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Assessing fitness of dormancy from reproductive values of dormant plants

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ABSTRACT

Questions: How can the fitness of dormancy as a life-history trait be assessed? Can comparisons of reproductive values between dormant and active plants be used as proxies for fitness comparisons of life histories with dormancy versus without dormancy? Must dormancy be a bet-hedge for it to be adaptive in cases where reproductive values of dormant plants are lower than for active plants?

Mathematical methods: Comparison of reproductive values and fitness across a range of variables using demographic population matrix modelling.

Key assumptions: Plastic phenotypes include dormancy in their life-history repertoire, while static phenotypes do not. These phenotypes have different fitness. The environment is heterogeneous such that individuals within a population experience different conditions in both deterministic and stochastic environments. Active plants have higher reproductive values in good sites and lower reproductive values in bad sites compared with dormant plants. Environments vary in their proportion of good sites as defined above. Phenotypes that include dormancy vary in the probability that an individual will go dormant when in a bad site.

Conclusions: To assess the fitness of dormancy as a life-history trait, one must know the proportion of good sites in the environment and the response accuracy of the plastic phenotype to environmental variation. The fitness of dormancy in a life-history repertoire cannot be determined solely from comparing reproductive values or their components between dormant and vegetative plants. Likewise, dormancy cannot be assessed as a bet-hedging mechanism without knowledge of variation in environmental conditions and plant responses to that variation.

Keywords: bet-hedging, dormancy, fitness, life history, *Lilium catesbaei*, reproductive value.

INTRODUCTION

How should we make inferences about whether particular traits are likely to be adaptive within a life history? The life history of an individual is a sequence of events, but this sequence is not the same for all individuals. While some events are hard-wired and

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experienced in an ordered progression by every individual of a given genotype, other events are plastic, occurring at different times in different individuals, or not at all.

Where plastic traits are concerned, there is a difference between having the ability to display a trait and the expression of the trait itself. However, it is easy to confound ability of expression with demonstrated expression in the field. To see this, consider two extreme but illustrative examples: traits such as inducible plant anti-herbivore defences or fever in response to infection. Individuals with high levels of the defence may well have reduced survival, reproduction, and/or reproductive value; however, the ability to put on such defences can clearly still be adaptive. While this distinction seems obvious, the problem can be fairly subtle when considering life-history traits such as dormancy.

Dormancy is among the life-history traits where the ability to enter a state may be adaptive while the display of this trait may be associated with obvious costs to survival and reproduction. Many plants and animals have the ability to enter a dormant state and persist for prolonged periods. Among plants with the geophytic growth form, dormancy is a temporary state easily distinguished from vegetative activity by the absence of above-ground leaves (Raunkiaer, 1934). Geophytes are found in many taxa that display long-term dormancy (Halevy, 1989; Lesica and Steele, 1994). As a result, dormancy is a widespread phenomenon in plants. Understanding the role of dormancy in the life history of these organisms will give us insight into their ecology and evolution.

Dormancy and stress

Dormancy is inducible, reversible, and commonly observed as a response to stress in plants (Lesica and Steele, 1994). Moreover, individual dormancy in geophytes can be induced by a variety of environmental factors, including light, moisture, pH, and nitrogen (Reintal *et al.*, 2010). For example, dormancy is induced by photoperiod and temperature in *Anemone coronaria* (Ben-Hod *et al.*, 1988). In addition, the frequency of dormant individuals in populations of *Silene spaldingii* is correlated with climate (Lesica and Crone, 2007). Similarly, dormancy in the small yellow lady's slipper orchid (*Cypripedium calceolus* ssp. *parviflorum* (Salisb.) Fernald) correlates with temperature and precipitation (Shefferson *et al.*, 2001). Biotic stimuli have also been observed to induce dormancy, as in the case of *Solidago missouriensis* following defoliation by the specialist herbivore *Trirhabda canadensis* (Morrow and Olfelt, 2003). Individual quality also seems to affect dormancy, as evidenced by a correlation between dormancy and small size in three lady's slipper orchids *Cypripedium* spp. (Shefferson, 2006). Consequently, the onset of dormancy appears to be due to complex interactions between individual quality and environmental variables.

Further evidence that dormancy is a plastic response to the environment comes from experimental manipulations. Dormancy was induced by experimental defoliation in the terrestrial orchids *Cypripedium calceolus* and *Cephalanthera longifolia* (Shefferson *et al.*, 2005). Moreover, increased flowering followed experimental fire and roller-chopping, and seems to be linked in particular to light availability in *Lilium catesbaei* (Huffman and Werner, 2000). Flowering and dormancy are mutually incompatible states in an individual, so we expect that dormancy may be more likely in inter-fire years when flowering is less common. These experimental manipulations align with observations noted above in confirming that dormancy is tightly linked to individual and environmental quality.

The plastic dormancy response varies not only among individual plants based on their current quality, but among populations as well. The sensitivity of the dormancy response of individuals to the environment varies among populations as a response to selection (Vaughton and Ramsey, 2001). Similar variation in the sensitivity of individual dormancy to environmental conditions was experimentally verified in the non-geophytic blackbrush *Coleogyne ramosissima* (Lei, 2005). Furthermore, variation in individual sensitivity to the environment and spatial variation in the environment may both help to explain asynchronous variation among populations in rates of dormancy (e.g. Kery and Gregg, 2004). Thus, not only do individuals respond to environmental variation based on their present state, there is also population-level variation in the onset of individual dormancy.

