

# REPORTS

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## EXTINCTION TIMES IN EXPERIMENTAL POPULATIONS

JOHN M. DRAKE<sup>1</sup>

*National Center for Ecological Analysis and Synthesis, 735 State Street, Ste. 300, Santa Barbara, California 93101 USA*

**Abstract.** Predicting population extinctions is a key element of quantitative conservation biology and population ecology. Although stochastic population theories have long been used to obtain theoretical distributions of population extinction times, model-based predictions have rarely been tested. Here I report results from a quantitative analysis of extinction time in 281 experimental populations of water fleas (*Daphnia magna*) in variable environments. To my knowledge, this is the first quantitative estimate of the shape of the distribution of population extinction times based on extinction data for any species. The finding that the distribution of population extinction times was extraordinarily peaked is consistent with theoretical predictions for density-independent populations, but inconsistent with predictions for density-dependent populations. The tail of the extinction time distribution was not exponential. These results imply that our current theories of extinction are inadequate. Future work should focus on how demographic stochasticity scales with population size and effects of nonrandom variable environments on population growth and decline.

**Key words:** *Cox proportional-hazards regression; Daphnia magna; environmental stochasticity; experimental populations; extinction; random environment; survival analysis; time to extinction; water flea.*

### INTRODUCTION

The distribution of population extinction times is a central question for theoretical population biology (Goel and Richter-Dyn 1974) and is foundational to conservation theory (Beissinger and McCullough 2002, Morris and Doak 2002). Although theoretical models of population extinction are abundant (Richter-Dyn and Goel 1972, Lande and Orzack 1988, Mangel and Tier 1993, Newman et al. 2004) and model-based estimates of the distribution of extinction times are routinely used for conservation planning (Heinsohn et al. 2004, Schtickzelle and Bagueette 2004, Kohlmann et al. 2005, Watson et al. 2005), only indirect evidence about the actual distribution of population extinction times has been gathered from natural populations (Pimm et al. 1993). In contrast, experimental studies have been examined only for qualitative agreement with theoretical predictions, with findings that distributions are highly skewed (Drake and Lodge 2004) and that small initial population size, small carrying capacity, and high environmental variation are risk factors for extinction (Belovsky et al. 1999, 2002, Drake and Lodge 2004). To date, no

analysis has attempted to characterize the distribution of extinction times, although predictions differ among models.

Here I provide a quantitative analysis of the distribution of extinction times for 281 replicate populations of water fleas (*Daphnia magna*) monitored during an experiment that lasted 104 days, in which each population was supported by an independently fluctuating supply of food resource, the green alga *Selenastrum* sp., at one of three levels of temporal variation (low, medium, and high). Time to extinction was previously reported to correlate negatively with environmental variation (Drake and Lodge 2004), although no analysis of the shape of the distribution of extinction times was performed.

In this paper, I report results from semiparametric modeling of those data using Cox proportional-hazards regression. Semiparametric models are useful for describing event-time data, such as data about time to extinction, when the shape of the time-to-event distribution is unknown, complex, or changes over time. The shape of the estimated time-to-extinction distribution was inconsistent with theoretical predictions and cannot be explained as the result of simple experimental artifacts, implying that a more complicated demographic theory will be required to understand how extinction occurs, even in simple populations. Future work should consider how the scaling of demographic

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<sup>1</sup> Present address: Institute of Ecology, University of Georgia, Athens, Georgia 30602-2202 USA.  
E-mail: drake.biosci@gmail.com

