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Inferring species extinction: the use of sighting records

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Abstract:

1. Accurate measures of extinction are needed in biodiversity monitoring and conservation management but ascertaining the exact time at which a species became extinct is difficult since a small population may go undetected for many years.

2. For little-studied species, often the only information available is historical sighting data. Several statistical tests have been developed which use this information to make inferences about a species' extinction. The increasing array of methods can present a daunting choice.

3. We review the more frequently cited methods, for each model explaining its assumptions, the data required, the scenarios it was developed for and power considerations, if known. We provide guidance on selecting the most appropriate method for a particular sighting record.

4. We give examples from the literature to show how the methods have been usefully applied across conservation research, informing conservation decision-making and extinction inference.

Introduction

Extinction, the disappearance of the last individual of a species, is rarely observed, is very difficult to detect, and therefore usually must be inferred (Diamond 1987). However, ensuring an accurate inventory of recent extinctions is important, not least to estimate a global measure of extinction rate to monitor biodiversity loss, particularly in light of international conservation targets (e.g. Convention on Biological Diversity 2010) and to provide a more detailed understanding of extinction trends over time. Eight hundred and sixty species have been documented as becoming extinct in the wild since 1500 AD (IUCN 2014) , almost certainly a considerable underestimation of the true extent of extinction during this period (Turvey 2009).

Listing a species as extant (still in existence) when it is actually extinct is undesirable since it can lead to misallocation of funds, incorrect reporting of current extinction rates and loss of public credibility in conservation science. It is hard, if not impossible, to know how often such a mistake occurs but there are numerous examples of the converse, species which have been declared to be extinct, only to be rediscovered (e.g. Fuller 2001; Keith & Burgman 2004; Butchart, Stattersfield & Brooks 2006; Fisher & Blomberg 2011). Whilst these incidences can be viewed as happy mistakes, they too can lead to the aforementioned undesirable effects and in at least one case, to the extirpation of species – the rediscovery of the Cebu flowerpecker along with historical evidence of primary forest where it had been thought none remained suggest that Cebu and 8 of its endemic birds were written off too early (Collar 1998).

When species extinction is not directly observed, observations can be used to infer the extinction date of a species. A variety of information can be used: a time series of historical sightings, a time series of absences (i.e. dates at which surveys have failed to record the species), the likelihood of detection given that the species is present, the effort expended in searching for the species, change in abundance over time (i.e. population trajectories), potential remaining habitat and its relationship to abundance, the severity and extent of processes threatening the species, and intrinsic taxon information (e.g. life history traits). Ideally all available information would be used to infer extinction (for example, non-sightings, measures of sighting effort, the likelihood of observing a species if it is extant). However, data is often restricted to sightings data and quantitative techniques have thus been developed for this purpose (Solow 1993a; Burgman, Grimson & Ferson 1995; Roberts & Solow 2003; McInerny *et al.* 2006) (see Table 1 for full list). There has been a tendency in the literature to apply multiple methods to a sightings record (e.g. Burgman, Grimson & Ferson 1995; Duffy *et al.* 2009) although the power of the methods differs depending on the nature of the sighting data (e.g. Rivadeneira, Hunt & Roy 2009). The aim of this review is to guide the user through the methods that use contemporary sightings data to infer extinction. We summarise these methods explaining the scenarios to which each could be applied, describe how they have been used in recent literature, and suggest how they could be incorporated into conservation decision-making.

Sighting records

We define a time series of sighting records as the times at which a species has been recorded as present. Although commonly referred to as a 'sighting' in the literature, the presence may be represented by a museum specimen, an acoustic record, a visual observation or some other diagnostic indicator of presence such as a hair or faecal sample. Following earlier literature, we also use the term 'sighting' to mean any reliable record of a species' presence. For the purposes of the methods described here, sightings must be independent of one another (see Box 1): multiple sightings of a taxon made at the same location and on the same day would not be viewed as independent.

Uncertain veracity of sighting data can present difficulties. In particular, anecdotal occurrence data should be verified before use. Recent developments for inferring extinction can incorporate uncertain sightings (Solow *et al.* 2012; Lee 2014; Lee *et al.* 2014; Solow & Beet 2014; Thompson *et al.* 2014) (see Table 3), the complications arising from uncertainty in sighting data are discussed in detail elsewhere (McKelvey, Aubry & Schwartz 2008; Elphick, Roberts & Reed 2010; Roberts, Elphick & Reed 2010; Lee *et al.* 2014; Solow & Beet 2014; Thompson *et al.* 2014).

Methods

Frequentist and Bayesian methods have both been developed to analyse sighting records (see Table 2) but they have important differences in their outputs. One type of frequentist method, null hypothesis significance testing (NHST) models generate a *p*-value, which is the probability of obtaining the sighting data (or more extreme sighting data further from the null hypothesis), given the null hypothesis that the species is extant. If this *p*-value is small enough, say < 0.05, we have observed an event that is highly improbable given that the species is extant and therefore can 'reject' the null hypothesis (understanding that there is still a chance that this rejection is incorrect). The probability statement can also be rearranged to generate an estimate of extinction time. In contrast, Bayesian methods give the probability that a species is extant, given the sighting data. There are several instances in which these two outputs have been confused in the existing literature (e.g. Burgman, Grimson & Ferson 1995; McCarthy 1998; McPherson & Myers 2009; Jaric & Ebenhard 2010; Chong *et al.* 2012). It is important to remember that in classical, frequentist statistics, the species either is or is not extinct; there is no 'extinction probability'. In Bayesian statistics, however, a hypothesis is treated as a random variable with a probability of being true, thus an extinction probability may be calculated. All of the methods assume that sightings occur as a Poisson process (Box 1).

