

# On the interpretation and application of mean times to extinction

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As a metric of population viability, conservation biologists routinely predict the mean time to extinction (*MTE*). Interpretation of *MTE* depends on the underlying distribution of times to extinction (*DTE*). Despite claims to the contrary, all information regarding extinction risk can be obtained from this single statistic, the *MTE*, provided the *DTE* is exponential. We discuss the proper interpretation of *MTE* and illustrate how to calculate any population viability statistic when only the *MTE* is known and the *DTE* is assumed to be exponential. We also discuss the restrictive assumptions underlying the exponential *DTE* and the conditions under which alternative models for the *DTE* are preferable to the conventional (exponential) model. Despite superficial similarities between the exponential and alternative *DTEs*, several key differences can lead to substantially different interpretations of the *MTE*.

**Keywords:** distribution of times to extinction; extinction; mean time to extinction; population viability analysis.

## Introduction

The assessment of population viability is fundamental to the theory and application of conservation biology (reviewed by Boyce, 1992; Caughley, 1994). One means of assessing population viability is to use numerical and analytical models to predict extinction risk in statistical terms, such as the mean time to extinction (*MTE*). However, in the absence of a full appreciation of their limitations, population viability analyses (*PVAs*) are easily misinterpreted. Inadequate information regarding population parameters and structure can lead to worthless estimates of population viability (Ginzburg *et al.*, 1990; Taylor, 1995). Another often unappreciated challenge is the interpretation of population viability estimates in the context of their statistical properties. Here, we discuss the proper interpretation and application of a widely reported population viability statistic, the *MTE*. Our analysis focuses on the assumption that the distribution of times to extinction (*DTE*) is exponential. We highlight some of the potential pitfalls of indiscriminate reliance on this assumption.

The mean time to extinction is a widely reported statistic for at least two reasons. First, in some cases it is the only easily estimable population viability statistic (e.g. Lande, 1993; Foley, 1994). Second, its meaning is seemingly intuitive. The near ubiquity and familiarity

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of *MTE* make it a primary interpretive tool in PVA. However, the meaning of *MTE* may be a misleading indicator of extinction risk for several reasons (Goodman, 1987; Burgman *et al.*, 1992; Nunney and Campbell, 1993; Mangel and Tier, 1994). First, the *MTE* is a poor indicator of central tendency since most populations are expected to go extinct prior to the *MTE*. It is widely reported that the *median* time to extinction is always much less than the *MTE* (e.g. Goodman, 1987; but see below). Moreover, the modal time to extinction approaches zero and is generally independent of the *MTE* when density dependence is strong or unpredictable catastrophic events pose the primary threat to extinction (Mangel and Tier, 1994). Second, the *MTE* alone provides no indication of population viability for specific time frames (Burgman *et al.*, 1992). Finally, *MTE* does not convey the highly variable nature of the extinction process and the enormous uncertainty in predicting extinction time (Ginzburg *et al.*, 1990; Foley, 1994). Here, we derive general quantitative expressions that reinforce some of our qualitative claims and refute other claims. We also show that the qualitative and quantitative properties of *MTE* are strongly dependent on the underlying DTE.

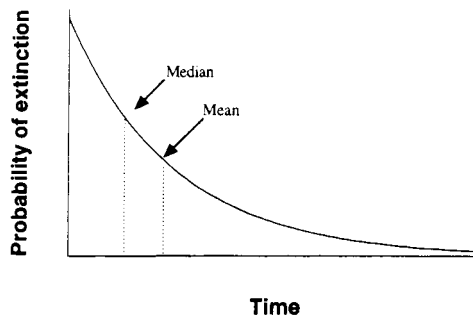
### The exponential DTE and the interpretation of *MTE*

Any population viability statistic can be derived from the *MTE* alone if an exponential DTE is assumed. This convenient property reflects the fact that the entire exponential distribution, and thus the probability of extinction at any time  $t$ , is defined by *MTE* (Fig. 1):

$$E(t) = MTE^{-1} \exp(-t/MTE) \quad (1)$$

The exponential assumption is satisfied if the annual risk of extinction is constant (Bain and Engelhardt, 1992), which may be approximately true when population dynamics are strongly density dependent (Nobile *et al.*, 1985; Gabriel and Bürger, 1992; Nunney and Campbell, 1993) or when catastrophic events constitute the primary risk of extinction (Mace and Lande, 1991). Hereafter, unless otherwise stated, the exponential assumption will be implicit.