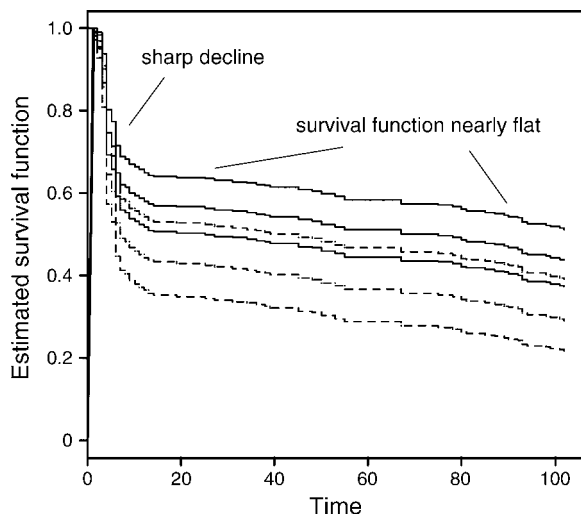


FIG. 1. Estimated survival functions with 95% confidence intervals for experimental populations of water fleas (*Daphnia magna*) in environments with high (dashed lines) vs. low or medium (solid lines) levels of environmental variation are significantly different in proportional-hazards regression ( $P = 0.011$ ). The sharp decline in the first 10 days of the experiment rapidly levels off, consistent with theoretical models in which small populations are not density regulated and quickly escape threat of extinction.

stochasticity (cf. Engen et al. 1998, Drake 2005) and how different regimes of environmental fluctuation (e.g., autocorrelation and environmental trends, such as seasonality and environmental deterioration and improvement) affect the distribution of extinction times (cf. Tuljapurkar 1990, Lande et al. 2003).

#### METHODS AND MATERIALS

##### Data

Data for this analysis were obtained from an experiment to test for effects of environmental variation on extinction and establishment of small populations of *Daphnia magna* in controlled (laboratory) environments (Drake and Lodge 2004). Populations were initiated with five individuals and were monitored daily for 104 days. Each population was supported by the daily addition of a quantity of food independently drawn from a lognormal distribution with specified variance, depending on treatment level (low, medium, high). Previously, a subset of these data was used to test hypotheses about how demographic variance scaled with population size (Drake 2005). For this study, the time series were filtered to obtain the date of extinction for each population that terminated during the experiment. Populations that persisted to the end of the experiment are “right-censored” in the sense of event-time analysis: although the date of extinction was not observed for these populations, the fact that they persisted for the course of the experiment contributes information that can be used to estimate the distribution of extinction times (see below). The complete set of observed

extinction times was used for the present analysis and is published online (see the Supplement). Extinction was observed for 53 of 93 populations in the low-variability treatment, 52 of 92 populations in the medium-variability treatment, and 67 of 96 populations in the high-variability treatment.

##### Analysis

I tested for the effect of the level of experimentally induced environmental variation as a categorical variable on extinction time using proportional-hazards regression (Venables and Ripley 1994). In survival analysis, the hazard function is a model for the instantaneous risk of extinction faced by the population and can be a function of characteristics of the population (i.e., the number of individuals that it contains) and the class of populations to which it belongs (i.e., experimental treatment), and may even change over time. Proportional-hazards regression is a semiparametric approach to modeling survival data without specifying a precise parametric model for the baseline hazard. This approach readily accommodates censored data, i.e., data from populations for which extinction was not observed (Cox and Oakes 1984). This model depends on the assumption, known as the proportional-hazards assumption, that the hazard function  $h(t)$  for any individual (in this case any population of *D. magna*) is related to a baseline hazard  $h_0(t)$  by the equation  $h(t) = h_0(t)e^{\beta^T \mathbf{x}}$ , where  $\mathbf{x}$  is a vector of covariates (e.g., experimental treatment) and  $\beta$  is a vector of coefficients. This assumption can be tested using a method proposed by Grambsch and Therneau (1994). Basically, nonproportional hazards can be modeled as time-varying coefficients that are visualized by plotting a smoothed function of weighted residuals, known as scaled Schoenfeld residuals, against event times. Departure from a horizontal line is evidence of nonproportional hazards.

After testing for effects of experimental treatments, I used the Kaplan-Meier estimator to obtain the fit survival function, which is defined as one minus the cumulative distribution of extinction times. The Kaplan-Meier estimator is widely used in biomedical applications and is the nonparametric maximum likelihood estimator of the survival function (Kaplan and Meier 1958). All analyses were implemented in R version 2.1.0 using the “survival” package (code available in the Supplement; R software, *available online*).<sup>2</sup>

#### RESULTS AND DISCUSSION

Because the estimated effect of medium vs. low environmental variation was not significant ( $P = 0.82$ ), observations from those treatments were pooled for analysis. As expected, the effect of high vs. low and medium levels of environmental variation was signifi-

<sup>2</sup> ([www.r-project.org](http://www.r-project.org))

