

# Evolution of flowering strategies in *Oenothera glazioviana*: an integral projection model approach

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The timing of reproduction is a key determinant of fitness. Here, we develop parameterized integral projection models of size-related flowering for the monocarpic perennial *Oenothera glazioviana* and use these to predict the evolutionarily stable strategy (ESS) for flowering. For the most part there is excellent agreement between the model predictions and the results of quantitative field studies. However, the model predicts a much steeper relationship between plant size and the probability of flowering than observed in the field, indicating selection for a 'threshold size' flowering function. Elasticity and sensitivity analysis of population growth rate  $\lambda$  and net reproductive rate  $R_0$  are used to identify the critical traits that determine fitness and control the ESS for flowering. Using the fitted model we calculate the fitness landscape for invading genotypes and show that this is characterized by a ridge of approximately equal fitness. The implications of these results for the maintenance of genetic variation are discussed.

**Keywords:** life history evolution; size-structured population; evolutionarily stable strategy; delayed reproduction; genetic variation; sensitivity analysis

## 1. INTRODUCTION

Evolutionary biologists have been fascinated by reproductive delays ever since Cole (1954) showed that 'for an annual species, the absolute gain in intrinsic population growth which could be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one individual to the average litter size'. In this simple model, if the annual produced two more offspring than the perennial it would eventually come to dominate the population. Hence, there is a potentially enormous benefit from early reproduction, and so it is natural to ask why are there any perennial species at all? Also, why do species that can reproduce often delay instead?

The main benefits of early reproduction accrue through reductions in mortality and generation time (Cole 1954; Charnov & Schaffer 1973; Roff 1992; Stearns 1992). Other things being equal, reductions in mortality increase fitness, whereas reductions in generation time only increase fitness under certain circumstances, and may have no effect on fitness in a density regulated population (Hastings 1978; Bulmer 1985; Kawecki 1993; Mylius & Diekmann 1995). The costs of early reproduction are reduced fecundity and/or quality of offspring (Bell 1980; Roff 1992; Stearns 1992). In addition to the benefits that accrue through increased growth and fecundity, delaying reproduction may provide an additional advantage via bet hedging. This requires temporal variation in the quality of the environment for growth and reproduction, and that members of a cohort reproduce in different years (de Jong *et al.* 1987).

Several studies have attempted to quantify the selective advantages of delayed reproduction in monocarpic plants

(Lacey & Pace 1983; Reinartz 1984; Kachi & Hirose 1985; Kelly 1985a,b, 1989; de Jong *et al.* 1989). Most were designed to show that delayed flowering is adaptive. Others attempted to predict the optimal size and age at flowering, with variable levels of success (Kachi & Hirose 1985; de Jong *et al.* 1989, 2000; Wesselingh *et al.* 1997; Rees *et al.* 1999, 2000). The calculation of the evolutionarily stable strategy (ESS) or optimal strategy is complicated because there is substantial variation between individual growth, which means that simple optimization approaches, such as the 1 year look-ahead approach introduced by Rees *et al.* (2000), only yield approximate solutions. Matrix models (Caswell 2001) provide powerful tools for analysing stage-structured populations; however, this approach requires that individuals be placed into categories and for continuous data, the choice of categories may influence the predictions of the model (Enright *et al.* 1995).

Here, we introduce integral projection models for monocarpic perennials and use these to analyse the flowering strategy of *Oenothera glazioviana*, using the detailed field studies of Kachi and Hirose (Kachi 1983; Kachi & Hirose 1983, 1985). These methods eliminate the need to divide data into discrete classes, without requiring any extra biological assumptions (Easterling *et al.* 2000). Equally importantly, the data required to parameterize integral projection models are no more complicated than those needed to construct an individual-based or matrix model of the same system. Underlying the integral projection model is a stochastic individual-based model, making the integral projection model a good alternative to simulation (Easterling *et al.* 2000). Integral projection models have many properties in common with matrix models, for example they allow the calculation of the stable size distribution, population growth rate  $\lambda$ , and sensitivities and elasticities of  $\lambda$ .

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First, we describe the integral projection model itself, and then proceed to describe the size-dependent demography of *Oenothera*. The integral projection model for *Oenothera* is then analysed: we estimate the sensitivities of  $\lambda$  and  $R_0$ , elasticities of  $\lambda$ , the fitness landscape of the flowering strategy, and question whether the observed strategy is an ESS.

## 2. MATERIAL AND METHODS

### (a) Integral projection models for *Oenothera glazioviana*

The integral projection model can be used to describe how a continuously size-structured population changes in discrete time (Easterling *et al.* 2000). The state of the population is described by a probability density function,  $n(x, t)$ , which can intuitively be thought of as the proportion of individuals of size  $x$  at time  $t$ . The integral projection model for the proportion of individuals of size  $y$  at time  $t + 1$ , one year later, is then given by

$$n(y, t + 1) = \int_{\Omega} [p(x, y) + f(x, y)] n(x, t) dx = \int_{\Omega} k(y, x) n(x, t) dx, \quad (2.1)$$

