DO LIFE HISTORY TRAITS AFFECT THE ACCURACY OF DIFFUSION APPROXIMATIONS FOR MEAN TIME TO EXTINCTION?

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Abstract. Estimating the risk of extinction is one of the central foci of conservation biology, but such estimates are often constrained by the available data. In the face of limited data, several authors have suggested using diffusion approximations to estimate the mean time to extinction as a means of quantifying the risk of extinction. However, the accuracy of the diffusion approximation for characterizing extinction processes has not been well tested. We develop a simulation model that includes life history parameters and incorporates both demographic and environmental stochasticity in population dynamics. We use the simulation model to study the effects of stochasticity on the accuracy of the diffusion approximation across different life history strategies. Our results show that predictions for mean time to extinction from the diffusion approximation may differ significantly from simulated ones, and that the amount and direction of the error in the approximation is not systematic. Given that this error is unpredictable and may be very sensitive to the exact demographic rates, we believe that the diffusion approximation should be used with caution as a basis for assessing extinction risk or making management decisions.

Key words: catastrophes; demographic; diffusion; environmental; extinction; life history; risk; simulation; stochastic; variation.

INTRODUCTION

Estimating the risk of extinction is one of the central foci of conservation biology. A wide variety of methods have been developed for characterizing extinction processes (Boyce 1992, Morris et al. 1998). Modeling approaches range in complexity from simple exponential growth models to Monte Carlo simulations that include age, stage, and/or spatial structure (Dennis et al. 1991, Burgman et al. 1993, Lacy 1993, Mangel and Tier 1993, Doak et al. 1994, Possingham and Davies 1995). However, one of the primary problems in modeling threatened species is the scarcity of data. In fact, for many threatened species the available data may be limited to intermittent survey data with no estimates of vital rates (Morris et al. 1998). Consequently, estimates of the risk of extinction are often constrained by the available data rather than the choice of applicable models. In the face of limited data, several authors have suggested using diffusion approximations to estimate the mean time to extinction as a means of quantifying the risk of extinction (Dennis et al. 1991, Foley 1994).

Diffusion approximations may be useful for estimating mean time to extinction for three reasons. First, they require relatively little data. One version of the approximation uses only the mean long-term population growth rate and its variance, parameters that can be estimated from intermittent survey data (Dennis et al. 1991, Foley 1994). Second, the approximations are analytic solutions, which makes them quick and easy for biologists and managers to use (Morris et al. 1998). Third, as interest in these solutions has increased, researchers have developed new approximations that can accommodate additional biological complexity such as limited forms of density dependence, catastrophes, and autocorrelation in growth rates (Lande 1993, Foley 1994). However, these more complex models may be less general and more difficult to parameterize because of the additional assumptions that they require. Mangel and Tier (1993) give a brief review of some of the developments in modeling extinction times using these methods. Diffusion approximations have been used to evaluate the risk of extinction for a variety of threatened species in taxa including birds, mammals, fish, and insects (Dennis et al. 1991, Foley 1994, Sæther et al. 1998, Hakoyama and Iwasa 2000). These papers generally attempt to make diffusion-based models accessible for managers, and these modeling methods have begun to be used by managers and agencies (Morris et al. 1998, USFWS 1999).

However, the accuracy of the diffusion approximation for characterizing extinction processes has not been well tested. This is particularly true for density-dependent versions of the approximation. The approximations used for predicting mean time to extinction assume that the probability of extinction is exponen-
tially distributed. They also require several assumptions about the transitions between population sizes at successive times that probably are not met by populations of many threatened species. The two assumptions inherent in the diffusion approximation that are most likely to generate an error are: (1) All possible population sizes can be reached from any current size in one time step. (2) Transitions between population sizes are drawn from a normal distribution.

Formally, the diffusion approximation for a system in which the change in population size \((N)\) in a unit of time \((\Delta t)\) is

\[
\Delta N = N(t + \Delta t) - N(t)
\]

assuming that \(N(t)\), the population size, is a continuous random variable such that:

\[
E[\Delta N|N(t) = n] = r(n)\Delta t + o(\Delta t)
\]

\[
E((\Delta N)^2|N(t) = n) = \sigma^2(n)\Delta t + o(\Delta t)
\]

with \(\Delta N \sim\) normal, where \(o(\Delta t)\) represents higher order terms of \(\Delta t\) such as \((\Delta t)^2\).

Lande and Orzack (1988), Foley (1994), and Middleton et al. (1995) evaluated the accuracy of the diffusion approximation for mean time to extinction by comparing it to simulation models. The approximations generally give accurate predictions of extinction risk when compared with risks calculated directly from many simulated population trajectories. However, the simulation models that have been used in these cases closely match the underlying assumptions of the approximation method and may not be biologically realistic. At a minimum, these comparisons are a somewhat circular test of the validity of the diffusion approximation because they assume normally distributed transitions in population size between time steps (Foley 1994, Middleton et al. 1995). Middleton et al. (1995) noted some differences between their simulations and the diffusion approximation that they used in predictions of probability of extinction over time (estimated by the inverse of the mean time to extinction); however, they discussed these differences only briefly. In other studies, diffusion approximations were not accurate for predicting extinction risk, particularly if the population size was small or if it was able to make large changes in size in short periods (Mangel 1990, Ludwig 1996, 1998). These results are in accord with both empirical and analytical tests of the diffusion approximation in other fields, in which approximations have been found to be accurate in limited cases, but inaccurate when assumptions are violated (Knessl et al. 1984, Matkowsky et al. 1984, Yoo et al. 1990, Page et al. 1995).

Given their growing popularity and the relative availability of time series data for parameterizing diffusion-based models, it is important to test the accuracy of the approximations. This is particularly true for density-dependent versions, for which there is very little validation, and which require additional assumptions regarding the form of density dependence (Foley 1994, Middleton et al. 1995). Questions about the effects of variation in birth and death rates and clutch sizes on the accuracy of the approximation are particularly important. Because organisms naturally have variable demographic rates, the error in the diffusion approximation may be more sensitive to some types of variation than others. Assessing how variation in demographic rates affects the diffusion approximation-based estimates for mean time to extinction may allow us to determine when the approximation will be useful and what the direction and magnitude of the error may be.