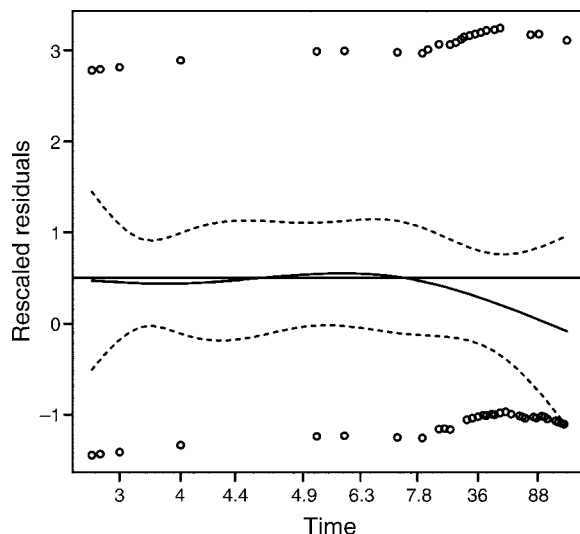


FIG. 2. The smoothed plot of scaled Schoenfeld residuals against time (solid curve; the  $x$ -axis has been log-transformed) is not significantly different from a horizontal line (heavy line) showing no evidence that the proportional-hazards assumption has been violated. Dashed lines are  $\pm 2$  SE for the smoothed (loess) residual plot.

cant ( $P = 0.011$ ). The estimated survival function shows a very sharp decline in the first 10 days, which slows dramatically thereafter (Fig. 1). There was no evidence that these data violate the proportional-hazards assumption, which is diagnosed by deviation from a horizontal line in the smoothed plot of Schoenfeld residuals vs. time (test for slope = 0:  $\chi^2 = 0.39$ ,  $P = 0.53$ ; Fig. 2).

In ecological theory (e.g., Sæther et al. 2005), it is customary to consider the probability distribution of extinction times, which is the negative of the derivative of the survival function with respect to time (Venables and Ripley 1994). Although several models have been developed to study the effect of density dependence on population persistence (e.g., Ludwig 1974, Tier and Hanson 1981, Foley 1994, Middleton et al. 1995, Näsell 2003, Newman et al. 2004), the effect of density dependence on the shape of the distribution of extinction times (rather than on the first few first moments, mean and variance) has not been adequately explored. However, two numerical examples might motivate some expectations.

First, Ludwig (1996) took a discrete-time Markov-chain approach to study effects on extinction times of individual variation in reproduction (demographic stochasticity), temporally uncorrelated variation in average reproduction (environmental stochasticity), and catastrophic mortality. This model belongs to a class of stochastic processes that are very well understood (time-homogeneous, finite state-space, discrete-time Markov chains) and has the benefit of straightforward numerical solution (Norris 1998). Density dependence is included as a Ricker-type stock-recruitment

relationship. This is a relatively mild form of regulation. The main conclusions from that study are that diffusion approximations are likely to be biased when populations are small or for populations that can change size very rapidly. However, we can exploit that study to obtain some insight into the behavior of at least one type of density-dependent model. Particularly, Fig. 7 of Ludwig (1996) shows the survival function for his model with positive intrinsic rate of increase, relatively small carrying capacity (40 individuals), and initial population size at 10% of carrying capacity (four individuals). With the exception that *Daphnia* reproduce continuously, this model is not an inappropriate approximation to the dynamical process that generated the present data. What that survival function shows is that extinctions are rapid at first and decline smoothly so that the probability density function of extinction times is not greatly peaked.

In a more empirically motivated paper, Middleton and Nisbet (1997) studied three models for density dependence applied to data on a population of Acorn Woodpeckers (*Melanerpes formicivorus*): a closed population with density-independent vital rates but an upper limit to population size, logistic and  $\theta$ -logistic regulated populations, and a regulated population with immigration and emigration. As before, these models were developed in discrete time, although overlapping generations resulted from the separation of reproduction and survival, and simulations were used to obtain extinction times rather than numerical solutions. Despite the much more severe density regulation in this model (the estimated value of  $\theta$  was 9.7), Fig. 3 of Middleton and Nisbet (1997) compares visually to Fig. 7 in Ludwig (1996): the distribution of extinction times is peaked and the transition to the tail is gradual. Indeed, Middleton and Nisbet conclude that the tail distribution is effectively exponential, which they suggest supports the practice of extrapolating from observed, estimated, or approximated mean extinction times to tail probabilities.

