

# Suboptimal timing of reproduction in *Lobelia inflata* may be a conservative bet-hedging strategy

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## Abstract

Age and size at reproduction are important components of fitness, and are variable both within and among angiosperm species. The fitness consequences of such life-history variation are most readily studied in organisms that reproduce only once in their lifetime. The timing of the onset of reproduction (bolting) in the monocarpic perennial, *Lobelia inflata*, occurs over a range of dates within a season, and may be postponed to a later year. Empirical relationships among life-history traits, derived from over 950 wild-growing and experimentally manipulated plants in the field, are used to model an optimal changing size threshold (norm of reaction) for bolting over the growing season. Comparisons are made between observed and expected norms of reaction governing bolting. An apparently suboptimal bolting schedule that precludes bolting beyond an early (conservative) date is observed, and is found to be qualitatively consistent with conservative bet hedging under unpredictable season lengths. On this basis we propose the schedule of bolting as a plausible example of a conservative bet-hedging strategy. The results underscore the critical need for long-term studies of fluctuating selection to distinguish suboptimality from bet hedging.

## Introduction

Life-history traits have proved useful in the study of adaptation because of their close relationship with fitness (Roff, 1992). An organism's schedule of reproduction can have an especially strong effect on fitness, and its evolution is influenced by the relationship between size and fecundity, as well as by the probability of survival to age at maturity (McLaren, 1966). Monocarpic (semelparous) plants offer a convenient system for the study of the life-history consequences of the onset of reproduction: the potentially complicating issue of resource allocation between immediate and future reproduction is avoided, and there is ample natural variation in the

timing of reproduction both within and among species. There exists an extensive literature on the fitness consequences of among-season reproductive delays (Young, 1984; Lacey, 1986; de Jong *et al.*, 1987; Klinkhamer *et al.*, 1991; Wesselingh *et al.*, 1997). A rosette that bolts (initiates reproduction by developing a flowering stalk) forgoes the additional growth it may have enjoyed had it remained vegetative until the following season, but it also evades the additional risk of mortality associated with the delay, and produces seeds a year earlier.

The fitness consequences of the timing of bolting are complicated by environmental uncertainty. For example, the date of last frost in the spring, first frost in the autumn, and accumulation of degree-days within a growing season are all characterized by year-to-year variation (Environment Canada, 1997; see Results and discussion). Bolting only initiates reproduction; considerable time is required to produce mature seed. At the time the bolting 'decision' is made, the length of the remaining season is unpredictable. Fitness might be

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increased, for example, by delaying bolting to the next season when reproduction is assured, rather than by bolting late in the season and risking low or zero fitness should the season be shorter than average. Optimal behaviour may differ among seasons, resulting in the evolution of a risk averse, or conservative bet-hedging bolting strategy that restricts bolting to early in the season. Bet-hedging strategies, rather than maximizing fitness under average conditions, have evolved to maximize geometric-mean fitness (Gillespie, 1974; Seger & Brockmann, 1987; Philippi & Seger, 1989). Bolting behaviour may thus appear to be suboptimal, and differ from expectations under 'average' conditions.

In this paper we propose that bolting behaviour in *Lobelia inflata* L. (Campanulaceae) provides a possible example of conservative bet hedging. Although diversification bet hedging has been used to explain apparently maladaptive phenotypes, examples of putative conservative bet hedging in nature have rarely been proposed (Hopper, 1999; Simons, 2002). This paper highlights an area in need of empirical work: long-term studies of fluctuating selection are necessary to understand the adaptive significance of traits such as the timing of reproduction (Benton & Grant, 1996; Rees *et al.*, 1999). In their absence, evidence for bet hedging is restricted to apparent suboptimality in qualitative agreement with the expectations of bet-hedging theory. Furthermore, because environmental unpredictability may be seen to include a wide range of stochastic events that occur over all time scales, its evolutionary effects may be broader than previously thought (Simons, 2002).

Studies of several plant species have found that bolting is influenced predominantly by rosette size (Lacey, 1986; Klinkhamer *et al.*, 1991; Wesselingh *et al.*, 1997). Models for the control of bolting have been based on monocarpic perennials that require vernalization. For plants that require vernalization for the initiation of bolting, individuals exceeding a threshold size for bolting anytime up to the end of a given season will bolt the following spring (Wesselingh *et al.*, 1997). However, for plants that do not require vernalization, such as *L. inflata*, the size threshold could be reached – and bolting could occur – at any time during the growing season. Upon bolting, an individual will successfully reproduce only if sufficient time remains in the season for the development of mature fruits. For plants that do not require vernalization, then, the fitness consequences of bolting depend critically on the time of year at which a size threshold is reached. Even under the assumption of invariable season length, expected fitness of a rosette attaining a large size only later in the season might be increased by overwintering as a rosette and bolting immediately the following spring if the improvement in fecundity, gained both through additional rosette growth and the greater length of time in which to develop mature fruits, compensates for the probability of mortality over the remainder of the season and over the intervening winter. Therefore, rather than a constant

threshold size for bolting through the season, selection should favour a changing threshold size that reduces the probability of bolting later in the season.

*Lobelia inflata* does not require vernalization, and its reproductive behaviour within a season is highly plastic, governed not only by rosette size attained but also by the interaction of rosette size and date (Simons, 1999). Plasticity in threshold size has been observed in other species: Young's (1985) work on life-history evolution of the semelparous *L. telekii* shows that flowering is influenced by both size and growth rate. For *L. inflata*, there is an increasing threshold rosette size requirement for bolting as the season progresses, which becomes prohibitively large by the beginning of August. Norms of reaction may evolve through natural selection (Gavrilets & Scheiner, 1993), and the norm of reaction for bolting would thus be expected to maximize fitness, given various constraints.