where  $k(y, x)$ , known as the kernel, describes all possible transitions from size  $x$  to size  $y$ , including births. The integration is over the set of all possible sizes,  $\Omega$ ; this was set at 0.9 times the minimum size observed and at 1.1 times the maximum size observed. The kernel is composed of two parts, a fecundity function,  $f(x, y)$ , and a survival-growth function,  $p(x, y)$ . In order to apply the model we must specify the dependence of survival, growth and fecundity on size. Specifically we will write the fecundity function as

$$f(x, y) = p_e p_f(x) f_n(x) f_d(x, y), \quad (2.2)$$

where  $p_e$  is the probability of seedling establishment,  $p_f(x)$  is the probability that an individual of size  $x$  flowers,  $f_n(x)$  is the number of seeds produced, and  $f_d(x, y)$  is the probability distribution of offspring size,  $y$ , for an individual of size  $x$ . The survival-growth function is given by

$$p(x, y) = s(x) [1 - p_f(x)] g(x, y), \quad (2.3)$$

where  $s(x)$  is the probability of survival of an individual of size  $x$ , and  $g(x, y)$  is the probability of an individual of size  $x$  growing to size  $y$ . The probability of flowering,  $p_f(x)$ , enters the survival function, as reproduction is fatal in monocarpic species. The form of the kernel is dictated by the life cycle of *Oenothera* (see fig. 1 of Kachi & Hirose (1985)). We now summarize the size-dependent demography of *Oenothera*, which will be used to construct the kernel.

### (b) Population biology of *Oenothera glazioviana*

*Oenothera glazioviana* is a monocarpic plant that often occurs in sand dune areas, and its demography has been extensively studied by Kachi and Hirose (Kachi 1983; Kachi & Hirose 1983, 1985). For an *Oenothera* rosette, growth can be described by a simple linear function

$$y = 0.96 - 0.59x + \varepsilon, \quad (2.4)$$

where  $x$  is log rosette diameter in May,  $y$  is the log rosette diameter the following year, and  $\varepsilon$  is a standard normal deviate with mean zero and standard deviation,  $\sigma = 0.67$ ; this represents the residual scatter, arising from measurement error and real bio-

logical variation about the regression line. Therefore the growth function  $g(x, y)$  is given by

$$g(x, y) = \frac{1}{\sigma \sqrt{2\pi}} \exp\left(-\frac{(y - (-0.59x + 0.96))^2}{2\sigma^2}\right), \quad (2.5)$$

which is the normal probability density function with the mean given by equation (2.4) and constant variance  $\sigma^2$ . The probability of flowering is given by

$$\text{logit}(p_f(x)) = -18.27 + 6.91x. \quad (2.6)$$

We used this function in preference to the linear function used in Kachi & Hirose (1985) so that we were consistent with previous studies (Rees *et al.* 1999), and the fitted values of the model lie in the interval  $[0, 1]$ . When we consider the evolution of this function we refer to the intercept and slope as  $\beta_0$  and  $\beta_s$ , respectively. The survivorship of vegetative rosettes is described by

$$s(x) = 0.36 + 0.17x, \quad (2.7)$$

where the probability of rosette survival has an upper bound of 0.7. The number of seeds produced as a function of rosette diameter is given by

$$f_n(x) = \exp(1.04 + 2.22x). \quad (2.8)$$

In constructing the kernel we use the expected value of  $f_n(x)$  which does depend on the scatter about the fitted relationship; it increases the intercept by an additive constant,  $\sigma_s^2/2$ ; where  $\sigma_s^2$  is the residual variance about the double-log regression. We do not have an estimate of the residual variance; however, this does not affect the outcome of any of the evolutionary calculations presented below, although it will result in the finite rate of increase,  $\lambda$ , and  $R_0$  being underestimated. The size distribution of recruits, on a log scale, follows a normal distribution with the mean  $-0.08$  and variance  $0.57$ . Data were not available on the size of recruits derived from seeds of plants of different size, but evidence from other systems indicates a low maternal effect on recruit size (Weiner *et al.* 1997), and so the distribution of offspring sizes was independent of parental size. The probability of seed becoming a seedling was  $0.0205$  and the probability of seedling survival was  $0.48$ . Combining these gives an estimated probability of establishment,  $p_e$  of  $0.00984$ . Note that the parameters in Kachi & Hirose (1985) are given for both natural logarithms and  $\log_{10}$  and we have converted these to natural logarithms. The number of recruits was independent of seed production suggesting density dependence acts on seedlings, such that the per seed probability of establishment declines with the density of seeds (Kachi 1983; Rees *et al.* 2000). In addition to this Kachi & Hirose (1985) state that plants 'show little competitive interaction between neighbouring individuals. Thus, it is unlikely that density is a major factor in determining plant growth in the dune system'. This strongly suggests that the main density-dependent process is recruitment. In the models that follow we model density-dependent recruitment implicitly by adjusting the parameter  $p_e$  so that  $\lambda = 1$ . This simple representation of density dependence corresponds to lottery competition between seedlings for microsites and assumes there is always sufficient seed production to allow all microsites to be colonized (Chesson & Warner 1981). This is a reasonable assumption as seed production is typically 1 to 2 orders of magnitude greater than the number of recruits (Kachi 1983; Rees *et al.* 2000).