Explaining dormancy

How do we investigate the effects of natural selection on geophyte dormancy if it is a response to stress? In a recent review, Shefferson (2009) concludes that long-term dormancy may be adaptive if the costs of vegetative activity outweigh the benefits. However, much of his reasoning is based on inferring fitness associated with the ability to go dormant based on comparison of survival of plants that are in the dormant versus active stages of their life cycle. Using similar reasoning, Lesica and Crone (2007) determined that prolonged dormancy in *Silene spaldingii* appeared to be advantageous based on a comparison of reproductive values associated with dormancy versus vegetative activity. Similarly, Shefferson *et al.* (2003) inferred that dormancy carries a fitness cost in *Cypripedium calceolus* based on survival and transition to flowering when compared with active individuals. Moreover, dormancy in *C. calceolus* is linked to smaller individual size, indicating that fitness costs may be the result of individual quality and not a direct result of dormancy (Shefferson, 2006). Here we argue that such comparisons of measures of current demographic statistics between dormant and non-dormant individuals miss the point that the most useful comparison is between the fitness of plants with the ability to become dormant versus that of plants without this ability.

For our part, we explicitly use the words ‘life history’ when we are referring to the appropriate phenotype on which natural selection acts. This is because natural selection acts on the life history as a whole, increasing the rate of population growth λ. Selection acts to maximize reproductive values of individual stages such as dormancy only within the context of the entire life history (Schaffer, 1981; Yodzis, 1981; Goodman, 1982). We ask, is it possible that the inclusion of dormant plants in a life-history repertoire can increase the fitness of a phenotype despite lower average reproductive values among dormant individuals? If so, how can we determine the conditions necessary for such a life history to evolve?

Although it appears that dormancy is a plastic response to stress, it does not have to be plastic for natural selection to favour it. One alternative possibility is that dormancy is a bet-hedging mechanism in stochastic environments. Bet-hedging involves a trade-off between the mean and variance of fitness, and is thus a relative term depending on a comparison with another non-bet-hedging genotype (Philippi and Seger, 1989). It follows that bet-hedging is explicitly not predictive of environmental quality, and does not depend on a plastic response to the environment.

When environmental quality is predicted or responded to, this will tend to increase the mean of fitness, rather than act to trade-off the mean and variance as in a bet-hedge.

However, it is possible that a life-history strategy with plastic dormancy could bet-hedge under the right circumstances, such as if the plastic response was imperfectly predictive or responsive. Accordingly, geophyte dormancy has been proposed as a bet-hedging mechanism in multiple species (Shefferson *et al.*, 2003; Shefferson and Tali, 2007; Shefferson, 2009). Much of the evidence for dormancy as a bet-hedge comes from seed dormancy (Clauss and Venable, 2000; Venable, 2007). Similarly, bet-hedging is common in invertebrates with dormant states (Caceres, 1997). Furthermore, bud dormancy may act as a bet-hedge against loss by herbivory (Nilsson *et al.*, 1996). The opportunities for bet-hedging are varied, as it is only required that a strategy sacrifice some average fitness for reduced variance in stochastic environments for it to be a bet-hedge.

Using a model of contrasting life histories, we map out a range of environmental conditions, the probability that plants will go dormant when appropriate, and the ultimate fitness consequences of varying proportions of dormant plants within a population. This provides us with a picture of when dormancy is adaptive in the sense that it increases fitness when permitted within a life-history repertoire, when expressed dormancy increases reproductive value compared with activity, and the conditions requiring that it does only one, both or neither. Furthermore, we analyse dormancy in stochastic environments to determine whether bet-hedging is necessary or sufficient to explain selection for dormancy in the face of lowered reproductive values.

We use a stage-based demographic model to carry out two comparisons: one between reproductive values of dormant and active plants, and the other between the intrinsic growth rates of life-history repertoires that permit or exclude dormancy as a possible state. The model allows us to explore the limitations on inferences that can be made about fitness from reproductive values of dormant individuals. Furthermore, we make fitness predictions in both deterministic and stochastic landscapes and determine the implications of bet-hedging. This model shows that reproductive values are predictive of fitness in competing life-history strategies only under a narrow range of conditions, and that dormancy may evolve under a much wider set of conditions in both deterministic and stochastic environments.

MODELLING

Matrix modelling fitness and reproductive values

We compare two life-history repertoires, one plastic with both dormancy and vegetative activity, and the other static (i.e. lacking dormancy). We expand each life history in a stage-based transition matrix to compare fitness between these two life histories. Furthermore, our life-history matrix approach allows us to relate fitness differences to the vital rates of vegetatively active and dormant individuals. Once we have two equations – one for fitness of a plastic life history and another for a static life history – we set them equal to each other to define the boundary where one life history is selected over the other. This boundary is defined in terms of the proportion of good sites in the environment and the accuracy with which plants go dormant under the correct conditions within the plastic life history. Accuracy, in this sense, is defined as the proportion of plants that are dormant in bad conditions, and is equivalent to the proportion of plants that are active in good conditions. Similarly, we define a boundary between reproductive values of vegetatively active and dormant plants within a plastic life history to find the environmental conditions and