From the exponential DTE (Equation 1), we derive several relationships between *MTE* and alternative population viability statistics. First, consider the  $(n \times 100)$ th percentile of the DTE. Percentiles express the number of years that a population is expected to persist



**Figure 1.** Exponential distribution of times to extinction, illustrating the strong skew and the relationship between the mean and median times to extinction.

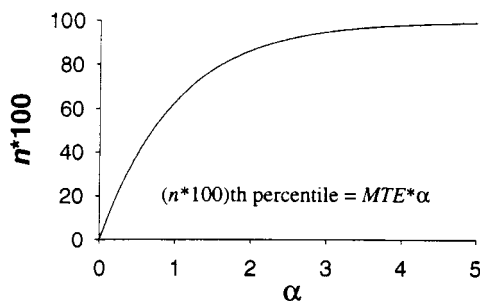
with  $(n \times 100)\%$  certainty, a practical and intuitively appealing population viability statistic. The relationship between  $MTE$  and the  $(n \times 100)$ th percentile is given the expression:

$$n = \int_0^{\alpha_n MTE} E(t) dt \quad (2)$$

where the product  $\alpha_n MTE$  is the  $(n \times 100)$ th percentile. The notation indicates that  $\alpha$  depends only on  $n$  (Fig. 2). Conveniently,  $\alpha$  is thus independent of  $MTE$ . Letting  $\alpha_n = 1$  and solving for  $n$  (in Equation 2) reveals that the  $MTE$  is approximately the 63rd percentile. Hence, a population has only a 37% chance of persisting beyond the  $MTE$ . This expression thus quantifies the claim that most populations go extinct prior to the  $MTE$  (see Goodman, 1987). Equation 2 also confirms that the median time to extinction is  $\ln(2) \times MTE$  (see also Rice, 1988).

More important, Equation 2 can be used to convert  $MTE$  to population viability statistics that reflects extinction risk for any specified time frame (cf. Burgman *et al.*, 1992). For example, consider a hypothetical population with a predicted  $MTE$  of 100 years. According to Equation 2 the expected persistence with 95% certainty would be only 5 years ( $= \alpha_{0.95} MTE = 0.05 \times 100$  years, where  $\alpha_{0.95}$  is obtained by letting  $n = 0.95$  and solving Equation 2). In addition, Equation 2 can also be used to derive the confidence interval for the time to extinction. For example, when  $MTE = 100$  years, the 95% confidence intervals of time to extinction is extremely wide (2.5–370 years), which highlights the point that  $MTE$ , by itself, is a poor indicator of the likely timing of extinction. More generally, the 50% confidence interval for the time to extinction is  $\{0.29MTE, 1.39MTE\}$ , the 70% confidence interval is  $\{0.61MTE, 1.90MTE\}$ , and the 90% confidence interval is  $\{0.05MTE, 3.00MTE\}$ . This application of Equation 2 illustrates that the  $MTE$ , if properly interpreted, reflects the highly uncertain nature of the time to extinction (cf. Ginzburg *et al.*, 1990; Foley, 1994).

The proposed criterion for placing a species on the IUCN red list is similarly expressed in terms of the probability of extinction within some time period (Mace and Lande, 1991; Mace *et al.*, 1992). The probability of extinction within  $x$  years can be predicted from the  $MTE$  alone:



**Figure 2.** Relationship between the multiple  $\alpha$  (by which the mean time to extinction is multiplied to obtain the  $n$ th percentile) and the  $(n \times 100)$ th percentile (beyond which a population is expected to persist with  $[n \times 100]\%$  certainty), assuming an exponential DTE. The  $(n \times 100)$ th percentile =  $MTE \times \alpha$ .