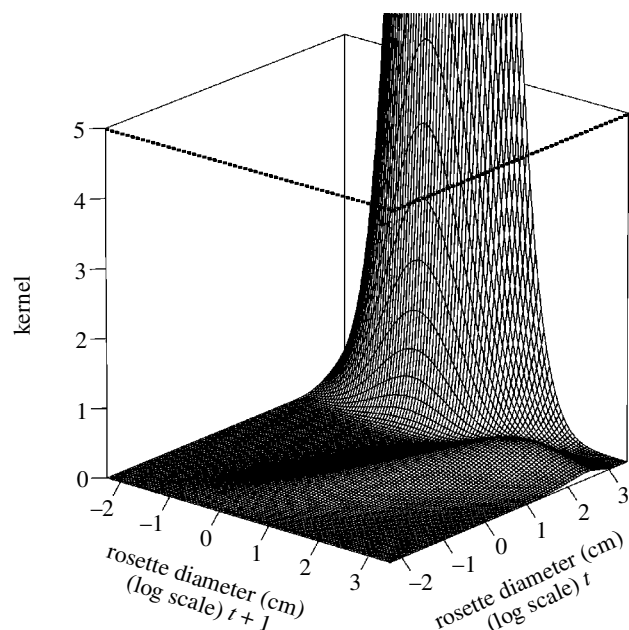


Figure 1. Fitted kernel for *Oenothera glazioviana*; the kernel represents all possible transitions from rosette diameter  $x$  in year  $t$  to rosette diameter  $y$  in year  $t + 1$ , see § 2a for details.

The functions described above can be used to construct the kernel (see figure 1). The low ridge across the surface describes growth and survival, and the large spike is reproduction.

### 3. RESULTS

#### (a) Analysis of the kernel

Given the kernel we can calculate the various demographic quantities, such as the finite rate of increase,  $\lambda$ . Using the methods described in Easterling *et al.* (2000) we find  $\lambda = 1.041$ , in excellent agreement with the value obtained by Kachi & Hirose (1985) using an individual-based simulation ( $\lambda = 1.04$ ). The right eigenvector corresponding to the dominant eigenvalue gives the stable size distribution,  $w(y)$ . Comparison of the predicted stable size distribution with the output from the individual-based model described in Kachi & Hirose (1985) shows excellent agreement between the approaches (figure 2). To calculate the mean size at flowering, used to compare model predictions with data, we first calculate the normalized stable size distribution of flowering plants,  $w_n^*$ , given by

$$w_n^*(y) = p_f(y)w(y) / \int_{\Omega} p_f(y)w(y)dy. \quad (3.1)$$

The arithmetic mean size at flowering is then given by

$$\mu = \int_{\Omega} w_n^*(y) \exp(y) dy.$$

We can now explore how variation in one of the parameters that defines the kernel affects  $\lambda$  by calculating sensitivities,  $\partial\lambda/\partial p$  (Caswell 2001). Sensitivities estimate the effect on  $\lambda$  of absolute changes in parameter values. They quantify the intensity and direction of selection, and may be interpreted as selection pressures (Metz *et al.* 1992; Rand *et al.* 1994; Caswell 2001). The calculated sensitivities (table 1) reveal strong selection operating for faster

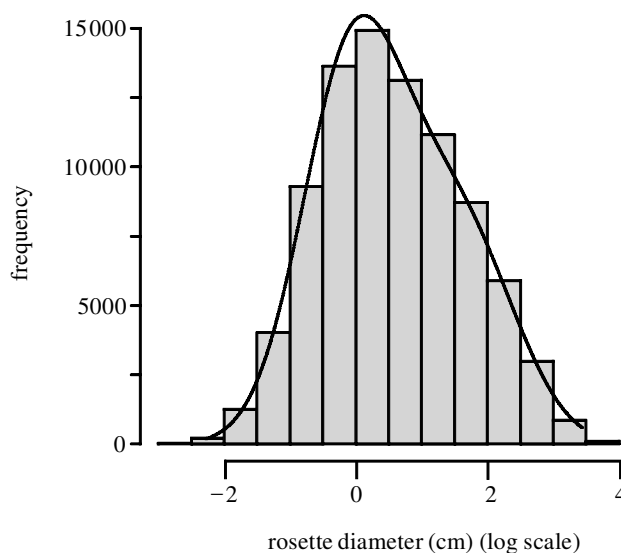


Figure 2. Comparison of the predicted stable size distribution from the integral projection model (solid line) with the output from the stochastic individual-based model of Kachi & Hirose (1985).

growth, higher survival and increased seed production. The variance term for growth is also under positive selection. By contrast, the parameters that define the probability of the flowering relationship are under weak selection; the importance of this result will be explored in the next section.

Elasticities can be used to measure the effect on  $\lambda$  of proportional changes in the kernel (Easterling *et al.* 2000), and are defined as

$$e(z_1, z_2) = \frac{k(z_1, z_2)}{\lambda} \frac{v(z_1)w(z_2)}{\langle w, v \rangle}, \quad (3.2)$$

where  $v$  and  $w$  are the right and left eigenvectors of  $\lambda$  and

$$\langle w, v \rangle = \int w(x)v(x)dx.$$

Unlike the previous analysis it is important to realize that at a particular point on the kernel there may be contributions from both  $p(x, y)$  and  $f(x, y)$  and elasticities do not distinguish between these contributions. The resulting surface shows the importance of reproduction and also transitions into the reproductive size classes (figure 3).