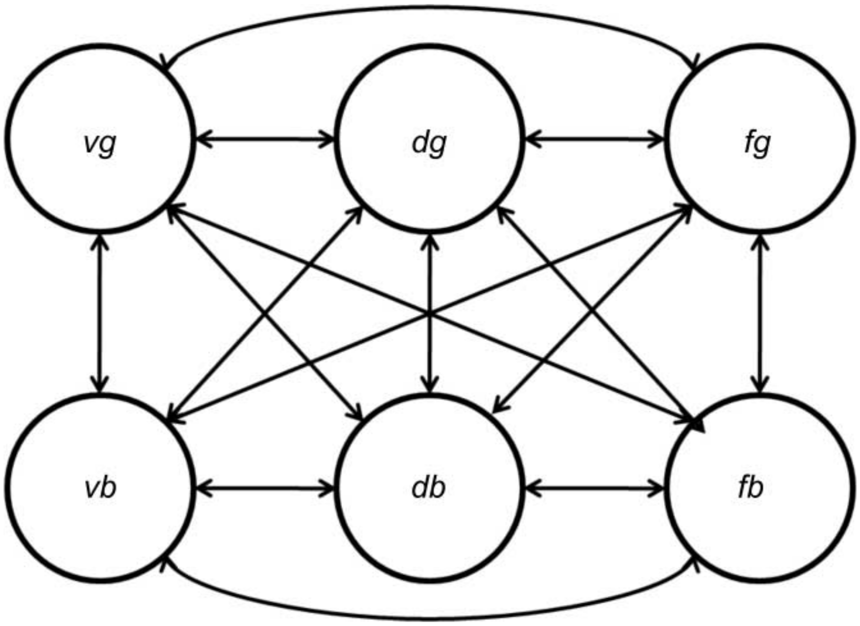

Fig. 1. Life cycle graph of a life history with vegetative (v), dormant (d), and flowering (f) plants across good (g) and bad (b) conditions. It is possible for an individual in any state to transition to any other state in the next time step.

response accuracies under which one stage will make a larger relative contribution to fitness. These two boundaries are then compared, and the delineated regions of parameter space explored.

We start by creating a plastic life history that has three stages: flowering (f), vegetative (v), and dormant (d); each experiences good (γ) or bad ($1-\gamma$) conditions (Fig. 1). Environmental conditions are good or bad depending on light availability/shading from neighbours, herbivory, or other microsite conditions known to be associated with dormancy (Lesica and Steele, 1994; Reintal *et al.*, 2010).

We model this life history in a 6×6 transition matrix to get estimates of fitness and reproductive values for each state (Table 1). Transition elements are based on reproduction in the sense of a branching process (Watson and Galton, 1875; Feller, 1939; Harris, 1963; Pollard, 1973), where each individual may give rise to zero, one, or more individuals in the following time step. What we call reproduction is actually a combination of biological reproduction and a later representation of the same individual in the next time step. In this way, survival and reproduction are both included in what we call reproduction: $\varphi = \varphi' + f$, where φ' is survival and f is biological reproduction. This combination of survival and reproduction carries with it some assumptions. First, there is no seed dormancy. Second, there is no age structure, such that newborns are the demographically same as adult vegetative, dormant, and flowering individuals. Each element of this matrix includes rates of reproduction φxy for individuals in a given stage ($x = v$, d, f) and conditions ($y = g$, b). To create transition elements, state-specific reproduction φxy is multiplied by the proportion of good conditions (γ) in the following year, the probability of flowering (ψ), and the accuracy (α) of being vegetative in good conditions and dormant in bad (Table 1).

Table 1. Life-history transition matrix for a plastic life history with dormancy

States	*vg*	*vb*	*dg*	*db*	*fg*	*fb*
vg	$\gamma\,\varphi vg\,(1-\psi)\,\alpha$	$\gamma\,\varphi vb\,(1-\psi)\,\alpha$	$\gamma\,\varphi dg\,(1-\psi)\,\alpha$	$\gamma\,\varphi db\,(1-\psi)\,\alpha$	$\gamma\,\varphi fg\,(1-\psi)\,\alpha$	$\gamma\,\varphi fb\,(1-\psi)\,\alpha$
vb	$(1-\gamma)\,\varphi vg\,(1-\psi)\,(1-\alpha)$	$(1-\gamma)\,\varphi vb\,(1-\psi)\,(1-\alpha)$	$(1-\gamma)\,\varphi dg\,(1-\psi)\,(1-\alpha)$	$(1-\gamma)\,\varphi db\,(1-\psi)\,(1-\alpha)$	$(1-\gamma)\,\varphi fg\,(1-\psi)\,(1-\alpha)$	$(1-\gamma)\,\varphi fb\,(1-\psi)\,(1-\alpha)$
dg	$\gamma\,\varphi vg\,(1-\psi)\,(1-\alpha)$	$\gamma\,\varphi vb\,(1-\psi)\,(1-\alpha)$	$\gamma\,\varphi dg\,(1-\psi)\,(1-\alpha)$	$\gamma\,\varphi db\,(1-\psi)\,(1-\alpha)$	$\gamma\,\varphi fg\,(1-\psi)\,(1-\alpha)$	$\gamma\,\varphi fb\,(1-\psi)\,(1-\alpha)$
db	$(1-\gamma)\,\varphi vg\,(1-\psi)\,\alpha$	$(1-\gamma)\,\varphi vb\,(1-\psi)\,\alpha$	$(1-\gamma)\,\varphi dg\,(1-\psi)\,\alpha$	$(1-\gamma)\,\varphi db\,(1-\psi)\,\alpha$	$(1-\gamma)\,\varphi fg\,(1-\psi)\,\alpha$	$(1-\gamma)\,\varphi fb\,(1-\psi)\,\alpha$
fg	$\gamma\,\varphi vg\,\psi$	$\gamma\,\varphi vb\,\psi$	$\gamma\,\varphi dg\,\psi$	$\gamma\,\varphi db\,\psi$	$\gamma\,\varphi fg\,\psi$	$\gamma\,\varphi fb\,\psi$
fb	$(1-\gamma)\,\varphi vg\,\psi$	$(1-\gamma)\,\varphi vb\,\psi$	$(1-\gamma)\,\varphi dg\,\psi$	$(1-\gamma)\,\varphi db\,\psi$	$(1-\gamma)\,\varphi fg\,\psi$	$(1-\gamma)\,\varphi fb\,\psi$

