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TECHNICAL COMMENT

Commentary on Holmes *et al.* (2007): resolving the debate on when extinction risk is predictable

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Abstract

We reconcile the findings of Holmes *et al.* (*Ecology Letters*, **10**, 2007, 1182) that 95% confidence intervals for quasi-extinction risk were narrow for many vertebrates of conservation concern, with previous theory predicting wide confidence intervals. We extend previous theory, concerning the precision of quasi-extinction estimates as a function of population dynamic parameters, prediction intervals and quasi-extinction thresholds, and provide an approximation that specifies the prediction interval and threshold combinations where quasi-extinction estimates are precise (vs. imprecise). This allows PVA practitioners to define the prediction interval and threshold regions of safety (low risk with high confidence), danger (high risk with high confidence), and uncertainty.

Keywords

Conservation biology, diffusion approximation, extinction, population forecasting, population viability analysis, PVA, risk, stochasticity.

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How precisely can extinction risk be estimated using only a time series of population abundance? Theoreticians have debated this question for > 25 years. Recently Holmes *et al.* (2007) showed that across a wide range of different population dynamics, a population's probability of crossing a quasi-extinction threshold can be estimated using a stochastic approximation, which they termed the CSEG model (Corrupted Stochastic Exponential with Gaussian errors):

$$\begin{aligned}\log X_t &= \log X_{t-1} + \mu + \varepsilon_{b,t-1}\\ \log N_t &= \log X_t + \varepsilon_{w,t}\end{aligned}. \qquad (1)$$

X_t is a stochastic exponential growth process with mean annual growth rate μ and random variability, ε_b, in population growth due to environmental stochasticity. N_t is X_t overlaid with random noise, ε_w, representing observation error, age structure fluctuations, and the like. Both noise terms are assumed Gaussian with zero mean, constant variances σ_b^2 and σ_w^2, respectively, and no temporal correlations. CSEG approximates the long-run statistical properties of population count data, N_t, and of the true unobserved population density, X_t. The CSEG approximation introduces no appreciable bias in many situations where the actual mechanisms of population change are completely different (Holmes *et al.* 2007), and its low parameter count makes precision as high as possible. These findings imply a general method for estimating quasi-extinction risks that does not require identifying the mechanisms driving the population dynamics.

Holmes *et al.* (2007) applied this method to over 100 20-year time series from vertebrate species of conservation concern. In many cases, their confidence intervals (CIs) on estimated 20–50 year quasi-extinction probabilities ($\hat{P}_e$) spanned only a fraction of the possible range from 0 to 1. These results challenge the '(0,1) criticism' that extinction risk estimates are fundamentally imprecise: unless $\hat{P}_e$ is near 0 or 1, 95% CIs typically cover most of (0,1) unless the prediction interval is significantly shorter (e.g. 80% shorter) than the length of the data series (Ludwig 1999; Fieberg & Ellner 2000). Holmes *et al.* argued that the vertebrate species in their database are characterized by low σ_b, the standard deviation of year-to-year population growth, and when σ_b is low the (0,1) criticism no longer holds. The mean and median σ_b for their database were 0.16 and 0.08, respectively, whereas studies finding extreme (0,1) problems typically used $\sigma_b = 0.3$–0.7. Thus, Holmes *et al.* argued that acceptably precise 20- to 50-year projections could often be made with only 20 years of data, at least for many vertebrates.

Rather than writing 'tit-for-tat' Ellner vs. Holmes commentaries on Holmes *et al.* (2007), we collaborated to help resolve the debate by developing new theory for the precision of count-based extinction risk estimation. We show that the theory underlying the (0,1) criticism remains valid for low-σ_b populations, indeed the CI widths reported by Holmes *et al.* (2007) closely match the theoretical CIs. Thus the original (0,1) criticism still holds at low σ_b. However, we show that as σ_b shrinks, the range of prediction intervals and quasi-extinction thresholds giving intermediate $\hat{P}_e$ and high uncertainty also shrinks, and finally collapses to a line when $\sigma_b = 0$. As a result, CIs for many risk estimates are actually much smaller than (0,1) when σ_b is small, as Holmes *et al.* (2007) found. This resolution of the (0,1) debate leads to general recommendations for selecting prediction intervals and quasi-extinction thresholds for count-based PVA, and for presenting assessments of extinction risk due to environmental stochasticity.