#### (b) Is the flowering strategy an ESS?

We can address this question using the invasibility techniques described in Mylius & Diekmann (1995), which examine the growth rate of an invading strategy in the environment set by the resident strategy. To do this we must be specific about the density-dependent processes operating in the population. For *Oenothera*, density dependence acts on seedling establishment and there is little evidence of intraspecific competition (Kachi & Hirose 1985; Rees *et al.* 2000). This means that the basic reproductive rate,  $R_0(I, R)$  for an invading strategy ( $I$ ) invading a resident strategy ( $R$ ) at equilibrium can be written as

$$R_0(I, R) = \sum l_x m_x p_c^R = p_c^R \sum l_x m_x = p_c^R R_0(I, 0), \quad (3.3)$$

where  $l_x$  is the probability of surviving to age  $x$ ,  $m_x$  is the

Table 1. Estimated sensitivities of  $\lambda$  and  $R_0$  for the parameters that define the kernel.

parameter, $p$	sensitivity $\lambda$ , $\partial\lambda/\partial p$	sensitivity $R_0$ , $\partial R_0/\partial p$
survival intercept (0.36)	1.242	5.732
survival slope (0.17)	0.894	4.153
flowering intercept (−18.27)	0.009	0.030
flowering slope (6.91)	0.027	0.095
growth intercept (0.96)	0.735	3.246
growth slope (0.59)	0.939	4.168
variance in growth (0.45)	0.301	1.244
fecundity intercept (1.04)	0.262	1.176
fecundity slope (2.22)	0.794	3.561
mean offspring size (−0.08)	0.256	1.119
variance in offspring size (0.57)	0.105	0.436

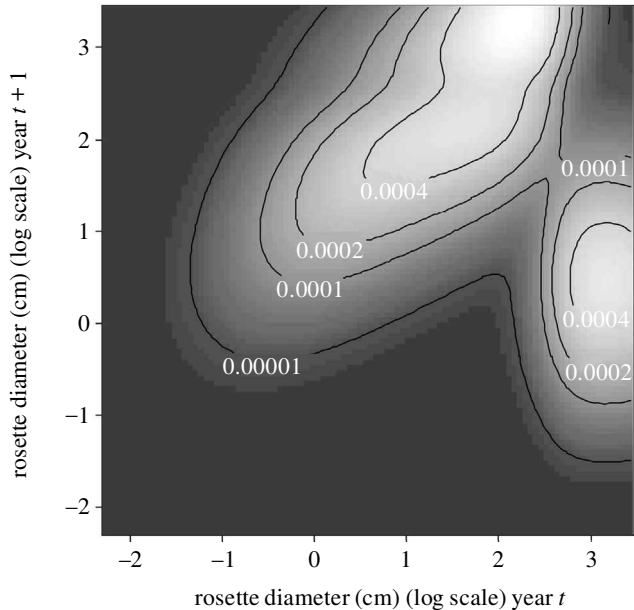


Figure 3. Elasticity contour plot for the *Oenothera glazioviana* kernel. The lighter areas indicate the importance of reproduction and transitions of individuals into the reproductive size classes (the smaller size in year  $t + 1$  than in year  $t$  indicates production of offspring) to  $\lambda$ .

age-specific seed production and  $p_e^R$  is the probability of seedling establishment, which is determined by the resident strategy. Finally  $R_0(I,0)$  is the basic reproductive rate of the invader in a virgin environment, that is, an environment in which individuals experience no negative effect from the presence of other individuals. From this we obtain the important result that the ESS flowering strategy maximizes  $R_0(I,0)$ . To see this, consider an invading strategy which has a larger  $R_0(I,0)$  than the resident strategy: then  $R_0(I,R) = p_e^R R_0(I,0) > 1$  because  $R_0(R,R) = p_e^R R_0(R,0) = 1$ , which means the invader will displace the resident strategy. It then follows that the ESS must maximize  $R_0(I,0)$ ; in fact this result holds for any environment, not just a virgin environment (Mylius & Diekmann 1995).

In order to apply these methods we need a way of calculating  $R_0$  for the integral projection model. To do this we apply the methods of Cochran & Ellner (1992) and Caswell (2001) that allow age-based life-history statistics to be calculated from stage-based models (see Caswell (2001, p. 126) for details of the calculations). These

methods assume that the demography of the population can be partitioned into transitions between different sizes and reproduction. As the kernel has this form it is straightforward to apply the methods to integral projection models.

To predict the ESS flowering strategy we assume the intercept of the probability of flowering, equation (2.6), is fixed and calculate the value of slope,  $\beta_s$ , which maximizes  $R_0$ . This gives a predicted flowering slope of 7.27, which is close to the estimated value of 6.91, indicating the observed flowering strategy is close to the predicted ESS. At the ESS  $R_0$  and  $\lambda$  are less than 1 for all alternative strategies (see figure 4). Using the predicted ESS gives a predicted mean size at flowering of 16.4 cm, in good agreement with the value observed in the field (*ca.* 18 cm). This explains why the estimated selection pressures on the flowering strategy were close to zero. If we assume evolution maximized  $\lambda$ , using the observed probability of establishment,  $p_e = 0.00984$ , we find the predicted value of  $\beta_s$  is 7.36, which corresponds to an average size of flowering of 16.05 cm.

