Scaling rules for the final decline to extinction
Blaine D. Griffen* and John M. Drake
Oдум School of Ecology, University of Georgia, Athens, GA 30605, USA

Space–time scaling rules are ubiquitous in ecological phenomena. Current theory posulates three scaling rules that describe the duration of a population’s final decline to extinction, although these predictions have not previously been empirically confirmed. We examine these scaling rules across a broader set of conditions, including a wide range of density-dependent patterns in the underlying population dynamics. We then report on tests of these predictions from experiments using the cladoceran Daphnia magna as a model. Our results support two predictions that: (i) the duration of population persistence is much greater than the duration of the final decline to extinction and (ii) the duration of the final decline to extinction increases with the logarithm of the population’s estimated carrying capacity. However, our results do not support a third prediction that the duration of the final decline scales inversely with population growth rate. These findings not only support the current standard theory of population extinction but also introduce new empirical anomalies awaiting a theoretical explanation.

Keywords: carrying capacity; Daphnia magna; population extinction; population growth rate; scaling rules

1. INTRODUCTION
The consistency of certain spatial and temporal dynamics among highly different nonlinear ecological systems is astounding (Damuth 1998; Schneider 2001). Such scaling rules have been found to characterize individual behaviour (e.g. Sims et al. 2008); the use of space by organisms (Jetz et al. 2004); life-history patterns of individuals (e.g. Enquist et al. 1999); population growth, regulation and abundance (e.g. Belgrano et al. 2002); community stability (Otto et al. 2007); and, by integrating across species ensembles, even patterns of biodiversity across regional landscapes (e.g. Bellwood & Hughes 2001; Volkov et al. 2007). Focusing at the population level, recent work has highlighted scaling rules for population dynamics, including the scaling rules for demographic stochasticity (Desharnais et al. 2006), population size (Carbone & Gittleman 2002) and population growth rate (Savage et al. 2004).

Scaling rules for population persistence time also have been empirically examined (e.g. Diamond 1984; Belovsky et al. 1999). These studies confirm that population extinction risk is negatively correlated with habitat area, population density, carrying capacity and individual longevity, and is positively correlated with the variation in population size and environmental variability. However, a population’s persistence time (i.e. the total time it exists before extinction) may be independent of the speed with which it disappears once it has started its final decline to extinction. Understanding this final decline to extinction could provide useful information for conservation by informing the amount of time available for implementing conservation strategies to avoid extinction.

Recently, Lande et al. (2003) have proposed scaling rules for the duration of the final decline of a population to extinction. They derived these scaling rules using a model based on a diffusion process confined to the interval between extinction and a fixed ceiling. Models of this sort are commonly used to represent population growth in a randomly fluctuating environment (e.g. Lande et al. 2006) and are standard in conservation biology (e.g. Lande 1993; Middleton et al. 1995; Meir & Fagan 2000; Morris & Doak 2002). The new approach taken by Lande et al. (2003) was to introduce an interval between some small positive population size (extinction or quasi-extinction) and larger population size (carrying capacity) and study the conditional diffusion process that enters the interval from above and proceeds to cross the (quasi-)extinction boundary without returning to the upper boundary. Such a process can be interpreted as the process of a population’s final decline. From their analysis (Lande et al. 2003, pp. 47–49), we have the following hypotheses (figure 1).

Hypothesis 1.1. If a population starts at carrying capacity \(K\), and if it has a positive long-run growth rate when it is below \(K\), then the expected duration of the final decline, \(T_E\) from \(K\) to extinction (or to quasi-extinction, \(T_Q\)) is generally much shorter than the mean persistence time of the population before extinction, \(T_K\), i.e. \(T_E \ll T_K\).

Hypothesis 1.2. The duration of the final approach to extinction, \(T_E\) (or \(T_Q\)), increases logarithmically with increasing carrying capacity, i.e. \(T_E \propto \ln(K)\).

Hypothesis 1.3. The duration of the final approach to extinction, \(T_E\) (or \(T_Q\)), is inversely proportional to the intrinsic growth rate, i.e. \(T_E \propto 1/(\lambda)\).