Frequentist methods

Using a time series of historical sightings, Solow (1993a) proposed a simple method for testing the hypothesis that a taxon is extant or estimating the time at which extinction occurred. This time series occurs over an observation period $[0,T]$, where T is usually the present time (Figure 1). There are n recorded sightings of the taxon within this time, with the most recent occurring at time t_n. Like all of the methods, Solow's 1993a method assumes the sighting record is a Poisson process (Box 1). The extinction of the taxon occurs at some unknown time T_E, until which the sighting rate $\lambda(t)$ is constant, and after which $\lambda(t)$ falls to zero. The method tests the null hypothesis that extinction has not already occurred (i.e. $T_E > T$) using the likelihood ratio statistic; an unusually large 'gap' between t_n and T makes it more probable that the population has gone extinct during that interval.

The p-value corresponding to the null hypothesis that extinction has not occurred is $(t_n / T)^n$. The smaller t_n is relative to T, the smaller this p-value, i.e. the smaller the probability that all n sightings would occur before time t_n given that the species is extant. (As mentioned earlier, the p-value should not be confused with the probability that the species is extant.) If a fixed significance level α is assumed, and extinction occurs at $T_E < T$, then by rearranging the probability statement an upper $(1-\alpha)$ confidence limit of $\alpha^{-1/n}\, t_n$ is obtained for the time of extinction T_E. Solow's original equation (1993a) has been modified in various ways: for example, Burgman, Grimson & Ferson, (1995) (equation 2) outline a discrete-time form that accommodates multiple independent sightings within a single time interval, while McInerny *et al*. (2006) aim to reduce the influence of the length of the observation period by using n/t_n as an estimate of the overall sighting rate. McCarthy (1998) introduced a 'Partial Solow equation', a discrete-time equation that used indices of the collection or survey effort expended each year. For worked examples of the methods, see Table 2, Box 2 and the Supplementary Information.

The above methods assume that the species is already in existence at the start of the observation period ($t = 0$). In some contexts (*e.g.* fossil records) this may not be appropriate, and Strauss & Sadler (1989) modify the basic method from Solow (1993a) to allow both the start and the end of the species sighting range to be unknown. Marshall (1997) further generalises this to allow $\lambda(t)$ to vary. We mention these two methods since they regularly crop up in the literature. However, they have limited conservation applications being mainly used to test for a common extinction time in a group of taxa known to be extinct and we do not discuss them further.

The Solow 1993a method extends naturally to the case when the sighting rate $\lambda(t)$ is not constant (McCarthy 1998). A general equation for the *p*-value of the null hypothesis that extinction has not occurred is $[\Lambda(t_n)/\Lambda(T)]^n$ where $\Lambda(t) = \int_0^t \lambda(u)du$. By making an assumption about the form of the sighting rate function $\lambda(t)$, it is possible to calculate this *p*-value. For example, Solow (1993b) calculates the significance level given a log-linear sighting rate function of the form $\lambda(t) = \exp(a + bt)$.

An alternative simple approach that does not require specifying a parametric form for $\lambda(t)$ is discussed by Solow & Roberts (2003). The method is based on the work of Robson and Whitlock (1964) who considered the estimation of the end point of a distribution using an independent sample of data. Again it relies on the property described in Box 1 that, given the number n of sightings, the sighting times are independently and identically distributed. The method tends to overestimate the extinction date, particularly when $\lambda(t)$ is constant or increasing (Rivadeneira, Hunt & Roy 2009; Clements *et al.* 2014) (Table 1).

Solow and Roberts' method has been modified by Jaric and Ebenhard (2010), replacing the time elapsed between the two last sightings with the average time elapsed between each pair of successive sightings. The equation is further modified for the case of a species where sighting rate has been changing over time, introducing a coefficient of trend in sighting intervals (c).

An alternative frequentist approach, optimal linear estimation, (Cooke & Li 1996; Roberts & Solow 2003) outputs the year of extinction although the model can be rearranged to produce an approximate p-value for testing for extinction (Solow 2005). Optimal linear estimation, also termed nonparametric, uses extreme value theory. This theory applies to the properties of the maximum of independent and identically distributed random variables (here, the latest sighting, t_n,) conditionally upon there being n observations in $[0,T]$. It shows that regardless of the distribution of the sightings, the distribution of the maximum is well-approximated by a particular 3-parameter distribution known as the generalised extreme value distribution. Note, however, that the justification is an asymptotic one, and the approximation will not be a good one unless n is large. This approach does not require the specification of a parametric form for $\lambda(t)$ but does still assume that the underlying process of sightings is a Poisson process. The extreme value theory is applied to the k most recent of the n sightings, so that the appropriate choice of k is an issue; if k is too small estimation will suffer from the small sample size but if k is too large the asymptotic assumption may not hold (Solow 2005). Collen *et al.* (2010) found that the technique generally gave accurate predictions when applied to more than 5 of the last sightings although upper confidence limits increased with increased gaps between sightings. The method was uninformative for assigning extinction times for species with 5 or fewer sightings since upper confidence limits were often millennia into the future. Rivadeneira *et al.* (2009) found that including large numbers of sightings increased the upper bounds of the estimates. Using experimental data from microcosms and considering extinction date alone, Clements *et al.* (2013) found, precision increased with the number of sightings used except when search effort decreased over time, and Clements *et al.* (2014) strongly recommend $k > 10$. Clements *et al*. (2014) found optimal linear estimation to be the most robust of the methods in general, showing no bias towards over or underestimation and having the lowest mean error of methods investigated for both experimental and real populations. It appeared to perform better than other methods when a species is undergoing gradual abundance decline and when the probability of observing the species is low (Rivadeneira, Hunt & Roy 2009; Clements *et al.* 2014) (Table 1).