In this system, evolution maximizes  $R_0$  and so sensitivities of  $R_0$  estimate how variation in model parameters affects the ESS flowering strategy. Calculating the sensitivities,  $\partial R_0/\partial p$ , we find an almost perfect linear relationship between the sensitivities of  $\lambda$  and those of  $R_0$  (slope = 4.53,  $r^2 = 0.999$ , see table 1). To see why this is, write  $R_0 = \lambda^T$  where  $T$  is the generation time (Caswell 2001), and then calculate  $\partial R_0/\partial p$ . This gives

$$\frac{\partial R_0}{\partial p} = \lambda^T \left[ \ln(\lambda) \frac{\partial T}{\partial p} + \frac{T}{\lambda} \frac{\partial \lambda}{\partial p} \right], \tag{3.4}$$

which, providing  $\lambda \approx 1$  so we can ignore the  $\partial T/\partial p$  term, results in a linear relationship with slope  $\lambda^{T-1}T$  (i.e.  $\partial R_0/\partial p \approx \lambda^{T-1}T \partial \lambda/\partial p$ ). For the fitted model,  $\lambda = 1.041$  and  $R_0 = 1.176$ , giving an estimated generation time of 4.021 years. Substituting these values into  $\lambda^{T-1}T$ , the predicted slope is 4.54, in excellent agreement with the regression analysis ( $4.53 \pm 0.03$ ). For density regulated populations,  $\lambda = 1$ , we obtain the simple result that  $\partial R_0/\partial p = T \partial \lambda/\partial p$ . We checked this by calculating  $p_e$  so that  $\lambda = 1$  and then regressed  $\partial R_0/\partial p$  against  $\partial \lambda/\partial p$ ; the estimated slope was  $4.24 \pm 0.04$ . The estimated generation time, calculated as the average age at reproduction, was 4.21, again close to the analytical prediction.

Using these methods we can calculate the fitness surface for any flowering strategy, using the estimated flowering

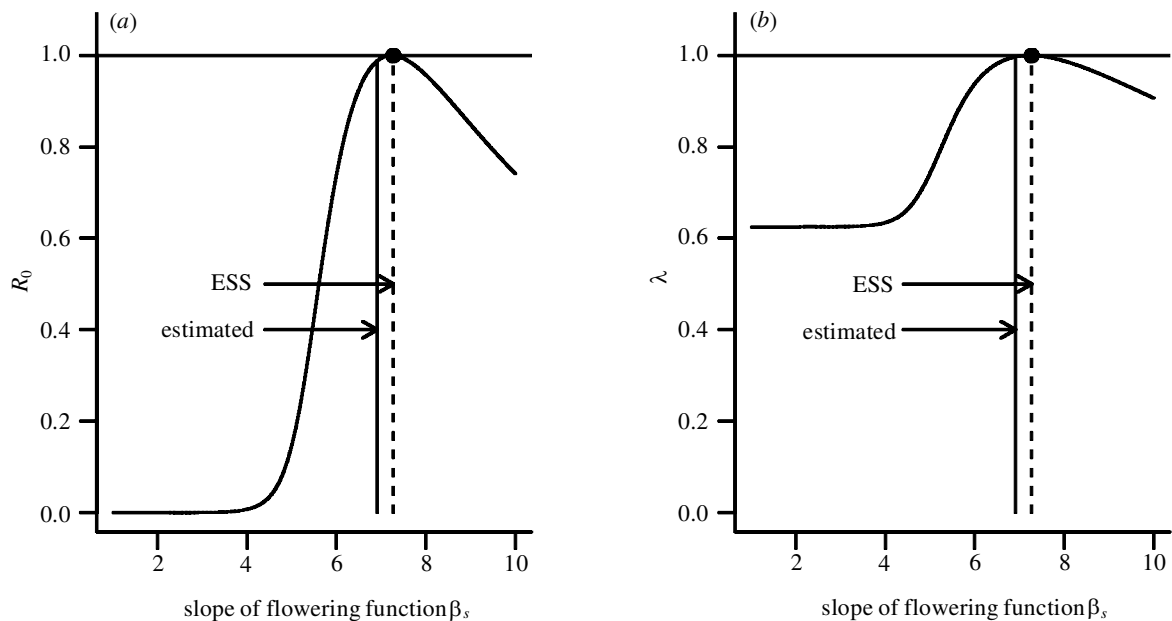


Figure 4. Relationship between (a)  $R_0$  and (b)  $\lambda$ , and the slope of the flowering relationship,  $\beta_s$ , assuming the resident population is at equilibrium, and follows the ESS for flowering predicted by maximizing  $R_0$ .