Based on these previous studies, we might suspect that the tail extinction probabilities for density-regulated populations will generally be exponential (Middleton and Nisbet 1997). To explore this possibility using the present experimental data, I obtained the estimated distribution of extinction times from the estimated survival functions for both the high and pooled low plus medium experimental treatments by dividing subsequent differences in the Kaplan-Meier estimated survival function by subsequent differences in the series of observation times. The resulting distributions appear extraordinarily peaked (Fig. 3), possibly much more than we would have guessed based on the prior analyses. Indeed, we can see this already in the shape of the estimated survival function, which after about day 15 is nearly horizontal, a notable contrast to Fig. 7 in Ludwig (1996). A somewhat more formal comparison can be obtained by inspecting plots of the natural logarithm of

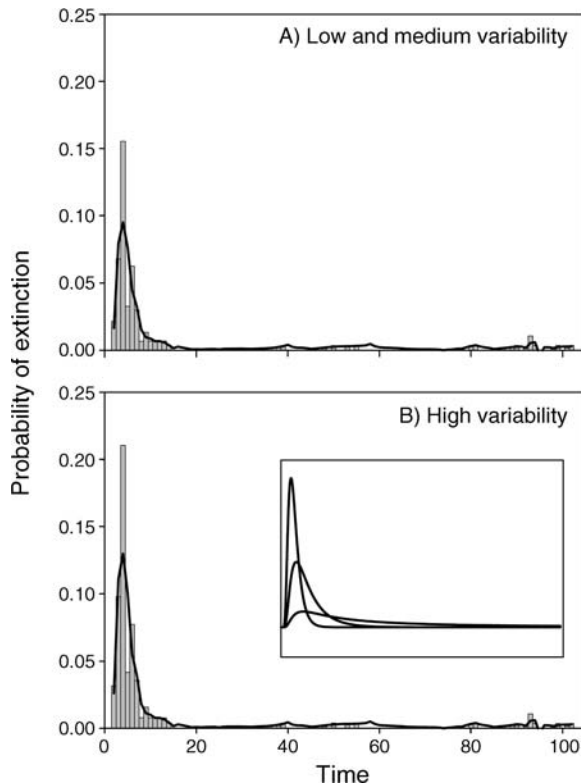


FIG. 3. Estimated distributions of extinction time in experimental populations are extremely peaked in (A) low-variability and medium-variability environments and (B) high-variability environments. These shapes are not predicted by density-dependent models, but the inverse Gaussian distribution of extinction time  $f(t) = x_d(2\pi\sigma^2t^3)^{-1/2} \exp[-(x_d - |\mu|t)^2 / (2\sigma^2t)]$  predicted by the Wiener process approximation, which is often used to model density-independent population growth in a fluctuating environment (Dennis et al. 1991, Middleton et al. 1995), can give these shapes (inset). In the inset plot, the inverse Gaussian distribution was evaluated at  $x_d = 5$ ,  $\sigma^2 = 1$ , and  $\mu = \{0.05, 0.5, 1\}$ . The solid lines overlying the histograms represent local linear regressions (loess) of the estimated distributions.

the estimated extinction probability density function (i.e., the plots in Fig. 3) against time. If the tail were exponential, the regression line fit through these points would be linear with negative slope. However, this pattern is not found in data from either experimental treatment (Fig. 4).

Curiously, the inverse Gaussian distribution of extinction times predicted by the Wiener process, a diffusion model that is often used to model density-independent population dynamics (Lande and Orzack 1988, Dennis et al. 1991, Middleton et al. 1995, Aalen and Gjessing 2001), can be coerced to give the extraordinarily peaked distribution of extinction times observed here (Fig. 3b, inset). Doubtless, alternative density-dependent models could be developed that would give this extraordinarily peaked distribution, although a systematic understanding of density-dependent stochastic models is currently lacking. One possi-

bility is to use chemostat models to develop semi-mechanistic models for the growth of *Daphnia* on the alga resource. A generalized Michaelis-Menten model for resource-limited population growth might exhibit nearly exponential growth until the population was very near carrying capacity, at which point regulation would be quite severe (Edelstein-Keshet 1988). A convenient and tractable phenomenological alternative is the  $\theta$ -logistic model adopted by Middleton and Nisbet (1997); see also Lande et al. (2003:110 ff). Limiting models of these forms function like exponential population growth with a maximum population size or ceiling, such as have been studied previously for both constant and fluctuating environments (MacArthur and Wilson 1967, Goodman 1987). However, both the Wiener process and its bounded counterpart retain the earlier result that the tail probabilities should be exponentially distributed. Thus,