The original theory underlying the (0,1) criticism is based on writing the probability of quasi-extinction for X_t in a CSEG model within prediction interval T as (Fieberg & Ellner 2000)

$$P_e(U, V) = \Phi(U - V) + \exp(2UV)\Phi[-(U + V)], \tag{2}$$

where $U = -\mu\sqrt{T}/\sigma_b$, $V = a/(\sigma_b\sqrt{T})$, Φ is the standard normal cumulative distribution function, a = log(initial population size/quasi-extinction threshold) = log (N_0/N_e). To calculate the theoretical minimum uncertainty (TMU) in $\hat{P}_e$, Fieberg & Ellner (2000) assumed that the only unknown parameter is μ, estimated from error-free population counts and that $V \gg 1$ (i.e. $\sigma_b\sqrt{T} \ll \log(N_0/N_e)$), in which case the second term in eqn (2) goes to 0. Under these assumptions, the TMU two-sided CIs are:

$$\Phi\left[\Phi^{-1}(\hat{P}_e) - z_{\alpha/2}\sqrt{T/n}\right] \le P_e \le \Phi\left[\Phi^{-1}(\hat{P}_e) + z_{\alpha/2}\sqrt{T/n}\right] \tag{3}$$

where n is the number of observed transitions (e.g. 20 successive counts gives $n = 19$), $100(1 - \alpha)$ is the confidence level (e.g. $\alpha = 0.05$ for a 95% CI), Φ and Φ^{-1} are the standard normal cumulative distribution function and its inverse function, and $z_{\alpha/2}$ is the upper $\alpha/2$ percentage point for the standard Normal distribution.

Equation (3) gives an *a priori* theoretical minimum CI for any CSEG-based quasi-extinction risk estimate where μ is estimated from the data, which depends only on n, T and $\hat{P}_e$. Remarkably, Holmes *et al.*'s (2007) CIs for extinction risk estimated from real data (their figure 8) come very close to the TMU CIs (Fig. 1), showing that their CSEG-parameterization methods, designed to correct for extraneous noise, nearly eliminate the extra uncertainty due to sampling errors and uncertainty in $\hat{\sigma}_b$. At the same time, Fig. 1 confirms that the (0,1) criticism *sensu* Fieberg & Ellner (2000) persists at small σ_b: if $\hat{P}_e$ is between 25% and 75% (the dotted vertical lines in Fig. 1), the 95% CIs cover most of (0,1). However, as Holmes *et al.* (2007) noted, relatively few of their CIs were extremely wide. The reason for this is indeed the smaller σ_b values in their data set. Decreasing σ_b increases $|U - V|$ and moves P_e towards 0 or 1, so $\hat{P}_e$ remains between 25% and 75% only for a restricted set of (N_e, T) combinations near the line μT = log (N_e/N_0) where $U = V$ (see Appendix S1).