Importantly, these scaling rules were derived using a ceiling model, in which population growth is assumed to be density independent up to some reflecting boundary or carrying capacity, \(K\), after which growth is density dependent. Since such processes are not typical

* Author and address for correspondence: Department of Biological Sciences and Marine Science Program, University of South Carolina, Columbia, SC 29208, USA (bgriffen@biol.sc.edu).

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2. MATERIAL AND METHODS  

(a) Extension of theoretical scaling rules  

Lande et al. (2003) derived the scaling rules given in hypotheses 1.1–1.3 using a ceiling model with demographic and environmental stochasticity. To study these scaling rules in more generality, we require a model that takes as some limiting form the logistic ceiling model of Lande (2003), while for 0 < \theta < \infty we represent a wide spectrum of possibilities for the form of density dependence. We incorporated environmental and demographic stochasticity as follows. The term in the right-hand side of equation (2.2) contained within the outer brackets can be viewed as a density-dependent growth rate, which we denote by \lambda_N. We incorporated environmental stochasticity by considering \lambda_N to be a random variable, unique for each t. As a growth rate, it must be positive and continuously distributed. The gamma distribution is a flexible distribution with these properties, and we therefore assumed that \lambda_N was drawn from a gamma distribution. We incorporated demographic stochasticity by assuming that the population size at time \tau was a discrete random variable with a mean equal to \lambda_N. We assumed that reproductive events were independent and could therefore be represented by a Poisson distribution with rate parameter equal to the gamma-distributed random variable, \lambda_N. Probability distributions in which the parameters themselves are random variables are known as mixture distributions. The parametrized version of equation (2.2) thus included environmental and demographic stochasticity using a gamma-mixed Poisson distribution (Johnson et al. 1993, p. 308), and can be approximated by a diffusion process with a mean

\[ M(N) = E[N_{t+1}] = N_t + M(N)dt + \left(\sqrt{V(N)}\right)dB, \]

and variance

\[ V(N) = \frac{\exp(\lambda(1 - (N/K)^\theta))}{(N\beta + 1)^{-1}}, \]

where \beta is the scale parameter of the gamma distribution which governs the degree of environmental stochasticity (see appendix I for a more complete description and a derivation of this model).

Our model simulations therefore followed Lande et al. (2003) by updating population size at \( t + 1 \) as

\[ N_{t+1} = N_t + M(N)dt + \left(\sqrt{V(N)}\right)dB, \]

where \( dt \) is the increment of time used in the diffusion process (0.1), and \( B \) is a normally distributed random number representing Brownian motion occurring in the time increment \( dt \). We extended the predictions of Lande et al. to a more general case by examining this model at \( \theta = 0.1, 0.25, 0.5, 1, 2, 4, 8, 16, 32, 64 \).

We varied population growth rate \( \lambda = 11, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0 \) and carrying capacity \( K = \{4, 8, 16, 32, 64\} \) in our model simulations for each \( \theta \) given above. Model simulations were started with \( N_0 = K \) and continued until the population went extinct (\( N_t \leq 0 \)). We also replicated this set of simulations over a range of values for \( \beta = 0.5, 2, 3.5, 5 \) to determine whether these scaling rules changed depending on the strength of environmental stochasticity.