$$P[T_0 < x] = \int_0^x MTE^{-1} \exp(-t/MTE) dt \tag{3}$$

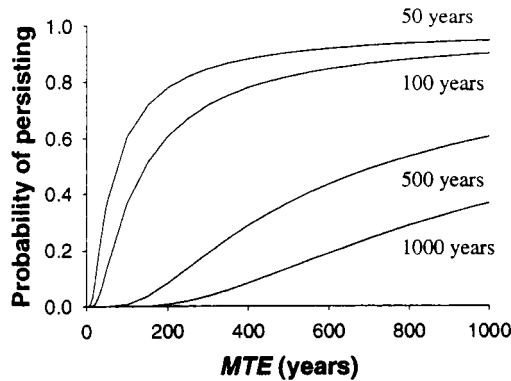
where  $T_0$  is time to extinction. This relationship permits the conversion of the proposed IUCN red-list criterion to a more familiar statistic, the  $MTE$  (Table 1). In reciprocal fashion, if the  $MTE$  has been predicted, then this relationship is useful because it permits the prediction of the probability of persistence over specific time frames (Fig. 3; cf. Burgman *et al.*, 1992).

PVA often takes into consideration the costs (financial) and benefits (improved population viability) of management plans. Suppose a PVA predicts that a particular plan will increase a population's  $MTE$  from 100 to 200 years. If the plan is implemented and the population persists for fewer than, say, 100 years, constituents may strongly object to the perceived squandering of resources. Policy makers may challenge the credibility of the PVA. Such scepticism is more likely to arise when the predictive power of  $MTE$  (and PVA in general) is misinterpreted. In this hypothetical example, there would be a 40% chance of extinction during the first 100 years. To obtain a more general expression of this relationship, let  $MTE_{plan}$  and  $MTE_{status\ quo}$  indicate the predicated  $MTE$  if a plan is implemented and if it is not implemented, respectively. Let  $\theta$  equal the ratio  $MTE_{plan} : MTE_{status\ quo}$ . Given that the plan is implemented, the probability of extinction prior to  $MTE_{status\ quo}$  is:

**Table 1.** Proposed criteria for placing species on the IUCN red list, expressed in terms of risk of extinction (Mace *et al.*, 1992); and the corresponding mean time to extinction ( $MTE$ ), calculated by integration of the exponential distribution

| Category   | Risk of extinction | $MTE$                   |
|------------|--------------------|-------------------------|
| Critical   | >50% in 5 years    | <7 years                |
| Endangered | >20% in 20 years   | <2 years <del>90</del>  |
| Vulnerable | >10% in 50 years   | <1 years <del>950</del> |

100



**Figure 3.** Relationship between mean time to extinction ( $MTE$ ) and the probability that a population will persist for various time periods.

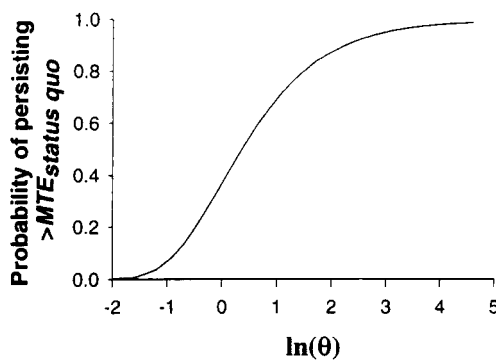
$$P[T_0 > MTE_{\text{status quo}}] = \int_0^{MTE_{\text{status quo}}} [(MTE_{\text{plan}})^{-1} \exp(-t/MTE_{\text{plan}})] dt \quad (4)$$

Inspection of Fig. 4 reveals that the plan must predict an  $MTE$  4.5 times longer than the  $MTE$  under the status quo (i.e.  $\theta$  must be  $> 4.5$ ) to achieve at least 80% certainty that the plan will increase persistence time beyond  $MTE_{\text{status quo}}$ .