Rigorously testing models of extinction requires extensive time series data, preferably on species that have gone extinct (Brook et al. 2000). There are few data sets of this type, and each one represents only a single replicate for the test (Ellner et al. 2002). In the face of this limitation, we used a simulation model to generate population trajectories that can serve as test data for the diffusion approximation. This is an increasingly common practice, and has generally been accepted as a reasonable strategy for testing extinction models (Ellner et al. 2002; but see Brook et al. 2000). The simulation model that we use is an individual-based stochastic population model that incorporates variation in birth and death rates and clutch sizes, yielding both demographic and environmental stochasticity in population dynamics. It also includes ceiling-type density dependence (MacArthur and Wilson 1967). After describing the diffusion approximation and our simulation model, we use the simulation model to study the effects of stochasticity on the accuracy of the diffusion approximation across five different hypothetical life history strategies. We hope to provide some guidance for when it might be reasonable to gather survey data and use a diffusion-based approach and when it would be better to use an alternate model that would include more extensive information on the life history characters of a species.

### The Diffusion Approximation

Foley’s (1994) formula for the mean time to extinction for a population starting at \(n_0\) with an average long-term growth rate of \(r\), a variance in the rate \(v\), and a population ceiling \(K\) is:

\[
T(n_0) = \frac{1}{2vr}(\exp(2sK)][1 - \exp(-2sn_0)] - 2sn_0) \tag{1}
\]

where

\[
s = \frac{rv}{2}
\]

and all parameters are scaled to the natural log of population size. This formulation for the mean time to extinction is based on a population that grows at a constant average rate, where the rate is normally distributed with some mean and variance. The upper boundary \((n = K)\) is reflecting, meaning that the population cannot exceed that size. The lower boundary...
with a common probability of reproduction for all individuals in that time step, $\beta_i$:

$$\Pr\{b_i = b\} = \binom{c}{b} \beta_i^b (1 - \beta_i)^{c-b}$$

(6)

where $c$ is the maximum clutch size, $b$ is the number of births, and $\beta_i$ is the reproductive probability for individual $i$.

The diffusion approximation assumes a constant value for the long-run population growth rate, and all of the life history information on a species is contained in that value and its variance. Our simulation model allows one to decompose the growth rate into the demographic parameters that affect it, namely the birth and death rates and the clutch size. We can use this detail to compare cases with similar growth rates but very different life histories, for instance, intermittent large clutches with a high mortality rate vs. more frequent small clutches with a lower mortality rate. We are also able to decompose the variation in the growth rate into demographic variation in births or in deaths and environmental variation in births or deaths.

**Measuring Approximation Accuracy**

We define accurate predictions by the diffusion approximation as those that fall inside the 95% confidence intervals of the mean time to extinction realized by the simulated trajectories. The difference between the analytic prediction and the nearer boundary of the confidence interval is then a measure of the amount of error in prediction. We ignore the effects of the quality of the estimates of the diffusion approximation parameters on the predictions made by the approximation, instead treating the approximation as a point estimator for mean time to extinction for any given parameter combination.

We explored the accuracy of mean time to extinction predictions for five idealized life history strategies: a top predator, an ungulate, a tree, an annual plant, and a songbird. We chose clutch sizes and probability distributions for the mean reproductive and survival probabilities to match each of the five generalized life history strategies, and initially set these parameters at high enough values to give long-term persistence (i.e., no
extinctions within the time range of our simulations; Fig. 1, Table 1). From these values, we then explored the effects of reducing the mean reproductive and survival probabilities and altering their variances. Our goal in choosing these parameters was not to specifically describe a particular species, or to explore the possible range of parameters, but rather to look at the effects of the stochastic behavior of several generalized life history strategies on the accuracy of the diffusion approximation.

In order to explore the accuracy of the diffusion approximation within each life history strategy, we varied the parameters for each strategy along five axes: (1) mean survival probability, (2) mean reproductive probability, (3) variance in survival probability, (4) variance in reproductive probability, and (5) population ceiling (Table 2). The potential parameter space that could be explored along these five dimensions is prohibitively large. Therefore, we first explored the fit between the simulation and the diffusion approximation across a range of survival values, from high values that result in populations oscillating near the ceiling to low values that result in rapid population crashes (Fig. 2). We then selected three mean survival probabilities for each of the life histories to obtain: (1) a persistent oscillating population, (2) a declining population, and (3) a crash-

Table 1. Parameter values yielding populations with the maximum persistence for the idealized life history strategies.

<table>
<thead>
<tr>
<th>Strategy type</th>
<th>Fecundity</th>
<th>Mortality</th>
<th>Maximum density-independent growth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>E[β_r]</td>
<td>Var[β_r]</td>
<td>E[β_m]</td>
</tr>
<tr>
<td>Top predator</td>
<td>0.5</td>
<td>0.0031</td>
<td>0.15</td>
</tr>
<tr>
<td>Ungulate</td>
<td>0.5</td>
<td>0.012</td>
<td>0.375</td>
</tr>
<tr>
<td>Tree</td>
<td>0.0000025</td>
<td>0.0000018</td>
<td>0.65</td>
</tr>
<tr>
<td>Annual plant</td>
<td>0.8</td>
<td>0.0076</td>
<td>0.89</td>
</tr>
<tr>
<td>Songbird</td>
<td>0.25</td>
<td>0.0046</td>
<td>0.45</td>
</tr>
</tbody>
</table>

Notes: β_r denotes the probability of reproduction, β_m the probability of mortality, and r the population growth rate. E[·] is the expected value of the parameter in brackets, and Var[·] is its variance, calculated as explained in the methods.
Table 2. Range of parameters explored for each life history.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean Pr{survival}</th>
<th>Mean Pr{birth}</th>
<th>Variance Pr{survival}</th>
<th>Variance Pr{birth}</th>
<th>Population ceiling (no. individuals)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top predator</td>
<td>0.85±0.5</td>
<td>0.5±0.4</td>
<td>0.001±0.01</td>
<td>0.0008±0.005</td>
<td>50–1000</td>
</tr>
<tr>
<td>Ungulate</td>
<td>0.625–0.35</td>
<td>0.5–0.4</td>
<td>0.002–0.015</td>
<td>0.003–0.02</td>
<td>50–1000</td>
</tr>
<tr>
<td>Tree</td>
<td>0.35–0.075</td>
<td>0.00000025–0.0000002</td>
<td>0.025–0.085</td>
<td>0.00000045–0.00000025</td>
<td>50–1000</td>
</tr>
<tr>
<td>Annual plant</td>
<td>0.11–0.01</td>
<td>0.8–0.7</td>
<td>0.0008–0.005</td>
<td>0.002–0.013</td>
<td>50–1000</td>
</tr>
<tr>
<td>Songbird</td>
<td>0.525–0.274</td>
<td>0.25–0.175</td>
<td>0.0013–0.009</td>
<td>0.001–0.008</td>
<td>50–1000</td>
</tr>
</tbody>
</table>

† The mean birth probability was varied across this range at each of three mean survival probabilities for each life history, and thus covers a similar range as the variation in the mean survival probability.