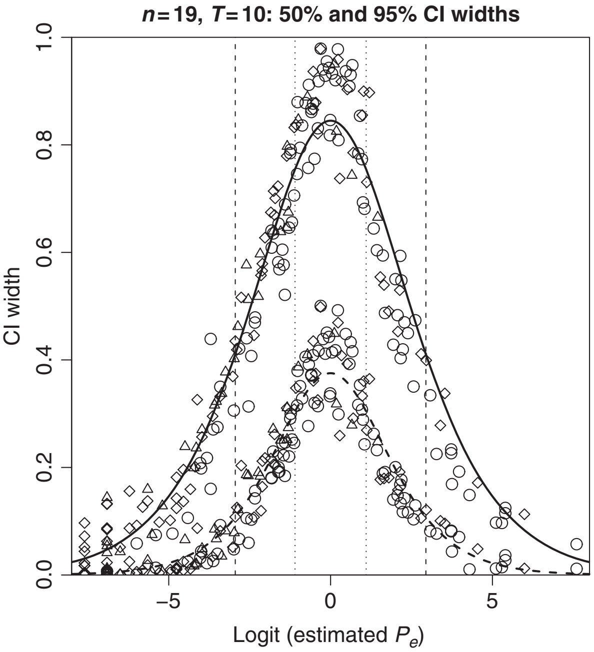
n = 19, *T* = 10: 50% and 95% CI widths

Figure 1 Comparison of theoretical minimum confidence interval (CI) widths on $\hat{P}_e$ (TMU CIs, eqn 3, which assume no uncertainty in $\hat{\sigma}_b$) with the CIs for $\hat{P}_e$'s estimated from vertebrate time series as presented in figure 8 of Holmes *et al.* (2007). The Holmes *et al.* CIs required estimation of $\hat{\sigma}_b$ from data corrupted with observation and other noise. All predictions of quasi-extinction probability are based on a projection interval $T = 10$ years and 20 successive population counts (hence $n = 19$ observations of population change). Curves show the TMU CIs (solid: 95% CI width, dash: 50% CI width), symbols are the Holmes *et al.* CIs for real data with three different quasi-extinction thresholds (triangles: decline to 20% of initial size, diamonds: decline to 50% of initial size, circles: decline to 80% of initial size). The dashed vertical lines are at $\hat{P}_e = 0.05$ and $\hat{P}_e = 0.95$, the dotted vertical lines are at $\hat{P}_e = 0.25$ and $\hat{P}_e = 0.75$. Code in R (R Development Core Team 2007) for producing this figure is provided in the online supplement to this article.

Because the TMU closely approximates actual CI widths (Fig. 1), the TMU can be used to explore the potential precision of CSEG risk projections. Using eqn (2), we can calculate TMU CI widths for different combinations of T and N_e as a function of $\hat{\mu}$ and $\hat{\sigma}_b$:

$$P_e(\hat{U} - z_{\alpha/2}\sqrt{T/n}, \hat{V}) \le P_e \le P_e(\hat{U} + z_{\alpha/2}\sqrt{T/n}, \hat{V}). \tag{4}$$

These are the two-sided limits; for one-sided limits, replace $z_{\alpha/2}$ with z_{α}. eqn (4), which uses both terms in eqn (2) rather than just the first, should always be used when analyzing real data rather than the large-V approximation eqn (3).

Figure 2 shows how the (N_e, T) region where estimates are 'certain' vs. 'highly uncertain' depends on σ_b. The high uncertainty region (dark grey) was defined as TMU CI width > 0.8. The high certainty regions (white) were defined as '$P_e < 0.05$ with high certainty' (upper one-sided 95% CI on P_e entirely below 0.05) or '$P_e > 0.95$ with high certainty' (lower one-sided 95% CI entirely above 0.95). In Fig. 2(a), σ_b is set at the median estimate (0.08) from the Holmes *et al.* (2007) vertebrate database. In this case, the region of high uncertainty is narrow despite having only 25 years of population counts for parameterization. In Fig. 2(b) where σ_b is much higher (0.25) the high uncertainty region is extensive, and much > 25 years of data would be needed to reduce the uncertainty. Plots such as Fig. 2 provide a comprehensive summary of the theoretical limits to precision of extinction risk estimates, and thus guide practitioners towards reliable forecasts and away from estimates that for theoretical reasons are inevitably highly unreliable. Figure 2 also shifts attention from extinction *probability* to extinction *time*, so that safe zones can be identified where extinction risk due to environmental stochasticity is low and uncertainty is also low.

