

LETTER

Speed of expansion and extinction in experimental populations

John M. Drake^{1*} and Blaine D. Griffen^{1,2}

¹*Odum School of Ecology, University of Georgia, Athens, GA 30602, USA*

²*Department of Biology, University of South Carolina, Columbia, SC 29208, USA*

*Correspondence: E-mail: jdrake@uga.edu

Abstract

Although the causes of population extinction are well understood, the speed at which populations decline to extinction is not. A testable, counter-intuitive prediction of stochastic population theory is that, on average, for any interior interval of the domain of biologically attainable population sizes, the expected duration of increase equals the expected duration of decline. Here we report the first empirical tests of this hypothesis. Using data from two experiments in which replicate populations of *Daphnia magna* were observed to go extinct under different experimental conditions, we failed to reject the null hypothesis of no difference between the growth and decline phases in populations under constant conditions and conditions with modest environmental variability, but find strong evidence to reject equal first passage time in highly variable environments. These results confirm the prediction of equal passage times entailed by diffusion models of population dynamics, supporting continued application in both population theory and conservation decision making under the restricted conditions where the approximation can be expected to hold.

Keywords

Daphnia magna, diffusion process, extinction, first passage time, fluctuating environments, microcosm, population dynamics, stochastic processes.

Ecology Letters (2009) 12: 772–778

INTRODUCTION

Population extinction is a fundamental problem in biogeography (Jablonski *et al.* 2006; Mittelbach *et al.* 2007), conservation (Morris & Doak 2002; Cardillo *et al.* 2006), ecology (Hanski 1999; Hubbell 2001), and evolutionary biology (Raup & Sepkoski 1982; Jablonski 1998). Important factors governing extinction are population age structure (Tuljapurkar & Orzack 1980; Lande & Orzack 1988), environmental fluctuations (Tuljapurkar 1990), individual variation (Gilpin 1992; Fox & Kendall 2002; Melbourne & Hastings 2008), population regulation (Tier & Hanson 1981; Sabo *et al.* 2004), and Allee effects (Dennis 2002). In the theoretical discussion about these phenomena, models based on univariate diffusion processes have come to dominate because of their generality, mathematical tractability, and because statistical estimation of key parameters is straightforward (Dennis *et al.* 1991; Fieberg & Ellner 2000; Holmes & Fagan 2002; Morris & Doak 2002; Lande *et al.* 2003; Holmes 2004; Sabo *et al.* 2004). A diffusion process is a continuous-time Markov chain with continuous state

variables and is the solution to a stochastic differential equation. In ecology, diffusion processes are often derived as an approximation to a mechanistically motivated branching process (Tier & Hanson 1981; Ludwig 1996). In applications, univariate diffusions are commonly used to model stochastic population growth and have been extended to cover most demographically relevant cases, including age- and stage-structured populations (Tuljapurkar & Orzack 1980; Lande & Orzack 1988), demographic and environmental stochasticity (May 1973; Tuljapurkar & Orzack 1980), nonlinear dynamics (Tier & Hanson 1981), and populations with mating structure (Engen *et al.* 2003). Further, univariate diffusion models are standard in population viability analysis (Dennis *et al.* 1991; Morris & Doak 2002), which is used for conservation planning and policy worldwide. Population viability analysis, if it shows that the probability of extinction in the wild population is at least 20% within 20 years or five generations, is an individually sufficient criterion for international red-listing of endangered species by the International Union for the Conservation of Nature under its Criterion E (Baillie *et al.* 2004).

Thus, these models are both foundational to the advance of ecological theory and of considerable significance in justifying environmental policy decisions that significantly affect species survival, sometimes at substantial cost to society. Accurate models are therefore a high priority for research.