An assessment of the fitness consequences of bolting behaviour requires empirical information on several parameters, including rosette size in autumn, overwinter survival, rosette size at bolting, bolting date, survival from bolting to fruit production and fecundity. Rosette size may influence the probability of surviving to reproduce, and should be closely related to number of flowers produced and therefore seed production. Seed production should also be influenced by the time of year at which bolting occurs: bolting too early or too late risks frost damage to flowers and fruits. Potential for rosette growth should also influence the evolution of bolting behaviour because a decision to bolt forgoes the additional fecundity that would be enjoyed by a larger rosette.

In this study, we measure the fitness consequences of bolting at different dates and sizes, using both wild plants and individuals with experimentally manipulated bolting times. Bolting in nature is constrained to the first few weeks of the season. To measure the fitness consequences of bolting at times outside the natural range, we induced plants to bolt under growth-chamber conditions and transplanted them to the field at intervals throughout the season. We then construct a model to predict the optimal decision (bolt/not bolt) for an individual of particular size at a given date. Using empirical data from over 950 wild-growing and transplanted rosettes of *L. inflata*, comparisons are made between observed and expected norms of reaction governing bolting. On this basis we propose the schedule of bolting as a plausible example of a conservative bet-hedging strategy.

## Empirical methods

Seed germination in *L. inflata* requires light (Baskin & Baskin, 1992; Simons & Johnston, 2000), and often follows soil disturbance. Therefore, rosettes may be of any size at a given time of year. *L. inflata* rarely flowers in its first season (pers. obs.); it may act as a 'biennial' or

winter annual and bolt only after overwintering as a rosette, or it may act as a monocarpic perennial.

For the analysis of overwinter survival, rosettes were marked along a gravel road ascending Martock Mountain, Hants County, Nova Scotia. Over three winters 412 individual rosettes were followed. Some (28) rosettes survived more than one winter, yielding a total sample size of 440 overwintering rosettes: 141 were followed in autumn 1995, 241 in 1996 and 58 in 1997. Because survival is a categorical response variable, and both continuous (autumn rosette size) and categorical (year) independent variables are of interest, PROC CATMOD (SAS, 1989) was used.

The fate of rosettes that survived the winter was documented, and additional rosettes were marked and followed during the growing season in both 1996 and 1997 for a total of 946 individuals. An area containing 227 rosettes was destroyed by a tree-harvesting vehicle. Although bet-hedging strategies may evolve in response to rare catastrophic events (Simons, 2002), this event was deemed unnatural, and these rosettes were excluded from analyses of survival. Survival, bolting behaviour, rosette size at bolting, the date and stem height at first flowering, as well as total fruit production and final stem height were recorded for the 719 remaining rosettes based on weekly visits to Martock.

The production of bolting individuals at dates beyond the natural range for *L. inflata* was achieved by satisfying bolting requirements of rosettes under long days (15 h 15 min light, and a 19°/13° thermoperiod of 12 h 30 min) in the growth chamber. Seeds were sown continually in the growth chamber to produce a range of germination and bolting dates. Individuals were transplanted to the field site at Martock as they bolted throughout the summer. Date of bolt was recorded for each plant, and the length of the longest leaf was measured weekly so that it could be recorded just prior to bolting. To ensure that bolting had occurred, individuals deemed to have bolted were allowed a short delay (11.93 ± 3.29 days) prior to transplant. A total of 233 newly bolted plants were transplanted to Martock over a period from 30 June to 24 October 1997. Date and stem height at transplant, date and stem height at first flowering, and final stem height and fruit production were recorded. Thirteen individuals were grazed and are excluded from analyses.

## Modelling methods

We next develop a model to ask, for a given rosette size and time of year, whether the optimal strategy is to bolt immediately or to delay bolting until the subsequent growing season. The model is parameterized based on empirically derived relationships. The goal is thus to find the bolting 'rule' or function that maximizes fitness. The plane containing every possible combination of time of year and rosette size can be divided into two areas: one for which immediate bolting maximizes fitness, one

containing combinations for which a delay maximizes fitness. The approach taken here is to divide these two areas with the function of equal fitness

$$w_b = w_{nb}, \quad (1)$$

where  $w_b$  is fitness associated with bolting in the first season, and  $w_{nb}$  is the fitness associated with not bolting, and delaying reproduction until the subsequent season. Expected fruit production, or fecundity, is used as a measure of fitness. We will first consider the fitness consequences of bolting within a season compared with a delay from one season to the next under the assumption of constant population size. Under the assumption of limited population growth, we may first proceed without regard to generation time (de Jong *et al.*, 1987).

The fitness consequence of immediate bolting at time  $t$  is modelled as dependent on rosette size ( $m_y$ ), survival from time  $t$  to fruit production ( $l_b$ ), and the effect of bolting date on realized fecundity ( $p_m$ ) expressed as a proportion of potential fecundity (later bolting reduces the time available in the present growing season for the development and maturation of reproductive structures). Expected fitness associated with the alternative strategy, namely a delay in bolting, is modelled as dependent on survival from time  $t$  to the end of the present growing season ( $l_t$ ), overwinter survival ( $l_o$ ), and fecundity the following year ( $m_{yt}$ ). Fecundity the following year depends on rosette growth over the remainder of the present growing season, rosette size at bolting ( $y_t$ ), and survival from the time of bolting to fruit production ( $l_b$ ). Thus

$$w_b = (m_y)(l_b)(p_m), \quad (2)$$

and

$$w_{nb} = (l_t)(l_o)(l_b)(m_{yt}). \quad (3)$$

## Rosette size and survival

Survival was recorded at eight times during the 1997 growing season (May 22–October 31). There was no significant ( $t = 0.32$ ;  $P = 0.75$ ) difference between the rosette size of survivors (mean = 9.2 mm) and nonsurvivors (mean = 9.4 mm). In a logistic regression to test the effects of date and rosette size on probability of survival, no significant effect of rosette size (Wald  $\chi^2 = 1.04$ ;  $P = 0.31$ ) was found. However, highly significant effects of date (Wald  $\chi^2 = 29.6$ ;  $P < 0.001$ ) and the interaction of date and rosette size (Wald  $\chi^2 = 19.2$ ;  $P = 0.004$ ) indicate that size dependence of survival changes over the season: mean size of survivors is less than that of nonsurvivors over five measurement intervals, and greater over two. It would be unreasonable to assume that the particular and complex pattern of size-dependent survival observed in 1997 may be extrapolated across years. Therefore, average instantaneous mortality,  $\bar{d}$ , is calculated for all rosettes observed under field conditions as