For each set of parameters, we simulated 250 trajectories for 200 time steps. Based on numerical experiments that we performed and on published analytical work, we determined that the starting population size had little effect on the results of our simulations. Thus, to be consistent with the diffusion approximation assumptions, we started populations at the ceiling (Ludwig 1978). We calculated the probability of extinction from the proportion of the 250 populations that went extinct in the simulations. This estimated probability was adjusted for the fact that we only observed populations for 200 time steps (right censoring), and thus may not have detected all of the extinctions that would occur over a longer time period (Gross and Clark 1975:62). Using this probability and assuming an exponential distribution of extinction times, we calculated the mean time to extinction. We also calculated the 95% CIs for the probability, and thus the mean time to extinction (following Gross and Clark 1975). The assumption of an exponential distribution for extinction times is generally accepted and is widely used to estimate survival processes (Gross and Clark 1975, Mangel and Tier 1993). We compared these simulation results to the mean time to extinction predicted by the diffusion approximation.

Our goal in this analysis was not to evaluate the effects of data limitations on the accuracy of the approximation, because this has been done elsewhere (Fieberg and Ellner 2000). Instead, we were interested in examining the effects of altering the mean birth probability at each of these survival probabilities. Although we varied the mean birth probability across a more narrow range than we used for survival probability, by repeating the process at multiple survival probabilities we were able to explore a similar amount of parameter space in terms of population behavior (rapidly increasing to crashing). We explored the effects of variance in the birth and survival probabilities by selecting the mean birth and survival probabilities for each life history that had the best match between the diffusion approximation and the realized extinction times. Using these mean probabilities, we increased and then decreased the variance in their distributions by 25%, 50%, and 75%. In order to separate the effects of variance in the demographic rates, we held the variance in one rate constant, while changing the other, resulting in a parameter set for the base variances in the rates set plus six other parameter sets for each rate. To examine the effects of the population ceiling on the accuracy of the diffusion approximation, we repeated all of the analyses for each life history strategy at six population ceilings: 50, 100, 250, 500, 750, and 1000 individuals. However, the important patterns are visible by examining the effect of changing the mean reproductive probability at different population ceilings, so we will focus on these results.

For each set of parameters, we simulated 250 trajectories for 200 time steps. Based on numerical experiments that we performed and on published analytical work, we determined that the starting population size had little effect on the results of our simulations. Thus, to be consistent with the diffusion approximation assumptions, we started populations at the ceiling (Ludwig 1978). We calculated the probability of extinction from the proportion of the 250 populations that went extinct in the simulations. This estimated probability was adjusted for the fact that we only observed populations for 200 time steps (right censoring), and thus may not have detected all of the extinctions that would occur over a longer time period (Gross and Clark 1975:62). Using this probability and assuming an exponential distribution of extinction times, we calculated the mean time to extinction. We also calculated the 95% CIs for the probability, and thus the mean time to extinction (following Gross and Clark 1975). The assumption of an exponential distribution for extinction times is generally accepted and is widely used to estimate survival processes (Gross and Clark 1975, Mangel and Tier 1993). We compared these simulation results to the mean time to extinction predicted by the diffusion approximation.

Our goal in this analysis was not to evaluate the effects of data limitations on the accuracy of the approximation, because this has been done elsewhere (Fieberg and Ellner 2000). Instead, we were interested in estimating the parameters for the top predator life history under three different mean survival probabilities. The mean reproductive probability and the variances used for these runs are the initial values, given in Table 1. The population ceiling is 100 individuals.
in the accuracy of the model, given that the parameters were estimated as accurately as possible. Thus we assumed that the population ceiling was known without error and used the exact values used in the simulation model. We parameterized the transitions and their variance for the diffusion approximation following Foley (1994), using the actual population size transitions from the model. Foley suggested using transitions in population size for populations well below the ceiling to estimate \( r \) for real populations, in order to avoid effects of density dependence. However, this method clearly biases the estimate of the variance in \( r \) if the population sizes ever exceed the ceiling. Foley (1994) noted this bias, but provided no guidance for correcting it. We ran the model 200 times starting from the population ceiling. For each run, we allowed 15 transitions for the population to move through any transient dynamics, and then collected data on the next five population size transitions to calculate the mean and variance of the long-term population growth rate. Because the underlying process is constant, there is no difference between estimating the model by collecting data in this manner vs. following a single trajectory for 1000 transitions. We excluded any transitions in which the population went extinct, because \( r \) would be infinitely negative. Additionally, one would hardly calculate extinction probability for an extinct population in a real setting (cf. Brook et al. 2000). Using the actual population transitions from the model to parameterize the approximation, rather than calculating the expected long-term growth rate and its variance analytically, makes the fitting of the approximation independent of the specific details of the simulation model.

**RESULTS**

**Effect of mean survival probability**

The diffusion approximation for mean time to extinction did provide accurate predictions for the realized mean time to extinction in the simulated data in a limited number of cases, for some of the life history strategies (Fig. 3). However, the approximation was inaccurate for some survival values for all of the life history strategies, and was never accurate for the tree strategy (Fig. 3). The life history strategies can be divided into three groups with respect to the accuracy of the approximation.

The first group consists of the top predator strategy, the ungulate strategy, and the songbird strategy, for which the pattern was overestimation of the mean time to extinction at high survival values and underestimation at low survival values (Fig. 3). At intermediate survival values, which translate into slowly declining populations, the diffusion approximation was fairly accurate (Figs. 2a and 3). Even in portions of the parameter space in which the approximation was relatively accurate, it was often outside the 95% CIs for the realized mean time to extinction (Fig. 3).