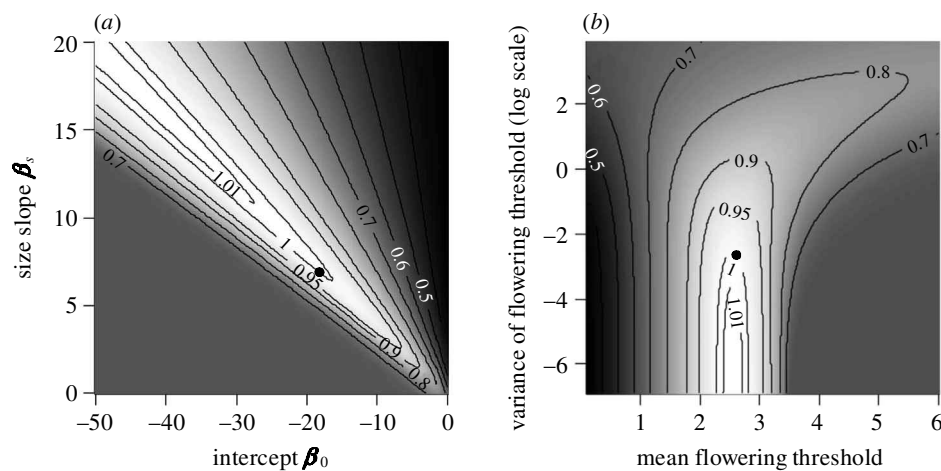


Figure 5. Fitness landscape for mutant flowering strategies invading a resident population with the observed flowering strategy. The solid circle indicates the observed flowering strategy. (a) Fitness landscape for flowering strategies characterized as  $\beta_0$  and  $\beta_s$ , and (b) fitness landscape for flowering strategies characterized by mean and variance in flowering threshold distribution.

strategy to define the resident population. To do this we first determine the value of the establishment probability such that the resident population has  $\lambda = 1$ . This defines the environment into which new strategies invade and is achieved when  $p_e = 0.00837$ . Invading strategies were defined by the intercept,  $\beta_0$ , and slope,  $\beta_s$ , of the probability of flowering function (equation (2.6)) and we calculated  $\lambda$  for each of these flowering strategies. The resulting fitness landscape is illustrated in figure 5a.

The landscape is characterized by a ridge of approximately equal fitness, and the estimated strategy lies on this. There are other strategies that achieve higher fitness than the observed strategy; these strategies approximate step-functions and therefore appear in the top-left corner of figure 5a. Assuming the step-function relationship gives a predicted average size at flowering of 17.28 cm, this is in excellent agreement with that observed in the field.

This formulation, while statistically well-grounded, is

biologically rather difficult to interpret as the mean and variance of the size at flowering are both functions of  $\beta_0$  and  $\beta_s$ . However, the fitted parameters of a logistic regression can be interpreted in terms of an underlying, unobserved distribution of threshold sizes for reproduction. Assume there is some distribution of threshold sizes for flowering,  $f_T$  within a population, then for a particular size,  $x$ , if 50% flower, this implies that 50% of the population have a threshold less than  $x$  (Wesselingh & de Jong 1995). In this way we may interpret the fitted logistic curve as a cumulative distribution function, calculating  $\partial p_T(x)/\partial x$ , using equation (2.6), we obtain

$$f_T(x) = \frac{\beta_s \exp(\beta_0 + \beta_s x)}{(1 + \exp(\beta_0 + \beta_s x))^2}, \quad (3.5)$$

which defines a general logistic distribution, with the mean  $-\beta_0/\beta_s$  and variance  $\pi^2/3\beta_s^2$ . In this way we may express the estimated parameters of the logistic flowering function

in terms of the mean and variance of the distribution of threshold sizes. The logistic distribution is symmetric and closely approximates a normal distribution, albeit with longer tails (Cox & Snell 1989). There are problems applying this approach to real systems, as there is growth between the time flowering decisions are made and flowering occurs. However, the approach is still useful for interpreting model parameters. Plotting the fitness landscape in terms of the mean and variance in the distribution of threshold sizes for reproduction (figure 5b) shows that the estimated mean threshold is close to the ESS prediction, but the variance is considerably larger than the ESS prediction.

#### 4. DISCUSSION

Integral projection models are powerful flexible tools for exploring population dynamics and evolution in size-structured populations. Because the operation of integration on the right-hand side of equation (2.1) is linear in  $n(x,t)$  we can regard equation (2.1) as a partial analytic solution of a stochastic individual-based model, and so we can compute expected population trajectories and population parameters without simulation (Easterling *et al.* 2000).

The model predictions (*ca.* 16/17 cm mean rosette diameter at flowering) are close to the observed flowering strategy (*ca.* 18 cm). Allowing both parameters to evolve results in a step-function relationship between the probability of flowering and plant size (figure 5), as expected from general models of evolution in a constant environment (Sasaki & Ellner 1995). Why is the observed relationship between the probability of flowering and plant size shallower than predicted by the models? There are several possible explanations. First, if plant size is not perfectly correlated with the threshold size for flowering then the slope of the probability of the flowering relationship will be attenuated (shallower) (Cox & Snell 1989), so making the distribution of thresholds in the population appear variable even if it is not. Second, other factors such as spatial or temporal variation in growth or survival, not included in the model, may allow the maintenance of genetic variation for threshold flowering sizes (Sasaki & Ellner 1995). Despite this discrepancy, it is clear that accurate prediction of average life-history phenomena in monocarpic perennials is possible (Rees *et al.* 1999, 2000; Rose *et al.* 2002). The elasticity surface for *Oenothera* demonstrates the importance of growth and reproduction; similar results have been found for monocarpic perennials using matrix models (Silvertown *et al.* 1993), indicating results obtained for *Oenothera* may be representative of other species.