$$\bar{d} = -\frac{\ln l_t}{162 - t}, \quad (4)$$

where  $l_t$  is survival from time  $t$  to the end of the growing season. Some rosettes were added to the data set as they were located during the growing season, and there is variation in the period over which rosettes were observed. Therefore, instantaneous mortality is weighted by the number of observations made: 82 rosettes were observed over the entire 162-day season, 18 over 155 days, 16 over 120 days, and 10 rosettes over shorter periods down to 64 days. The weighted average,  $\bar{d} = 0.00564$ , is similar to instantaneous mortality calculated using only the 82 rosettes observed over the entire season ( $= 0.00562$ ). Survival from time  $t$  to the end of the season is thus modelled as

$$l_t = e^{-\bar{d}(162-t)}. \quad (5)$$

Overwinter rosette survival ( $l_o$ ) of naturally growing plants averaged 44% over the three winters (43, 47 and 34%), and did not differ significantly among winters (PROC CATMOD; d.f. = 2;  $\chi^2 = 4.31$ ,  $P = 0.116$ ). Overwinter survival was independent of rosette size in late autumn (PROC CATMOD; d.f. = 1;  $\chi^2 = 0.50$ ;  $P = 0.48$ , year as covariate to accommodate differences in final rosette size); survivors averaged 15.4 mm and nonsurvivors 16.2 mm. Therefore, the best estimate of overwinter survival is simply  $l_o = 0.44$ .

### Rosette size and fecundity

The expected fruit production for a wild rosette of size  $y$  at the time of bolting (Fig. 1) is given ( $N = 50$ ;  $r^2 = 0.376$ ) by the power function

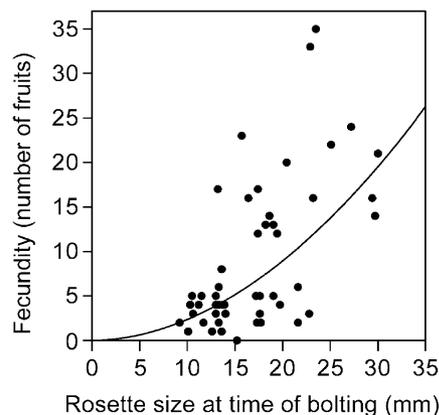
$$m_y = 0.028y^{1.925}. \quad (6)$$

Because bolting in wild-growing rosettes does not occur after 10 July (day 40), this function is assumed to represent true reproductive potential for a given rosette size, whereas the results of the manipulation experiment (below) consider the effects of deteriorating conditions associated with bolting later in the season. The relationship is only slightly altered ( $m_y = 0.022y^{2.010}$ ) if the analysis is restricted to individuals bolting only during the first 20 days, and results in a small (0–6%) difference in predictions of fruit numbers over realistic rosette sizes of 10–35 mm.

There is a weaker relationship between final rosette size for overwintering rosettes ( $y_f$ ) and expected fruit production ( $m_{y_f}$ ) than that for immediate bolters, and is given by the power function

$$m_{y_f} = 0.370y_f^{0.866} \quad (7)$$

Survival from the time of bolting to fruit production is very high (>95%) in the field: no wild-growing plants were grazed or destroyed, and 13 of 233 of the transplants were grazed. Furthermore, on the assump-



**Fig. 1** The dependence of fruit production on the size of a rosette (length of longest leaf) for wild rosettes bolting at Martock early in the growing season.

tion that post-bolting survival does not differ for immediate and delayed bolters, this parameter appears on both sides of the equation describing equal fitness of bolters and delayed bolters and thus cancels.

If a rosette is of size  $y$  at time  $t$ , the expected rosette size at the end of the growing season,  $y_f$ , is given by

$$y_f = ye^{\bar{g}(162-t)}, \quad (8)$$

where  $\bar{g}$  is an average growth exponent over a given time interval. However, the growth exponent over the remainder of the season is dependent on time of year: spring and fall are characterized by low average growth rates, regardless of rosette size. Therefore, size-independent growth rate cannot be represented by a single value; it is modelled instead as a function. We proceed in two steps: we first obtain a typical growth exponent function from the changing growth rates of an 'average rosette', and then apply this  $\bar{g}$  to individual rosettes to obtain size-dependent growth and, thus, final rosette size.

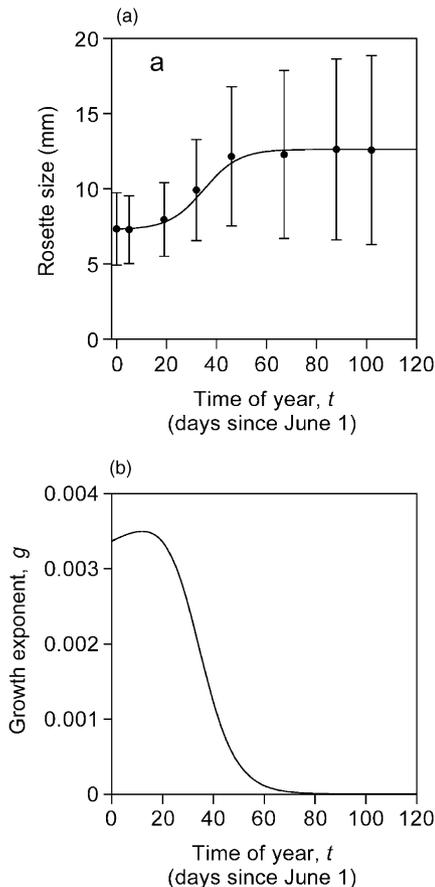
The size-independent effect of seasonality on the average growth rate of a typical rosette over the time remaining in the season after time  $t$  is modelled as