An examination of the values of the instantaneous per capita growth rate \( (r) \) for the top predator strategy shows that, at these intermediate levels of survival, the populations are generally below the population ceiling.
Fig. 4. Values of $r$ for three life histories across the range of mean survival probabilities, illustrating their dynamic behavior. Open diamonds show values of $r$ between time $t$ and time $t+1$ for populations that were extant at time $t+2$ (note log scale of $y$-axis). Filled squares show corresponding values of $r$ for populations that went extinct at time $t+2$. The data are taken from 20 trajectories lasting for 20 time steps. The total number of points indicates the relative persistence of populations for each panel. The upper diagonal dotted line shows the $r$ value that would take the population above the ceiling in the next time step. The lower diagonal dotted line shows the value that would result in extinction in the next time step. Future population size can be predicted from this graph. For instance, in panel (a), populations in quadrant 1 will be in quadrant 1 in the next time step; those in 2 will be in either 3 or 4 in the succeeding time; from 3, populations can either remain in 3 or move to 4 or 1; from 4, populations remain in 4. Thus, a rapidly oscillating population would have points mostly in 2 and 4, e.g., panel (i), resulting from high values of $r$ below the ceiling and low values above it. A more slowly oscillating population would have values in 2, 3, and 4, e.g., panel (f), which would indicate that populations below the ceiling increase rapidly to exceed it, but those above it may drop back quickly (quadrant 4) or may decay down more slowly (quadrant 3).

and while they are decreasing, on average ($r < 0$), they stay at reasonably large population sizes for some period (Fig. 4b). Populations that go extinct in this parameter range tend to drift slowly toward zero from the population ceiling, and finally go extinct from smaller sizes (Fig. 4b). At higher survival values, where the approximation did not provide accurate predictions for the mean time to extinction, the populations tend to oscillate just below the population ceiling, occasionally making excursions above the ceiling, but dropping back below it within one time step (Fig. 4c). Because of a positive instantaneous growth rate at population sizes below the ceiling, extinctions tend to occur only when populations that are above the ceiling experience very high mortality in a single time step and go to extinction (Fig. 4c). In contrast, for low survival values, where the diffusion predictions were also inaccurate, the populations do not reach the ceiling after their initial start (Fig. 4a). Here most values of $r$ are below 0, indicating that the populations are steadily declining. Extinction generally occurs from small population sizes, although there is a wider range of population sizes immediately preceding extinction compared with extinctions occurring at the intermediate survival values (Fig. 4a, b).

Variance in the observed values of $r$ tends to increase with decreasing population size for the life histories in this group (Figs. 4b, c, and 5). This increase in variance is a general property of these life histories, independent of the probability of survival, but is particularly significant for simulations with lower survival values. The increase in variance results from smaller populations representing fewer samples of the underlying random process (i.e., fewer individuals reproducing and dying). Thus, as population size decreases, the variance in $r$ increases, even if the underlying random process is constant. Thus as the mean survival probability decreases, populations spend a larger portion of the period they are extant at small sizes, resulting in an increase in the variance in $r$ as the survival probability goes down.

The diffusion approximation consistently underestimates the mean time to extinction for the tree life history. The tree life history strategy represents an extreme contrast to the dynamics of the first group of strategies (top predator, ungulate, and songbird). The tree life history has a lower average survival probability but a larger variance in survival. It also has a very low mean probability of birth, but a long tail on
Fig. 5. Variance in r values for populations in a size range for top predator and tree life histories with different mean survival probabilities (values in keys). Bars show estimates of variance in r calculated from populations in a particular size range over 20 simulated population trajectories lasting a maximum of 20 yr. Numbers above the bars show the sample size for each population range/parameter combination. Mean birth probability and variance in survival and birth are as for the initial values, given in Table 1.

the distribution, resulting in occasional time steps with large amounts of reproduction. These two factors, along with the large number of seeds, result in populations with pronounced oscillations that are frequently above the ceiling, even if the populations are going extinct over a short time period (Fig. 4d–f). Thus, populations not only can decline slowly to extinction, as in the first group, but also can go extinct through the effect of large oscillations, even from very large population sizes.

Populations in this life history also have fairly slow dynamics, as can be seen by the large number of populations above the ceiling that remain above the ceiling in the following time step, despite no reproduction (Fig. 4d–f; points above the upper diagonal line and to the right of the ceiling). These slow decreases in population size for populations above the ceiling introduce autocorrelation in r. Because no reproduction is possible above the ceiling, populations will experience successive negative values of r until they are below the ceiling (Fig. 4d–f). In fact, for the highest mean survival probability, almost all populations below the ceiling have large values of r that take them above the ceiling in the next time step, after which all populations experience at least one negative value of r and some experience multiple negative values if the first transition does not take them back below the ceiling (Fig. 4f).

The tree life history shares some of the patterns of the previous group of strategies: as mean survival probability increases, population trajectories make fewer excursions to very low sizes, and the variance in r increases as mean survival decreases (Fig. 4d–f). However, the effect of population size on the variance in r is not apparent as it was for the first group of strategies (Fig. 4a–c). The explanation for this lack of sampling error is that the values of r have a lower bound. Because r cannot be calculated for populations that go extinct, the range of possible r values has a lower bound that increases toward zero as population size gets closer to one (Fig. 4d–f). In addition, the tree strategy has a fairly large variance throughout the range of population size; thus, this lower bound constrains the variance to be nearly constant across population size.

For the annual plant strategy, the diffusion approximation is accurate at some survival rates, but does not show a consistent trend in its accuracy (Fig. 3). The population dynamics for this strategy are somewhat similar to those of the tree strategy; both have strong oscillatory tendencies (Fig. 4g–i). However, the annual plant strategy has a much lower mean survival probability with a smaller variance, and a higher mean birth probability with a larger variance (Fig. 1). In addition, the tree strategy has a bimodal distribution for reproduction, resulting in most time steps having little or no reproduction, with sporadic reproductive booms. In contrast, the annual plant has a unimodal distribution for reproduction, resulting in a more even distribution of reproduction across time steps. Thus, the dynamics for this strategy are much more rapid than for the tree strategy. This can be seen in the lack of populations
above the ceiling that remain there in the next time step (Fig. 4g–i; see points above the upper diagonal and right of the population ceiling). These more rapid dynamics result in oscillations with a much shorter period, and thus more negative autocorrelation in $r$ (Fig. 6). As with the tree strategy, there is no increase in the variance of the $r$ values at smaller population sizes within runs for a given mean survival probability. Similarly, variance in $r$ increases as the mean survival probability decreases, despite a constant variance in the underlying distribution of survival probabilities (Fig. 4g–i).