Note: States are a combination of life-history stage (v = vegetative, d = dormant, f = flowering) and environmental condition (g = good, b = bad). Transitions depend upon the proportion of good sites γ, reproduction φ, rate of flowering ψ, and the accuracy α of plastic response to the environment. Transitions may be read ‘from’ columns ‘to’ rows.

The fitness of this plastic life history with dormancy is calculated as the dominant eigenvalue of the matrix given in Table 1:

$$\lambda d = \varphi vg\ \alpha\ \gamma\ (1-\psi) + \varphi vb\ (1-\alpha)\ (1-\gamma)\ (1-\psi) + \varphi dg\ (1-\alpha)\ \gamma\ (1-\psi) + \varphi db\ \alpha\ (1-\gamma)\ (1-\psi) + \varphi fg\ \gamma\ \psi + \varphi fb\ (1-\gamma)\ \psi \quad (1)$$

This is just the weighted average reproduction with the probability of transitioning into each state as the weights. For example, take the first element in the sum. The reproduction of vegetative plants in good sites φvg is scaled by the accuracy rate α of being vegetative under good conditions, the proportion of good conditions γ, and the propensity $1-\psi$ for not flowering. Each of the other reproduction rates is scaled by the probability of transitioning into the respective state as well.

How does this plastic life history with dormancy compare with a static life history without dormancy? To make this fitness comparison, we need to construct a new, alternative life history that does not have any dormant plants. This life history will have vegetative and flowering plants in both good and bad conditions for a total of four states. The transition matrix is 4 × 4, with the same fecundities and transition probabilities as in the more extensive life history with dormancy, except that there is no accuracy rate for being vegetative under good conditions (Table 2).

This static life-history matrix results in the following fitness calculated as the dominant eigenvalue:

$$\lambda nd = \varphi vg\ \gamma\ (1-\psi) + \varphi vb\ (1-\gamma)\ (1-\psi) + \varphi fg\ \gamma\ \psi + \varphi fb\ (1-\gamma)\ \psi \quad (2)$$

We want to find the boundary where the fitness of a plastic life-history strategy with dormancy (λd) is equal to the fitness (λnd) of a static life-history strategy in which there is no dormancy. To do this, we set the fitness of the life history with dormancy λd (equation 1) equal to that without dormancy λnd (equation 2). These two fitness values are equal under a specific set of circumstances:

$$\gamma \mid \lambda d = \lambda nd = \gamma^* = \alpha(\delta-\varepsilon)/(\alpha(2\delta-\varepsilon-1)-\delta+1) \quad (3)$$

When parameters vary from this exact relationship, one life history will be selected for over the other. This set of parameter values can be plotted as a line in parameter space delineating conditions where one life history is selected over the other (Fig. 2).

Table 2. Life-history transition matrix for a constant life history without dormancy

	vg	*vb*	*fg*	*fb*
vg	$\gamma\ \varphi vg\ (1-\psi)$	$\gamma\ \varphi vb\ (1-\psi)$	$\gamma\ \varphi fg\ (1-\psi)$	$\gamma\ \varphi fb\ (1-\psi)$
vb	$(1-\gamma)\ \varphi vg\ (1-\psi)$	$(1-\gamma)\ \varphi vb\ (1-\psi)$	$(1-\gamma)\ \varphi fg\ (1-\psi)$	$(1-\gamma)\ \varphi fb\ (1-\psi)$
fg	$\gamma\ \varphi vg\ \psi$	$\gamma\ \varphi vb\ \psi$	$\gamma\ \varphi fg\ \psi$	$\gamma\ \varphi fb\ \psi$
fb	$(1-\gamma)\ \varphi vg\ \psi$	$(1-\gamma)\ \varphi vb\ \psi$	$(1-\gamma)\ \varphi fg\ \psi$	$(1-\gamma)\ \varphi fb\ \psi$

Note: States are a combination of life-history stage (v = vegetative, f = flowering) and environmental condition (g = good, b = bad). Transitions depend upon the proportion of good sites γ, reproduction φ, and rate of flowering ψ. This life history mirrors that of a plastic life history with dormancy (see Table 1), but with all rates associated with dormancy removed.