$$\bar{g} = \frac{\ln \bar{y}_f - \ln \bar{y}(t)}{162 - t}, \quad (9)$$

where average measured rosette size at time of year,  $\bar{y}(t)$ , is well described (Fig. 2a;  $r^2 = 0.99$ ;  $P < 0.001$ ) by the sigmoid function

$$\bar{y}(t) = \frac{\bar{y}_f - \bar{y}_{\min}}{1 + e^{-r(t-t_{\text{mid}})}} + \bar{y}_{\min}. \quad (10)$$

We use an average final rosette size,  $\bar{y}_f = 12.63$  mm; average initial rosette size,  $\bar{y}_{\min} = 7.28$  mm; the time corresponding to the point at which rosette growth begins to decelerate,  $t_{\text{mid}} = \text{day } 35$ ; and  $r = 0.143$ . This function is then used in the calculation of the average



**Fig. 2** Seasonal effects on rosette growth at Martock: (a) average size and standard deviations of wild-growing rosettes measured through the growing season and (b) the average growth exponent,  $g$ , over the time remaining in the season from time  $t$ . The fitted sigmoidal growth function is used to estimate seasonal changes in the average growth exponent necessary for the calculation of expected rosette size at the end of the growing season and  $\bar{g}$ .

growth exponent ( $\bar{g}$ ; Fig. 2b), for the period from time  $t$  to the end of the season (eqn 9). Substituting  $\bar{g}$  from eqn 9 into eqn 8 yields a final expected rosette size for a rosette of size  $y$  at time  $t$  of

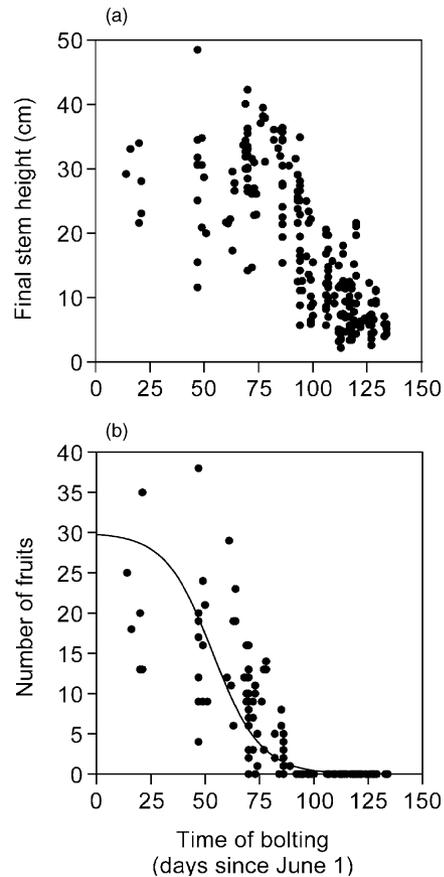
$$y_f = ye^{\frac{\ln(12.63) - \ln\left[\frac{12.63 - 7.28}{1 + e^{-0.143(t-35)}} + 7.28\right]}{(162-t)}} \quad (11)$$

or

$$y_f = ye^{2.54 - \ln\left[\frac{5.35}{1 + e^{-0.143(t-35)}} + 7.28\right]} \quad (12)$$

**Within-season timing of bolting, natural and transplant field observations**

Under natural field conditions the median date of bolting of wild-growing rosettes was 20 June and no wild rosette



**Fig. 3** Results of a manipulation experiment in which the natural period of bolting of *Lobelia inflata* was extended. Rosettes were transplanted to a field site shortly after they had been manipulated to bolt under growth chamber conditions. Shown are the relationships between date of bolt and (a) final plant height, and (b) the number of fruits produced. The curve indicates the fitted least-squares function  $p_m$  included in the optimality model to describe the declining fecundity associated with later bolting dates.

bolting after 10 July. The transplant experiment indicates that bolting up to 29 August (day 89) can result in the successful production of fruit. However, a decline in both the final plant height (Fig. 3a) and number of fruits produced (Fig. 3b) in the manipulated transplants is observed with later bolting dates. This manipulation experiment is used to quantify the dependence of fruit production on time of bolting. The sigmoid function of best fit (Fig. 3b;  $r^2 = 0.511$ ), constrained to predict <1 fruit following day 89 (no plants bolting later produced a single fruit), and expressed as a proportion of maximum fruit production, is

$$p_m = \frac{1}{1 + e^{0.091(t-53.6)}}, \quad (13)$$

where  $t$  is time of bolting, expressed as days since June 1.

## Results and discussion

### Model predictions and evaluation

Substituting the above empirical relationships from *L. inflata* of eqns 2 and 3 into eqn 1 yields the equation describing equal fitness for immediate and delayed bolting:

$$\begin{aligned} & (0.028y^{1.925}) \left[ \frac{1}{1 + e^{0.091(t-53.6)}} \right] \\ &= \left[ e^{-0.00564(162-t)} \right] 0.44 \\ & \times \left[ 0.370 \left[ ye^{2.54 - \ln \left[ \frac{12.63 - 7.28}{1 + e^{-0.143(t-35)}} + 7.28 \right]} \right]^{0.866} \right]. \end{aligned} \quad (14)$$

