$$f(q) = 1\ 0 < q < 1. \qquad (11)$$

The sense in which this is non-informative is clear: a priori, all possible values of q are equally likely. It follows that

$$\pi_j = \int_0^1 \text{pr}\left(\tau_j | q\right) f(q)\, dq = 1/(j\,(j+1)) \qquad (12)$$

which is a special case of the Yule-Simon distribution (Simon 1955). Other choices of $f(q)$ or, more generally, of specifying π_j are also possible.

Returning to the example of the Dodo, in this case, $r = 64$, and Alroy's method takes $\pi_{m+j} = 0.011\exp(-0.011\,(m+j))$: or, by virtue of the memoryless property of the exponential distribution, $\text{pr}\left(\tau_{m+j} | \tau_E < m\right) = 0.011\exp(-0.011j)$. The corresponding posterior probability $\text{pr}(T_{10}|n,\ s_{m+10})$ given by Eq. 9 is 0.19. If instead, the standard Bayesian approach is used, $\pi_{m+j} = 1/((m+j)\,(m+j+1))$ and $\text{pr}(T_{10}|n,\ s_{m+10})$ is 0.28. It cannot be said that one of these is right and the other wrong. The point is that the choice of prior distribution matters and the one in Eq. 12 has a clear justification.

In summary, to a reader lacking Alroy's intuition, the method he proposed is something of a black box. The purpose of this comment has been to open this box. Doing so has clarified (a) that this method produces sequential extinction probabilities; (b) that it treats an estimate of the sighting probability as correct; (c) that the prior distribution of extinction time on which it is based is actually posterior to the sighting record, and (d) that the specification of this distribution is without a clear justification. In contrast, the standard Bayesian approach (the results of which are summarized in Eqs 9 and 12) addresses the same problem in a straightforward and transparent way, and there is something to be said for sticking with it unless it can be shown to be inferior.

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A simple Bayesian method of inferring extinction: reply

John Alroy[1]

The purpose of Solow (2016) is to comment on a recently published method of mine (Alroy 2014). It also presents two new Bayesian methods of inferring extinction. These methods, like several others, are based on ecological or paleontological observations such as the monk seal sightings reported by Solow (1993*a*) or the dodo sightings listed by Roberts and Solow (2003).

Solow first proposes a retrospective equation (number 7) that uses fixed per-interval sampling probabilities derived from the observed data. Solow goes on to develop a second, sequential equation (number 9) that is instead based on combinatorial computations. He notes that in his view a "good reason" must be given to use sequential inference—i.e., inference based only on the data observed up to a time interval in the past that is of interest—when an entire sighting record could be used instead.

Neither of the new equations produce superior results.

This fact can be shown by applying Solow's equations to two Monte Carlo simulation data sets reported by Alroy (2014), each of which summarized histories of 1,000 species observed across 50 time intervals. Extinction was assumed to be a geometric process. In one trial of interest (Alroy 2014, Fig. 3A), the per-interval sighting rate was 20% and the per-interval extinction rate was 5%. The latter rate was selected in order to avoid having all species go extinct during the trial and to create enough extinctions for the process to be visible. In another trial (Alroy 2014, Fig. 3C), the sighting rate was instead 50% but there was no extinction (making it possible to test for false positives).

Solow's two equations perform very differently (Fig. 1). When cumulative counts are employed, equation 7 appears to be generally more accurate than the others given ongoing extinction (Fig. 1A). It is shown to be extremely aggressive at the end of the time series, however, even when there is no extinction (compare Fig. 1A,B). The reason that equation 7 appears to work well here is that it nearly amounts to declaring a species extinct as soon as it is last