Effect of mean birth probability

We explored the effect of changing the mean birth probability across a range of values at three different mean survival probabilities for each life history (Table 2). A number of these sensitivity analyses showed patterns similar to those for the analysis of mean survival probability. For the top predator, ungulate, and songbird life histories at the high and intermediate survival probabilities, increasing the mean birth probability resulted in the diffusion approximation overestimating the mean time to extinction. This overestimation increased as the mean birth probability increased, similar to the effects of increasing mean survival. The tree life history also showed a pattern similar to the survival sensitivity analysis; the diffusion approximation underestimated the mean time to survival for all mean birth probabilities at all three mean survival probabilities.

At the low survival probability, the results for all of the life histories, with the exception of the tree, were more complex (Fig. 7). At low mean survival probabilities (top predator, 0.625; ungulate, 0.475; annual plant, 0.03; and songbird, 0.375), the diffusion approximation was fairly accurate in the sensitivity analysis for mean survival (Fig. 3). However, it is clear that even modest changes in the mean birth probability can have significant effects on this accuracy for some of the strategies (Fig. 7). Although the magnitude of these effects is fairly modest within this narrow range of parameter space, the direction of the error changes for three of the life histories, such that the approximation overestimates the mean time at some parameter combinations and underestimates it at others (Fig. 7). The direction of this error also is not consistent across life history strategies; for example, the error changes in opposite directions for the songbird and annual plant across the range of birth probabilities explored (Fig. 7). For the ungulate strategy, this error even changes direction two times over the range of parameters explored (Fig. 7). The effects of changes in the mean birth probability do scale with the maximum clutch size, although not strictly, because the largest effects are for the songbird (Table 1, Fig. 7).

Inspecting the patterns for the annual plant and songbird strategies gives some indication of the mechanisms underlying the error in the diffusion approximation. The effect of increasing the mean probability of reproduction for the annual plant is to increase the number of excursions above the population ceiling and to decrease the time between excursions (Fig. 8a, b). Because $r > 0$ most of the time for populations below the ceiling, excursions above the ceiling, which result in reproductive failure, represent the main source of extinctions for this life history (Fig. 8a, b). Thus, increasing reproduction increases the frequency of exceeding the ceiling, reducing the mean time to extinction. On the other hand, extinctions for the songbird life history generally occur as slow declines, and for the lower mean probability of reproduction, they are
Fig. 7. Mean time to extinction (log scale) predicted by the diffusion approximation and actual values realized by the simulated populations. Symbols designate diffusion predictions for the life histories. The observed mean time to extinction for each life history is displayed along the same range of reproductive probabilities. Error bars show the 95% confidence intervals for the simulated trajectories. The population ceiling is 100 individuals, and the life history abbreviations and mean survival probabilities are: TP, top predator (0.625); UG, ungulate (0.475); AP, annual plant (0.03); and SB, songbird (0.375). The variances in the survival and reproduction probabilities are given in Table 1. Letters a–d correspond to panels in Fig. 8.

Fig. 8. Values of \( r \) and population size (log scale) for annual plant and songbird life histories across the range of mean reproductive probabilities, illustrating the dynamic behavior in the life histories. Panel letters correspond to labels in Fig. 7. Open diamonds show values of \( r \) between time \( t \) and time \( t + 1 \) that were extant at time \( t + 2 \). Filled squares show corresponding values of \( r \) for populations that went extinct at time \( t + 2 \). Data are taken from 10 trajectories lasting for 20 time steps. See Fig. 4 for more detail.
Fig. 9. Difference between mean time to extinction predicted by the diffusion approximation ($t_{\text{diff}}$) and the realized time for the simulated populations ($t_{\text{sim}}$). Panel (a) shows the effect of increasing or decreasing the variance in the reproductive probability by 25%, 50%, and 75%. Panel (b) shows the effect of altering the variance in the survival probability across the same range. The mean survival and reproductive probabilities were those that gave the most accurate results for the diffusion approximation. Mean survival and reproductive probabilities, respectively, for the five life histories were: top predator (TP), 0.625, 0.5; ungulate (UG), 0.475, 0.5; tree (TR), 0.175, 0.0000025; annual plant (AP), 0.03, 0.8; songbird (SB), 0.375, 0.25. It was not possible to explore the 50% or 75% increases in variance in the reproductive probability for the tree strategy because of limitations of the beta distribution; thus, the maximum increase in variance is 40%.

certainly not due to oscillations above the ceiling (Fig. 8c, d). However, the variance in the realized values of $r$ increases as population size decreases, as noted for this strategy in the survival sensitivity analysis (Figs. 8c, d, and 5a). Thus, as the mean probability of birth is reduced, trajectories are at small population sizes for a higher proportion of the time that they are extant, increasing the estimate of the variance in $r$ and resulting in underestimates of the mean time to extinction by the diffusion approximation. Conversely, as the mean reproductive probability is increased, the songbird populations begin to reach and exceed the ceiling, resulting in oscillatory dynamics that lead to overestimation of the mean time to extinction by the diffusion approximation (Fig. 8d).

Effect of variance in the demographic rates

Modifying the variance in the demographic rates had only minor effects on the accuracy of the diffusion approximation for mean time to extinction (Fig. 9). For this analysis, we chose the parameters for the mean reproduction and survival probabilities that had given the best match between the diffusion approximation and the realized mean times to extinction. For most of the life histories at most parameter values, there was little effect (Fig. 9). The approximation was fairly ac-
curate for the top predator strategy, and the variance in the demographic rates had little effect on this pattern (Fig. 9). Similarly, the approximation was not accurate for the tree strategy, and altering the variance in the demographic rates only changed this difference quantitatively (Fig. 9).

Changes in variance did affect the annual plant and songbird strategies. The sensitivity analyses for mean birth and survival probabilities have demonstrated the sensitivity of the diffusion approximation to the specific parameter values in the annual plant life history relative to the other life histories (Fig. 3). The results for alterations in the variance in the probability of birth show a similar pattern, with erratic increases in the difference between the diffusion approximation and the realized mean time to extinction across the range of parameters explored. For the songbird strategy, the mean survival and birth probabilities that we used for this analysis gave a slowly declining population (Fig. 2). Decreasing the variance in the demographic rates for this combination of parameters resulted in populations spending longer periods at very small population sizes before going extinct, a phenomenon similar to that observed for this species in the other sensitivity analyses (Fig. 5). This results in a larger estimate of the variance in $r$. In addition, there appears to be an interaction between the change in the variance of the probability of birth and the distribution of survival probability, such that the estimated value of $r$ decreases as the variance in the birth rate either increases or decreases (Table 3).

