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Evolution of size-dependent flowering in a variable environment: partitioning the effects of fluctuating selection

Mark Rees[1]*, Dylan Z. Childs[1], Karen E. Rose[1] and Peter J. Grubb[2]

[1] *Department of Biological Sciences and NERC Centre for Population Biology, Imperial College, Silwood Park, Ascot SL5 7PY, UK*
[2] *Department of Plant Sciences, University of Cambridge, Cambridge CB2 3EA, UK*

In a stochastic environment, two distinct processes, namely nonlinear averaging and non-equilibrium dynamics, influence fitness. We develop methods for decomposing the effects of temporal variation in demography into contributions from nonlinear averaging and non-equilibrium dynamics. We illustrate the approach using *Carlina vulgaris*, a monocarpic species in which recruitment, growth and survival all vary from year to year. In *Carlina* the absolute effect of temporal variation on the evolutionarily stable flowering strategy is substantial (*ca*. 50% of the evolutionarily stable flowering size) but the net effect is much smaller (*ca*. 10%) because the effects of temporal variation do not influence the evolutionarily stable strategy in the same direction.

Keywords: nonlinear averaging; non-equilibrium dynamics; evolutionarily stable strategy

1. INTRODUCTION

Temporal variation in demographic rates is a ubiquitous property of natural systems (Reinartz 1984; Verkaar & Schenkeveld 1984; Klemow & Raynal 1985; de Jong & Klinkhamer 1986, 1988; Crawley & Gillman 1989; de Jong *et al.* 1989, 2000; Kelly 1989; Watkinson 1990; Louda & Potvin 1995; Klinkhamer *et al.* 1996; Campbell 1997; Wesselingh *et al.* 1997; Rees *et al.* 1999, 2002; Rose *et al.* 2002). Despite this, we know almost nothing about the role and importance of temporal variation in the evolution of plant life histories in natural systems. This is caused, in part, by a lack of suitable data, but also reflects the complex way that temporal fluctuations affect fitness. There are two distinct ways that temporal variation influences fitness. First, average demographic rates vary owing to nonlinear averaging (NLA) (Ruel & Ayres 1999). For example, probabilities of survival and growth are nonlinear functions and so demographic rates in the average environment will differ systematically from average demographic rates. Second, there are non-equilibrium fluctuations in fitness caused by variation in both demographic rates and the size and age structure of the population; this means that the fitness of a particular strategy varies, and bet-hedging may become an important component of fitness (Seger & Brockmann 1987). It is important to separate the effects of NLA and non-equilibrium dynamics (NED) because there is no reason to assume that they act in the same direction, and so potentially large effects of temporal variation on fitness may be masked if they act equally but in opposite directions. How these different mechanisms influence life-history evolution in the field is an important, but still unanswered, question.

Despite the presence of a well-developed theoretical framework for estimating fitness in stochastic environments (Tuljapurkar 1990), there are few examples of studies that have applied the techniques to empirical datasets. Rees *et al.* (1999) and Rose *et al.* (2002) attempted to separate the effects of stochastic recruitment, growth and mortality on the evolutionarily stable flowering size, by fitting statistical models with and without year effects and comparing their predictions. The problem with this approach is that the constant- and stochastic-environment models have different fitted functions. For example, in *Carlina* the probability of survival is independent of size if one ignores year effects and size dependent when year effects are included (Rose *et al.* 2002). This means that the influence of stochastic variation is confounded by changes in the fitted functions, making it difficult to assess the impact of temporal variation on life-history evolution. In addition, these studies did not attempt to separate the effects of NLA and NED.

We investigate the selection pressures acting on the flowering strategy of *Carlina*, extending the analysis of Rose *et al.* (2002) and Childs *et al.* (2003, 2004) by developing a method for systematically decomposing the effects of stochastic variation on the evolutionarily stable strategy (ESS). The methods are derived for the *Carlina* system but are applicable to any system where variation in demographic rates has been quantified. We derive appropriately averaged versions of the statistical models for recruitment, growth and survival, which allow the effects of different sources of stochasticity on the evolutionarily stable flowering size to be quantified. Methods for constructing size- and age-dependent stochastic models and calculating evolutionarily stable flowering strategies are described in Childs *et al.* (2003, 2004).

2. METHODS

(a) *General approach and rationale*

The main aim of this study is to understand how the evolutionarily stable flowering size is influenced by: (i) different

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* Author for correspondence (m.rees@imperial.ac.uk).