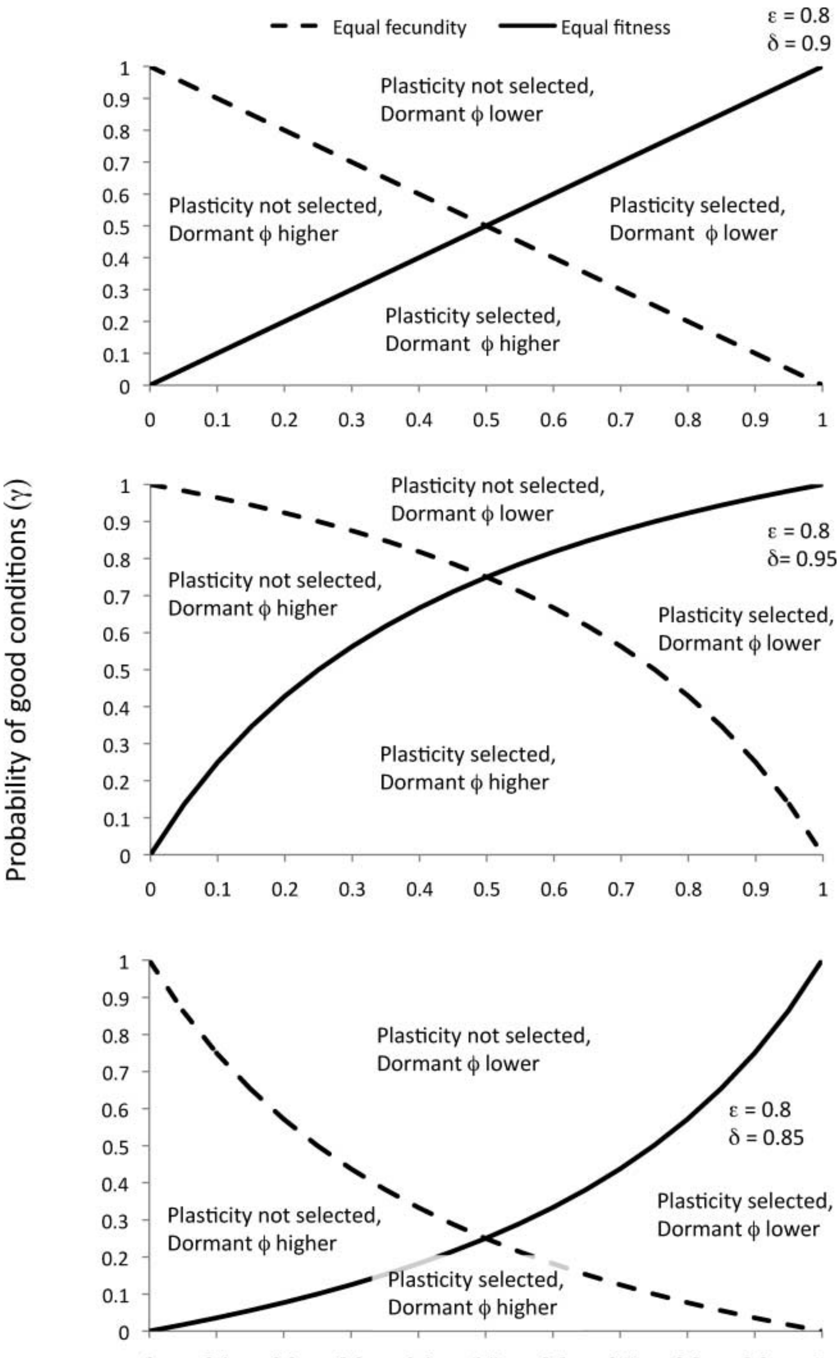

Fig. 2. Boundaries delineating the environmental conditions and plastic response accuracy where fitness of one life history is selected over another (solid lines) and where the reproductive values are different (dashed lines).

The reproductive values for each state within the plastic life history that includes dormancy are calculated as the dominant left eigenvector of the transition matrix given in Table 1:

$$v = \varphi vg,\ \varphi vb,\ \varphi dg,\ \varphi db,\ \varphi fg,\ \varphi fb \tag{4}$$

As seen here, when we calculate the reproductive value of the matrix in Table 1, all of the transition rates simplify out, leaving only reproduction (in the branching process sense) as contributing to reproductive values. Therefore, reproductive value comparisons are equivalent to reproduction comparisons.

The reproductive values we would observe if we sampled a population will include vegetative and dormant plants in both good and bad sites. Because vegetatively active and dormant plants are found in both good and bad sites, reproductive values must be averaged across all environmental conditions. This average or expected value is:

$$E\varphi vx = xp(\varphi vx)\varphi vx \tag{5}$$

where $x = (\gamma, 1 - \gamma)$. In other words, the expected reproductive value is the weighted average of reproductive values in good and bad sites, weighted by the probability of being in good and bad sites. When we apply this to vegetative plants, the expected reproductive value is

$$\varphi v = \varphi vg\ \alpha\ \gamma\ \alpha\ \gamma + (1 - \alpha)\ (1 - \gamma) + \varphi vb\ (1 - \alpha)\ (1 - \gamma)\ \alpha\ \gamma + (1 - \alpha)\ (1 - \gamma) \tag{6}$$

This expected reproductive value depends on reproductive values in good and bad conditions scaled by the probabilities of experiencing each condition.

At this point, we introduce a couple of key assumptions. Reproductive values of vegetative plants vary across conditions. This is because vegetatively active plants are exposed to the vicissitudes of the environment. It is convenient to relate reproductive values across environments by a coefficient ε; $\varphi vg\ \varepsilon = \varphi vb$. Dormant plants, on the other hand, have identical reproductive values across conditions; they are not exposed, and thus environmental conditions have no bearing on their vital rates. However, the reproductive value of dormant plants is lower than that of vegetative plants in good conditions by a factor δ; $\varphi vg\,\delta = \varphi d$. We constrain this factor δ to be always greater than ε, so that dormancy is always associated with higher reproductive value than vegetative activity in bad sites. This means that we can consider bad sites as being defined by lowering vegetative reproductive value below dormant reproductive value.