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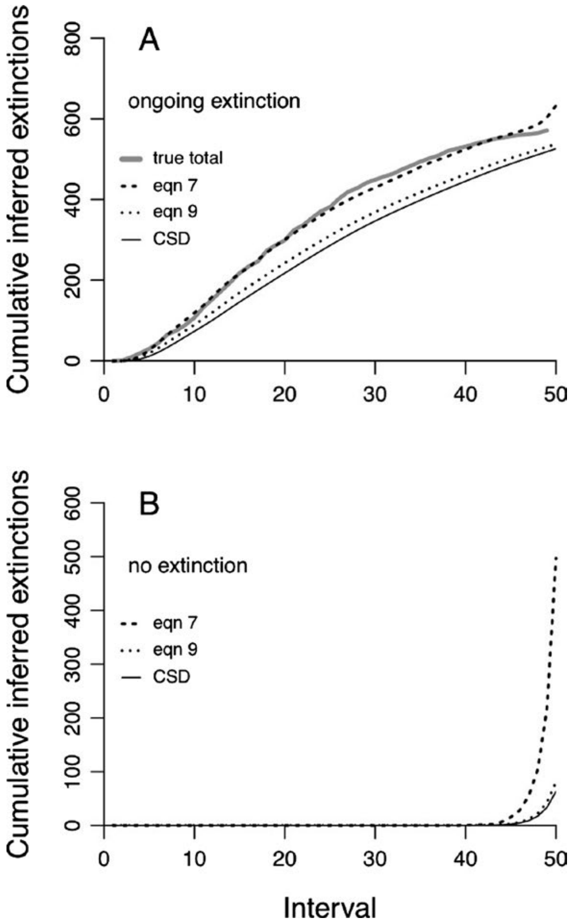

FIG. 1. Results of simulation trials in which cumulative sums of posterior extinction probabilities are computed using simulated data and the equations of Solow (2016) and Alroy (2014). Estimates are retrospective and carried out at time step 50. There are 1,000 species and 50 intervals in each trial. The curves fall short of 1,000 because undersampled or unsampled species are omitted from calculations. Thick gray line = true total; dashed line = based on equation 7 of Solow; dotted line = based on equation 9 of Solow; solid line = based on the creeping-shadow-of-a-doubt (CSD) equation of Alroy (2014). (A) Results based on applying the methods to the data of Alroy (2014, fig. 3A) in which the per-interval extinction probability was 0.05 and the sampling probability was 0.2. The "true total" for interval 50 is omitted because a computational error in Alroy (2014) inflated this one number. (B) Results based on applying the methods to the data of Alroy (2014, fig. 3C) in which there was no actual extinction and the sampling probability was 0.5.

seen. By contrast, the other two equations express uncertainty about the date of extinction that is appropriate given the poor sampling of the scenario illustrated by Fig. 1A. They therefore lag in declaring extinction, and cumulative lines therefore depart from the true running tallies.

Switching to a noncumulative representation of the data (Fig. 2) more strongly highlights differences amongst the methods. This representation emphasizes that when sampling is poor and there is ongoing extinction, the equation 7 curve eventually becomes upward biased (Fig. 1A). Meanwhile, it is now made more clear that on an interval-by-interval basis, the sequential equation 9 yields almost exactly the same results as does my creeping-shadow-of-a-doubt (CSD) method (Fig. 1). This latter finding indicates that Solow's concern about the use of point sampling probability estimates is misplaced.

The bias in Solow's equation 7 would be less problematic if it consistently produced low posteriors that happened to yield high sums because they were evenly distributed across species. In other words, perhaps

