Variable offspring size as an adaptation to environmental heterogeneity in a clonal plant species: integrating theory and data

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Summary

1. The production of variably sized offspring has been hypothesized to be adaptive to temporal variability in environmental conditions.
2. This is difficult to verify empirically, and theoretical models are typically generic and not parameterized with data from real populations; studies integrating theoretical and empirical approaches to this problem are rare.
3. Here, we present field and experimental data on the growth of *Scirpus maritimus*, a clonal aquatic macrophyte that grows through vegetative extensions involving tubers.
4. The experiments show that offspring fitness (biomass productivity) is dependent on environmental conditions (water depth).
5. Both field and experimental data indicate that variation in offspring (tuber) sizes of individual ramets can be approximated by a lognormal distribution.
6. We use these data to develop a difference equation model of *S. maritimus* growth in order to test whether producing variably sized offspring is adaptive. The model compares fitness under the lognormal strategy to several hypothetical strategies with qualitatively different variance in offspring size.
7. The model results suggest that lognormal variation in *S. maritimus* tuber size may be adaptive to the temporal variation in water levels that characterize its natural Mediterranean environment.
8. We illustrate how the underlying principles that lend adaptive value to offspring size variation may apply to other species experiencing similar environmental conditions.
9. *Synthesis*: Close integration of data and theoretical models creates a unique tool for investigating the adaptive value of life history traits in clonal aquatic plants.

Keywords: *Scirpus maritimus*, mathematical model, size-number tradeoff, environmental variability, theoretical model, lognormal distribution, bet-hedging

Introduction

One of the central issues that have informed life history theory is the tradeoff between size and number of offspring (Stearns 1992, Moles & Westoby 2006). For a given level of resource investment, a parent may choose to produce a few large-sized offspring (with higher individual probabilities of survival to reproductive maturity) or many small-sized offspring (with lower probabilities of survival). A standard mathematical model predicts the evolution of a single optimal offspring size that maximizes maternal fitness, in situations where offspring fitness increases with size according to a certain functional form (Smith & Fretwell 1974). Subsequent work has extended this model and related it to ecologically important phenomena including competition, dispersal, predation, and host-parasite relationships (Parker & Begon 1986, Venable 1992, Fox et al. 1997, Marshall et al. 2006).

One such extension investigates whether the single-sized offspring strategy is still optimal when the environment varies unpredictably in time or in space. In this case, an alternative to a single-size strategy is for an individual to produce variably sized offspring. This may provide a buffer against environmental variability and constitutes a form of bet hedging (Philippi & Seger 1989, Marshall et al 2008, Olofsson et al 2009). Since the 1970s various authors have described offspring size variability in a large range of taxa among plants, insects, fishes, birds, vertebrate and suggested its possible adaptive value in variable habitats (for references, see

McGinley et al. 1987, Geritz 1995, Geritz et al. 1999, Westoby et al. 1996, Moles & Westoby 2006). However, variable offspring size within a species can arise from a number of genetic and environmental sources and can be partitioned in numerous ways: among populations, among individuals in the same population, within individuals, within a year or a clutch, or between years (Hangelbroek & Santamaria 2004). As a consequence it is often difficult to determine if the observed offspring size variation simply reflects developmental or resource constraints or whether it might also have adaptive value (Sakai 1995, Wolfe 1995, Simons & Johnston 1997, Vinuela 1997, Vaughton & Ramsey 1998, Forbes 1999, Simons & Johnston 2000, Einum & Fleming 2004). A second obstacle to establishing the adaptive value of offspring size variation is that the stipulation of specific functional forms relating fitness to offspring size and number is often difficult to establish (Einum & Fleming 2000, Torres-Vila & Rodriguez-Molina 2002, Moles et al 2003, Gómez 2004, Moles & Westoby 2006). For example, it is generally admitted that the survival of seedlings increases with seed size, however large seeds can also have higher risks of predation or reduced dispersal, resulting in a co-evolution of traits (Venable & Brown 1988, Moles et al 2003). The relationship between offspring size and fitness may also vary between different stages of development or depend on parental behavior (Hendry et al. 2001). Hence, although there have been several empirical studies indicating that variation in offspring size can indeed be an adaptive response to unpredictable environmental variation (Fox et al. 1997, Kudo 2001), empirical support for the hypothesis remains rare and largely hypothetical. Such obstacles also prevent the forging of more intimate links between theoretical and empirical approaches to the problem.