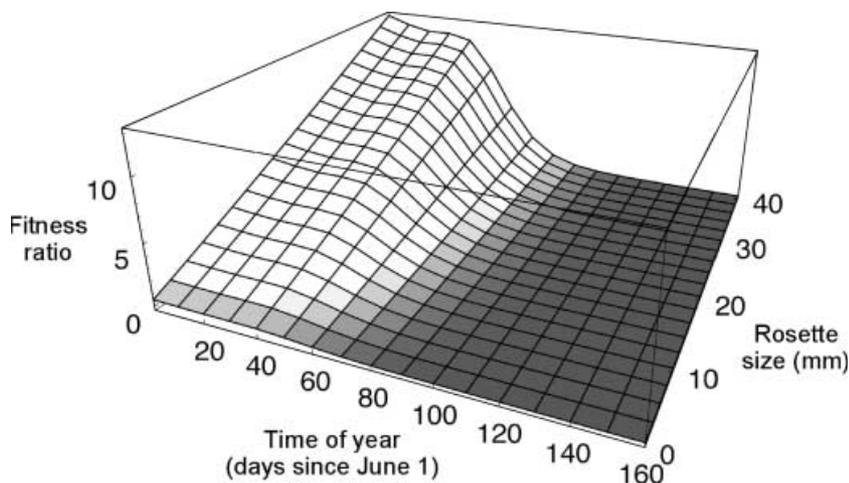
Each side of the equation forms a fitness surface associated with immediate or delayed bolting, with height  $w_b$  and  $w_{nb}$ , respectively, for any combination of time of year ( $t$ ) and rosette size ( $y$ ). We are interested in the relative success of the two strategies, or a comparison of the values of  $w_b$  and  $w_{nb}$  at any point ( $t, y$ ). The surface of fitness ratios (Fig. 4) shows how the fitness ratio  $w_b : w_{nb}$  changes with time of year and rosette size. Ratios above unity indicate that bolting in the current season is the fitter strategy, whereas ratios below unity indicate that delayed bolting is favoured. Points with a height of unity (Fig. 4) form the isocline for which the two strategies confer equal fitness. This isocline is shown in two dimensions in Fig. 5.

The function of equal fitness for the conditions under study (Fig. 5) suggests that rosette behaviour should evolve such that bolting is prevented late in the season by an ever-increasing size requirement. The area at the upper left bounded by the plotted function contains values of rosette size and time of year at which fitness of immediate bolters would be higher than that of rosettes delaying bolting until the subsequent season; fitness of

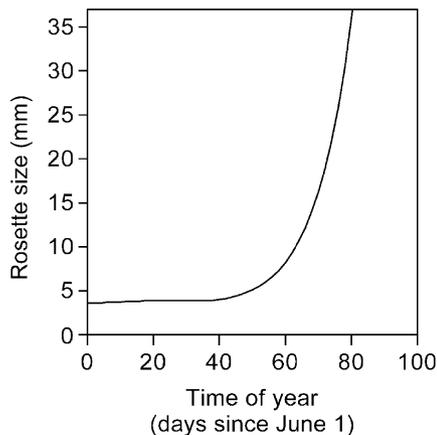
delayed bolters would be higher for all other combinations of  $y$  and  $t$  (Fig. 5). Note that a relative fitness advantage of immediate bolting implies that a rosette should not delay bolting until the subsequent season, but should bolt either now or at a later date during the current season if additional growth places the rosette at a higher point on the fitness surface (Fig. 4). This becomes apparent especially at early values of  $t$  on the  $w_b = w_{nb}$  curve (Fig. 5).

The function thus indicates that the optimal size threshold for bolting should increase through the season up to a time after which no rosette will bolt (Fig. 5). Specifically, any rosette that is physiologically capable of bolting at the beginning of the season is expected to bolt, and bolting of large rosettes is expected to continue into August. For example, rosettes of 35 mm or more should bolt until 19 August (day 80) according to the model. No lower limit on rosette size was used to impose physiological constraints on bolting in the model, although the minimum observed bolting rosette size in the field was 9.2 mm. Unrealistic model predictions of fewer than one fruit may thus result from bolting at small rosette sizes. For example, the model shows that  $w_b > w_{nb}$  for rosettes with a longest leaf of only 4 mm near the beginning of the season. However, both  $w_b$  and  $w_{nb}$  are low (<1 fruit); a within-season delay would yield a new combination of  $y$  and  $t$  for which  $w_b$  might be higher. A further prediction of the model, then, is that all rosettes present at the beginning of a season – provided they have reached the physiological lower limit for bolting – should bolt that season.

This model result is only qualitatively similar to rosette behaviour under field conditions. In the field, bolting is restricted to a period during early summer: of the rosettes followed under field conditions, 58 were observed to bolt; one bolted on 10 July, but all other bolting was restricted to between 1 June and 4 July (Fig. 6a). This restriction is caused by abstinence rather than absence:



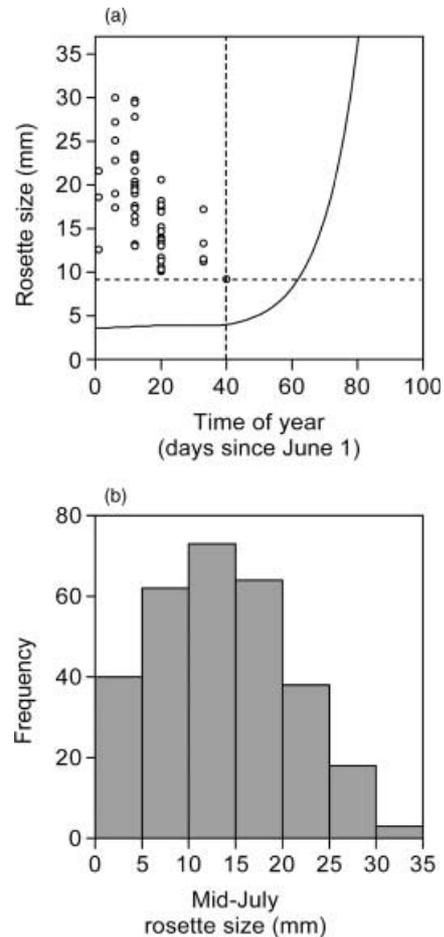
**Fig. 4** The surface of fitness ratios for immediate bolting vs. delayed bolting. Each elevation is an isocline in relative fitness; fitness thus depends on both rosette size and time of year. Higher elevations (light shading) imply stronger selection for immediate bolting; lower elevations (dark shading) imply selection for delayed bolting. The area of intermediate shading corresponds to the isocline of equal fitness associated with immediate and delayed bolting.