Model selection

Much of the literature covering the frequentist models is devoted to testing their performance using either simulated data (e.g. Burgman *et al.* 2000; Solow & Roberts 2003; Rivadeneira, Hunt & Roy 2009; Collen, Purvis & Mace 2010) or species of known conservation status (e.g. Burgman, Grimson & Ferson 1995; Solow & Roberts 2003; Collen & Turvey 2009; Duffy *et al.* 2009), with a recent addition testing models on experimental microcosm data (Clements *et al.* 2013; Clements *et al.* 2014). Each model has different responses to variation in number of records and change in $\lambda(t)$ (summarised in Table 2), being sensitive to different patterns of change in abundance and search effort and therefore to different patterns of deviation from homogeneity (Burgman, Grimson & Ferson 1995; Burgman *et al.* 2000) (but see (Vogel *et al.* 2009). In studies to date, optimal linear estimation (Roberts & Solow 2003) seems to give the most accurate extinction estimates in the majority of, but not all, circumstances (Rivadeneira, Hunt & Roy 2009; Clements *et al.* 2014). However, given that the number of actual cases in which extinction is known with certainty is so small, we would caution against extrapolating these findings into a general rule.

The performance of hypothesis testing methods can be assessed by examining rates of Type I (the null hypothesis is true but rejected) and Type II (the null hypothesis is false but not rejected) errors. These error rates can be calculated through simulation, and compared with expected levels given the significance level of the test (usually 0.05) (Collen, Purvis & Mace 2010). Simulations can also be used to compare estimated dates of extinction with actual dates (Clements *et al.* 2014), and to assess the coverage of confidence intervals around the estimated date of extinction, that is, the probability that the true parameter value occurs within the bounds of the confidence interval (Rivadeneira, Hunt & Roy 2009). Ideally, coverage should equal the nominal level of the confidence interval so that, for example, a 95% confidence interval covers the true extinction time of 95% of simulation runs on average (Rivadeneira, Hunt & Roy 2009).

Tests performed on simulated and microcosm data have shown a tendency for higher accuracy across models when population decline is rapid (except Solow 1993b) (Rivadeneira, Hunt & Roy 2009; Clements *et al.* 2013; Clements *et al.* 2014) and accuracy tends to increase with number of sightings (Clements *et al.* 2014). The sighting rate (affected by search regime) also affects accuracy, models responding differently to different rates (Clements *et al.* 2014) (see Table 1). If information regarding $\lambda(t)$ is known, the most appropriate model can be selected (Tablee 2). However, care must be taken in interpreting sighting records. Contrary to expectations based on simulations and microcosm data, tests on well-studied wild populations showed greater accuracy on populations experiencing gradual rather than rapid decline (Clements *et al.* 2014). This is probably due to the limited time from which temporally sporadic sightings of wild populations can be gathered, meaning the change in sighting rate does not mirror the population trajectory (Clements *et al.* 2014). When the probability of observing a species decreases over time, the species is less likely to be observed in the period immediately preceding extinction, overstating evidence for early extinction and producing confidence intervals that are too narrow (Rivadeneira, Hunt & Roy 2009).

It has been suggested that sightings data should be analysed using multiple models in order that significant changes are not missed due to one test faring poorly on a particular dataset (Grimson, Aldrich & Wanzer Drane 1992; Burgman, Grimson & Ferson 1995; Burgman *et al.* 2000). This is broadly sensible providing of course models are not applied to data that violate their assumptions (see Table 2), dueallowance is made for multiple model testing and that the models' underlying processes are understood. The different models can give quite different results, as illustrated in Box 2 by the three hypothetical sighting records containing a typical (Collen, Purvis & Mace 2010) 7 records spanning 126 years, with the last sighting 60 years ago. The effect of constant, decreasing and increasing sighting rates is explored (Box 2) with *p*-values ranging from 0.032 to 0.271, 0.356 to 0.920 and 0.032 to 0.123 respectively. (When interpreting results, it must be remembered that the *p*-value does not relate to the species' threat status. A very recent sighting of the last remaining individual of a species will lead to a high *p*-value despite the species' rapidly approaching and unavoidable extinction, see the sensitivity analysis in Table 2.) These examples illustrate the importance of understanding the underlying processes of the models and the 'natural history' of a sighting record (Solow & Beet 2014).

Three of the frequentist methods (Solow (1993a), Burgman, Grimson & Ferson (1995) and McInerny *et al*. (2006)) can only be used for records with a constant sighting rate. With *p*-values ranging from 0.044 to 0.065, these methods indicate that the null hypothesis might be rejected and thus that extinction is plausible. The methods use only the first and last sightings and number of records, thus give the same *p* value regardless of sighting rate. However, applying these methods to records with a decreasing/increasing sighting rate would violate their assumption of a constant sighting rate meaning extinction might be incorrectly inferred/dismissed.

The other methods (Solow (1993b), Roberts & Solow (2003), Solow & Roberts (2003) and Jaric & Ebenhard (2010)) do not assume a constant sighting rate and thus are affected by the distribution of one or more gaps within the sighting record, giving lower *p*-values when the sighting rate is increasing and higher *p*-values when the sighting rate is decreasing. Solow

(1993b) assumes an exponentially declining population and cannot be used if the sighting rate is increasing although can be run on records with a constant sighting rate (an infinitely slow decline). Jaric & Ebenhard's (2010) method makes most use of the sighting record data, reflecting the change in sighting rate and might thus be preferred (if data available) over Solow & Roberts (2003) which uses only the last two sighting records. Optimal linear estimation, which makes no assumptions about the sighting rate, estimates the year of extinction at 1988, 2089 or 1956 depending whether the sighting rate is constant, decreasing or increasing (Table 2).

A sensitivity analysis using the hypothetical sighting records given in Box 2 shows the effect on the p-values/estimated extinction year if the last sighting is moved forward in steps of 10 years to 50, 40,…10 years ago (Table 2). As the last sighting year becomes more recent, the gap between p-values/extinction year tends to widen. Even with a last sighting of 10 years ago there is a wide variation of p-values ranging from 0.642 (Burgman, Grimson & Ferson 1995) to 0.989 (Solow 1993b decreasing sighting rate) although none of the methods gives reason to doubt that the species is extant. The upper confidence limits given by optimal linear estimation increase as the last sighting year becomes more recent and, in the case of the decreasing sighting rate, reach over 2000 years into the future.