**Effect of the population ceiling**

The simulated populations had qualitatively similar patterns of mean time to extinction across differing mean probabilities of survival as the population ceiling increased (Fig. 10). For instance, the top predator strategy had a relatively constant mean time to extinction across the low and intermediate survival values and increased rapidly at the highest values, independent of the population ceiling (Fig. 10). However, the pattern of mean time to extinction predicted by the diffusion approximation changed with increasing population ceiling (Fig. 10). The changes in the diffusion approximation across increasing population ceilings are similar to the differences across the mean probability of survival at a constant population ceiling (Figs. 10 and 3). This can be seen most clearly for the top predator, ungulate, and songbird strategies; at a ceiling of 50 individuals, the predicted and realized mean times to extinction look like those for smaller values of survival at a ceiling of 100 (Figs. 10 and 3). In contrast, the patterns for these three life histories at a ceiling of 1000 resemble the patterns for the same strategies with higher survival probabilities at a ceiling of 100 (Figs. 10 and 3).

For the tree and annual plant strategies, which show more oscillatory dynamics, increasing the population ceiling generally caused the diffusion approximation to change from underprediction to overprediction of the mean time to extinction (Fig. 10). This pattern varied along the axis of mean survival probability, with different population ceilings resulting in changes from underprediction to overprediction at particular mean survival probabilities (Fig. 10). Additionally, changing the ceiling in some cases had little effect on the accuracy of the extinction, e.g., at the higher mean survival probabilities for the tree strategy (Fig. 10). This is probably due to the interaction between the survival probability and the population ceiling, which determines the oscillatory behavior of the strategies. Thus at low population ceilings or at relatively higher survival values, the approximation is more inaccurate.

**Discussion**

The diffusion approximation has been proposed as an alternative to other, more data-hungry approaches, such as stochastic age-structured models, for modeling threatened and endangered populations. However, our results show that predictions for mean time to extinction from the diffusion approximation may differ significantly from realized extinctions generated by individual population simulations. Moreover, the amount and direction of the error in the approximation is not systematic. In some cases, the approximation overestimates the mean time to extinction; in others, the approximation underestimates it. Both the direction of the error and the magnitude of the error varied across the idealized life histories that we compared and within life histories across the various demographic parameters. The pattern in the error was often complex with respect to the demographic parameters, and did not appear to be easily predictable.

However, there were some patterns that may be helpful in determining when the approximation will be less accurate. In general, there was a pattern of increasing error with life histories that more strongly violated the assumptions of the approximation. For strategies similar to those of a tree (long-lived with intermittent periods of high reproductive success) or a songbird (relatively short-lived with frequent periods of high reproductive success), the approximation was particularly poor. In most cases, the approximation will be

| Table 3. Variance in parameters for reproduction and the resulting mean and variance in the realized instantaneous growth parameter $r$ for the songbird strategy. |
|----------------------|-------|----------------------|
| Variance in $Pr(birth)$ | Estimated $mean \ r$ | Estimated Variance $r$ |
| 0.00004              | 0.040 | 0.42                 |
| 0.00015              | 0.017 | 0.28                 |
| 0.00034              | 0.029 | 0.46                 |
| 0.00061              | 0.055 | 0.43                 |
| 0.00096              | 0.050 | 0.40                 |
| 0.00140              | 0.008 | 0.43                 |
| 0.00160              | 0.023 | 0.47                 |
FIG. 10. Mean time to extinction predicted by the diffusion approximation and actual values realized by the simulated populations across a range of population ceilings. Symbols designate diffusion predictions for the life histories (Abbreviations: TP, top predator; UG, ungulate; TR, tree; AP, annual plant; SB, songbird). The observed mean time to extinction for each life history is displayed along the same range of survival probabilities. Error bars show the 95% confidence intervals for the simulated trajectories. The parameters for the mean reproductive probability and the variances in the rates are given in Table 1. Note the different y-axis scales for left- and right-hand panels.

accurate for some parameter values for a particular life history. However, this range may be fairly narrow and somewhat difficult to predict, as in the case of the annual plant life history in our analysis.

The inaccuracy in the diffusion approximation for predicting mean times to extinction in our analysis can be ascribed to three general sources: (1) inaccuracy in the method used to estimate \( r \) or its variance; (2) biases in estimating \( r \) inherent in particular types of dynamics, such as density-dependent growth or rapid declines to extinction; and (3) structural differences between the diffusion approximation and dynamical systems that do not meet the underlying assumptions of the approximation. The first of these factors potentially can be resolved using better methods for estimating \( r \) and its variance. The remaining two may be more difficult, as they are either inherent biases in the data or limitations of the modeling approach.

We found that the method of estimating \( r \) for a diffusion approximation with a population ceiling using the log of the ratio of successive values of population size gave a poor estimate of the variance in \( r \) (Foley 1994). We identified two important mechanisms underlying this problem: inflation of the variance in \( r \) as population size decreases and the effect of the population ceiling. Ignoring the transitions in population size near or above the ceiling and using a single term to represent the variance in \( r \) gave poor estimates of the variance in \( r \), even though the mean of \( r \) and its variance estimated below the ceiling were, in fact, the true values realized by the simulation model.

The first mechanism generating inaccuracy in the diffusion approximation is the increase in the variance in \( r \) at small population sizes (Fig. 5a). Because there are fewer samples of the distribution of births and deaths at small population sizes (i.e., fewer individuals reproducing and dying), the estimated variance in \( r \) tends to increase at small population sizes. Thus, for declining populations that are at small population sizes, the variance in \( r \) increases even if the variance in the underlying demographic rates is constant. One of the underlying assumptions in many diffusion approximations is that the effect of demographic stochasticity is small except at very small population sizes. Thus, by setting a quasi-extinction boundary above this level, the effects of demographic stochasticity can be ignored.
(Foley 1994, Middleton et al. 1995). In these diffusion approximations, where a single term is used to represent stochastic effects on population size, ignoring demographic stochasticity, the variance estimated for \( r \) will depend on the range of population sizes used in estimation. This will lead to inaccuracies in the approximation due to overestimates or underestimates of the variance in \( r \), unless the population size does not move outside the range of sizes used to parameterize the approximation. This will, of course, be less important for populations that are not at small sizes, are not declining to a small size, and do not experience periodic oscillations to small sizes. In addition, recent advances in the application of diffusion approximations to extinction processes have included both demographic and environmental stochasticity as separate terms in the approximation, and thus can accommodate this sampling effect (Sæther et al. 1998, Hakoyama and Iwasa 2000).