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sources of temporal variation; (ii) NLA; and (iii) NED. To partition these effects, we use statistical models including year effects to derive appropriately averaged functions for the different demographic transitions. Comparison of the ESS predictions of the different models then allows the impact of stochastic effects to be estimated. We assume that a model, $f(\theta_t)$, which contains parameters, denoted collectively by θ_t that vary from year to year, describes some demographic rate. This function could depend on plant size or age, and may also contain parameters that do not vary from year to year. The average demographic rate is given by averaging $f(\theta_t)$ with respect to the distribution of yearly parameters, θ_t, that is $E[f(\theta_t)]$. If $f(\theta_t)$ is nonlinear then this expectation will depend on the variance of θ_t. By contrast, if $f(\theta_t)$ is linear then $E[f(\theta_t)] = f(E[\theta_t])$, so the difference between $E[f(\theta_t)]$ and $f(E[\theta_t])$ measures the impact of NLA on demographic rates. If we define $\bar{f}_\sigma = E[f(\theta_t)]$ and $\bar{f} = f(E[\theta_t])$ then the difference between the ESS predictions of models that use these functions will provide an estimate of the effect of NLA. We will refer to $\bar{f}$ and $\bar{f}_\sigma$ as the average-environment (AE) model and NLA model, respectively.

The second way that temporal variation could influence the ESS is through NED. To separate the effects of NLA and NED we need to define a model where demographic rates vary from year to year, but the effect of NLA is removed. To do this we define the function

$$\bar{f}_\tau = f_\tau - (\bar{f}_\sigma - \bar{f}), \tag{2.1}$$

where f_τ is the demographic rate in year type τ; the term in brackets is the effect of NLA. The average of $\bar{f}_\tau$ with respect to θ_t is $\bar{f}$, because $E[f_\tau] = E[f(\theta_t)] = \bar{f}_\sigma$. In this way, the difference between the ESS predictions of models that use $\bar{f}_\tau$ and $\bar{f}$ provides an estimate of the effect of NED. We will refer to $\bar{f}_\tau$ as the non-equilibrium dynamics (NED) model. Therefore, by carefully averaging the functions that define a model we can estimate the effects of NLA and NED on model predictions.

(b) *Alternative models for demography in* Carlina

In *Carlina*, the number of recruits and the intercepts of the size-dependent growth and survival functions vary from year to year (Rose *et al.* 2002). None of the estimated parameters is correlated within years (Spearman's rank correlation, $p > 0.2$ in all cases), and so any differences in the predictions obtained with different models may be attributed to specific stochastic effects.

A single alternative model for recruitment was derived by replacing the number of recruits in a particular year, R_τ, with the mean number of recruits, $\bar{R}$. We refer to this as the average-recruitment model. Survival is described by a logistic regression, and so the NLA survival function, conditional on plant size, x, is given by

$$\bar{s}_\sigma(x) = \frac{1}{N}\sum_{\tau=1}^{N} \frac{\exp(m_0 + \gamma_\tau + m_s x)}{1 + \exp(m_0 + \gamma_\tau + m_s x)}, \tag{2.2}$$

where N is the number of year types, m_0 is the average intercept, γ_τ is the deviation from m_0 in year type τ, and m_s is the size-dependent slope. The average-environment survival function is

$$\bar{s}(x) = \frac{\exp(m_0 + m_s x)}{1 + \exp(m_0 + m_s x)}. \tag{2.3}$$

The functions $\bar{s}_\sigma(x)$ and $\bar{s}(x)$ are the NLA and AE survival functions, respectively. The NED survival function, $\bar{s}_\tau(x)$, was generated using

$$\bar{s}_\tau(x) = s_\tau(x) - (\bar{s}_\sigma(x) - \bar{s}(x)), \tag{2.4}$$

the expectation of which, with respect to the distribution of yearly intercepts, is $\bar{s}(x)$. To ensure that $\bar{s}_\tau(x) \in [0, 1]$, the function was truncated to lie inside the unit interval. The expectation of the truncated functions was compared against $\bar{s}(x)$ and found to give the same ESS predictions.