Given the paucity of data for many species and lack of understanding of their sightings history these models can rarely be expected to provide a definitive answer to whether a species is extinct. However, in the absence of additional information, they can be used to decide whether further survey effort/conservation action might be justified alongside factors such as the available financial resources and the role of the species (see 'Deciding to declare extinction' below).

Table 2 shows each models' data inputs and assumptions, with the aim of allowing the reader to quickly select which models may (not) be appropriate for their data. For example, choice of model may be constrained by the number of sightings, or the sighting rate.

An understanding of the process by which sightings data were generated is imperative when using these models since the majority of methods assume some level of continual survey effort across the observation period (Table 2). If sightings arise from systematic surveys (e.g. Pan-European Common Bird Monitoring Scheme (European Bird Census Council 2006)) or from incidental observations then this assumption may be reasonable (Solow & Roberts 2003). However, if sightings occur from sporadic expeditions separated by periods of no effort or if survey effort has been halted perhaps due to a period of political instability, this assumption may not be justifiable. Additionally, since the observed $\lambda(t)$ is proportional to effort as well as to abundance there is a risk that the recent trend in increasing survey effort for threatened species (e.g. Boakes *et al.* 2010) could mask an abundance decline. The relationship between sightings rate and abundance may not be linear according to how factors such as group size and population density change with abundance (McCarthy *et al.* 2013). This relationship may differ across species and could lead to a premature estimation of extinction time. If search effort is well understood, the sighting record could be standardised across periods of equal effort rather than years.

Applications

One widely cited application of the probabilistic methods is in conservation priority-setting; ranking taxa according to their *p*-value is a strategy that has been used to assess relative taxon vulnerability in several plant groups (Burgman *et al.* 2000; Ungricht, Rasplus & Kjellberg 2005; Robbirt, Roberts & Hawkins 2006; Maxted *et al.* 2008). However, as mentioned above, it is incorrect to use the *p*-value as a measure of extinction risk since the methods test for extinction rather than population decline, and a very recent sighting will generate a high *p*-value regardless of trends in population abundance or sighting frequency. There are alternative statistical methods that can be used to infer population declines from sighting data (McCarthy 1998; Solow 1999; McPherson & Myers 2009).

To our knowledge there are no instances in which the hypothesis-testing methods have been used to support a formal declaration of a taxon's global extinction. Indeed, in this respect their most useful application may be to provide a quantitative check on more qualitative conclusions about extinction (Solow 2005). However, these methods do not need to be restricted to the topic of global extinction and we advocate their application to other conservation problems. There are several instances in which they have been applied informatively at smaller spatial-scales. For example, they have been used to infer the probability of local extinctions of the Atlantic sturgeon *Acipenser sturio* and the ship sturgeon *A. nudiventris* (Dulvy *et al.* 2004; Jaric *et al.* 2009) and of the smalltooth sawfish

Pristis pectinata (del Monte-Luna *et al.* 2007; del Monte-Luna, Castro-Aguirre & Brook 2009). The methods can be used in protected area management; Patten, Gomez de Silva & Smith-Patten (2010) were able to establish a sightings history for non-migrant birds in the Palenque national park, Mexico, prior to 1970, finding that species which were likely to have been lost from the park had also been the first to be lost from forest fragments in other areas of the Neotropics and lending support to theories that some species are particularly vulnerable to extinction (e.g. Bennett *et al.* 2005).

In a similar vein, van der Ree and McCarthy (2005) used the methods to infer the persistence of mammals in the greater Melbourne area, Australia, comparing persistence between inner and outer local government areas and investigating how persistence varied between species groups. Hamer and McDonnell (2010) repeated the exercise for frogs and reptiles. Likewise, Farnsworth and Ogurcak (2006) inferred persistence of plant taxa in New England states. On an even more local scale, survey data has been used in conjunction with the methods to estimate survey site abandonment in the endangered Cape Sable seaside sparrow *Ammodramus maritimus mirabilis* in the Everglades (Cassey, Lockwood & Fenn 2007). Cassey, Lockwood & Fennl (2007) concluded that long-term survey data, even if statistically flawed with regard to their original collection purpose, actually contain far more information than many managers realise and their study provides an excellent example of how sightings data can be used to provide new insights into population dynamics.

Jaric et al (2012) make innovative use of Solow's 1993a model to investigate the expansion of an invasive species, the Amur sleeper *Perccottus glenii*, in the Danube River. By substituting the one dimensional spatial distribution of river length for temporal distribution, ordering sighting records from the most downstream to the most upstream, they estimate the probability that a species is present at a certain locality in the river. Although the method gives a very simplistic species distribution assessment it is quick to apply and therefore of potential value to conservation managers as a preliminary assessment of riverine invasive species distributions.

Bayesian methods

As can be seen in Table 2, not all the current methods in the literature use sighting records to calculate a *p*-value for the null hypothesis that the taxon is extant. Bayesian methods can be used to make probabilistic statements about the state of the world (McCarthy 2007). In the context of sighting record methods, they can directly calculate the variable of interest: the probability that the taxon is extant, given the observed data. This is an advantage firstly because it avoids any potential confusion over interpretation of *p*-values and secondly because it obtains a measure that can be applied unambiguously in a structured framework to inform management decisions (see next section).