The second mechanism generating inaccuracy in the approximation was a result of excursions above the ceiling by the simulated populations. The method of estimating \( r \) and its variance that we used ignores transitions near or above the population ceiling, causing the estimate of \( r \) to be artificially high and its variance to be artificially low (Foley 1994). However, it is unclear in the current modeling framework (a diffusion approximation with ceiling density dependence) how else to estimate \( r \). We tried including transitions for populations above the ceiling, which gives the true value of \( r \) and its variance for the simulated trajectories. However, when used in the current form of the diffusion approximation, these values give even less accurate predictions for mean time to extinction than do values estimated at small population sizes. Again, other researchers have proposed alternate formulations of the diffusion approximation that include logistic density dependence, which should be able to accommodate some aspects of how \( r \) might be estimated at or above the ceiling (Hakoyama and Iwasa 2000, Sæther et al. 2000). However, these models have not been tested extensively for data generated from sources for which the underlying dynamics are known, e.g., from simulation models, so it is hard to assess their accuracy. In addition, they present the complication of estimating additional parameters and, in some cases, require detailed knowledge about individuals in the populations, such as individual reproductive success, in order to estimate parameters (Sæther et al. 1998).

There are also difficulties in estimating \( r \) and its variance for particular types of dynamics that are independent of the method for estimating these values. In particular, rapidly declining populations represent a difficult situation. The primary reason is that the distribution of estimable \( r \) values is bounded on the lower end by extinction. For instance, censusing a population of >1000 individuals, one might see an occasional huge crash in numbers that leaves something on the order of 10s of individuals, giving \( r \sim -4.5 \). However, if the population is only 10 individuals, the largest decline for which \( r \) can be calculated is nine individuals (e.g., \( r \sim -2.3 \)), as any larger decline will result in extinction (and thus \( r \sim -\infty \), and cannot be estimated). Thus if we have a population, estimate its growth rate and variance over some past period for which it has been extant and fairly small, and then make projections about its future extinction, we may have an underestimate of the probability of extinction. Clearly, this is an extreme example; however, it is important to keep in mind that the \( r \) we estimate for populations is actually the \( r \) conditional on them being currently extant. Thus our estimate of \( r \), and particularly of its variance, may be biased, with \( r \) being high and variance being low in relation to the true value of \( r \) and its variance. This effect can be seen clearly in the life histories that have larger variances in \( r \), e.g., in the tree strategy, when they reach smaller sizes (Fig. 4d, e; note the points along the lower diagonal dotted line at population sizes of <30 individuals). This point is particularly important for populations in which the mean size is small relative to its variance, i.e., either small or declining populations, and will apply to any estimation of changes in population size or its variance.

Excursions above the population ceiling also make estimation of \( r \) difficult because they introduce temporal structure in the values of \( r \), which cannot be captured by the current formulations of the diffusion approximation for mean time to extinction. There were both positive and negative autocorrelations in \( r \) in our simulated trajectories, and the magnitude and sign of this autocorrelation depended on the general life history pattern and the specific probabilities of reproduction and survival for that life history. It is important to note that there is no autocorrelation in the mean reproductive or survival probabilities in the simulation model; the autocorrelation is a function of the population regulation mechanism in the larger stochastic process. For instance, the tree life history has large bouts of reproduction that occur intermittently, and mortality is relatively low by comparison. This results in occasional excursions above the population ceiling that slowly decay back down, yielding positive autocorrelation in the value of \( r \) until the population declines back below the ceiling (Fig. 6; see time steps 11–14). By contrast, the annual plant life history also has large bouts of reproduction, but these occur much more frequently and survival is much lower. This results in negative autocorrelation in \( r \) as the populations oscillate rapidly around the ceiling (Fig. 6). Thus, the method of fitting \( r \) and its variance from populations below the ceiling not only ignores these transitions and incorrectly estimates the realized mean \( r \) and its variance, but also leaves out this temporal structure in \( r \).

Furthermore, it is unclear how these dynamics, which are a result of a realistic upper boundary on population size and a bounded distribution of popu-
lation growth rates that does not extend \(-\infty\) to \(+\infty\), might be accommodated in a model that assumes normally distributed transitions and a reflecting upper boundary on population size (both of which would prevent excursions above the ceiling). Even in more recently developed versions of the diffusion approximation, which have logistic density dependence and thus avoid some of the problems with the estimation of \(r\), population transitions are still assumed to be normally distributed, resulting in similar difficulties in matching bounded transitions (Sæther et al. 1998). Middleton et al. (1995) noted a similar problem in comparing the diffusion approximation for mean times to extinction with population trajectories generated from a simulation model, and suggested that the approximation may be valid only when population size is small.

In general, white noise approximations, similar to the diffusion approximation, have been found to be inaccurate in estimating extinction risk when population growth rates are correlated (Johst and Wissel 1997). The accuracy of simulated white noise approximations was dependent on the size of the transitions and the time scale of the correlation (Johst and Wissel 1997). Our results suggest that population growth rates may have correlation structure, even if the underlying demographic rates do not, extending this result for correlation in demographic rates more generally to density-dependent dynamics.

As interest in modeling extinction stimulates more work on the application of diffusion approximations to predict extinction risk, some of the problems previously outlined may be overcome. Diffusion approximations have already progressed from early versions that included only simple demographic stochasticity and exponential growth to much more complex forms of density-dependent regulation that include multiple types of stochasticity (MacArthur and Wilson 1967, Sæther et al. 1998). A number of researchers have developed alternate formulations for density-dependent versions of the diffusion approximation (Sæther et al. 1998, 2000, Hakoyama and Iwasa 2000, Hakoyama et al. 2000, Iwasa et al. 2000). These approaches all assume logistic density dependence in the population, and find either an analytic approximation via numerical integration or develop regression formulae for predicting measures of extinction such as mean time to extinction. The parameters in the approximations include the instantaneous growth rate \((r)\), its variance, the carrying capacity (in the strict logistic sense), and, in the case of the theta-logistic model, an exponent on the density-dependent term in the equation. Environmental and demographic stochasticity are then additive terms that modify the population size or its growth rate between time steps, scaling with either the log of population size or its square root (Sæther et al. 1998, Hakoyama and Iwasa 2000). Some testing has been done with these methods to determine their error in predicting extinctions; however, this testing generally has used simulated data from models that matched the underlying assumptions of the approximation (Hakoyama and Iwasa 2000).