Diffusion approximations make several idealizing assumptions, however (Ludwig 1996). For instance, for species with age-structured demography, the univariate process is only asymptotically correct (Tuljapurkar & Orzack 1980) and populations far from the stable age distribution may exhibit prolonged transients. Further, diffusion approximations may be inaccurate at small population sizes for any species in which change in abundance occurs through the reproduction, growth, and survival of distinct individuals (Ludwig 1996). Thus, whether or not diffusion processes represent a satisfactory theory of extinction is an empirical, not conceptual, question. These extinction models have nonetheless rarely been tested (Griffen & Drake 2008a, 2009).

Here we present such a test based on an overlooked phenomenon predicted by diffusion models – the equal expected duration of the growth and decline phases of a population’s trajectory – that has both substantive biological implications and provides a unique test of the diffusion modelling framework. Although the univariate assumption might appear to be restrictive, it has previously been shown that numerous multivariate demographic processes can be represented by a suitably chosen univariate process (Tuljapurkar & Orzack 1980; Ovaskainen & Hanski 2004). Drawing on the work by Karlin & Taylor (1981), concerning the first passage times of conditional univariate diffusion

processes (including both density-dependent and density-independent processes), Lande *et al.* (2003) made the counterintuitive observation that if the diffusion process is a suitable model for stochastic fluctuations in population size, then for any interval within the range of positive population sizes, the average time to transit the interval in the increasing direction (population growth) is equal to the average time to transit the interval in the decreasing direction (population decline). The quantities compared by this hypothesis are illustrated in Fig. 1. For concreteness, we designate an upper boundary by K and a lower boundary by Q , reflecting the fact that we are typically interested in the fluctuations between some quasi-stationary state (carrying capacity, conventionally K) and quasi-extinction, though we underscore that K and Q may be any arbitrarily chosen values, $Q < K$. The duration of population growth (\mathcal{G}) is the interval between the time at which the population trajectory last crosses Q and the time it first crosses K (assuming that it does so). Similarly, the duration of the final decline to extinction (\mathcal{E}) is the time between last crossing K and first crossing Q (assuming that it does so). We remark that the restriction that the process actually crosses K or Q is important, because it means the processes under consideration are conditional diffusion processes. Denoting by S the first passage time of the unconditional process, the equal first passage-time hypothesis may be expressed as $E[\mathcal{G}] = E[S|K \text{ is attained from } Q] = E[S|Q \text{ is attained from } K] = E[\mathcal{E}]$, which explicitly identifies the role of conditionalization in establishing the equivalence that is at the centre of the equal first passage-time hypothesis. Because population trajectories are stochastic, \mathcal{G} and \mathcal{E}