### Alternative DTEs and the interpretation of $MTE$

Many investigations have relied on the statistical convenience of assuming an exponential DTE (e.g., Foley, 1994; Lande *et al.*, 1995; Hanski *et al.*, 1996). Here, we consider the degree to which our interpretations of  $MTE$  depend on this assumption. A full treatment of this subject is beyond the present scope, but we offer a brief summary. At least three alternative models for the DTEs have been developed. First, the inverse Gaussian distribution describes the (conditional) DTE for populations whose growth is density independent, whose size is unrestricted, and whose primary risk of extinction is environmental stochasticity (Lande and Orzack, 1988). A second model for the (unconditional) DTE applies when the inverse Gaussian model is altered to incorporate a carrying capacity (Schwartz, 1992; Middleton *et al.*, 1995). A third model for the DTE describes extinction in a collection of isolated subpopulations, where each subpopulation's DTE is exponential (Burkey, 1995). Under biologically realistic conditions, these models deviate from the exponential model in several significant respects, which we summarize below.

Alternative models also differ markedly from the exponential model in the degree of unpredictability in time to extinction. This unpredictability can be characterized by the variance in time to extinction ( $VTE$ ). Under the exponential DTE,  $VTE = MTE^2$ . Under the alternative models for DTE, the  $VTE$  can be much greater or much less than  $MTE^2$  (e.g. see Equations 18 and 19 in Dennis *et al.*, 1991). When  $VTE < MTE^2$ , the time to extinction is more predictable and  $MTE$  is a more reliable estimator of population viability. The converse is true when  $VTE > MTE^2$ . For a sample of seven populations (those analysed by Dennis *et al.*, 1991), the  $VTE$  ranged from  $MTE^{1.4}$  to  $MTE^{2.7}$ .



**Figure 4.** Relationship between  $\theta$  (the ratio  $MTE_{\text{plan}}:MTE_{\text{status quo}}$ ) and the probability of extinction prior to  $MTE_{\text{status quo}}$ , where  $MTE_{\text{plan}}$  and  $MTE_{\text{status quo}}$  represent the predicted  $MTE$  if a management plan is implemented and if it is not implemented, respectively. The relationship is determined by Equation 4.

Unlike the exponential model, which is completely defined by a single parameter (i.e. *MTE*), alternative DTE models generally depend on multiple parameters. Consequently, additional population viability statistics cannot be derived when only the *MTE* is known. For example, the ( $n \times 100$ )th percentile for the inverse Gaussian DTE depends on the *MTE* as well as the *VTE*:

$$n = \int_0^n \frac{1}{2} \left( \frac{2}{\pi \times VTE} \right)^{1/2} \left( \frac{MTE}{t} \right)^{3/2} \exp \left[ - (t - MTE)^2 \frac{MTE}{2t \times VTE} \right] \quad (5)$$

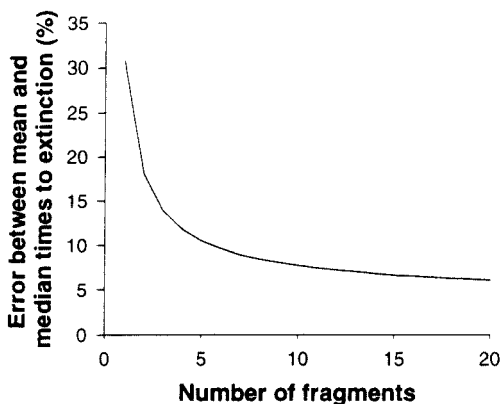
Except in the case of the exponential DTE, the *VTE* is not easily predicted from the *MTE*. Therefore, population viability statistics (e.g. median, mode, percentiles, or probabilities of persistence to some time period) cannot be estimated when only the *MTE* is known.

Alternative models can differ greatly in their predictions of extinction risk in the near future. Under both the inverse Gaussian and Schwartz DTEs, increases in the current population size significantly reduce the risk of extinction in the immediate future (Lande and Orzack, 1988; Middleton *et al.*, 1995; for empirical support see Pimm *et al.*, 1988; Berger, 1990; Schoener and Spiller, 1992; Tracy and George, 1992). Therefore, the exponential model tends to overestimate the probability of extinction in the immediate future, except when density dependence is especially strong. The exponential model also tends to underestimate lower-tail percentiles and overestimate probabilities of persistence beyond specified timeframes (where such probabilities are near unity).