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(Sibly et al. 2005), our first goal was to establish the generality of these rules within a larger class of models of which the ceiling model studied by Lande et al. (2003) is a special case. Second, we sought empirical support for these putative scaling rules using data on extinction trajectories in laboratory populations of Daphnia magna (Griffen & Drake 2008a). Support for hypothesis 1.2 is available for vertebrate populations (Fagan & Holmes 2006), but to our knowledge hypotheses 1.1 and 1.3 have not been examined. We show that the scaling rule given in hypothesis 1.1 is indeed predicted for populations where growth is approximately density-dependent population growth processes, and that this hypothesis is supported by extinction trajectories of empirical populations. However, we show that the scaling rules given in hypotheses 1.2 and 1.3 are only predicted for populations where growth is approximately density independent up to \( K_c \) and further that these scaling rules are only partially supported by empirical data. These findings represent an important step towards predicting population extinction dynamics.
We determined the duration of the final decline to extinction, \( T_{E1} \), for each simulation by calculating the interval from the last time the population dipped below \( K \) until extinction (figure 1). The distributions of \( T_{E1} \) and \( K \), from our simulated populations were both strongly right-skeewed. We therefore determined whether the scaling rule given in hypothesis 1.1 above, \( T_{E1} \approx K \), held for model populations over the full range of values for \( \theta \) by comparing \( T_{E1} \) and \( K \) using a paired Wilcoxon signed-rank test at each \( \theta \). Next, we determined whether the scaling rule given in hypotheses 1.2 and 1.3 above, \( T_{E2} \propto \ln(K) \) and \( T_{E3} \propto 1/\ln(\lambda) \), held over the full range of values for \( \theta \) using model comparison to select the best model from a field of alternatives comprising both the predicted scaling rules and the untransformed \( K \) and \( \ln(\lambda) \) in all combinations. Thus, the following four linear models were fit to the simulated data, assuming a normal error distribution:

\[
\begin{align*}
(1) & \quad T_{E1} = a(\ln(\lambda)) + bK + c \\
(2) & \quad T_{E2} = a\left(\frac{1}{\ln(\lambda)}\right) + bK + c \\
(3) & \quad T_{E3} = a(\ln(\lambda)) + b(\ln(K)) + c \\
(4) & \quad T_{E3} = a\left(\frac{1}{\ln(\lambda)}\right) + b(\ln(K)) + c
\end{align*}
\]

where \( a \) and \( b \) are coefficients and \( c \) is the intercept. We then used AIC to determine which model provided the best fit to the simulated data. Model 4 is the model that agrees with both hypotheses 1.2 and 1.3, thus, selection of this model would concurrently support both of these hypotheses.

**c) Statistical examination of scaling rules**

Two important parameters in the hypotheses given by Lande et al. (2003) are the intrinsic rate of increase, \( \ln(\lambda) \), and the carrying capacity, \( K \). We estimated both of these parameters simultaneously by fitting the Ricker model to each time series of population sizes from the experimental populations (all parameter estimates were significant at the 0.05 level). We then determined \( T_{E1} \) and \( K \) for each experimental population as described above for the model-generated population data. We also performed a duplicate set of analyses with parameters that we estimated independently. Specifically, we estimated \( \ln(\lambda) \) as \( \lambda = \ln(N_f/N_i) \), using \( N_f \) rather than \( N_i \) because the generation time in our experimental systems was approximately twice the length of our sampling interval (B. D. Griffen 2007, unpublished data), and using the median population size as an estimate of \( K \). However, results with these parameter estimates were not qualitatively different from that when both parameters were estimated simultaneously using the Ricker model. We therefore report only the results with simultaneously estimated parameters.

While the experiment included a total of 96 populations (see Griffen & Drake 2008a), not all of these were included in the analyses. Hypotheses 1.1–1.3 above apply only to populations with positive long-run growth rates at population sizes below \( K \) (Lande et al. 2003). Fifty-one of the sixty-nine experimental populations had \( \lambda \leq 1 \). These populations were excluded from the analyses, leaving a total of 45 populations. There was a single outlying population that had \( T_{E1} \) that was nearly twice that of any other population. However, the results of analyses were qualitatively the same with and without including this population. We therefore report only the results with this population included.

Hypotheses 1.1–1.3 apply equally to the decline to complete extinction and the decline to some previously stipulated population size, i.e. quasi-extinction (see figure 1). We tested each of these hypotheses using our experimental data for both the decline to complete extinction (population size \( k=0 \)) and the decline to quasi-extinction (population size \( k=5 \)). This provided two separate tests of each theory. \( T_{E1} \) and \( T_{E2} \) were determined for each population using the same method as described above for the analysis of model-simulated populations.