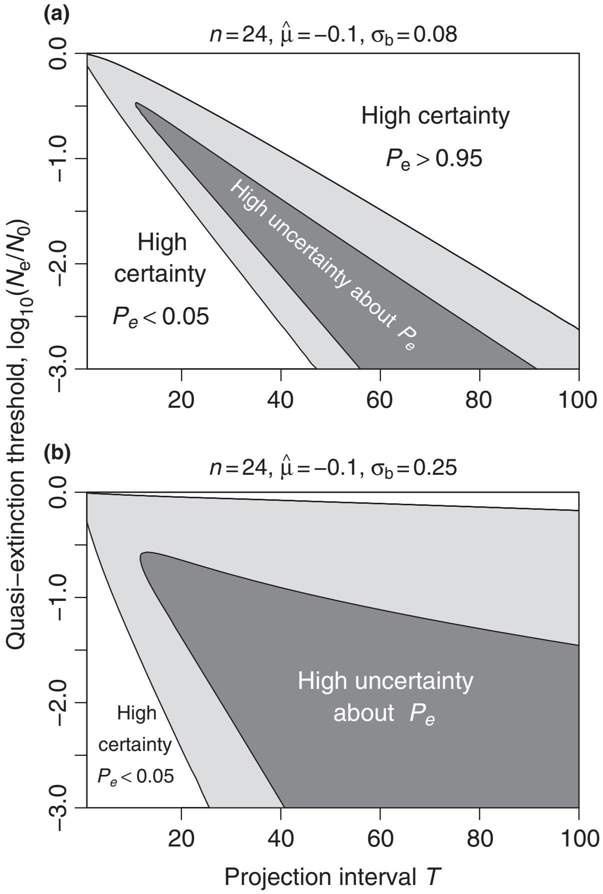

Figure 2 Combinations of prediction interval and quasi-extinction threshold where estimates of quasi-extinction are highly uncertain (confidence interval (CI) width > 0.8) and highly certain (one-sided 95% CIs on $\hat{P}_e$ are entirely below $P_e = 0.05$ or above $P_e = 0.95$). The light grey region shows where uncertainty is intermediate between these extremes. These plots were drawn using the TMU CIs for the CSEG model, eqn (4), which does not involve the large-V approximation. Panel (a) represents a rapidly declining species ($\mu = -0.1$), with σ_b set to the median value (0.08) in the Holmes *et al.* (2007) database of vertebrate species. In panel (b), σ_b is set much higher to 0.25. In both cases, 25 years of count data with no observation error are assumed ($n = 24$). Complete code in R (R Development Core Team 2007) for drawing this figure is provided in the online supplement to this article. The supplement also includes an Appendix S1 explaining why the wide-CI region is wedge-shaped, and showing that the size of the wide-CI region is proportional to σ_b as $\sigma_b \to 0$.

Figure 2 uses the TMU, which assumes σ_b is known rather than estimated. In Fig. 3, we show how uncertainty in σ_b increases uncertainty in P_e. We estimated μ and σ_b from simulated data corrupted with observation errors and calculated CIs using parametric bootstrapping (following methods for corrupted data described in Holmes *et al.* 2007). The grey-shaded wedges in Fig. 3 show where the TMU CI-width is > 0.8. The contours around the grey wedges show how this wide-CI region expands when observation errors ($\sigma_w = 0.2$, 0.3 or 0.7) are added to the data. The top panels show that for high σ_b, wide CIs are a barrier to all but the shortest projections. Uncertainty in $\hat{\sigma}_b$ only makes CIs wider. However, at lower σ_b, representative of the Holmes *et al.* (2007) vertebrate database, the wide-CI region becomes a narrow wedge, especially for rapidly declining populations. The estimation methods presented in Holmes *et al.* (2007) effectively deal with observation error, except when observation error is very high ($\sigma_w = 0.7$ and over an order of magnitude > σ_b). Figure 3 supports the argument that 20- to 50-year projections can be made with *c.* 20 years of data for some populations of concern. But this is not true for all populations, or for any one population at all (N_e,T) combinations, so it is critical to report CIs along with point estimates of P_e.

Although we have shown that long-range estimates of quasi-extinction risk due to environmental stochasticity are possible for some populations, in general long-range (25–100 year) projections based solely on environmental stochasticity are problematic. PVA practitioners are well aware that environmental stochasticity is only one of many risk factors facing species of conservation concern (e.g. Coulson *et al.* 2001; Doak *et al.* 2008). Other important risks include: demographic stochasticity, genetic factors (random fixation of disadvantageous alleles, inbreeding depression, or reduced genetic variability), and extreme catastrophic events