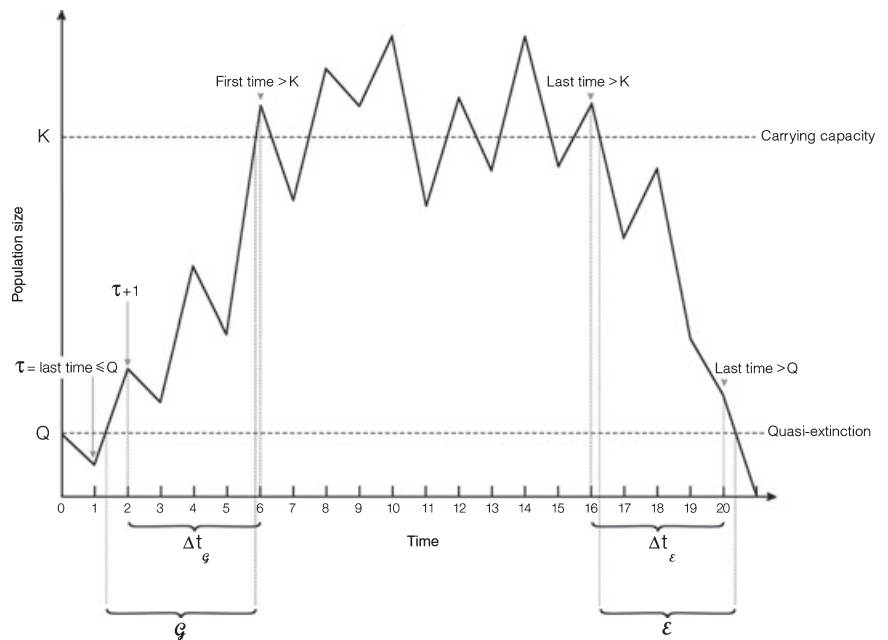


Figure 1 An idealized representation of the changes in population size in a discretely sampled trajectory exhibiting growth, quasi-stationarity, and decline to extinction. The equal passage-time hypothesis holds that the average interval of population growth between quasi-extinction (Q) and carrying capacity (K) should equal the average interval of population decline from K to Q . Since the growth and decline intervals \mathcal{G} and \mathcal{E} are unobserved, the hypothesis test was performed on the unbiased estimators $\Delta t_{\mathcal{G}}$ and $\Delta t_{\mathcal{E}}$.

are random variables. The equal passage-time hypothesis, then, entails that the means of the distributions of \mathcal{G} and \mathcal{E} , $\mu_{\mathcal{G}}$ and $\mu_{\mathcal{E}}$, are equal. An important consequence of equal first passage time is that those populations whose growth is most explosive are also most vulnerable to rapid extinction. That is, although extinction is rare in such populations (because the average population growth rate is relatively large), when it does occur it will typically be fast. A corollary is that the duration of a population's final decline (the expected conditional first passage time) is typically short compared with its expected unconditional first passage time.

We tested the equal passage-time hypothesis using data from two previously reported experiments that tracked the growth and decline of replicated *Daphnia magna* populations under laboratory conditions to test hypotheses about extinction rates in fluctuating environments (Experiment I) and under various habitat size and resource-supply conditions (Experiment II). *Daphnia magna* is a large-bodied, parthenogenetic, herbivorous zooplankton and is commonly used as a model for experimental ecological and evolutionary studies (Ebert *et al.* 2000; Nelson *et al.* 2005; Lampert 2006). These experiments support the equal first passage-time hypothesis in constant environmental conditions but not highly variable environment. Importantly, the predictions we tested do not depend on conditions stronger than that the diffusion is univariate and time-invariant. Particularly, the equal first passage-time hypothesis applies to both density-dependent and density-independent population dynamics. The consistency of findings across these two experiments, carried out with different treatments under different experimental conditions, suggests that the finding of these patterns is not accidental. How general the phenomenon is in nature is unknown.

MATERIALS AND METHODS

Experiments

The details of these experiments have been reported previously (Drake & Lodge (2004), Drake (2005, 2006), Griffen & Drake (2008b)). The datasets used in this analysis may be downloaded from <http://dragonfly.ecology.uga.edu/drakelab/data.html>.

The original aim of Experiment I was to test the hypothesis that the rate of population extinction increased with the variance of random environmental fluctuations. The experiment consisted of 281 populations, started with five individuals each, and subject to different supply regimes of the food resource, the green alga *Selenastrum* sp. (Drake & Lodge 2004; Drake 2005, 2006). Populations were censused daily and monitored for 104 days (median extinction time: 37 days). At censusing times, populations larger than nine individuals were categorically scored as 'abundant'. These

data showed an effect of high environmental variation on population extinction rate, but little evidence for a difference between moderate and zero environmental variation (Drake 2005).

The original aim of Experiment II was to test for interactions between two regulators of population growth (habitat size: two levels; food supply: three levels) predicted to differently affect reproductive ratio and carrying capacity (Griffen & Drake 2008b). Treatments were fully crossed and replicated 16 times, yielding a total of 96 populations. Populations were started with one non-gravid adult and four juveniles, censused weekly, and monitored until all populations were extinct (median extinction time: 12 weeks). These data showed that extinction time was correlated with both carrying capacity and reproductive ratio. Further, both habitat size and food supply affected both carrying capacity and reproductive ratio, implying that the causal pathways by which environmental characteristics influence extinction rate are intertwined.