Solow (1993a) included a Bayesian adaptation of his aforementioned hypothesis test. As with the analogous hypothesis test, this Bayesian model assumes the sighting record represents a Poisson process, and that extinction occurs at some unknown time T_E until which the sighting rate $\lambda(t)$ is constant but unknown and after which $\lambda(t)$ falls to zero (Table 2). From Bayes theorem, the probability that the taxon is extant given the sighting record **t** is:

$$p(T_E > T \mid \mathbf{t}) = \frac{p(\mathbf{t} \mid T_E > T)\pi}{p(\mathbf{t} \mid T_E > T)\pi + p(\mathbf{t} \mid T_E \le T)(1-\pi)},$$

where $p(\mathbf{t} \mid T_E > T)$ is the likelihood of the sighting record **t** given that the species is extant at time T, $p(\mathbf{t} \mid T_E \le T)$ is the likelihood of the sighting record if the species is extinct by T, and π is the prior probability that the taxon is extant, independent of the observed sighting record. Studies that have applied this method to species data (e.g. (van der Ree & McCarthy 2005; Gerlach 2007; Hamer & McDonnell 2010) appear to have used non-informative prior probabilities of 0.5, which means that without the information from the sighting data, the taxon is judged as equally likely to be extant or extinct. Using a non-informative prior allows the sighting data to dominate the calculation of the posterior probability. The influence of the prior then depends on the amount of sighting data available. If sighting data are scarce and thus contain little information, the probability that the species is extant will remain close to the prior probability of 0.5. When specified appropriately, informative priors can increase the precision of estimates without systematically reducing accuracy (Morris *et al.* 2015). Priors can be elicited from experts (Martin *et al.* 2005) or predicted through meta-analysis (McCarthy & Masters 2005). An informative prior for the probability a taxon is extant could be generated independently from sighting history by considering, for example, the type and extent of threats affecting the species. Within the above equation, the prior could be expressed as a probability distribution instead of a fixed value, although this would make the calculation less accessible.

As with the analogous frequentist method, this simple model provided a basis for further development. It has been extended to account for a decreasing sighting rate, as would occur in a population declining to extinction (Rout, Salomon & McCarthy 2009). Because of difficulties in obtaining analytical solutions for this more complex Bayesian model, a probability of extinction was obtained by estimating the magnitude of sighting rate decline from the sighting record rather than providing a solution for all possible magnitudes (Rout, Salomon & McCarthy 2009). (Similarly, Rout, Heinze & McCarthy (2010) used trapping data to estimate the magnitude of decline in sighting rate – we have not included this in Table 2 because it uses additional data outside of the historical sightings record).

Solow's 1993a Bayesian method has also been extended to accommodate uncertainty as to the validity of sightings (Solow *et al.* 2012; Lee 2014; Lee *et al.* 2014; Solow & Beet 2014; Thompson *et al.* 2014) as summarised in Table 3. For example, sightings based on visual or aural observation can be termed 'uncertain' since they could potentially be false (mistaken) as opposed to valid. Decisions on whether to exclude uncertain sightings or treat them as valid can be difficult to make and often have a substantial effect on the results of extinction calculations (Roberts, Elphick & Reed 2010; Rout, Heinze & McCarthy 2010). Solow *et al*. (2012) extended the 1993a Bayesian method to incorporate sightings of uncertain validity, using as an example the controversial sighting record of the ivory-billed woodpecker *Campephilus principalis*. Sightings based on physical evidence are classed as certain, the others as uncertain. Certain and uncertain sightings were assumed to follow independent stationary Poisson processes, with certain sightings occurring first, followed by uncertain sightings. Uncertain sightings comprised both false uncertain and valid uncertain sightings, with the latter occurring at the same rate as certain sightings.

Subsequent papers aimed for more general characterisations of this problem where uncertain sightings can occur at any time throughout the sightings record, and at a different rate to certain sightings (Thompson *et al*. 2014, Lee *et al.* 2014, Solow and Beet 2014). Thompson *et al*. 2013 and Lee *et al*. 2014 account for the fact that different types of sightings vary in uncertainty, e.g. photographs, expert visual records, audio records, local reports. Both methods partition the sighting record into discrete uniform time intervals rather than continuous time. Thompson *et al*. 2014 also takes into account historical search effort, accommodating cases where sightings occur both within and outside of structured surveys, using expert-derived estimates of the probability of sighting the species during a survey. Whilst this feature reduces the uncertainty in extinction when compared to three other Bayesian models in which search effort is not incorporated (C.F. Clements, T.E. Lee & M.A. McCarthy, unpublished data), in practice, search effort is rarely known. One of Thompson *et al*.'s (2014) solution methods is provided within a freely available Excel spreadsheet that can also include uncertainty in the prior probability the species currently persists (Lee 2014).

Regan *et al*. (2006) developed a simple model for calculating the probability a species is extant given its annual probability of detection, calculated from its sighting record, and the probability it will persist from year to year. In assuming constant probabilities of detection and persistence, this essentially assumes a constant population size up until the point of extinction (we have not included this in Table 2 because it uses additional data outside of the historical sightings record). Caley and Barry (2014) used this as a basis for a more general model in which detection and persistence probabilities can vary as a function of population size. Using only the sighting record as input, this model can be applied to species where population size is not constant prior to extinction, but no assumptions are made about the population trajectory (it could be decreasing or increasing).

Applications

Fewer tests on simulated and/or real data have been conducted on the Bayesian methods described here (Table 1) than the frequentist. This is likely due to a number of factors: the relative recentness of many of the Bayesian methods compared to frequentist, several of the Bayesian methods being developed for a particular set of circumstances and thus being less comparable, a lack of communication between theorists and empiricists (Alroy 2014), and perhaps conservation biologists tending to be more familiar with frequentist than Bayesian statistics. Consequently, less is known regarding the performance of the Bayesian methods. The incorporation of prior information can be an advantage of Bayesian methods because it allows the user to combine and utilise different types of information in a transparent way

(McCarthy 2007). Additional information relevant to assessing extinction but independent of a historical sighting record includes information about the timing and severity of threatening processes (including the interaction between threatening processes and the species' life history traits), and the outcomes of recent targeted surveys. For example, experts estimated a prior probability of between 0.24 and 0.48 that the Pohnpei Mountain Starling *Aplonis pelzelni* was extant in 2014, based on the severity, duration and geographic scope of threats to which it has been exposed (Lee 2014). Regardless of the type of information used, prior probabilities can have an important influence on the calculation of the posterior, so they must be constructed in a logical and repeatable fashion (McCarthy 2007) (A recent 'Bayesian' method which uses the sighting data to set the prior (Alroy 2014) appears to be robust in predicting extinction, but we urge caution in its use since Bayesian principles require the prior to be set independent of the data.)