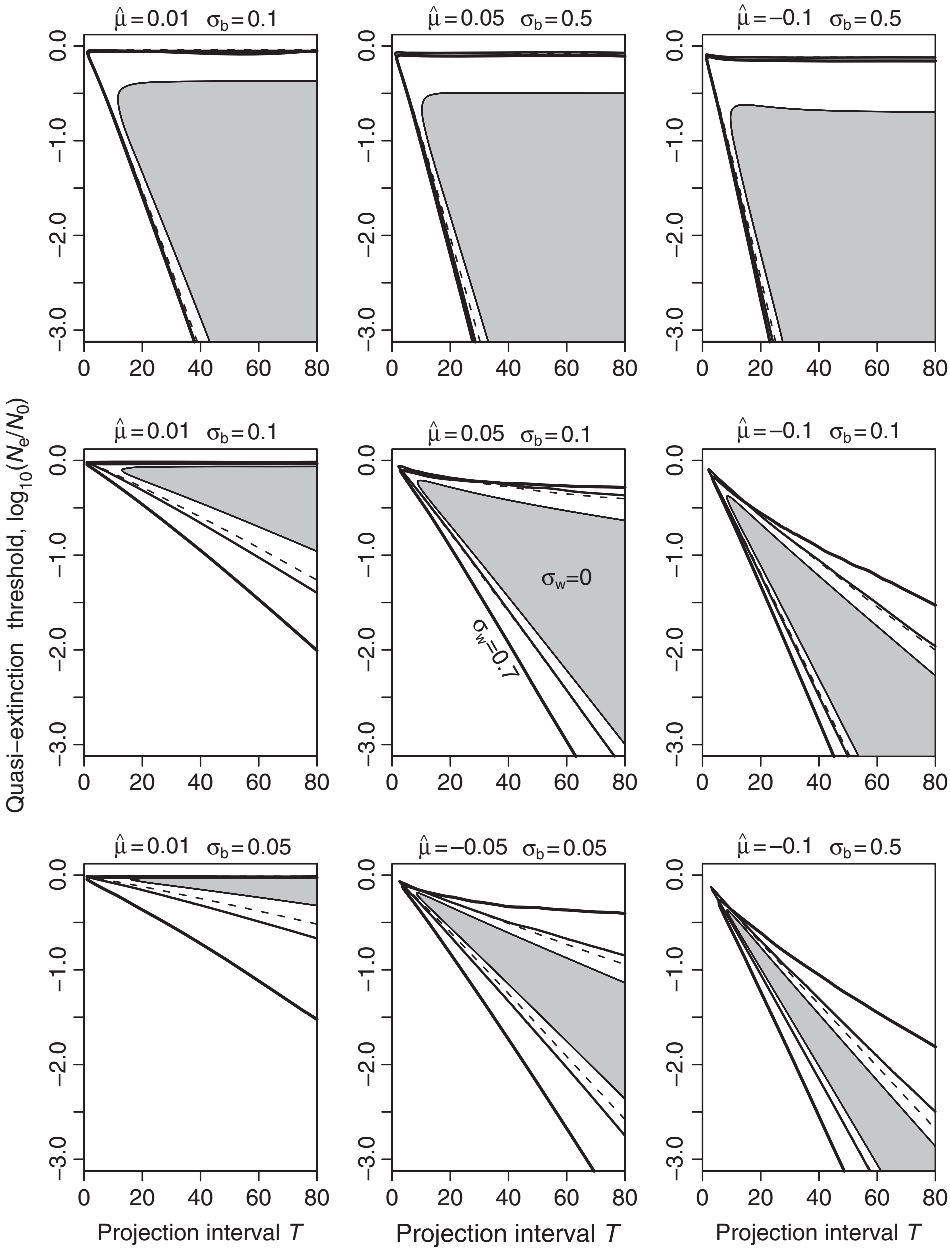

Figure 3 The T and N_e regions where 95% confindence intervals (CIs) on quasi-extinction probability cover > 80% of the possible (0,1) range when σ_b is known vs. estimated. The different panels show the results as a function of the mean and standard deviation of the interannual population growth rate (μ and σ_b), respectively, for a 20-year time series of population counts ($n = 19$). The wedge shaded in grey identifies the combinations of T and N_e where CI width > 0.8 when σ_b is known and $\sigma_w = 0$ (using eqn 4). The lines moving outward from the grey wedges show how the region of CI width > 0.8 grows when σ_b is estimated under different levels of observation error ($\sigma_w = 0.2$, 0.3 and 0.7 from closest to farthest from the grey wedge). The CIs for the σ_b-unknown cases are estimated using parametric bootstrapping: using $\hat{\mu}$, $\hat{\sigma}_b$, and $\hat{\sigma}_w$ (following Holmes *et al.* 2007), bootstrapped abundance time series are generated using eqn (1). From each bootstrapped time series, $\hat{\mu}$, $\hat{\sigma}_b$, and $\hat{\sigma}_w$, are estimated and from the bootstapped $\hat{\mu}$, $\hat{\sigma}_b$ estimates, bootstapped P_e's and bootstrapped CIs are obtained. Complete code in R (R Development Core Team 2007) to draw this figure is provided in the online supplement to this article.

that are hard to estimate because of rarity. In addition, risk analyses based solely on environmental stochasticity do not account for unanticipated changes in environmental conditions (habitat loss, climate change, impeded movement) or in ecological interactions such as introduced predators or pathogens. Sorting out how risk factors interact and when one dominates the others is a difficult challenge. However, summarizing the risk from each factor as a function of prediction interval and threshold, as in our Fig. 2, would clarify the time scales over which different risks are important. Such a comparison moves discussion away from debates about whether 100-year forecasts from CSEG models capture all the risks facing a population (clearly not!), and towards more productive discussions about how much time remains until different risk factors may put a species in imminent danger of extinction.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Analytic approximation to the wide-CI region.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2008.01211.x.

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