Hypothesis 1.1 \( (T_{E1} \ll T_{E2} \text{ and } T_{E2} \ll T_{E3}) \): As with model-simulated populations, the distributions of \( T_{E1} \), \( T_{E2} \) and \( T_{E3} \) from our experimental populations were all strongly right-skewed. We therefore used a Wilcoxon signed-rank test to test the hypothesis that the duration of the final decline to extinction \( (T_{E1}) \) or the decline to quasi-extinction \( (T_{E2}) \) are much shorter than the persistence time of the population after it first reaches \( K \) and before extinction \( (T_{E3}) \).

Hypotheses 1.2 and 1.3 \( (T_{E1} \text{ and } T_{E2} \text{ increase proportionally with } \ln(k) \text{ and with the inverse of } \ln(\lambda) \)): The estimates of carrying capacity and the intrinsic rate of increase were positively correlated across populations (Pearson’s correlation \( = 0.71, p < 0.0001 \)). We therefore simultaneously tested the hypotheses that the duration of the final decline to extinction increases logarithmically with \( K \) and with the inverse of \( \ln(\lambda) \), using identical analyses as we used with model data.

Specifically, we tested hypotheses 1.2 and 1.3 by fitting the four linear models described above. As with the analysis of model data, we then used AIC to determine which of the four models best fit the experimental data. Model 4 is the model that agrees with both hypotheses 1.2 and 1.3, thus selection of
this model would concurrently support both of these hypotheses. Some populations included in the analyses had values of $l$ which were only slightly greater than one, resulting in $\ln(l)$ values that were very close to zero and $1/\ln(l)$ values that were extremely large (i.e. outliers). To avoid this, we instead used $\ln(C_1/C_0/C_1)$. We repeated these analyses using both $T_E$ and $T_Q$ to test the scaling of the final decline to both total extinction and quasi-extinction, respectively. All model simulations and statistical analyses were performed using R v. 2.4.1.

3. RESULTS

(a) Extension of theoretical scaling rules

Results of our model simulations did not change qualitatively across the range of environmental stochasticity examined. For brevity, we therefore report only model results at intermediate levels of environmental stochasticity ($\beta = 2$), but the patterns reported apply equally to the range of tested values for $\beta$ (0.5–5). Simulated populations started at carrying capacity, and most fluctuated around carrying capacity for some time (depending largely on the magnitude of $K$), and then rapidly declined to extinction.

Our model simulations demonstrate that the scaling rules, predicted by Lande et al. (2003) for the special case where density dependence moderates only population growth after the carrying capacity has been reached (when $q/N$), may in part be generalized to a broader range of types of density-dependent population growth. Specifically, our simulations show that hypothesis 1.1, which $T_K \sim \ln(K)$, applies for all types of density-dependent growth examined ($p \ll 0.0001$ for all combinations of $\theta$, $K$ and $\ln(l)$). The difference between $\ln(T_K)$ and $\ln(T_E)$ for model-simulated populations increased logarithmically with $K$, regardless of the value of $\theta$. Absolute differences between $T_K$ and $T_E$ ranged from 2 or 3 time steps at low $K$ to more than 25 000 time steps at the highest values of $K$ examined.

Our simulations demonstrate that hypotheses 1.2 and 1.3, however, have a much more limited application. At high values of $\theta$, although at values below infinity used in the ceiling model, scaling rules of hypotheses 1.2 [$T_E \sim \ln(K)$] and 1.3 [$T_E \sim 1/\ln(l)$] still apply (as...
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Table 1. Results from linear models and model selection to test hypotheses 1.2 (that $T_E$ or $T_Q$, increases proportionally with $\ln(K)$) and 1.3 (that $T_E$, or $T_Q$, increases proportionally with $1/\ln(\lambda + 0.1)$). (p-Values give significance of parameters estimated in each linear model. AIC values compare the fit of the four models. ΔAIC>2 for a given model would indicate that it is substantially less supported compared with the best model (the lowest AIC).)

<table>
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<th>$\ln(\lambda + 1)$</th>
<th>$K$</th>
<th>$1/\ln(\lambda + 1)$</th>
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<th>$\ln(K)$</th>
<th>$1/\ln(\lambda + 1)$</th>
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<td>0.03</td>
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<td>0.21</td>
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then rapidly declined to extinction (see plots of time series from all 96 experimental populations in appendix III). Support for hypotheses 1.1–1.3 was similar when examining both the decline to final extinction and the decline to quasi-extinction.