The NLA growth function is derived in an analogous manner. Growth in *Carlina* is well described by a simple linear model,

$$y = a_g + \alpha_\tau + b_g x + \varepsilon, \tag{2.5}$$

where y and x are size (on a log scale) next year and this year, respectively, $a_g + \alpha_\tau$ is the intercept in year type τ, b_g is the size-dependent slope and ε is a normally distributed random variable with variance, σ^2, that describes the scatter about the fitted line. The probability that an individual grows from size x to size y is therefore normally distributed, and so the NLA growth function is given by

$$\bar{g}_\sigma(x,y) = \frac{1}{N}\sum_{\tau=1}^{N} \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(y - (a_g + \alpha_\tau + b_g x))^2}{2\sigma^2}\right). \tag{2.6}$$

The average-environment growth function is

$$\bar{g}(x,y) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(y - (a_g + b_g x))^2}{2\sigma^2}\right). \tag{2.7}$$

The functions $\bar{g}_\sigma(x,y)$ and $\bar{g}(x,y)$ are referred to as the NLA and AE growth functions, respectively. These are used to generate the NED growth function, $\bar{g}_\tau(x,y)$:

$$\bar{g}_\tau(x,y) = g_\tau(x,y) - (\bar{g}_\sigma(x,y) - \bar{g}(x,y)), \tag{2.8}$$

the expectation of which, with respect to the distribution of yearly intercepts, is $\bar{g}(x,y)$. To ensure that $\bar{g}_\tau(x,y) \in [0, 1]$, the function was truncated to lie inside the unit interval and then renormalized so that the conditional growth function is a true probability density function. The expectation of the truncated functions was compared against $\bar{g}(x,y)$ and found to give the same ESS predictions. The model using the average recruitment and the average-environment growth and survival functions is referred to as the constant-environment model.

(c) *Partitioning the effects of temporal variation*

To partition the effects of temporal variation in the vital rates on the evolutionarily stable flowering strategy, we use an ANOVA decomposition of the different stochastic effects. The evolutionarily stable flowering strategies were calculated using the techniques described in Childs *et al.* (2004). By comparing the predictions of models using the AE and NLA survival and/or growth functions we can estimate the effect of NLA. Comparing the predictions of models incorporating the AE survival and/or growth functions with those of the NED models allows the effect of NED to be estimated. Interactions between the effects of NLA and NED can then be estimated by applying the NLA and NED models in a factorial manner. We write the evolutionarily stable mean flowering size in a fully stochastic, variable environment, μ_V, as a linear function of the corresponding mean size in the average (constant) environment, μ_C, a stochastic recruitment effect, ΔR_V, stochastic survival effects, ΔS_{NLA} and ΔS_{NED}, stochastic growth effects, ΔG_{NLA} and ΔG_{NED}, and interaction terms, such that

$$\mu_V = \mu_C + \Delta R_V + \Delta S_{NLA} + \Delta S_{NED} + \Delta G_{NLA} + \Delta G_{NED} + \text{interactions}, \tag{2.9}$$

Table 1. ANOVA table summarizing the effects of different sources of stochastic variation on the evolutionarily stable flowering size, partitioned into the effects of NLA and NED.
(Only main effects and first-order interactions were fitted to the fully factorial design.)

	d.f.	SS	MS	F-value	p-value
R_V	1	163.24	163.24	812.38	$3.837 \times 10^{-15***}$
S_{NLA}	1	224.72	224.72	1118.36	$3.096 \times 10^{-16***}$
S_{NED}	1	161.31	161.31	802.80	$4.212 \times 10^{-15***}$
G_{NLA}	1	264.57	264.57	1316.70	$< 2.2 \times 10^{-16***}$
G_{NED}	1	292.21	292.21	1454.23	$< 2.2 \times 10^{-1***}$
$R_V \times S_{NLA}$	1	1.63	1.63	8.11	0.0116297^{*}
$R_V \times S_{NED}$	1	0.00	0.00	0.00	0.9555731
$R_V \times G_{NLA}$	1	0.04	0.04	0.21	0.6519315
$R_V \times G_{NED}$	1	4.78	4.78	23.77	0.0001685^{***}
$S_{NLA} \times S_{NED}$	1	0.41	0.41	2.04	0.1723841
$S_{NLA} \times G_{NLA}$	1	0.01	0.01	0.06	0.8036207
$S_{NLA} \times G_{NED}$	1	0.04	0.04	0.18	0.6756577
$S_{NED} \times G_{NLA}$	1	0.05	0.05	0.23	0.6415143
$S_{NED} \times G_{NED}$	1	0.15	0.15	0.75	0.3985939
$G_{NLA} \times G_{NED}$	1	20.12	20.12	100.12	$2.724 \times 10^{-8***}$
residuals	16	3.22	0.20		

$^{*}p < 0.05$; $^{***}p < 0.001$.