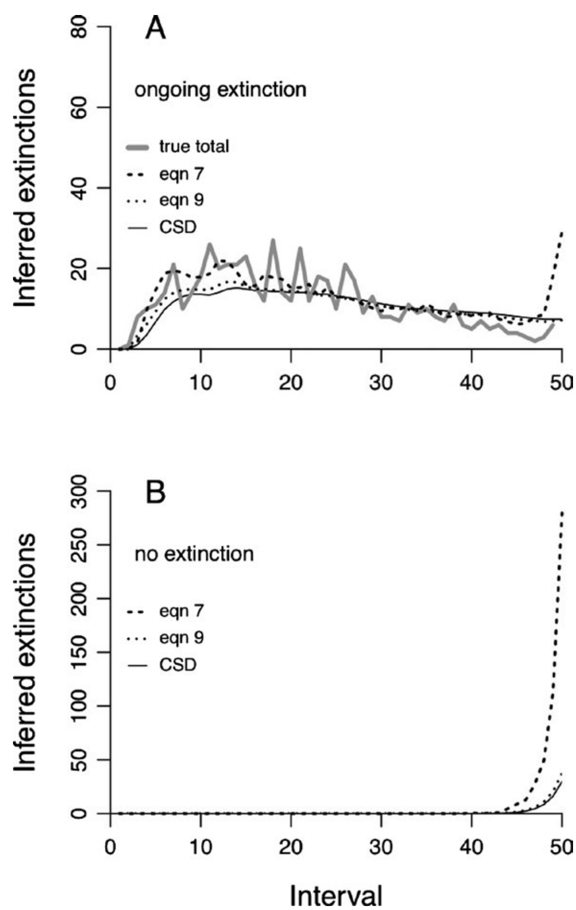

FIG. 2. Noncumulative sums of inferred extinctions based on 50-interval simulation trials. By contrast, figures in Alroy (2014) and the current Fig. 1 show cumulative sums. Lines are as in Fig. 1. (A) Results based on the same data as in Fig. 1A. (B) Results based on the same data as in Fig. 1B.

equation 7 is unique because it rarely infers with any confidence that extinction has occurred but often infers extinction with low confidence. There is no particular reason to believe that this conjecture is true, and it is not: counts of species with posteriors >0.5 (not shown) are nearly identical to simple sums of posteriors regardless of which methods are used.

It is important to note that for ease of computation, these illustrations only include extinction probabilities computed after last sightings. By contrast, I earlier illustrated cases where probabilities had also been computed for gaps within sighting ranges (see Alroy 2014, Figs. 10 and 12). Treating the data this way is simpler, and it is sufficient to make the point that the first new equation is inferior and the second is no improvement (Figs. 1 and 2).

On an unrelated point, Alroy (2014, Fig. 2 and following) presented true extinction totals that were based only on taxa recorded from at least two observations within the sampling window. For consistency, the same cutoff is used here. The example data are therefore not based on the full distribution of extinction events, but rather on the distribution of events that can be computed sensibly because the relevant species have been sighted repeatedly.

Note that in implementing Solow's equations I have used his preferred specification of the prior distribution (equation 12). Said distribution is extremely steep, implying a 1/2 prior chance of extinction in the first interval; a 1/6th chance in the next; and so on. It is also of questionable realism because it is scale-dependent: if intervals are years, then there is a 50% chance of extinction in the time series' first year, but if they are millions of years then the chance is 50% per million years. Thus, the results depend on how the analyst chooses to resolve the time scale. By contrast, my method uses a prior calculation that is not scale-dependent in any way, except for the inevitable fact that rounding error might distort the value. For example, if a species' duration is 500 yr long then the per-year prior extinction probability is 0.00138 and it makes no difference if the analytical intervals are years, decades, or centuries (Alroy 2014, p. 586).

In addition to presenting two equations of questionable utility, Solow's paper includes a number of comments on my method that are either debatable or not criticisms in the first place. (1) Solow does not attempt to show that there is an actual error in the math. (2) He notes that his equations provide different results, and as shown in Figs. 1 and 2, the main difference is that his first method is too aggressive. (3) He notes that my method's extinction prior is based on the data, which is not Bayesian in the narrow and strict sense of the term. However, I only termed my method "Bayesian" because it employs Bayes' theorem. (4) He is uncomfortable with the way I computed my exponentially distributed prior, which he says was "without justification." The prior was in practice treated as geometric by Alroy (2014) because intervals were assumed to be discrete, the same as with Solow's new methods. In any case, a full discussion of my reasons for defining the prior in the way that I did is to be found in the previous paper.

The equations of Alroy (2014) are not erroneous and were shown repeatedly to provide accurate results. By contrast, Solow generally does not evaluate the performance of his own methods, having proposed at least five earlier ones in at least four different papers (Solow 1993*a*,*b*, Roberts and Solow 2003, Solow and Roberts 2003). Although Solow's new equations are internally consistent and seem to be correctly derived, he now dismisses my new equation without presenting simulation results showing that any of his methods outperform it. By contrast, evidence that his methods are in general either too liberal or too conservative has been provided elsewhere (Rivadeneira et al. 2009, Clements et al. 2013, Alroy 2014).

Readers may be interested to know that another method meeting all requirements under discussion here already exists (Alroy 2015). It uses a combinatorial and retrospective approach, it is fully Bayesian, it assumes a geometric prior that is not scale dependent, and it produces the same accurate results as does the method of Alroy (2014).

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