The very meaning of the *MTE* depends on the underlying model for the DTE. Under the exponential DTE, the median time to extinction (50th percentile) is significantly shorter than the *MTE* (62nd percentile). Consequently, the *MTE* is not a good estimator of the central tendency of the DTE. Under alternative DTEs, the *MTE* may be much closer to the 50th percentile. For example, consider a population with 1000 individuals and an expectation and variance in annual growth rate of  $-0.03$  and  $0.002$ , respectively. Under these conditions, the inverse Gaussian DTE predicts modal, median, and mean times to extinction of 97, 99, and 100 years, respectively. In this case, the *MTE* is quite representative of the central tendency of the DTE as well as the most likely time to extinction. Consider an example involving the DTE derived by Burkey (1995). A key parameter for the Burkey DTE is the number of isolated population fragments. Inspection of Equations 5 and 6 in Burkey (1995) reveals that the percent error between the mean and median times to extinction depends only on the number of fragments and that this error falls quickly as the number of fragments increases (Fig. 5). Contrary to the common assertion that the median time to extinction is always much less than the *MTE*, we have described a biologically plausible scenario where the median is only slightly less than the *MTE*.

## Discussion

Any population viability statistic can be derived from the *MTE* provided the DTE is adequately described by the exponential model. As examples, a population has only a 38% chance of persisting past the *MTE*, an expected persistence with 95% certainty that is only 5% of the *MTE*, a 95% confidence interval that is bounded by extinction times corresponding to 2.5% and 370% of the *MTE*. In contrast, when the DTE is better described an alternative model, population viability statistics such as the median, mode, and percentiles typically cannot be calculated from *MTE* alone. Since interpretation of the *MTE*



**Figure 5.** Percent error between the mean and median times to extinction depends only on the number of isolated population fragments under the Burkey (1995) DTE. (The case where there is only one fragment is equivalent to the exponential DTE.)

depends on the underlying DTE, it is important to recognize biological conditions under which alternative DTE models may be appropriate. Unfortunately, direct empirical evidence will typically be unavailable to guide the selection of an appropriate DTE. Instead, an appropriate model for the DTE can be selected by simulating or deriving the DTE associated with the population dynamics model that best describes the observed population dynamics (see Dennis *et al.*, 1991). Nevertheless, additional theoretical and empirical exploration of DTEs is likely to improve our ability to interpret *MTE* and extinction risk under a variety of contexts.

To dismiss *MTE* as a misleading or inadequate indicator of extinction risk would be overly pessimistic. Consider the claim that the median time to extinction is less misleading than *MTE* since it accurately reflects the central tendency of the time to extinction (i.e. a population has an equal chance of going extinct either before or after the central tendency). We have shown conditions for which the median can be calculated from *MTE* (Equation 2) and other conditions for which *MTE* itself is a reasonable approximation of the central tendency (Fig. 5). More important, the median and *MTE* have similarly low precision for predicting the time to extinction. While a population is unlikely to go extinct near the *MTE*, it is also unlikely to go extinct near the median. For example, Equation 2 can be used to show that a population has only a 35% chance of going extinct within 50% of the calculated median time to extinction. In this regard, the median and *MTE* are similarly inadequate. We do not mean to imply, however, that the probability of persistence to some time period is a fully satisfactory population viability statistic. This statistic too, like population viability statistics in general, is inadequate; it considers only a single time frame and level of certainty.

Statements of risk are inherently fraught with potential for misinterpretation (Piattelli-Palmarini, 1994). Perhaps in an attempt to prevent such misinterpretation, *MTE* has been characterized as a poor indicator of extinction risk under an exponential DTE. The standard criticism is that it does not approximate the median or modal time to extinction, and does not reflect the highly variable nature of time to extinction. Given that *MTE* is nonetheless widely reported (and is the only tractable statistic for many analytical models), we have provided a simple framework for its proper interpretation.

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