Table 2. Estimated change in the evolutionarily stable flowering size resulting from different sources of stochastic variation, from the main-effects-only model, partitioned into the effects of NLA and those of NED.
(The baseline evolutionarily stable flowering size in a constant environment is also given.)

		estimate (mm)	net change (mm)	absolute change (mm)
mean flowering size constant environment	μ_C	56.8		
recruitment	ΔR_V	$+4.5^{***}$	+4.5	4.5
survival	ΔS_{NLA}	-5.3^{***}	−9.8	9.8
	ΔS_{NED}	-4.5^{***}		
growth	ΔG_{NLA}	$+5.8^{***}$	−0.2	11.8
	ΔG_{NED}	-6.0^{***}		

$^{***}p < 0.001$.

where the NLA and NED subscripts refer to the effects of NLA and NED, respectively. To estimate these effects, the evolutionarily stable flowering size was calculated using every combination of AE, NLA, NED and stochastic models for survival, growth and recruitment. The resultant design of the simulation experiment is a five-way fully factorial ANOVA without replication (i.e. $\bar{R}$ versus R_τ, $\bar{s}(x)$ versus $\bar{s}_\sigma(x)$, $\bar{s}(x)$ versus $\bar{s}_\tau(x)$, $\bar{g}(x,y)$ versus $\bar{g}_\sigma(x,y)$ and $\bar{g}(x,y)$ versus $\bar{g}_\tau(x,y)$). The size slope of the flowering function, β_s, was constrained during the simulation experiment to fix the variance in the threshold-size distribution (see Childs *et al.* (2004) for a justification of this approach).

3. RESULTS

(a) *Partitioning the effects of temporal variation*

The ANOVA model (equation (2.9)) with main effects and two-way interactions accounted for 99.6% of the variation in the evolutionarily stable mean flowering size. All the main effects and two of the interactions ($R_V \times G_{NED}$ and $G_{NLA} \times G_{NED}$) were highly significant ($p < 0.001$). Only one other interaction ($R_V \times S_{NLA}$) was significant ($p < 0.05$) (table 1). The ANOVA model with only the main effects accounts for 97.2% of the variance, suggesting that the effects of variable recruitment, survival and growth on the evolutionarily stable flowering size are approximately additive. Consequently, to simplify model interpretation, the main-effects model was used to derive estimates of the stochastic effects (table 2). The net effect of stochastic survival was greatest ($\Delta S_{NLA} + \Delta S_{NED} = -9.8$), followed by that of recruitment ($\Delta R_V = 4.5$) and then that of growth ($\Delta G_{NLA} + \Delta G_{NED} = -0.2$). Variable recruitment selects for larger sizes at flowering, which suggests the operation of a bet-hedging strategy: large sizes at flowering, coupled with variable growth, distribute reproduction over several years, thereby mitigating the effects of low-recruitment years. By contrast, the non-equilibrium effects of variable survival and growth select for smaller flowering sizes (i.e. $\Delta S_{NED} = -4.5$, $\Delta G_{NED} = -6.0$): individuals flower earlier to reduce the risk of suffering occasional high-mortality or low-growth years. When we consider the absolute values of the different terms, variable growth had the largest impact ($|\Delta G_{NLA}| + |\Delta G_{NED}| = 11.8$), followed by survival ($|\Delta S_{NLA}| + |\Delta S_{NED}| = 9.8$) and recruitment ($|\Delta R_V| = 4.5$). The significant interactions involving the variable-recruitment term ($R_V \times G_{NED}$ and $R_V \times S_{NLA}$, not presented) both increased the evolutionarily stable flowering size, while the interaction involving the growth terms ($G_{NLA} \times G_{NED}$, not presented) reduced the evolutionarily stable size.

4. DISCUSSION

By calculating the evolutionarily stable flowering size with a set of carefully chosen analogues of the stochastic model, we have partitioned out the effects of different sources of stochasticity. The absolute change in the evolutionarily stable flowering size caused by these effects is *ca.* 50% of the evolutionarily stable size in the constant environment, though the net effect is much smaller (*ca.* 10%) because the processes do not influence the ESS in the same direction. Without quantifying the total effect of stochasticity in this way, it would be easy to underestimate the influence of temporal variation. For example, reducing temporal variation in survival could increase flowering sizes by as much as 19% of the current observed mean. NED induced by variable survival and growth select for smaller flowering sizes. Presumably, this reflects the cost associated with occasional low-survival or low-growth years: individuals that wait too long before flowering increase the risk of suffering such an event. By contrast, variable recruitment selects for larger flowering sizes, which indicates that a bet-hedging mechanism is operating. To spread the risk of suffering a poor year for recruitment, a particular flowering strategy needs to distribute reproduction over several years. When individuals are subject to variable growth (within or between years) increasing the size at flowering achieves this by increasing the variance in the age at flowering. We suggest that, in a system with density-dependent recruitment, these mechanisms are generic, and the direction of change in the ESS resulting from NED should be consistent across systems.