We want to create a boundary where reproductive values are equivalent to allow comparison with the boundary where fitness of contrasting life histories with and without dormancy are equivalent (equation 3). To do this, we find a critical proportion of good conditions where the reproductive values of vegetatively active and dormant plants are equal to each other:

$$\gamma \mid \varphi v = \varphi d = \gamma' = \varepsilon\ (\alpha - 1) + \delta\ (1 - \alpha)/(\varepsilon\ (\alpha - 1) + \delta\ (1 - 2\alpha) + \alpha) \tag{7}$$

When these reproductive values are equal, there is a constant relationship between reproductive value factors δ and ε and the accuracy of being dormant in bad conditions α. When these parameters deviate from this exact ratio, one stage's reproductive value will be greater than that of the other.

The result of comparing both reproductive values (equation 7) and fitness (equation 3) is that the reproductive value comparisons between dormant and vegetatively active plants do not mirror fitness comparisons between a plastic life history with dormancy and a constant life history in which plants are never dormant (Fig. 2). Notably, there is a large region of parameter space where vegetative plants have greater reproductive values than dormant plants, yet a plastic life-history repertoire with dormancy is selected for.

Letting costs vary

So far, we have not addressed the effect of coefficients δ and ε on fitness and reproductive value comparisons. Changing the values of these parameters changes the curvature of the boundaries between reproductive values and fitness (Fig. 2). However, the boundaries γ^*(equation 3) and γ' (equation 7) intersect at a constant plastic response accuracy α^*.

$$\alpha \mid \gamma^* = \gamma' = \alpha^* = 0.5 \tag{8}$$

When the survival of dormant plants is half way between vegetative plants in good and bad sites, the equivalence lines are straight, and the areas above and below the equilibrium contours are equal. However, when the reproductive values of dormant plants become more similar to good-site vegetative plants ($\delta \rightarrow 1$), there is a greater range of plastic accuracy and proportion of good sites where plasticity is selected for and dormant plants have higher observed reproductive values. On the other hand, when the reproductive value of dormant plants drops closer to that of vegetative plants in bad sites ($\delta \rightarrow \varepsilon$), the opposite effect occurs, and vegetative plants have higher reproductive values while selection favours constant vegetation over a wider range of accuracies and environments. Behaviour at the extremes is unchanged by the relationship between dormant and vegetative reproductive values, so that constant vegetation is always selected for when all individuals experience good conditions or all ‘guesses’ made by plants are wrong. At the opposite extremes, when all conditions are bad and/or the response to the environment is perfect, plasticity is always selected for.

The general qualitative relationship between accuracy, environmental quality, and reproductive values remains the same regardless of the exact parameter values for dormant and vegetative plants, as long as they are within their constraints (Table 3). Variation in parameter values only affects the range of the variables where one life history will be

Table 3. Parameters and variables describing life histories

Parameter or variable	Meaning	Constraint
φxy	Reproduction/reproductive value of stage x under conditions y	$0 \leq \varphi xy \leq 1$
γ	Probability of good conditions	$0 \leq \gamma \leq 1$
ψ	Rate of flowering	$0 \leq \psi \leq 1$
α	Accuracy of response	$0 \leq \alpha \leq 1$
δ	Relative reproductive rate, dormant	$\varepsilon \leq \delta \leq 1$
ε	Relative reproductive rate, vegetative bad environments	$0 \leq \varepsilon \leq \delta$

selected for over the other, and where plants in one state will have greater reproductive values.

Environmental stochasticity and bet-hedging

Environmental stochasticity creates the possibility for the plastic life-history strategy with dormancy to act as a bet-hedge compared with a constant strategy without dormancy. So far, our analyses deal with evolutionary outcomes and reproductive value comparisons when the average proportion of good and bad conditions is constant among years. When the probability of good conditions varies from year to year, this creates the environmental stochasticity necessary for bet-hedging while maintaining heterogeneity in conditions experienced by individuals within the population.

Bet-hedging is a trade-off between the mean and variance of fitness. In stochastic environments, bet-hedging results in a trade-off between the arithmetic and geometric mean fitness. A life-history strategy that increases the geometric mean fitness while decreasing the arithmetic mean fitness is a bet-hedging strategy. In contrast, if a strategy increases both the arithmetic and geometric mean fitness, it cannot be considered a bet-hedge because it is selected for in both stochastic and deterministic scenarios, and does not require a trade-off.

We simulated different stochastic environments by assuming a progression of good and bad years with variable proportions of good sites in the habitat at any given time. There is no temporal autocorrelation linking probabilities of good and bad sites from one year to the next. The fitness of each genotype is calculated using equations (1) and (2). The stochastic fitness was calculated as the square root of the product of good and bad year fitness. Fitness was scaled relative to a perfectly good year with all vegetative plants.

A few scenarios of good and bad years are shown in Table 4. For example, a perfectly good year will have all good sites, but a year still may be considered ‘good’ as long as it has a greater proportion of good sites than in bad years. Good years and bad years are relative to one another, and need not be absolutely good or absolutely bad in the sense that they consist of only good or bad conditions experienced by all individuals in the population. In other words, there is still micro-site heterogeneity among individuals. In scenario A (Table 4), good years are perfect, with 100% of the population experiencing good events, and bad years have only 51% good sites. In this case, the arithmetic mean fitness for the constant, no-dormancy life history is higher, but the plastic life history with dormancy has the higher geometric mean fitness. This is a case of selection for plasticity as a bet-hedging strategy. Note that both arithmetic and geometric mean comparisons of vegetative and dormant reproductive values favour vegetative plants.