Statistical analysis

To prepare data for analysis, we first chose Q and K as follows. For analysis of both experiments, the quasi-extinction threshold Q was set at the initial population size $N_0 = 5$. For Experiment II, K was chosen to be carrying capacity and obtained for each population from the least squares estimate using a Ricker model (Griffen & Drake 2008b). In Experiment I, population sizes ≥ 10 were not distinguished. However, as the equal first passage hypothesis holds for any interior interval in the population state space, we may set the upper boundary to any convenient population size $K > Q$. Accordingly, for Experiment I we used $K = 9$, i.e. the maximum uniquely distinguished population size. Having chosen Q and K , we filtered the observed time series to include only those populations that were observed both to exceed K at some point and to proceed to extinction. These criteria were met by 116 out of 281 (41%) populations from Experiment I and 78 out of 96 (81%) populations from Experiment II.

Although diffusion models represent population fluctuations as variations in a continuous variable over a continuous time interval, the data are discrete in two ways. First, observed population sizes are discrete, reflecting the fact that organism abundance is integer-valued, a property that gives rise to several important demographic phenomena in nonlinear systems. Second, our time intervals were artificially discretized by periodic censusing. As population abundance does not explicitly appear in the equal passage-time hypothesis, the first discretization is not confounding. To address the second discretization, we estimate the unobserved intervals \mathcal{G} and \mathcal{E} using the following unbiased estimators. For \mathcal{G} , we used $\Delta t_{\mathcal{G}}$, the interval with endpoints

$\tau + 1$, where τ is the last time the population was observed to be less than or equal to the lower boundary, and Q and the first time the population was observed to exceed K (Fig. 1). Analogously, \mathcal{E} is replaced by the interval $\Delta t_{\mathcal{E}}$, the endpoints of which are the time of the last observation greater than K and the time of the last observation greater than Q . Using these estimated quantities, we tested the null hypothesis $H_0: \mu_{\Delta t_{\mathcal{G}}} = \mu_{\Delta t_{\mathcal{E}}}$ with nonparametric bootstrap. From 100 000 resampled datasets, we calculated the mean difference between the growth and decline phases, the 95% confidence limits on the mean difference, and a P -value for the null hypothesis from the empirically obtained cumulative distribution function.

Data from Experiment II, where populations were fully censused at all population sizes, were also used to test the prediction that populations with the fastest expansion also exhibited the fastest decline. To quantify expansion, we obtained the basic reproductive ratio λ from the ratio of the second censused population size to the initial population size, $\lambda = N_2/N_0$, as the generation time was roughly 2 weeks (Griffen & Drake 2008b). We then used a

Spearman's rank-order correlation to test for a relationship between $\log(\lambda + 1)$ and $\log(\mathcal{E} + 1)$ and analysis of covariance to rule out experimental treatments as confounding factors.

RESULTS

Overall, 194 out of 377 (51%) time series were analysed in this study. Of 281 populations from Experiment I, 137 (49%) went extinct before attaining K and 28 (10%) were censored at the end of the experiment. Of 96 populations in Experiment II, 18 (19%) were discarded because they failed to first reach K before going extinct, or because estimates of K were not estimated to be greater than Q . (These populations typically exhibited rapid population crash). The remaining 78 (81%) populations commonly rose rapidly to K , fluctuated around this quasi-stationary state, and then declined rapidly (Fig. 2). In Experiment I, the average duration of growth was 1.36 days (± 0.16 SE) and the average duration of decline was 0.97 days (± 0.18 SE). In Experiment II, the average duration of growth was