The effect of NLA depends on the shape of the survival and growth functions. For survival, the standard small-variance approximation of equation (2.2) shows that, provided $\bar{s}(x) > 1/2$, temporal variability reduces the probability of survival and so selects for smaller sizes at flowering. For all plants with a longest leaf length of greater than 10 mm, we find that $\bar{s}(x) > 1/2$ and therefore selection favours flowering at smaller sizes, as found in the simulation experiment. The biological reason for this is that the probability of survival is bounded at one, and plants that make the decision to flower are large and have high chances of survival. This means that in good years the probability of survival hardly changes, whereas in bad years the probability of survival is substantially reduced. Clearly, the effect of bad years will outweigh that of the good years and as a result the probability of survival decreases when the environment fluctuates. In long-lived monocarpic species, where the probability of survival is high for large plants, we suspect that ΔS_{NLA} will be negative, as in *Carlina*. However, in short-lived species the opposite may be true, because in bad years the probability of survival is bounded at zero.

A similar approach can be used to understand the effect of variance in the growth intercept. The number of microsites captured by a plant depends on its seed production, which is a function of plant size on an arithmetic scale (i.e. not log transformed), and arithmetic plant size is given by $\exp(y) = \exp(a_g + \alpha_\tau + b_g x + \varepsilon)$ (equation (2.5)). This function is concave up (has a positive second derivative), which means that large values of ε and α_τ result in dramatic increases in plant size, whereas small values are bounded by zero. The net effect is an increase in arithmetic size when ε and α_τ fluctuate, which selects for larger sizes at flowering (Rees *et al.* 2000; Rose *et al.* 2002; Childs *et al.* 2003), as found in the simulation experiment. For a wide range of species growth is well described by the simple linear model (equation (2.5); Metcalf *et al.* 2003) and so we expect that ΔG_{NLA} will generally be positive.

Our method for partitioning out the effects of stochasticity is only one of several approaches that could be used. For example, one could argue that the geometric (rather than arithmetic) mean of the fitted survival functions is most appropriate, because the probability of surviving to a given age is the product of several size-dependent mortality terms. The advantage of our adopted method is that the effects of NLA and NED are easy to interpret in terms of simple underlying models (Rees *et al.* 2000; Rose *et al.* 2002; Childs *et al.* 2003).

The techniques developed in this article should be broadly applicable to any system where temporal variation in demographic rates has been quantified and an appropriate model that allows the prediction of the evolutionarily stable or optimal strategy has been defined. A wide range of life-history problems can be addressed within this framework. For example, species with multiple reproductive delays arising from seed dormancy and delayed reproduction or complex reproductive strategies, combining clonal growth and seed production, can easily be analysed.

In *Carlina*, the main-effects-only ANOVA model accounts for over 97% of the variance in the results of the simulation experiment. We suspect that this is a consequence of the lack of covariation between the yearly parameter estimates. In systems where there is covariation between parameter estimates, for example, a good year for growth could also be a good year for survival, interaction terms may well be important. These effects can be explored in the current framework by randomizing the yearly parameter estimates, repeating the analysis and calculating the covariation between the parameter estimates in the randomized dataset. Plots of the effect size of the interaction against the covariance of the parameter estimates then allow the impact of covariance to be assessed.

Life-history analyses have traditionally measured the success of a model in terms of how well it is able to predict a trait. An adequate model must lead to accurate predictions, but this should not be viewed as a sufficient measure of model validity, especially if the aim of a study is to understand the selective forces acting on the trait. We demonstrated that in *Carlina* variable recruitment, growth and mortality influence the evolutionarily stable flowering size, though their net effect is relatively small because they act in different directions. It is possible to imagine a scenario in which a constant-environment model might accurately predict flowering size, not because stochasticity is unimportant, but because the various stochastic effects are balanced. Conclusions about the role of stochasticity should be reached only after a stochastic model has been analysed.

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