There has been much recent development of Bayesian methods for inferring extinction (e.g. Thompson *et al.* 2014, Lee *et al*. 2014, Lee 2014) and with code generally now being provided with published methods we hope that conservation practitioners will feel more confident to test the power and accuracy of Bayesian methods as well as to utilise them (as appropriate) in management decisions.

Deciding to declare extinction

While these statistical methods provide a measure of the certainty of extinction, it still falls to decision makers to determine the level of certainty at which a taxon should be declared extinct, i.e., what is a "reasonable level of doubt"? (IUCN 2001). In setting this threshold, it is important to consider the implications of declaring extinction, such as the cessation of conservation management, and the risks and consequences of making the wrong decision.

Regan *et al*. (2006) provide the first formal analysis of this decision for a taxon, although in the context of declaring eradication of an invasive species. They argue that the level of certainty at which a species should be declared eradicated depends on the cost of increasing certainty by performing more surveys, balanced against the cost of declaring eradication when the species is still present. For invasive species, falsely declaring eradication can lead to damaging impacts caused by a remnant population allowed to grow undetected. Regan *et al*. (2006) calculate when a species should be declared successfully eradicated, expressed as a number of surveys without detection, to minimise the total expected cost.

Rout, Heinze & McCarthy (2010) adapt this approach to making cost-effective decisions about declaring extinction. They describe the consequence of wrongly declaring extinction as the increased expectation that the species will go extinct if management intervention is ceased. They translate this into an expected monetary loss, and calculate when taxa should be declared extinct to minimise the total expected cost. Chadès *et al*.(2008) also take an economic approach to the management of possibly extinct taxa, finding scenarios when it is cost-effective to manage and when it is cost-effective to survey, given the probability that the taxon is extant.

Within these decision analyses, a variety of methods have been used to calculate the probability an undetected taxon is extant (Regan *et al.* 2006; Chadés *et al.* 2008; Ramsey, Parkes & Morrison 2009), including the Bayesian analysis of historical sighting records (Rout, Salomon & McCarthy 2009; Rout, Heinze & McCarthy 2010).

Conclusions

In this review we summarise the range of statistical methods used to infer extinction from a time series of sighting records. By providing information on the assumptions and limitations of each method (main text and Tables 1, 2 and 3), we hope to enable users to choose the most appropriate method for their taxon. In the instances in which knowledge of a population is limited to opportunistic sightings, these methods are a practical way to put this limited knowledge to use. Their correct application can increase our understanding of a population's status and help inform conservation decision-making. However, when assessing the status of a population it is important to incorporate all available information, not just the limited information contained in a sighting record and we strongly recommend the development of a framework for the systematic integration of sighting records with other forms of information relevant to the assessment of extinction.

Two related developments are required to make further progress in inferring extinction using sighting records. First, many of the assumptions that are required for the various models are either extremely hard to judge, or rarely achievable in the haphazard manner with which many sightings records are accumulated. Better ways are needed to incorporate uncertainty into analyses of time-series of records, account for record quality, and incorporate survey effort and threat intensity. Second, many of the limitations of inferring extinction are no longer the models, but the data required to produce them. Techniques such as those covered here, will be most appropriate in settings, where quality, survey effort and decisions on thresholds can be made dependent on the desired use.

Box 1: The Poisson process

The basic assumption underlying most statistical methods for inferring extinction is that species sightings can be represented by a Poisson process, one in which events occur singly in continuous time and numbers of events in non-overlapping intervals of time are statistically independent of one another. In the statistical methods discussed here, the events of interest are sightings of a particular taxon through time.

We denote the rate function of a Poisson process by λ, which in this case represents the rate of sightings of the taxon. A taxon is sighted if it is observed (or otherwise detected) anywhere in the study region at a particular time. The chance of any given sighting depends on both the abundance of the taxon, and the amount of effort that is made to observe it as well as the conspicuousness of the taxon, i.e. whether it is cryptic, camouflaged, nocturnal etc. The interpretation is that $\lambda(t)$ is the instantaneous rate of sightings at time t and a natural assumption is that $\lambda(t)$ is directly proportional to both abundance and effort so that, for example, if abundance were decreasing but sufficient effort were made to obtain and record sightings then the overall sighting rate could remain constant or even increase. If $\lambda(t)$ is a constant for all t, then the Poisson process is homogeneous (stationary).

For a Poisson process, the number of sightings in a fixed time period $[0,T]$ has a Poisson distribution, where the mean of the distribution is given by the integrated rate $\Lambda(T) = \int \lambda(t)\, dt$ over that time interval. Then, given that there are n sightings in $[0,T]$, these sightings are *independently and identically distributed* over the time period with probability density $f(t) = \lambda(t)/\Lambda(T)$. In the special case when $\lambda(t)$ is a constant, $f(t) = 1/T$ so that the sightings are uniformly distributed over the time period. The standard methods for testing extinction are based particularly on this last property.

In a Poisson process, events occur in continuous time, while in practice, sightings data are often discretised. That is, rather than being a list of exact times of sightings at a particular location, they consist of records of the presence or absence of sightings in a discrete set of time intervals (usually years although any unit may be used provided the data are adequately resolved (Burgman, Grimson & Ferson 1995)). In the descriptions below, it is convenient to ignore this distinction and assume that the sightings occur in continuous time. As long as the sightings are relatively rare in the study region, then this distinction is unlikely to be important. However, if data are aggregated into larger spatial regions resulting in frequent sightings, then the Poisson assumption will become less appropriate; this situation can be resolved if temporal resolution allows the time intervals to be shortened.

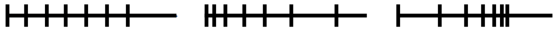
Box 2: Example Calculations

Here we calculate *p*-values (as calculated for $T = 2014$) or estimated year of extinction using three hypothetical sighting records with constant, decreasing and increasing sighting rates using 7 of the frequentist methods described. To illustrate the case of multiple sightings within one time period in the discrete time form (Burgman, Grimson & Ferson 1995) we calculate the *p*-value based on an extra sighting in one of the time periods.