**Fig. 5** The function describing the combinations of date and rosette size at which expected fitness of rosettes making a 'decision' to bolt is equal to the expected fitness of those delaying bolting until the subsequent season. Individuals below the curve maximize fitness by delaying reproduction and those above the curve by immediate bolting.

an abundance of rosettes of all sizes is present immediately following this period (Fig. 6b). Field observations are corroborated by observed bolting behaviour under growth chamber conditions. In an experiment conducted under three photoperiods mimicking early, mid, and late summer and repeated for two generations, a consistent decline – to nearly zero – in the frequency of bolting was observed with later simulated dates (Simons & Johnston, 2000). It should be noted that bolting behaviour is not uniform: a significant proportion (42%) – although measured under growth chamber conditions, and should be viewed as an overestimate of the true value (Simons & Roff, 1994, 1996) – of the observed variation is composed of additive genetic variation for the size threshold for bolting (Simons & Johnston, 2000).

That in the field only one rosette bolted later than 4 July whereas the model predicts bolting until mid-August suggests that bolting behaviour is suboptimal. Conservative bet hedging, however, is also consistent with the observation of restricted bolting, and will be discussed below. Conclusions must be drawn with an awareness of the model's deficiencies. First, the effect of delayed reproduction on fitness through an increase in generation time has not been considered. Secondly, the sensitivity of the result to variation in model components may be important because these are estimated with error. Finally, the model is based on data gathered over a relatively short time scale. If parameter values fluctuate over time, conclusions are valid only for the conditions under which data were collected. We consider these deficiencies in turn, and conclude with a treatment of the effects of environmental variance on the evolution of bolting behaviour.



**Fig. 6** Rosette bolting behaviour under field conditions: (a) the distribution of the timing of bolting for wild rosettes growing at Martock and (b) the size distribution of nonbolting rosettes. Fifty-eight rosettes bolted over two growing seasons (a), whereas 298 nonbolting rosettes (b) were present at Martock immediately following 10 July, the end of the bolting period. Horizontal and vertical dashed lines indicate the smallest rosette size at bolting observed in the field and the latest bolting date observed, respectively. The optimality model result from Fig. 5 is included for comparison (solid line).

In a population that increases without limit, rate of increase is sensitive to generation time (Lewontin, 1965). For a monocarpic perennial under unconstrained population growth, an individual delaying reproduction from season  $n$  to season  $n + 1$  must produce seeds in the ratio of  $(n + 1)/n$  to have the equivalent fitness of an immediate bolter. However, for monocarpic plants under limited population growth, generation time may be unimportant (de Jong *et al.*, 1987): delayed flowering is appropriate simply if increased fecundity outweighs the risk of mortality (de Jong *et al.*, 1987). Here, although relative fitness of immediate bolting compared with delayed bolting increases dramatically for large, early

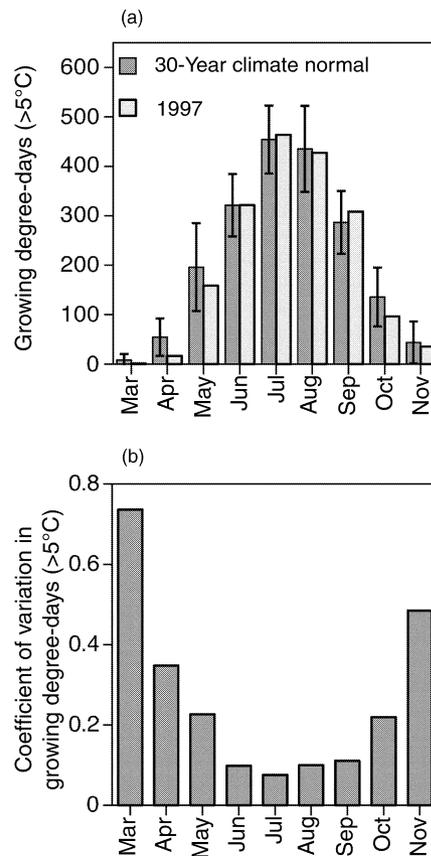
bolters when generation time is considered, the function of equal fitness described by the model remains almost unchanged. Here we assume a delay from the second to third year of growth (rosettes rarely bolt during the first season) only; additional possibilities not considered include all other single-season delays (first to second, etc.), and two-, three-, etc. year delays. For a delay from the second to third year, the latest date of bolting for a 35-mm rosette, for example, increases by only 3 days, and this difference is smaller with smaller rosette sizes. Therefore, whereas the fitness differences between strategies become more pronounced, the identity of the fittest strategy is robust to generation time.

All component model parameters are estimated with uncertainty. We therefore attempt to assess the sensitivity of the model result to alterations in these parameters. Because the solution is not a single value but a function – latest bolting date as a function of rosette size – we express sensitivity as a change in the predicted latest date for bolting for two rosette sizes: 15 and 35 mm. Changes in the model solution are explored for these two rosette sizes in response to a  $\pm 10\%$  change in modelled parameters (Table 1). Slight differences in conclusions would result from changes in within-season survival (modelled as  $\pm 10\%$  in average instantaneous mortality,  $\bar{d}$ ; eqn 5), overwinter survival, and expected final rosette size (modelled as change in growth rate resulting from  $\pm 10\%$  in  $y_f$ ; eqn 9), but the model appeared to be most sensitive to changes in  $p_m$  (Table 1), the decline in production of fruits later in the season (modelled as a  $\pm 10\%$  horizontal shift in the sigmoidal function; Fig. 3b).