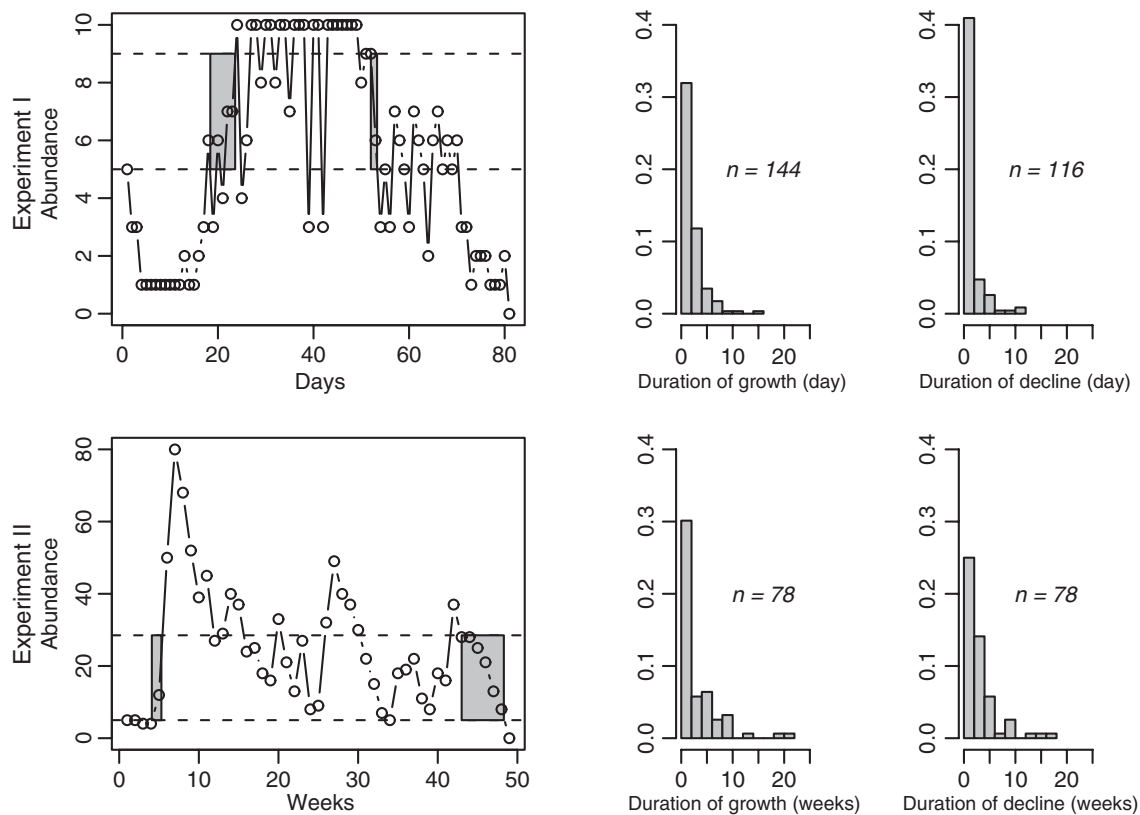


Figure 2 Fluctuations and distributions of growth and decline phases for representative populations from two experiments. Estimated duration of growth, $\Delta t_{\mathcal{G}}$, and decline, $\Delta t_{\mathcal{E}}$, are defined in the main text. The population trajectory in the upper left panel is for population 51 (high variability treatment) from Experiment I. The population trajectory in the lower left panel is for population 12 (treatments: large chamber size, medium food) from Experiment II. The grey regions identify the true intervals of growth and decline.

Experiment	Treatment	<i>P</i> -value	EMD	95% CI
I	All treatments pooled	0.059	0.388 day	−0.10, 0.84
I	Low variability	0.238	0.238 day	−0.43, 0.86
I	Medium variability	0.443	0.048 day	−0.88, 0.83
I	High variability	0.025*	1.03 days	0.03, 2.00
II	All treatments pooled	0.448	0.077 week	−0.90, 1.08

EMD, estimated mean difference.

*Significant at the $\alpha = 0.05$ level.