Sighting records:

Constant sighting rate	1828	1849 1849	1870	1891	1912	1933	1954
Decreasing sighting rate	1828	1830	1834	1842	1858	1890	1954
Increasing sighting rate	1828	1892	1924	1940	1948	1952	1954

Sighting record



Method	Constant sighting rate	Decreasing sighting rate	Increasing sighting rate
Solow 1993a frequentist[1]	0.065		
Solow 1993b[1]	0.271	0.920	
Discrete time form (Burgman, Grimson & Ferson 1995)[1]	0.044		

Solow & Roberts (2003)[1]	0.259	0.516	0.032
McInerny *et al*. (2006)[1]	0.032		
Jaric & Ebenhard (2010) eqn 6[1]	0.258	0.356	0.123
Optimal linear estimation (Roberts & Solow 2003)[2]	1988 (1956, 2178)	2089 (2020, 2089)	1956 (1954, 2006)

[1] p-value for the null hypothesis that the species is extant

[2] Estimated year of extinction with lower and upper confidence limits calculated for α = 0.05 given in brackets

Model	Tends to underestimate extinction time	Tends to overestimate extinction time	Accuracy increases with number of sightings	Notes
Solow 1993a	✓[1]		✓[1]	Accuracy decreases with decreasing search effort[1] and gradually decreasing population[2].
Solow 1993b	✓[1]		✓[1]	Low power if extinction time is close to the end of the observation period[3] , if *n* < 15[3] or if search effort is increasing[1] . Upper confidence interval can be infinitely high[3].
Discrete-time form (Burgman, Grimson & rson 1995).		✓[1]		Tends to overestimate extinction time, particularly when search effort is constant or increasing[1] .
Partial Solow Equation (McCarthy 1998).				Accuracy decreases with gradually decreasing population[2] .
Optimal Linear Estimation (Roberts &			✓[1,4]	No bias towards under/over estimation but greater mean error in

Solow 2003).				underestimates[1] . Accuracy increases with number of sightings[1,4] with a recommended *k* >5 and preferably >10. Type I (extant species declared extinct) and Type II (extinct species declared extant) errors high under exponential, accelerating and linear abundance declines. Upper confidence interval can be millennia into the future for species with few or widely spaced sightings[4] . Accuracy declines with irregular and/or decreasing search effort[5] . Robust to gradual population decline and low sighting probability[2] .
Solow and Roberts 2003		✓[1,2]		Tends to overestimate extinction time, particularly when search effort is constant or increasing[1,2]. Confidence interval can be very wide (Solow 2005).
McInerny *et al.* 2006				Unaffected by *n* and by the length of the observation period thus suitable for taxa that have been discovered relatively recently. Accuracy decreases with gradually declining population[2] .

Jaric and Ebenhard 2010		✓[6]		Unaffected by *n* and by the length of the observation period .

Table 1. Summary of the frequentist models' performance on simulated and microcosm data. For a detailed study of the models' error rates see [1]Clements *et al*. (2014), [2]Rivadeneira, Hunt & Roy (2009), [3]Solow (1993b), [4]Collen, Purvis & Mace (2010), [5]Clements *et al*. (2013) and [6]Jaric & Ebenhard (2010)**.**

Table 2. Summary of the models' outputs, assumptions, data requirements and code availability. Sensitivity analyses have been conducted for models which do not require information additional to sighting records using the hypothetical records given in Box 2 and with the last sighting data increasing in increments of 10 years from 1954 to 2004, constant sighting rate -blue, decreasing sighting rate - red, increasing sighting rate - yellow), corresponding in an increase in *p*-value, extinction year or *P(extant)*.

[1] sExtinct package (2013), in R: A Language and Environment for Statistical Computing (2012)

[2] Lee *et al*. (2014)

[3] Lee (2014)

[4] Caley and Barry (2014)

Table 3. Summary of the data requirements of the Bayesian models that allow for uncertainty in sightings.

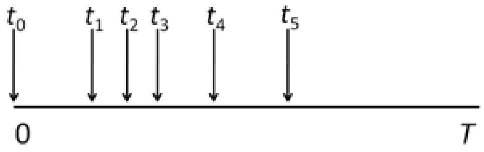


Figure 1: A schematic representation of a sighting record (with credit to Burgman, Grimson & Ferson (1995)). The first sighting may be used to define the start of the observation period t_0, and in this case would be omitted from the total number of sightings to leave $n = 5$. For example, consider that $T = 100$, and the most recent observation t_5 was made at $t = 55$. Using Solow's 1993a method, the *p*-value of the null hypothesis that the species is extant is $p = (55/100)^5 = 0.0503$ (Burgman, Grimson & Ferson 1995).

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Data Accessibility

The manuscript does not include data.