Hypothesis 1.1 ($T_E$ or $T_Q < T_K$): Consistent with the theoretical predictions, time before the final decline to extinction (15.8 ± 11.0 weeks, mean ± s.d.) was longer than the duration of the final approach to extinction (2.8 ± 1.7 weeks) (Wilcoxon signed-rank test, $p < 0.0001$; figure 3). The results were qualitatively unchanged when comparing the time before the final decline to the duration of the decline to quasi-extinction (2.2 ± 1.7 weeks, $p < 0.0001$).

Hypotheses 1.2 and 1.3 ($T_E$ or $T_Q$ increases proportionally with $\ln(K)$ and with $1/\ln(\lambda + 0.1)$): Experimental results provided mixed support for these predicted scaling rules. Specifically, when examining the decline to final extinction ($T_E$), none of the terms with $\lambda$ in models 1–4 were significant, while all the terms with $K$ were significant (table 1, figure 4). This supports the hypothesis that $T_E$ scales proportionally with $\ln(K)$ (hypothesis 1.2), but does not support the hypothesis that $T_E$ scales with $1/\ln(\lambda + 0.1)$ (hypothesis 1.3). However, model selection of the linear models with experimental data did not detect a difference between any of the models, indicating that $T_E$ scaled just as closely with untransformed $K$ as with $\ln(K)$ (table 1, figure 3e–h). These patterns were replicated closely when examining the decline to quasi-extinction, with the exception that terms with untransformed $K$ were also marginally non-significant, while terms with $\ln(K)$ were significant (table 1), lending additional support to hypothesis 1.2 (figure 3e–h).

4. DISCUSSION
In this paper, we report that the scaling rules for the final decline to population extinction given by Lande et al. (2003) partially extend to a broader range of density-dependent

(b) Empirical tests of scaling rules
Most of the 45 populations rose quickly from the initial population size of five individuals to carrying capacity, fluctuated around carrying capacity for some time and

Figure 3. Duration of final decline to extinction as a function of (a, e) carrying capacity, $K$; (b, f) $\ln(K)$; (c, g) intrinsic rate of increase, $\ln(\lambda + 1)$; and (d, h) $1/\ln(\lambda + 1)$. (a–d) Time to total extinction, $T_E$ and (e–h) time to quasi-extinction, $T_Q$.

indicated by the best fit of linear model 4 to the simulated data; figure 2). However, at lower values of $\theta$ the scaling rules are much less clear, as alternative models were selected (figure 2). To examine this more closely, we varied $\theta$ more finely within this transition range and found that the cut-off is around $\theta = 2.49$. Above this cut-off, scaling rules proposed by Lande et al. (2003) apply; below this cut-off, scaling of the final decline to extinction is less clear, with model selection most frequently showing the best fit to simulated data by linear models 1 or 2 (appendix II). All coefficients in linear models 1–4 were highly significant ($p < 0.0001$) for all model simulations, except for simulations at $\theta = 0.1$, where none of the coefficients that including $\lambda$ were significant.
conditions. Hypothesis 1.1 \( (T_E \text{ or } T_Q \ll T_K) \) applied across the entire range of conditions examined. By contrast, hypotheses 1.2 and 1.3 \( (T_E \text{ or } T_Q \text{ increases proportionally with } \ln(K)) \) and with \( 1/\ln(\lambda + 0.1) \) were applicable only when density dependence is relatively unimportant for populations that are below \( K \), i.e. under the ceiling model conditions used by Lande et al. (2003). When density dependence also influences populations that are far below \( K \) \( (\theta < 2.49) \), other scaling relationships apply (figure 2). We also note here that demographic stochasticity is an important driver of extinction dynamics and that this may more appropriately be modelled using a discrete process. However, we used a diffusion model for consistency with the original scaling rules proposed by Lande et al. (2003) so that deviations from their predictions under different density-dependent conditions could not be attributed to differences in modelling approaches. Our experimental results provide mixed support for the scaling rule predictions. Specifically, we found strong support for the prediction that the duration of final decline is small relative to population persistence prior to extinction (hypothesis 1.1). Our data also supported the more specific prediction that the duration of the final decline to extinction scales with \( \ln(K) \) (hypothesis 1.2). However, our data did not support the prediction that the duration of the final decline to extinction scales with the inverse of the long-run population growth rate (hypothesis 1.3).