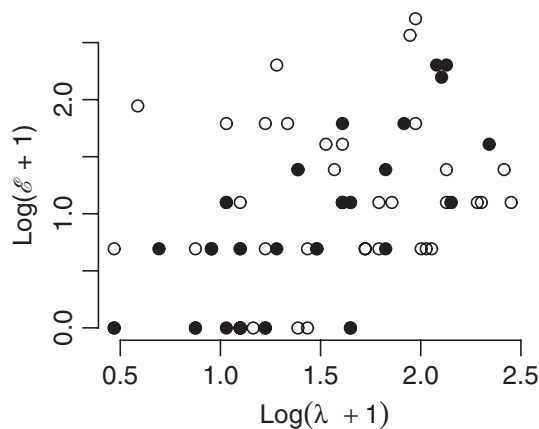


Figure 3 Time to quasi-extinction is correlated with population growth in Experiment II. There was no evidence for a difference between small chambers (filled circles) and large chambers (open circles).

Table 2 Analysis of covariance table showing tests for effects of $\log(\lambda + 1)$ and experimental treatments on $\log(\ell + 1)$

	d.f.	Sum of squares	Mean sum of squares	<i>F</i> -value	Pr ($> F$)
$\log(\lambda + 1)$	1	9.935	9.935	22.795	< 0.0001
Size	1	0.055	0.055	0.126	0.724
Food	2	0.357	0.178	0.410	0.666
Residuals	73	31.817	0.436		

2.6 weeks (± 0.45 SE) and the average duration of decline was 2.5 weeks (± 0.37 SE). These intervals of expansion and decline were 1–2 orders of magnitude smaller than typical extinction times in these populations.

For populations from Experiment I, in which environmental conditions were manipulated to fluctuate randomly, a bootstrap test for a difference of means narrowly failed to provide evidence to reject the prediction of equal passage times at the $\alpha = 0.05$ level when all treatments were pooled for analysis (Table 1). To further investigate, we repeated the analysis separately for each treatment of

Table 1 Results of bootstrap test for a difference of means between the estimated growth and crash phases of a population trajectory

zero, moderate, or high levels of experimentally imposed random environmental variation. For populations from zero and moderate variability treatments, we again failed to reject the null hypothesis of equal first passage time (Table 1). By contrast, the hypothesis of equal first passage times was strongly rejected for populations from the high variability treatment (Table 1). For populations from Experiment II, in which environments were held constant with food and habitat size treatments, the same procedure failed to provide evidence for a difference between Δt_g and Δt_ℓ (Table 1). Finally, there was strong evidence for a correlation between $\log(\lambda + 1)$ and $\log(\ell + 1)$ in Experiment II (Fig. 3; Spearman rank-order correlation: $\rho = 0.49$, $P < 0.0001$) and no evidence for any additional effects of experimental treatments (Table 2). In conclusion, we therefore find evidence to reject equal first passage times in treatments with high variability environments, but not treatments with constant or low variability environments.

DISCUSSION

Population extinction models used in conservation have rarely been tested with replicated data (Griffen & Drake 2008a) and univariate diffusions are among the most commonly used stochastic models of population extinction (Dennis *et al.* 1991; Morris & Doak 2002; Lande *et al.* 2003). Here, we draw attention to a previously untested prediction of these models and report on an empirical test using data from two experiments. The results of our analysis are mixed. In one experiment, we find no reason to reject the equal passage hypothesis, a phenomenon that implies equivalence between population growth and decline, despite the fact that experimental conditions were contrived to impose the small population sizes at which the assumptions of the diffusion approximation are most likely to be violated. In another experiment, we detect an estimated mean difference of 1.03 days in high variability treatments, but not zero and moderate variability treatments. Although small in absolute terms, this deviation is large relative to the estimated average duration of decline in these populations (0.75 day).