In order to estimate the ESS flowering strategy we assumed that density dependence acts on seedling establishment, so that  $R_0$  is maximized (Mylius & Diekmann 1995). The integral projection approach can easily be modified to incorporate other forms of density dependence. For example, the effect of density on growth can be quantified by incorporating density as a covariate in the growth model (Rees *et al.* 1999) (equation (2.4)) and this incorporated into the kernel. Analysis of such density-dependent models is rather more complicated but poses no new problems. Likewise, age-dependent demographic

rates can easily be accommodated. Similar predictions of the average size at flowering are obtained (*ca.* 16 cm), assuming evolution maximizes  $R_0$  or  $\lambda$ . Maximizing  $\lambda$  gives a slightly lower predicted value; this is a result of  $\lambda$  being dependent on generation time, which favours earlier and so smaller sizes, at reproduction. In addition to this, sensitivities and elasticities of  $\lambda$  and  $R_0$  are proportional, providing  $\lambda \approx R_0$  (equation (3.4)), and so similar predictions arise if one uses either of these commonly used fitness measures.

At equilibrium  $R_0 = \lambda = 1$  and so  $\lambda$  provides an estimate of the growth rate of rare mutants introduced into the resident population. Sensitivity analysis (table 1) reveals strong selection operating for faster growth, higher survival and increased seed production, indicating that these are the key processes influencing the evolution of delayed reproduction in *Oenothera*. Given that strong selection operates on all these parameters, it is clear that physical or genetic constraints or trade-offs must be operating. There are several possibilities, for example *Oenothera* has a taproot and it is probable that survival could be improved by increased allocation to storage in the taproot, which would allow plants to recover after damage, however this would decrease allocation to the rosette and presumably slow growth.

Fitness also increases with increasing variance about the growth curve, as found by earlier studies (Rees *et al.* 1999, 2000; Rose *et al.* 2002). This occurs because the variance about the growth curve increases the equilibrium plant size, on an arithmetic scale. This is given by

$$l = \exp((a_g + \sigma^2/2)/(1 - b_g)), \quad (4.1)$$

where  $a_g$  and  $b_g$  are the intercept and slope of the growth function (equation (2.4)) and  $\sigma^2$  is the variance about the fitted relationship. This results in increased fecundity and so increases  $R_0$  and as a result increases fitness.

The weak selection pressure operating on the flowering strategy is a consequence of the flowering strategy being close to the ESS (see figures 4 and 5). The ridge of approximately equal fitness arises because there is strong negative covariance between the estimates of the intercept,  $\beta_0$ , and slope,  $\beta_s$ , of the probability of the flowering relationship. This means that a wide range of combinations of  $\beta_0$  and  $\beta_s$  provide a similar description of the data, and so have approximately equal fitness. This provides a potential mechanism allowing the maintenance of genetic diversity, and indeed selection experiments have shown that natural populations harbour extensive genetic variation for threshold sizes of flowering (Wesselingh & de Jong 1995; Wesselingh & Klinkhamer 1996). Rose *et al.* (2002) draw the same conclusion from the fitness landscape of the monocarpic thistle *Carlina vulgaris*, which is remarkably similar to that calculated here for *Oenothera*.

The techniques presented here allow considerable insight into the evolutionary forces acting on plant populations in the field without relying on the development of computationally intensive individual-based models (Rees *et al.* 1999). With the development of the techniques presented here, it is now possible to compare the observed parameters with the ESS, and to estimate precisely the selection pressures on each parameter. The consequences of the estimated selection pressures will depend on the genetic architecture of the traits and particularly any

trade-off present (Lande 1982). Further insights into the evolutionary ecology of semelparous herbs are dependent on understanding the selection pressures that operate on many species, in different habits, and determining the allocation constraints that prevent plants achieving simultaneously higher growth and survival.