By contrast, in scenario B, good years have 90% good events and bad years maintain 70% good events. In this situation, the constant life history without dormancy has a higher fitness in stochastic and deterministic environments, and plasticity is selected against. The opposite is true in scenario C, where plasticity has higher geometric and arithmetic mean fitness despite consistently higher reproductive values in vegetative plants. Lastly, situation D presents a case of what we call false bet-hedging. In this scenario, dormant plants have lower arithmetic and higher geometric mean survival, making dormancy appear to be a bet-hedging mechanism. However, the plastic life history with dormancy actually has the higher arithmetic mean fitness as well as geometric fitness, and thus is selected for, but not as a bet-hedge because there is no trade-off between these two measures of fitness.

Table 4. Results of fitness comparisons between plastic and static life histories in stochastic environments

Scenario	**A**				**B**			
Year type	Good	Bad	Arithmetic	Geometric	Good	Bad	Arithmetic	Geometric
	1.0000	0.5100	0.7550	0.7141	0.9000	0.7000	0.8000	0.7937
Plastic	0.9750	0.9260	0.9505	**0.9502**	0.9650	0.9450	0.9550	0.9549
Static	1.0000	0.9020	**0.9510**	0.9497	0.9800	0.9400	**0.9600**	**0.9598**
Vegetative	1.0000	0.9515	**0.9757**	**0.9754**	0.9929	0.9750	**0.9839**	**0.9839**
Dormant	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9
Scenario	**C**				**D**			
Year type	Good	Bad	Arithmetic	Geometric	Good	Bad	Arithmetic	Geometric
	0.9000	0.5000	0.7000	0.6708	0.7000	0.0500	0.3750	0.1871
Dormancy	0.9650	0.9250	**0.9450**	**0.9448**	0.9450	0.8800	**0.9125**	**0.9119**
No dormancy	0.9800	0.9000	0.9400	0.9391	0.9400	0.8100	0.8750	0.8726
Vegetative	0.9929	0.9500	**0.9714**	**0.9712**	0.9750	0.8273	**0.9011**	0.8981
Dormant	0.9	0.9	0.9	0.9	0.9	0.9	0.9	**0.9**

Note: Bet-hedging in stochastic environments is indicated by greater geometric mean fitness in conjunction with lower arithmetic mean fitness between the two genotypes. False bet-hedging is indicated when arithmetic mean reproduction is lower while geometric mean reproduction is greater. The larger fitness or reproduction between strategies and states is shown in **bold** for each of four scenarios labelled A–D. In each scenario, the stochastic probability of any given year being good or bad is 50%. The scenarios differ only in the quality of good and bad years based on the proportion of good events. The values shown were calculated with the parameters.

DISCUSSION

Reproductive values are important measures of life-history states that can be used to assess the fitness of contrasting life histories. However, to make inferences about the fitness consequences of states such as dormancy, their role within the context of the entire life history must be taken into account. This means analysing entire contrasting life histories and comparing their fitness values. In this respect, recent speculation about the adaptivity of dormancy in geophytes (Shefferson *et al.*, 2003; Shefferson, 2006, 2009; Lesica and Crone, 2007) has been necessarily inconclusive. Our model makes it clear why this is so.

Rather than relying on reproductive values alone, we assessed the fitness of plant dormancy by comparing a plastic life history that includes dormancy in the repertoire of possible states to a static life history in which plants never go dormant. The results show that the fitness of including dormancy in a life history cannot be assessed exclusively on reproductive values of vegetative and dormant plants. This is illustrated by the considerable regions of parameter space in our model where vegetative plants have higher reproductive values than dormant plants within which selection can favour either a plastic life history with dormancy or a constant life history without dormancy (Fig. 2). This means that in situations where dormant plants have lower reproductive values than vegetatively active plants, the fitness of a plastic phenotype that includes dormancy in its life history may still be greater than that of a constant phenotype without dormancy. In other words, dormancy may be selected for even when dormant plants have lower measured reproductive values. Interestingly, the converse may be true as well. These results for dormancy reflect the more general relationship between reproductive value and fitness of individual life-history events.

Plants in natural environments experience a range of light, moisture, pH, nutrients, and other abiotic and biotic stresses. Environmental heterogeneity does not only vary across time, it also varies across space within the habitat occupied by a population. Because dormancy is a plastic response to stress (see Reintal *et al.*, 2010 and references therein), dormant plants are very likely to be experiencing stressful conditions in the same years, while at the same exact time vegetative plants within the same population are experiencing more amenable conditions. As a result of spatial variation in the environment, reproductive value comparisons between vegetative and dormant plants are inappropriate for use as measures of fitness.

Across the board, geophyte dormancy seems to be a plastic response to stressful conditions (Reintal *et al.*, 2010). Moreover, dormant plants have different rates of survival and reproduction than active plants (Hutchings, 1987a, 1987b; Shefferson *et al.*, 2001, 2003; Vaughton and Ramsey, 2001; Shefferson, 2006; Lesica and Crone, 2007). Unfortunately, this is not sufficient evidence to make claims about the adaptivity of dormancy. In fact, our calculations show no pattern between survival or reproduction and fitness without considering environmental conditions and plant response to them (Fig. 2). Nonetheless, efforts have been made to make the inferential leap from vital rates to fitness.