It is plausible that the different results for the two experiments result from the severity of environmental fluctuations, which were manipulated in Experiment I and held constant in Experiment II. After all, one of the main consequences of environmental stochasticity, especially in the presence of density dependence, is that population dynamics become erratic. This explanation is supported by the failure to reject the null hypothesis when analysis was restricted to the zero- and moderate-variability treatments. We remark that this difference between the high variability treatment and pooled zero- and moderate-variability treatments is consistent with the results of a previous analysis in which time-to-extinction was the focus (Drake 2005). Further, it is precisely the assumption of smoothness that permits population dynamics in variable environments to be approximated by a univariate diffusion process (Tuljapurkar 1990). To our knowledge, all of the various derivations in the ecological literature make the assumption that the variance of the process is small compared with the growth rate of the population. How small is small enough? Previous writers have answered this question on theoretical grounds (Tuljapurkar 1990; Ludwig 1996). Here we augment these arguments with data. Particularly, we find that over a range of environmental variabilities consistent with variabilities observed in the field (Drake & Lodge 2004), the environmental noise in zero- and moderate-variability treatments was indeed small enough, but that noise in the high-variability treatments exceeded what could be tolerated for the diffusion approximation to remain valid. We conclude that the magnitude of environmental variation may be a critical phenomenon that determines whether or not diffusion models of population fluctuation are satisfactory models of the extinction process.

The, perhaps counterintuitive, predicted equivalence between the duration of population growth and population decline has important implications for understanding population expansion and decline. First, as pointed out by Lande *et al.* (2003) and empirically supported by Griffen & Drake (2009), the duration of a population's final decline generally will be orders of magnitude smaller than the expected time to extinction from its quasi-stationary state, implying that when populations are destined to extinction, a future condition that cannot be known in advance, the process of decline may be very fast. Second, the equivalence between the expected duration of growth and expected duration of decline also entails the weaker relationship that those populations that expand fastest can also exhibit the most rapid declines. The conservation implications of this property are immediate: we cannot separate the 'small-population paradigm' from the 'declining-population paradigm' (Caughley 1994). Although populations with higher growth rates have smaller chances of extinction, in the event that extinction does occur it will typically happen faster, all

else being equal. Applying this general rule to conservation particularly, we conclude that a cost of taking actions to promote the growth rate of a population is that when extinction does occur it will be fast and surprising, unless actions are taken simultaneously that reduce the amount of variation in population trajectories. Caughley (1994) has written, 'One of the most distressing characteristics of the declining-population paradigm is its dearth of theoretical underpinning'. We submit that the connection between population growth rate and the expected duration of final decline, predicted by the diffusion theory of stochastic population growth and illustrated empirically here in Fig. 3, comprises a starting point from which the needed theory might be developed.

Future research is needed to test this theory in the field, however. In an early contribution to this question, Holmes & Fagan (2002) reported on declines in natural populations. But, their definition of a population's final decline, the subtrajectory leading to extinction in which no population increases are observed, differs from that defined by the diffusion theory used in this paper and of Lande *et al.* (2003) and so does not allow straightforward comparison. To our knowledge, the diffusion theory of population extinction does not make any specific testable predictions concerning the interval of non-increasing decline.

In conclusion, although we have provided some evidence for the equal first passage hypothesis, how generally this phenomenon holds is unknown. Our failure to reject equal first passage times in most experimental treatments explored provides some optimism that this pattern may hold more generally. Of course, the conditions under which these experimental populations persisted were highly contrived. In the light of the high variability treatment of Experiment I, it is reasonable to wonder if the non-stationary, heterogeneous conditions that buffet natural populations may well render these patterns far more complicated.

ACKNOWLEDGEMENTS

This research was supported by the University of Georgia and a grant from the University of Georgia Research Foundation. We thank A. Silletti for assistance with experiments and K. Carter for assistance drawing Fig. 1. We thank R. Lande and B. Dennis for discussions on reversible stochastic processes.

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Editor, Michael Bonsall

Manuscript received 15 December 2008

First decision made 26 January 2009

Second decision made 29 March 2009

Manuscript accepted 7 April 2009