The growing season during which data were collected and for which the model was constructed may not be representative of the conditions under which bolting behaviour evolved. An environmental parameter derived for agricultural applications as an indication of a season's quality for growth is the accumulation of degree-days above 5 °C (Fig. 7a; Environment Canada, 1997). At Martock, the degree-day accumulation above 5 °C was

**Table 1** Sensitivity of model predictions of latest date of bolting to a  $\pm 10\%$  change in component parameter values. Last date of bolting (days since 1 June) is given for two rosette sizes and for changes in mortality ( $\bar{d}$ ), overwinter survival ( $l_o$ ), final rosette size ( $\bar{y}_f$ ), and the seasonal decline in fecundity ( $p_m$ ). The original model for 15 mm and 35 mm rosettes yields values of 70 and 80 days, respectively. See text for description of how upper and lower 10% values were established for each parameter.

Model parameter	15 mm rosette		35 mm rosette	
	-10%	+10%	-10%	+10%
$\bar{d}$	69	70	80	81
$l_o$	71	68	81	79
$\bar{y}_f$	68	71	79	81
$p_m$	65	75	75	85



**Fig. 7** Meteorological data for the field site at Martock, Nova Scotia: (a) the 30-year normal ( $\pm 2$  SD) is compared with values for the year in which the transplant experiment was performed and (b) unpredictability in the effective length of the growing season over a 30-year period. Unpredictability is measured as the coefficient of variation in degree-day accumulation and is shown month-by-month.

1680 for May–September 1997, which is very close to the 30-year climate normal (1694) for the Martock weather station (Fig. 7a). Therefore, the argument that observed bolting behaviour is apparently suboptimal only because it was assessed under unusually favourable conditions is not supported.

### Conservative bet hedging

Apparent suboptimality over a short time scale may result from the maximization of geometric mean fitness under environmental unpredictability (Gillespie, 1974; Slatkin, 1974; Seger & Brockmann, 1987; Philippi & Seger, 1989). Degree-day accumulation has been variable as estimated over a 30-year period at Martock (Fig. 7a), and is less predictable at the early and late extremes of the growing season (Fig. 7b; Environment Canada, 1997). Variance in season length cannot be

confidently included in a model because, even when accurate climate records are available, the quantitative relationships between a potentially infinite set of environmental variables and plant fitness are unknown. However, the conservative bet-hedging hypothesis can be tentatively assessed, at least qualitatively, by comparing the behaviour of rosettes in the field to expectations when season-length variability is incorporated into the model.

We assume that variation in effective season length affects both  $w_b$  and  $w_{nb}$ . The fitness associated with immediate bolting is affected primarily through among-year variance in the decline in fruit production over the season (eqn 13), whereas  $w_{nb}$  is affected through among-year variance in expected rosette growth. Although growth is affected by season length, survival of the frost-hardy vegetative rosettes is assumed – for the purposes of this speculative analysis – to be unaffected.

Season length variance is included in the model by adding a random normal deviate to the function describing the decline in fecundity through time (eqn 13). For simplicity, season length variance is modelled by assuming that the horizontal position of the point of inflection of the fecundity decline function is normally distributed: ‘poorer’ seasons are characterized by an earlier decline in fecundity. More complex possibilities involving a change in shape of the relationship (such as adding variation to the steepness of the decline) are not considered here. The geometric-mean fitness associated with bolting ( $gw_b$ ) at a given size,  $y$ , and time of year,  $t$ , is calculated over 30 generations of simulated environmental variance in season length. Because the sequence of 30 environments is sampled at random, different runs can yield different estimates of geometric-mean fitness. Therefore, each estimate of geometric-mean fitness is based on 100 runs of the 30-generation model. The simulation is performed for different levels of environmental unpredictability by altering the standard deviation of the random normal distribution to correspond to a coefficient of variation (CV) of 0–1.2.

Expected fitness of delayed bolters ( $w_{nb}$ ) is influenced by season length variance because of its effect on variance in final rosette size (eqn 11): average rosette growth rates are lower for poorer seasons. The effect of environmental variance on growth rate over the remainder of the season (eqn 9) is simulated by assigning the same random normal deviate as for the calculation of  $w_b$  (above) to average rosette growth over the season (eqn 10) for the calculation of  $w_{nb}$ . To generate variation in growth rates, the difference between average initial and average final rosette size ( $\bar{y}_f - \bar{y}_{min}$ ) was given a standard deviation ranging from 0 to 1.2. Geometric-mean fitness for each rosette size and time of year is thus computed for a final rosette size that is based on a randomized average growth rate over the remaining season. Again, environmental vari-

ance is simulated over 30 generations, and the geometric mean fitness associated with a delay in bolting ( $gw_{nb}$ ) is calculated for each level of environmental unpredictability using 100 runs of the model.