There have been a number of theoretical modeling studies of strategies for offspring size distribution and/or offspring numbers in the presence of temporally or spatially varying environments (Kaplan and Cooper 1984, Schultz 1991, Geritz 1995, Sasaki and Ellner 1995,

Geritz et al 1999, Kisdi 2007, Simons 2007, Olofsson et al 2009). The process generally followed by mathematical models is to compare the fitness of a single-size strategy to a strategy of producing variably sized offspring under different conditions of habitat variability in space and/or time. Most of these theoretical approaches conclude that, under certain assumptions, the optimal solution to the tradeoff between size and number of offspring in a spatially and/or temporally variable environment is the production of variably sized offspring (Kaplan and Cooper 1984, Schultz 1991, Geritz 1995, Geritz et al 1999). However, one modeling study concluded that variability in offspring size does not necessarily provide a fitness advantage over single-size strategies in a temporally varying environment that can be either “good” or “bad” (McGinley et al 1987). These studies have generally not parameterized their models with empirical data, aiming for generality instead.

Another possible adaptive response to temporally varying environmental conditions is dormancy, and several studies have used empirical data and/or models parameterized with empirical data to investigate this issue (Simons & Johnston 2006; Venable 2007). For example, two studies that parameterize a simulation model with empirical data suggest that seed banking may be an adaptive response to temporally variability in environmental conditions (Kalisz and McPeck 1993, Evans et al 2007). Another study parameterizes a simulation model of marine copepods using field data to determine evolutionarily stable diapause strategies in a temporally varying environment (Hairston & Munns 1984). In contrast, a modeling study by Einum & Fleming (2004) based on data from Atlantic salmon found that within-clutch variability more likely reflects difficulties in allocating resources equally among offspring rather than evolutionary adaptation *per se*.

Studies that parameterize theoretical models with empirical data in order to investigate the adaptive value of producing variably sized offspring in temporally varying environments remain uncommon. Here, we describe experiments carried out to investigate offspring size variation in a clonal plant species and use the experimental data to develop a species-specific mathematical model of growth dynamics. In particular, we (1) experimentally determine the relationships between offspring size and fitness in the clonal plant *Scirpus maritimus* under different environmental conditions, and (2) use these experimental data, together with longitudinal historical data on the temporally varying environment of *S. maritimus*, to develop a difference equation model of *S. maritimus* growth dynamics. The model allows us to compare the fitness under the offspring size distribution observed in natural populations to the fitness under several hypothetical alternative offspring size distributions, and under different conditions of temporal environmental variability. The objective is to determine whether the observed variation in *S. maritimus* offspring sizes is adaptive to a temporally varying environment. This integrated approach allows us to address issues that could not be addressed with empirical or theoretical approaches in isolation from one another. In addition to its relevance to the theory of parental investment, this question is also important to ecology because its answer could shed light on the potential geographic extent of the species (e.g., its ability to colonize areas with highly variable rainfall/water levels) or how it might respond to environmental change in its present habitat. Finally, by conducting further simulations, we also investigate the impact of representing environmental variability through a discrete number of possible states, rather than a continuous distribution of possible states. In the following section we describe materials and methods (for field data, experimental, and modelling components of the study), results (for field data, experimental, and modelling components), and we conclude with a discussion.