There are two main arguments for using diffusion approximations: (1) they are analytic and thus do not require large amounts of computational time; and (2) they can be parameterized with generally available data, such as counts of abundance (Dennis et al. 1991, Foley 1994). However, as these approximations become more complex, analytical solutions are no longer available. When solutions must be obtained numerically, they require similar computational effort to simulation methods. In addition, as the approximations become more complex, they require larger amounts of data on the species being modeled (Sæther et al. 2000, Hakoyama and Iwasa 2000). Thus the realism available in the more complex approximations comes at the cost of more time and data requirements (Dennis et al. 1991, Foley 1994, Middleton et al. 1995). When comparing the requirements of these approximations with simulation methods, researchers have also assumed that the simulation methods will be very complex, including explicit space or age structure for instance. However, there is no necessary requirement for complexity in simulation methods; in fact, it is possible to tailor the model exactly to the data available.

Although this may seem a straightforward point, diffusion approximations are being applied to species in cases in which the assumptions of the approximation are violated and adequate data are available for other approaches (Oli et al. 2001). In part, this problem may have to do with the difficulty of falsifying tests regarding the applicability of the diffusion approximation for particular data sets. To illustrate this point, we subsampled the data from our simulated trajectories and asked how often one would reject the observed \(r\) values as being non-normal for a given sample size. We took 1000 random samples of 5, 10, and 20 successive transitions and evaluated them for normality. We did this by using the observed mean and variance from the subsample to parameterize a normal distribution, drawing the same number of samples from it and then comparing the samples using a Kolmgorov-Smirnov two-sample test (Sokal and Rohlf 1981). We found that it was fairly difficult to reject the assumption of normality, even for the tree strategy. Across all of the survival probabilities that we explored for the tree strategy, we were able to reject an assumed normal distribution of \(r\) less the 12% of the time with 10 samples and <55% of the time with 20 samples of \(r\), although the distribution of \(r\) values is clearly bimodal for this strategy (Fig. 4f). Furthermore, there appeared to be little relationship between the frequency of rejection of normality and the accuracy of the approximation in predicting mean time to extinction. For instance, the rejection rates were consistently higher for the top
predator strategy than for the tree, although the approximation was more accurate for the top predator.

Our results regarding the inaccuracy of the diffusion approximation are similar to those from experimental tests in other fields, such as particle and wave transmission in random media, where the accuracy of the approximation is sensitive to how well the transitions in the process being modeled match the underlying approximation assumption of normally distributed transitions (Yoo et al. 1990). Although the diffusion approximation may be useful for estimating mean time to extinction in some cases, our results argue for caution in applying it. It is important to carefully analyze the life history strategy and population trajectory of the population in question to determine if approaches based on diffusion approximation are appropriate to use at all. If the population makes large, infrequent transitions or if there is bias in the direction of the transitions with respect to size or frequency, e.g., due to catastrophic mortality or reproductive failure, the approximations are not appropriate and may be very inaccurate with respect to the realized trajectory. Although there are diffusion approximations that can accommodate phenomena that violate the basic assumptions, such as catastrophic mortality, these modifications make them more complex, potentially difficult to fit to data, and less intuitive because they require rescaling of population sizes and transitions (Lande 1993). Diffusion approximations may be useful in some cases if their assumptions are met. For instance, in our comparisons the diffusion approximation was accurate for strategies that were declining relatively slowly and had reasonably small variances in the distribution of \( r \). One approach for determining the applicability of the approximation in particular cases may be to build a simulation model that includes the features of the species’ biology that are thought to be important, and then to use this to test the accuracy of the approximation in that particular case, much as we have done.

At a minimum, when a diffusion approximation is used, it should be compared to at least one alternate modeling strategy. Although it was difficult in the past to find alternate models that could be parameterized with very limited data, the advent of powerful and inexpensive computing has made alternative models readily available. Simulations can be designed with the appropriate level of complexity for the data available and the questions being investigated. Moreover, if they are parameterized using maximum likelihood methods, there is some indication of the validity of both the parameters in the model and the structure of the model as a whole for representing the species under study. Alternative analytical models are also available. For instance, the birth–death process model proposed by MacArthur and Wilson can be parameterized with limited knowledge about the birth and death rates of adults in a population (MacArthur and Wilson 1967, Mangel and Tier 1993). Ludwig (1996) also offers an alternate approach to analytic modeling of extinction dynamics. Halley and Iwasa (1998) have also proposed an analytic model that can be applied in similar situations. All of these alternative approaches have their own weaknesses. For instance, to develop an empirically based probability distribution for population transitions, the birth–death process model requires data on transitions over a wide range of population sizes (Mangel and Tier 1993). Moreover, recent work by Ludwig (1998) shows that the confidence intervals on analytic models might be quite wide because of observation or process uncertainty. This is potentially a general property of extinction. Because waiting times for random processes happening at a constant rate are generally exponentially distributed, the variance of the time to extinction will increase with the mean, resulting in wide confidence intervals (Ross 1980). Clearly there is no perfect solution to the problem of predicting extinctions. In some cases, even nonbiological approaches, such as using land zoning information and rates of urban growth to predict habitat loss, and thus future carrying capacity, may be more effective than any type of population modeling.

Finally, models of extinction processes are often used as a basis for making recommendations about management (Possingham and Davies 1995). Diffusion-based PVA models may be particularly tricky in this application, because of the structure of their errors. For example, assume that a manager wanted to establish a reserve for a threatened population that would give a mean time to extinction of 1000 yr (using the diffusion approximation), and planned to use the population ceiling as a measure of the necessary reserve size. Depending on where the proposed reserve size falls on the curve of mean time to extinction vs. population ceiling, and on how the real curve and the diffusion approximation curve are shaped, the diffusion approximation could have either a large or a small error and the error could be biased high or low. For instance, the approximation is accurate for some population ceilings for the top predator strategy, but it is unclear how to predict this range a priori. Given that this error is unpredictable and may be very sensitive to the exact parameters that go into the model, it is difficult to know whether the size of the resulting reserve would provide the desired level of security from extinction. This uncertainty flies in the face of the usual assumption that, although quantitative predictions of extinction risks may be inaccurate, relative risks should be less sensitive to inaccuracies in the models. This generalization may not be true for diffusion approximations. In light of this unpredictability, the diffusion approximation should be used with caution as a basis for making management decisions, or should form only one part of the decision process.

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LITERATURE CITED