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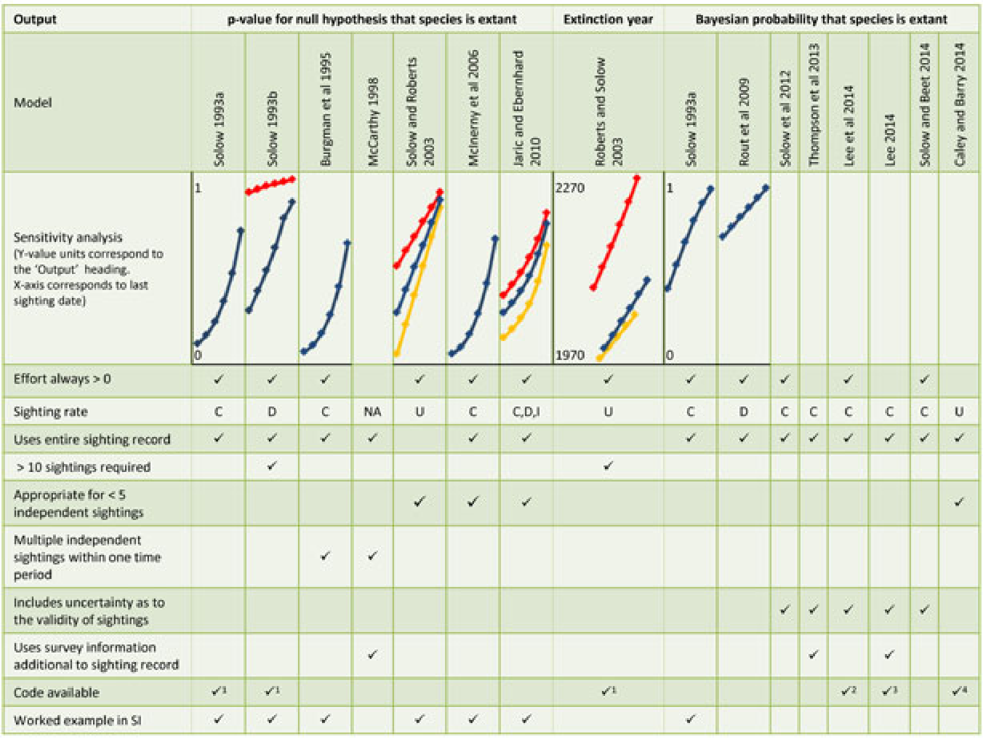
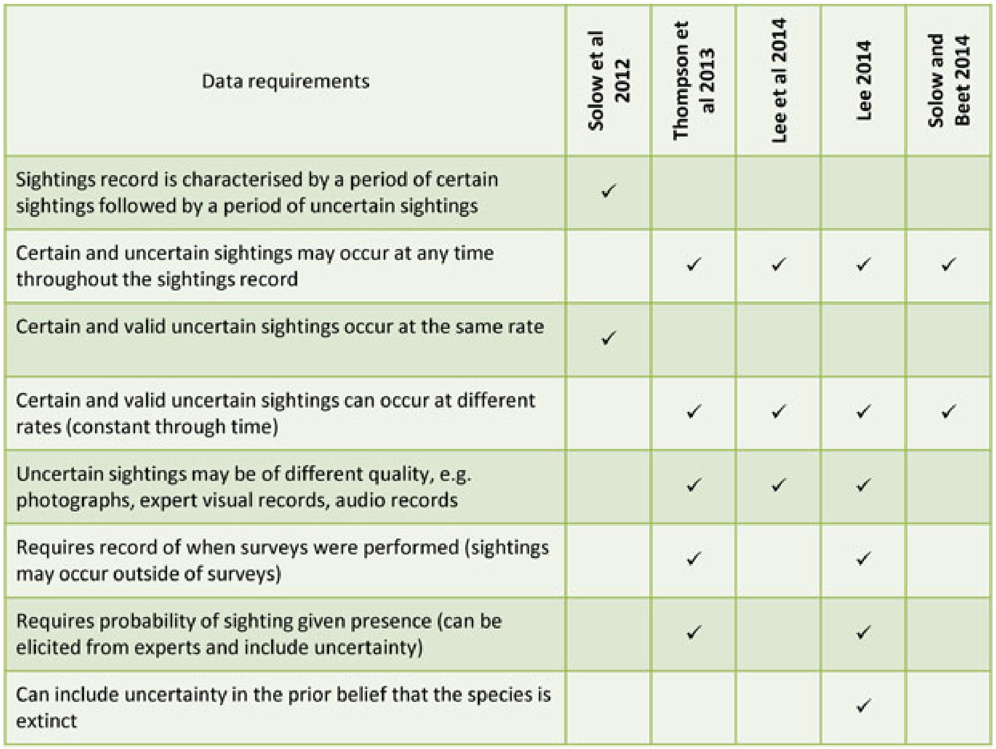


Output	p-value for null hypothesis that species is extant							Extinction year	Bayesian probability that species is extant							
Model	Solow 1993a	Solow 1993b	Burgman et al 1995	McCarthy 1998	Solow and Roberts 2003	McInerny et al 2006	Jaric and Ebernhard 2010	Roberts and Solow 2003	Solow 1993a	Rout et al 2009	Solow et al 2012	Thompson et al 2013	Lee et al 2014	Lee 2014	Solow and Beet 2014	Caley and Barry 2014
Sensitivity analysis (Y-value units correspond to the 'Output' heading. X-axis corresponds to last sighting date)	1 0							2270 1970	1 0							
Effort always > 0	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓		✓		✓	
Sighting rate	C	D	C	NA	U	C	C,D,I	U	C	D	C	C	C	C	C	U
Uses entire sighting record	✓	✓	✓	✓		✓	✓		✓	✓	✓	✓	✓	✓	✓	✓
> 10 sightings required		✓						✓								
Appropriate for < 5 independent sightings					✓	✓	✓									✓
Multiple independent sightings within one time period			✓	✓												
Includes uncertainty as to the validity of sightings											✓	✓	✓	✓	✓	
Uses survey information additional to sighting record				✓								✓		✓		
Code available	✓[1]	✓[1]						✓[1]					✓[2]	✓[3]		✓[4]
Worked example in SI	✓	✓	✓		✓	✓	✓		✓							



Data requirements	Solow et al 2012	Thompson et al 2013	Lee et al 2014	Lee 2014	Solow and Beet 2014
Sightings record is characterised by a period of certain sightings followed by a period of uncertain sightings	✓				
Certain and uncertain sightings may occur at any time throughout the sightings record		✓	✓	✓	✓
Certain and valid uncertain sightings occur at the same rate	✓				
Certain and valid uncertain sightings can occur at different rates (constant through time)		✓	✓	✓	✓
Uncertain sightings may be of different quality, e.g. photographs, expert visual records, audio records		✓	✓	✓	
Requires record of when surveys were performed (sightings may occur outside of surveys)		✓		✓	
Requires probability of sighting given presence (can be elicited from experts and include uncertainty)		✓		✓	
Can include uncertainty in the prior belief that the species is extinct				✓	