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On the flux ratio method and the number of valid species names

Andrew R. Solow and Michael J. Benton

Abstract.—The flux ratio method is a simple method for estimating the rate of synonymy within a group based on variations over time in the status of species names. Here, we correct an error in this method.

Andrew R. Solow. Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543. E-mail: asolow@whoi.edu
Michael J. Benton. Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, United Kingdom. E-mail: Mike.Benton@bristol.ac.uk

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Introduction

Taxonomies are constructed by classifying individual specimens into species and then grouping (and subdividing) species to form an inclusive hierarchical arrangement. Because classification is an imperfect process, taxonomies are subject to error. One type of taxonomic error is synonymy. Synonymy refers to the situation in which two (or more) species names actually refer to the same species. The observed rate of synonymy, defined as the ratio of the number of synonyms to the total number of names, can exceed 50% in some groups (Gaston and Mound 1993). Elevated rates of synonymy can pose a challenge to understanding biological diversity and the processes that produce and maintain it.

Solow et al. (1995) noted that the observed rate of synonymy will underestimate the true rate when recent names have not had a chance to be synonymized and went on to propose a method for estimating the true rate of synonymy that accounts for this effect. Alroy (2002) pointed out that this method does not allow for the re-validation of synonymized names and proposed a different method—the flux ratio method—that does. The flux ratio method has been used by Alroy (2003) to analyze taxonomic inflation in North American fossil mammals and by Benton (2008a) in a study of dinosaur taxonomy and is now widely cited (e.g., Scotland and Wortley 2003; Agapow et al. 2004; Wang and Dodson 2006; Butterfield 2007). The purpose of this note is to identify and correct an error in this method.

The Flux Ratio Method

The flux ratio method is based on the following stochastic model of variations in the status of species names over time. Consider a single name. At its first appearance, this name is valid. As time goes by, it faces a constant instantaneous risk λ of being invalidated. Once it is invalidated, the name faces a constant instantaneous risk μ of being re-validated. The process continues *ad infinitum*. This model is called an alternating renewal process (e.g., Ross 1995). Under it, the length of each uninterrupted stretch during which a name is valid has an exponential distribution with mean λ^{-1}, the length of each uninterrupted stretch during which a name is invalid has an exponential distribution with mean μ^{-1}, and the long-run proportion of time that a name is in the former is

$$f = \frac{\lambda^{-1}}{\lambda^{-1} + \mu^{-1}}. \quad (1)$$

The flux ratio method seeks to estimate the quantity f in equation (1). Toward that end, suppose that there is a collection of n species names, all independently following the same alternating renewal process. Let $n_{v,j}$ be the number of stretches in which name j is valid and let $d_{v,j}$ be the total duration of these stretches. Similarly, let $n_{i,j}$ and $d_{i,j}$ be the

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number and total duration, respectively, of stretches in which name j is invalid. The estimates of λ and μ proposed by Alroy (2002) are

$$\hat{\lambda} = \frac{\sum_{j=1}^{n} n_{v,j}}{\sum_{j=1}^{n} d_{v,j}} \quad (2)$$

and

$$\hat{\mu} = \frac{\sum_{j=1}^{n} n_{i,j}}{\sum_{j=1}^{n} d_{i,j}} \quad (3)$$

respectively, and the proposed estimate of f is

$$\hat{f} = \frac{\hat{\lambda}^{-1}}{\hat{\lambda}^{-1} + \hat{\mu}^{-1}}. \quad (4)$$

An Error and Its Correction in the Flux Ratio Method

Alroy (2002) claimed that $\hat{\lambda}$ and $\hat{\mu}$ are the maximum likelihood (ML) estimates of λ and μ so that, by the invariance property of ML estimation, $\hat{f}$ is the ML estimate of f. In fact, $\hat{\lambda}$ and $\hat{\mu}$ are *not* the ML estimates of λ and μ. The problem is that the length of the terminal stretch for each name is, in statistical terminology, censored by the end of the observation period. For example, consider a name that has been viewed as valid since 1999, so that the terminal stretch is ten years long (it now being 2009). Because the end of this terminal stretch is not observed, its duration does not have an exponential distribution—all we know is that this valid stretch is *at least* ten years in length.

Briefly, under the exponential model, the contribution to the log likelihood of λ from a non-terminal stretch of duration d during which a name is valid is $\log \lambda - \lambda d$. However, if this stretch is terminal, then this contribution is only $-\lambda d$. This reflects the fact that, for the exponential distribution, the probability that a valid stretch has duration of at least d is $\exp(-\lambda d)$. It follows that the complete log likelihood for λ is

$$\log L(\lambda) = \log \lambda \sum_{j=1}^{n} n_{v,j} - \lambda \sum_{j=1}^{n} d_{v,j} - n_v \log \lambda \quad (5)$$

where n_v is the number of names that are currently valid. Alroy (2002) essentially neglected the last term on the right-hand side of equation (5). It is straightforward to show that the correct ML estimate of λ is

$$\tilde{\lambda} = \left(1 - \frac{n_v}{\sum_{j=1}^{n} n_{v,j}}\right) \hat{\lambda}. \quad (6)$$

An analogous correction holds for the ML estimate of μ.

As an illustration, we considered the status histories compiled by Benton (2008a) for 1400 dinosaur species names. As with other fossil groups, these status histories include errors other than synonymy—for example, the misclassification of species as dinosaurs. For these names, $\sum_{j=1}^{n} n_{v,j} = 1586$ and $\sum_{j=1}^{n} d_{v,j} = 62696$, so that $\hat{\lambda} = 0.025$. Also, $\sum_{j=1}^{n} n_{i,j} = 874$ and $\sum_{j=1}^{n} d_{i,j} = 23849$, so that $\hat{\mu} = 0.037$. Thus, the flux ratio method estimates f as 0.60. However, of the 1586 valid stretches, $n_v = 712$ are terminal, so that the correct ML estimate of λ is 0.014. Also, of the 874 invalid stretches, $n_i = 688$ are terminal, so that the correct ML estimate of μ is 0.008. Thus, the correct ML estimate of f is 0.36.

Discussion

The purpose of this note has been to identify and correct an error in the flux ratio method. As the example of the previous section shows, this can have a dramatic effect on the estimate of the quantity f. Whether or not the flux ratio method is used, the analysis of status histories should account for changes over time in the quality of taxonomic work (Benton 2008b). There is evidence in at least some groups that taxonomic practice has improved over time through the use of improved standards and techniques. Such an improvement would likely increase the mean duration of both valid and invalid stretches, and, depending on the relative magnitudes of the effects, failure to account for it could lead to either under- or overestimation of f.

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