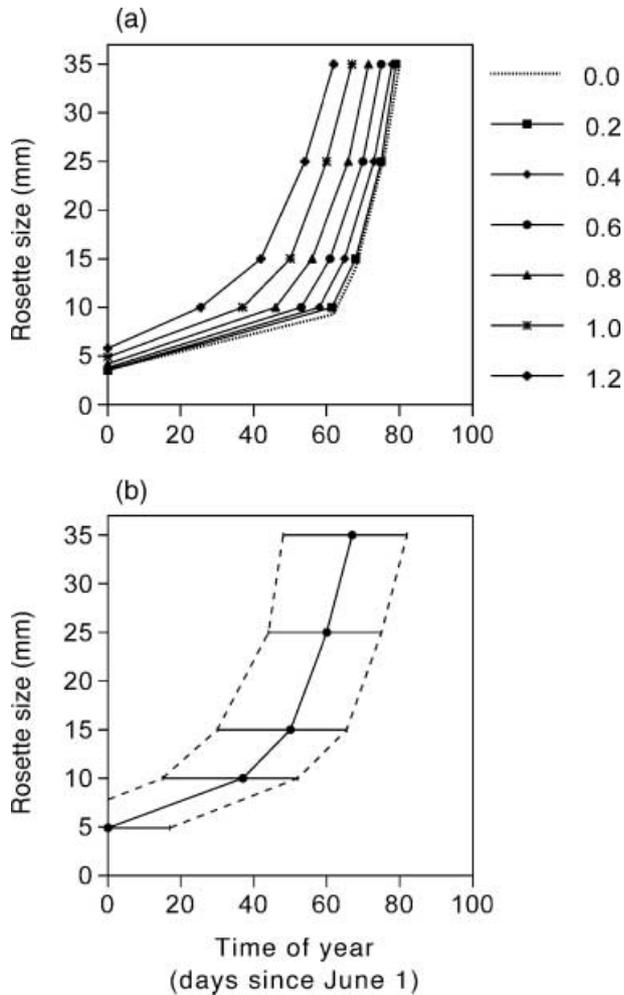
The simulation model shows that for any combination of rosette size and time of year falling along the original function of equal expected fitness ( $w_b = w_{nb}$ ), the geometric-mean fitness associated with immediate bolting is lower than for a delay in bolting. For example,  $w_b : w_{nb} = 1$  for a rosette size of 35 mm at 80 days, whereas the ratio  $gw_b : gw_{nb}$  is reduced to 0.72 when environmental CV = 0.5.

A function of equal geometric-mean fitness for immediate vs. delayed bolting ( $gw_b = gw_{nb}$ ) may now be constructed for any level of environmental variance. Results of the simulation model suggest that higher levels of environmental unpredictability should select for earlier final dates of bolting (Fig. 8a) through the maximization of geometric-mean fitness. Therefore, confinement of bolting to the period between early June and early July is qualitatively consistent with conservative bet hedging: although, in an average year, rosettes might maximize fitness by bolting, longer-term fitness might be maximized by remaining vegetative ‘in case’ the season is shorter than average.

The function of equal geometric-mean fitness ( $gw_b = gw_{nb}$ ) is estimated with error, and this sampling error increases with environmental variance. When the environmental CV = 1.0, for example, 5% of the 30-generation fitness ratios ( $gw_b : gw_{nb}$ ) are <1 at day 48, as estimated over 10 trials of the 100-run, 30-generation model (Fig. 8b). The 90%, rather than 95%, confidence intervals are used (Fig. 8b) because we are primarily interested in the lower confidence limit, or the final date of bolting for which 95% of  $gw_b : gw_{nb}$  values are >1. A simulated environmental CV of 1.2 or greater is necessary before the 90% confidence interval includes day 40 as a latest day for bolting. Although the level of environmental variance is assigned arbitrarily in the model, the results are qualitatively consistent with the hypothesis that the evolution of bolting behaviour is shaped by anomalous environmental events. A quantification of among-season unpredictability as it relates to fitness, however, would be an essential step in assessing the importance of bet hedging in the evolution of the timing of reproduction.

## Conclusions

Apparent suboptimality of bolting behaviour may be explained as a conservative bet-hedging strategy that has evolved in response to environmental unpredictability. It is possible, however, that bolting behaviour is simply suboptimal, or that other, unmeasured, parameters might be important in explaining the confinement of bolting to the first few weeks of the season. Fitness effects imposed by factors such as seedling density (Geritz,



**Fig. 8** The effect of among-year environmental variance on the geometric-mean fitness of bolting strategies. Simulation model results show functions of equal geometric-mean fitness for immediate and delayed bolting when among-year variation in growing season quality was added to the single-season life-history model. The effects of simulated coefficients of environmental variation, ranging from 0.2 to 1.2, on the average geometric-mean fitness over 30 generations (a) are based on 100 runs of the model. For comparison, the dashed line joins values of equal fitness from the original empirically derived optimality model that assumes no among-year environmental variance. The function of equal geometric-mean fitness is shown with 90% confidence intervals (b) under a coefficient of environmental variation of 1. Each upper and lower confidence limit is based on 10 trials of the 100-run, 30-generation model.

1995), herbivory (Simons & Johnston, 1999), and competition were not considered, and might well influence the outcome of the optimality model. A quantitative test of the predictions of the model would require observation under field conditions over many generations, using rosettes of known age.

The validity of any optimality model depends on the time scale over which natural selection can be effective. That bolting behaviour was not found to be optimal according to the present model during the season in which the study was performed does not rule out optimality over a longer time scale (Simons, 2002). Ironically, bet-hedging strategies are seldom assessed empirically because such studies are inherently risky. For example, obtaining a single value for trait optimality of a bet-hedging strategy over 10 generations requires an investment an order of magnitude greater than for a simple test of optimality, but the benefit of performing this long-term research cannot be predicted. Because of the difficulties inherent to the evaluation of bet hedging, evidence of suboptimality that is in qualitative agreement with bet-hedging theory remains our only evidence for bet hedging (Rees *et al.*, 1999). Furthermore, this scant evidence is largely restricted to that for the existence of diversification bet hedging in traits such as seed germination and insect diapause (Philippi & Seger, 1989; Simons & Johnston, 1997). Whereas the study of diversification bet hedging may be prompted by clues to its existence in the form of otherwise unexplained trait variance, conservative bet hedging offers no such clues. Very little attention has been paid to conservative strategies (Hopper, 1999); yet their evolution may, in theory, occur over any time scale, and in response to environmental events of any magnitude (Simons, 2002). The prevalence of conservative strategies should thus be considered an important problem because even powerful evidence of trait suboptimality under average conditions does not preclude optimal conservative bet hedging over a longer time scale. The present results provide an example of a possible conservative bet-hedging strategy, and encourage rigorous empirical study of temporal fluctuations in selection.

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