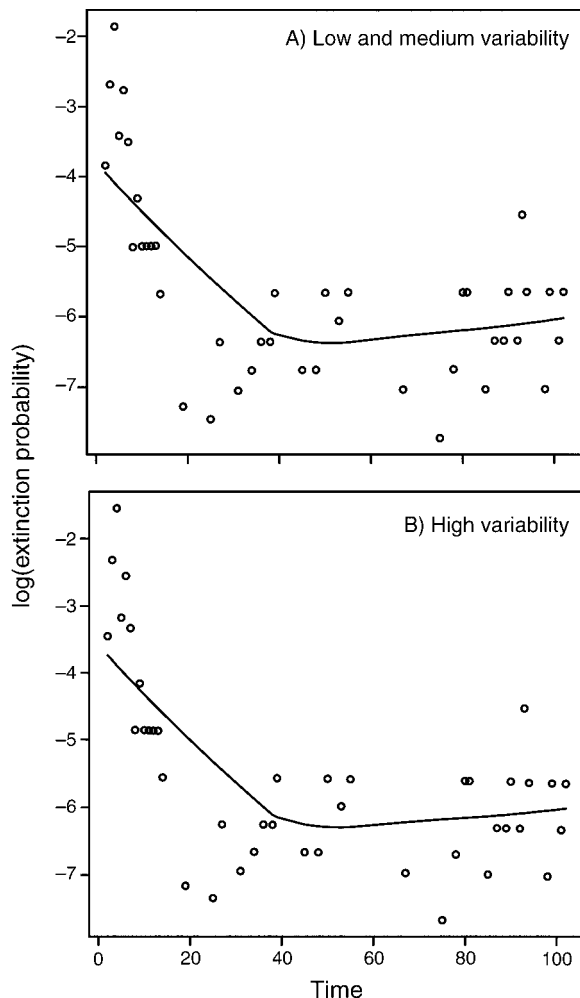


FIG. 4. Plots of the natural logarithm of the estimated extinction probability against time for (A) low- and medium-variability environments and (B) high-variability environments show that the tail of the distribution of extinction times is not exponential. The solid lines are scatterplot smooths obtained from local linear regression (loess).

although regulation of this sort might be postulated to explain the peaked character of the distribution of extinction times observed in this study, it fails to account for the distribution tails (Fig. 4). These inconsistencies are intriguing and warrant further theoretical consideration.

One idea is that per capita demographic variance is an increasing function of population size due to the force of regulation (cf. Engen et al. 1998). The effect would be to render density dependence in the average population growth rate demographically irrelevant from the standpoint of extinction because extinction would be reachable in a short period of time from any population size, whereas populations that declined to small size would quickly (and nearly deterministically) bounce back, a kind of stochastic buffering. A previous analysis of these data showed the opposite pattern, however; i.e., demographic variance in these populations declined with population size (Drake 2005: Fig. 1). Thus, this explanation fails at least in the present case. A further plausible explanation for the shape of the estimated survival function is the presence of trends in the environment. However, to explain the distribution of extinction times observed in this experiment, environmental conditions would have to have been improving over time on average, not deteriorating, which is unlikely under experimental conditions.

In conclusion, these results are the first quantitative estimates of the distribution of population extinction times based on extinction data for any species. The failure of these data to conform to distribution characteristics predicted by theory implies that a better understanding of demographic processes leading to extinction is required for accurate application. Evidently, the relationship between population dynamics and the distribution of extinction times in these experimental populations is quite complicated, and plausible explanations appealing to the scaling of density dependence and the effect of environmental trends should be evaluated. The extent to which extinction times of natural populations are determined by these phenomena or others not yet considered by theory is even less clear.

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#### SUPPLEMENT

Data and R code for analyzing extinction times of experimental *Daphnia* populations (*Ecological Archives* E087-135-S1).