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## REFERENCES

- Bell, G. 1980 The costs of reproduction and their consequences. *Am. Nat.* **116**, 45–76.
- Bulmer, M. G. 1985 Selection for iteroparity in a variable environment. *Am. Nat.* **126**, 63–71.
- Caswell, H. 2001 *Matrix population models. Construction, analysis and interpretation*. Sunderland, MA: Sinauer.
- Charnov, E. L. & Schaffer, W. M. 1973 Life-history consequences of natural selection: Cole's result revisited. *Am. Nat.* **107**, 791–793.
- Chesson, P. L. & Warner, R. R. 1981 Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* **117**, 923–943.
- Cochran, M. E. & Ellner, S. 1992 Simple methods for calculating age-based life-history parameters for stage-structured populations. *Ecol. Monogr.* **62**, 345–364.
- Cole, L. C. 1954 The population consequences of life-history phenomena. *Q. Rev. Biol.* **29**, 103–137.
- Cox, D. R. & Snell, E. J. 1989 *Analysis of binary data. Monographs on statistics and applied probability*. London: Chapman & Hall.
- de Jong, T. J., Klinkhamer, P. G. L. & Metz, J. A. J. 1987 Selection for biennial life histories in plants. *Vegetatio* **70**, 149–156.
- de Jong, T. J., Klinkhamer, P. G. L., Geritz, S. A. H. & van der Meijden, E. 1989 Why biennials delay flowering: an optimization model and field data on *Cirsium vulgare* and *Cynoglossum officinale*. *Acta Bot. Neerlandica* **38**, 41–55.
- de Jong, T. J., Klinkhamer, P. G. L. & de Heiden, J. L. H. 2000 The evolution of generation time in metapopulations of monocarpic perennial plants: some theoretical considerations and the example of the rare thistle *Carlina vulgaris*. *Evol. Ecol.* **14**, 213–231.
- Easterling, M. R., Ellner, S. P. & Dixon, P. M. 2000 Size-specific sensitivity: applying a new structured population model. *Ecology* **81**, 694–708.
- Enright, N. J., Franco, M. & Silvertown, J. 1995 Comparing plant life histories using elasticity analysis: the importance of life-span and the number of life-cycle stages. *Oecologia* **104**, 79–84.
- Hastings, A. 1978 Evolutionary stable strategies and the evolution of life histories: I. Density dependent models. *J. Theor. Biol.* **75**, 527–536.
- Kachi, N. 1983 *Population dynamics and life-history strategy of Oenothera erythrosepala in a sand dune system*. Japan: University of Tokyo.
- Kachi, N. & Hirose, T. 1983 Bolting induction in *Oenothera erythrosepala* borbas in relation to rosette size, vernalization, and photoperiod. *Oecologia* **60**, 6–9.
- Kachi, N. & Hirose, T. 1985 Population dynamics of *Oenothera glazioviana* in a sand-dune system with special reference to the adaptive significance of size-dependent reproduction. *J. Ecol.* **73**, 887–901.
- Kawecki, T. J. 1993 Age and size at maturity in a patchy environment: fitness maximisation versus evolutionary stability. *Oikos* **66**, 309–317.
- Kelly, D. 1985a On strict and facultative biennials. *Oecologia* **67**, 292–294.
- Kelly, D. 1985b Why are biennials so maligned? *Am. Nat.* **125**, 473–497.
- Kelly, D. 1989 Demography of short-lived plants in chalk grassland. I. Life-cycle variation in annuals and strict biennials. *J. Ecol.* **77**, 747–769.
- Lacey, E. P. & Pace, R. 1983 Effect of parental flowering and dispersal times on offspring fate in *Daucus carota* (Apiaceae). *Oecologia* **60**, 274–278.
- Lande, R. 1982 A quantitative genetic theory of life-history evolution. *Ecology* **63**, 607–615.
- Metz, J. A. J., Nisbet, R. M. & Geritz, S. A. H. 1992 How should we define fitness for general ecological scenarios. *Trends Ecol. Evol.* **7**, 198–202.
- Mylius, S. D. & Diekmann, O. 1995 On evolutionarily stable life-histories, optimization and the need to be specific about density dependence. *Oikos* **74**, 218–224.
- Rand, D. A., Wilson, H. B. & McGlade, J. M. 1994 Dynamics and evolution: evolutionarily stable attractors, invasion exponents and phenotype dynamics. *Phil. Trans. R. Soc. Lond. B* **343**, 261–283.
- Rees, M., Sheppard, A., Briesse, D. & Mangel, M. 1999 Evolution of size-dependent flowering in *Onopordum illyricum*: a quantitative assessment of the role of stochastic selection pressures. *Am. Nat.* **154**, 628–651.
- Rees, M., Mangel, M., Turnbull, L. A., Sheppard, A. & Briesse, D. 2000 The effects of heterogeneity on dispersal and colonisation in plants. In *Ecological consequences of environmental heterogeneity* (ed. M. J. Hutchings, E. A. John & A. J. A. Stewart), pp. 237–265. Oxford: Blackwell.
- Reinartz, J. A. 1984 Life-history variation of common mullein (*Verbascum thapsus*). 1. Latitudinal differences in population-dynamics and timing. *J. Ecol.* **72**, 897–912.
- Roff, D. A. 1992 *The evolution of life histories. Theory and analysis*. London: Chapman & Hall.
- Rose, K. E., Rees, M. & Grubb, P. J. 2002 Evolution in the real world: stochastic variation and the determinants of fitness in *Carlina vulgaris*. *Evolution* (In the press.)
- Sasaki, A. & Ellner, S. 1995 The evolutionarily stable phenotype distribution in a random environment. *Evolution* **49**, 337–350.
- Silvertown, J., Franco, M., Pisanty, I. & Mendoza, A. 1993 Comparative plant demography: relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J. Ecol.* **81**, 465–476.
- Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press.
- Weiner, J., Martinez, S., Müller-Schärer, H., Stoll, P. & Schmid, B. 1997 How important are environmental maternal effects in plants? A study with *Centaurea maculosa*. *J. Ecol.* **85**, 133–142.
- Wesselingh, R. A. & de Jong, T. J. 1995 Bidirectional selection on threshold size for flowering in *Cynoglossum officinale* (Hound's tongue). *Heredity* **74**, 415–424.
- Wesselingh, R. A. & Klinkhamer, P. G. L. 1996 Threshold size for vernalization in *Senecio jacobaea*: genetic variation and response to artificial selection. *Funct. Ecol.* **10**, 281–288.
- Wesselingh, R. A., Klinkhamer, P. G. L., de Jong, T. J. & Boorman, L. A. 1997 Threshold size for flowering in different habitats: effects of size-dependent growth and survival. *Ecology* **78**, 2118–2132.

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