and the second censuses was 2.9 ± 0.2 y (average and SD among populations) and the range of the census duration within a population was 1.8

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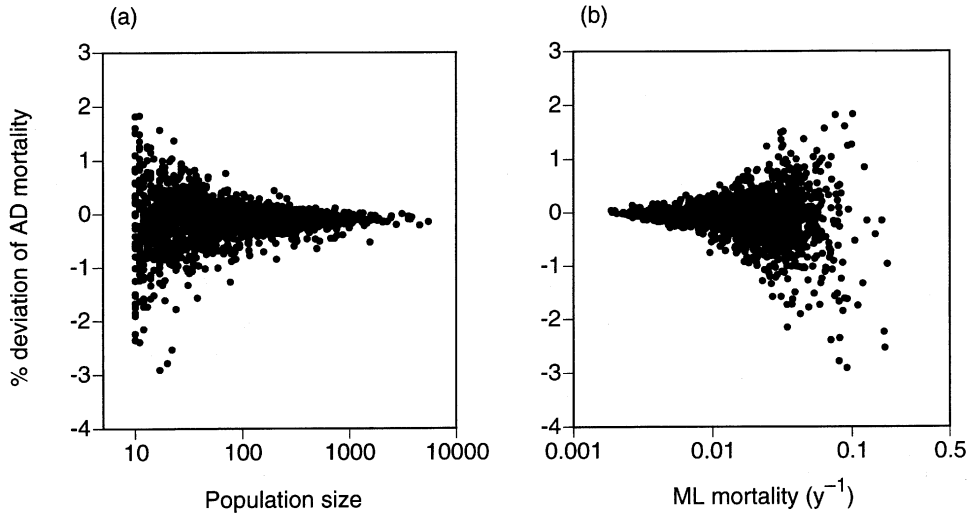


Figure 1. Distribution of the % deviation of average duration (AD) mortality from maximum liklihood (ML) duration, calculated as [(AD mortality) − (ML mortality)]×100/(ML mortality), in each size class of each species in the Pasoh 50-ha plot (during first census period), plotted against (a) the initial population size, and (b) ML mortality estimate. Total 1950 populations from 612 species were analysed.

± 0.5 y. The relative difference between the two estimates was usually smaller than 3% as Condit *et al.* expected. The difference between ML estimate and AD estimate was increased with decreasing population size, and with increasing mortality (i.e. increasing contribution of the term of dead trees in equation (3) relative to that of survivors) (Figure 1). Distribution of errors were both positive and negative, although they were significantly biased toward underestimation ($P < 10^{-28}$; binomial test based on sign of errors), contrary to the persistent negative bias in the simulation of Condit *et al.* (1995).

As it turned out that there were close agreements between the ML and AD estimates, we can practically adopt either of them for a constant-mortality model. However, we recommend an accurate procedure of ML estimation for census data with a wide range of duration variation, particularly when population size is small and when mortality is high. Furthermore, ML estimation has an advantage that its derivation is based on an explicitly defined stochastic model, so that we may easily extend the ML model into a more realistic mortality model such as that depending on growth (Pacala *et al.* 1996) and on both size and local competition (Kubo & Ida 1998). The ML estimation of mortality is valuable not only for duration-variable plot census data of tree populations, but also for similar types of data, such as individual-based sporadic records of survival and death in populations of large mammals.

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