Laboratory experiments provide a valuable venue for testing population extinction theory (Griffen & Drake 2008a). Our laboratory system allowed strict control of factors affecting carrying capacity and population growth rate, but may have provided a stringent test of the scaling rules for the final decline to extinction. Experimental variations in \( \lambda \) and \( K \) resulting from our experiments were relatively small compared with variations that might be expected under natural conditions where habitat size and quality can themselves be much more variable, and are combined with variation in other environmental variables such as temperature, availability of refuge habitat and the densities of interacting species. In addition, the food resource we used (Spirulina) is less nutritious than live algae and subsequently supports fairly small clutch sizes at food levels used in our experiment \( (1.9 \pm 0.9 \text{ mean } \pm \text{s.d.}, \text{ B. D. Griffen, unpublished data). This probably resulted in a lower range of population growth rates than are to be expected under natural conditions. Our laboratory experiments therefore provided less resolution (i.e. a smaller range of values) for \( \lambda \) and \( K \) than that may be expected in the field, reducing our power to discriminate subtle differences in the relationships between these population parameters and the duration of the final decline to extinction. These limitations of the experimental system are modest and unlikely to lead to spurious conclusions.

We found that the duration of the final decline to extinction increased with the logarithm of carrying capacity and with untransformed carrying capacity (hypothesis 1.2, figure 3a,b). \( T_E \) may increase with \( K \) either because the rate of population decline is constant, but the population has farther to fall when \( K \) is higher, or because the rate of population decline decreases as \( K \) increases. To differentiate between these two scenarios, we examined the rate of decline for each population during the final decline to extinction as a function of \( K \). Neither of these two scenarios occurred in our experiment; rather, the decline rate was higher for populations with larger \( K \) (figure 4), suggesting that while populations with larger \( K \) fell to extinction at a faster rate, this was more than that compensated by the greater distance they had to fall, and a net effect of longer duration of the final decline to extinction with larger \( K \). A previous analysis of these data demonstrated overall time to population extinction increased with \( K \) (Griffen & Drake 2008a). Confirmation of hypothesis 1.1 demonstrates that at least a part of this effect is accounted for by the increased time before a population enters the final decline. Results here, however, show that increasing \( K \) has the further beneficial effect of lengthening the extinction process once the final decline has begun (figure 3a,b).

Our experimental data did not support the model-predicted relationship between \( T_E \) and population growth rate (hypothesis 1.3). The reason for this discrepancy is unclear and warrants further investigation.

The success of scaling rules across a broad range of ecological relationships provides a promising step towards ecological prediction. Predicting population extinction is a major goal of ecology (Clark et al. 2001), for instance in population viability analyses of threatened and endangered species (Morris & Doak 2002). However, much of the extinction process, particularly the final decline, is influenced by stochastic processes that hamstring prediction. Reliable scaling rules for extinction, which incorporate this stochasticity, would therefore be broadly applicable and desirable. Our examination of the scaling rules, suggested by Lande et al. (2003) at a broad range of density-dependent conditions, broadens the applicability of hypothesis 1.1 to a wide range of natural systems that experience different forms of density dependence (Sibly et al. 2005), but suggests that hypotheses 1.2 and 1.3 may apply to a more limited set of populations. The lack of empirical support for our experiment for one of these scaling rules \( [T_E \propto 1/\ln(\lambda)] \) suggests that important aspects of the extinction process remain to be explained. However, empirical support for the other scaling rules suggests that they accurately capture the dynamics of the extinction processes, including the duration of the final decline.

Figure 4. Proportional decline in population size during each time step of the final decline to extinction as a function of carrying capacity, \( K \). \( \text{Ind./time step} = 0.44 \times K + 1.08, F_{1,43} = 24.28, p < 0.001. \)
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