Shefferson (2009) asserts that for dormancy to be adaptive, the costs of vegetative activity must overcome the benefits at some time. While this holds true, we have shown that these costs cannot be assessed by comparisons of survival or reproductive success in dormant and vegetatively active plants. Similarly, the reproductive values of active and dormant individuals of *Silene spaldingii* (Lesica and Crone, 2007), as well as survival rates in *Cypripedium calceolus* (Shefferson *et al.*, 2003; Shefferson, 2006), do not act as evidence for or against the adaptivity of dormancy. Evidence of lower reproductive value, either from decreased survival or reproduction, does imply decreased arithmetic mean fitness, as has been suggested (Shefferson *et al.*, 2003; Shefferson, 2006, 2009). Moreover, increased reproduction following dormancy is not evidence for the adaptivity of dormancy any more than decreased reproduction would be, contrary to the conclusions of Lesica and Crone (2007). Natural selection will act to maximize the rate of increase or fitness of a life history, but this does not mean that maximizing fitness requires eliminating all life-history stages but the one with the highest reproductive value, even if such a thing were possible.

If we use reproductive values to determine the adaptivity of dormancy, we need to know the distribution of good and bad sites in the environment, as well as the accuracy of plant response to variation. In particular, our model shows that we need to quantify the proportion of sites (γ) in which vegetative activity results in either higher or lower reproductive values than dormancy. In addition, the degree with which reproductive value is affected by microsite quality (ε) and dormancy (δ) must be quantified. Furthermore, an estimate of the accuracy (α) of the plastic dormant response to environmental quality must be made. Only once these parameter values are known can reproductive values of dormant and vegetatively active plants be used to determine the fitness of dormancy in a life-history repertoire. This presents a considerably more complicated picture than a simple comparison of vital rates between dormant and active plants.

On the one hand, the conclusions of this model indicate that we cannot infer fitness from the vital rates of dormant and vegetative plants alone (Fig. 2). Furthermore, to make claims about the evolution of dormancy from vital rates, we would have to assume a population occupies exact regions of parameter space reflecting proportions of good conditions and responses to those conditions. On the other hand, these results tell us that it is likely that dormancy provides a selective advantage to geophytes, regardless of vital rate comparisons. At a minimum, the evidence of lower vital rates in dormant plants (e.g. Hutchings, 1987a, 1987b; Shefferson *et al.*, 2001, 2003; Vaughton and Ramsey, 2001; Shefferson, 2006) is not enough to infer fitness of dormancy.

Despite the fact that dormant plants are neither growing nor reproducing, they may confer a selective advantage by avoiding costs associated with production of above-ground structures (Shefferson, 2009). What the reproductive value and fitness comparisons calculated here show us is that we may actually see the effects of this without knowing it. In particular, our results show that when survival or reproductive value is lower in dormant plants, the inclusion of the dormant state in a plastic life history may nonetheless increase arithmetic mean fitness.

In more complicated life histories, it may be possible for dormant plants to increase their reproductive value by being more likely to flower in the future (Lesica and Crone, 2007). However, our model shows that a plastic life history that includes dormancy may increase fitness even when the total reproductive value of dormant plants is lower than that of vegetative plants. Thus, a life history that includes dormancy may also be selected for in the cases where survival and reproductive value are lower than in vegetative plants (Shefferson *et al.*, 2001, 2003; Vaughton and Ramsey, 2001). While the opposite is also true, that a life history with dormancy may be selected against, we have no reason to think that this is more likely.

The addition of environmental stochasticity does not change these fundamental results. For a trait to be a bet-hedge, it must be selected against in deterministic environments and selected for in stochastic ones. However, the reproductive values of dormant and vegetatively active plants do not indicate if this is true. It is possible for the inclusion of dormancy in a life history to be a bet-hedge when the reproductive values of vegetative plants are greater than those of dormant plants (Table 4). However, it is possible for plasticity in dormancy to be selected either for or against when vegetative reproductive values are greater than dormant ones even in deterministic environments. From this we conclude that bet-hedging is not necessary for dormancy to be adaptive, despite lower reproductive values associated with dormant plants. While bet-hedging is not necessary to explain the evolution of dormancy even when dormant reproductive values are lower than in vegetative plants, it is nonetheless a possibility in stochastic environments.

It is likely that dormancy does increase fitness in the life history of geophytes, although this inference is based on circumstantial lines of reasoning. First, the conditions or events experienced by an individual may vary because of variation in landscape patch quality within a population (van Noordwijk and de Jong, 1986; Clark, 1991; Levin, 1992; Wiens *et al.*, 1993). We also know that geophytes go dormant in response to stress, and population-wide dormancy rates correspond to herbivory, temperature, light, pH, nitrogen, and moisture (Shefferson *et al.*, 2001, 2005; Morrow and Olfelt, 2003; Shefferson, 2006; Lesica and Crone, 2007; Reintal *et al.*, 2010). The combination of landscape variation and plastic response of dormancy to environmental variation indicates that concurrent dormant and vegetative plants likely experience different environmental conditions, causing asynchronous dormancy within a population.

When evaluating a life-history strategy, all we need to know is whether the strategy, on the whole, increases fitness compared with some viable alternative. For a state or stage such as dormancy, this means evaluating the fitness of the entire life-history context in which the particular state or stage is included. It is misleading to assume that at some time and place, dormant plants must have better vital rates than vegetative plants on average across a population. The environmental and vital rate heterogeneity that exists among individuals across a population will result in selection for traits that appear to be selected against if this heterogeneity is not taken into consideration.

The state of dormancy is different from the ability to go dormant. Reproductive values may pertain to the state of dormancy, but they do not reflect the fitness of the ability to go dormant. However, the fitness of the ability to go dormant can be evaluated by comparing fitness of contrasting life histories, as we have shown here.

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