Materials and methods

STUDY SPECIES

We investigate the adaptive value of variable offspring size in the emergent macrophyte *Scirpus maritimus*. The species grows clonally by producing underground sympodial rhizomes. The initial above-ground shoot of a seedling produces from one to three rhizomes at its base which grow horizontally and turn upwards to form erect above-ground shoots. Each new above-ground shoot then produces from one to three new rhizomes. Branched systems composed of several tens of sympodial rhizomes can be produced from an initial shoot during a single growing season (Clevering 1995, Charpentier et al. 1998). During the growing season each shoot forms a tuber at its base. Among the tubers produced in a single growing season, tuber biomass increases from the early- to the later-produced tubers along rhizome systems (Lieffers & Shay 1982, Clevering 1995, Charpentier & Stuefer 1999). Clonal growth stops at the end of summer. Aboveground shoots dry out and die in the autumn, while tubers persist in the soil. In spring, new shoots are produced from axillary buds situated on overwintering tubers and start to produce from one to three rhizomes.

Several studies have described in detail the variation in tuber size in this species (Lieffers & Shay 1982, Clevering 1995, Charpentier et al. 1998, Charpentier & Stuefer 1999). The variation arises within individuals during a single season: tuber size increases gradually from the first to the last produced tubers. This pattern is observed in the field as well as in single plants grown in pots under stable conditions, suggesting that this variation can be attributed to a developmentally programmed syndrome rather than environmental stress or changes in environmental conditions during the season.

1
2 The ecology of this species allows us to expect a strong relationship between size and fitness
3 of offspring. In emergent macrophytes, because of the low efficiency of underwater
4 photosynthesis, it is generally assumed that the maximum water depth they can overcome in
5 spring depends on the amount of reserve stored in overwintering organs (e.g. tubers,
6 rhizomes) (Spencer 1982, Grace 1989, Clevering et al. 1995). We can thus suppose that in *S.*
7 *maritimus*, the ability of shoots to emerge above the water surface in spring is crucial for
8 survival and depends on tuber size, i.e. the amount of stored reserves. (Nutrient availability,
9 particularly that of oxygen, is also reduced at greater depths, and therefore larger tubers with
10 more reserves are more likely to be able to reach shallow depths where more nutrients are
11 available.) Therefore, (1) we can use offspring tuber biomass as an analog for vegetative
12 offspring size in *S. maritimus*, (2) we can use water depth as an analog for environmental
13 quality, and (3) we can use total tuber biomass produced by an initially present tuber during a
14 growth season as an analog for fitness of the initial tuber. The water regime of wetlands that
15 support *S. maritimus* worldwide are variously described as irregularly exposed, temporary,
16 irregular, seasonally and permanently flooded, all characterized by a strong variability of
17 water levels (Kantrud 1996). Therefore, we can also suppose that the variability and
18 unpredictability of water regime represents a strong environmental pressure for the evolution
19 and ecology of this species.

20 21 22 FIELD DATA

23
24 To examine the natural variability in offspring tuber sizes in *S. maritimus*, 550 tubers were
25 collected from a population in the wildlife reserve of the Tour du Valat, Rhone delta,

Southern France in autumn 1998. Tubers were stored under moist dark conditions at 5°C. In spring 1999, the fresh weight of all the tubers was measured. The size distribution was fit to several functions to determine the best goodness of fit using the statistical software program JMP (version 5.1 for Macintosh).

The population was located in a temporary marsh in a region that experiences strong between-year variation in water level due to the unpredictable rainfall patterns characteristic of a Mediterranean climate. Rainfall data for 1932-2003 were obtained from a meteorological station a few kilometers from the marsh. The water depth in the marsh was monitored from 1995 to 2003. The relationship between the total rainfall from September to March and the water level at the end of March (start of the growing season) was determined for 1995-2003 (Supporting Information, Fig. A1). Using this relationship, the yearly water level was then derived for the period 1932-2003 based on the historical rainfall data for 1932-2003. The frequency distribution of water levels was fit by several distributions using the statistical software program JMP (version 5.1 for Macintosh) and MATLAB (version for Macintosh).

EXPERIMENT

An experiment was performed at Utrecht University in 1999 to test the hypothesis that biomass productivity of *S. maritimus* is dependent on environmental quality and the size of the initial tuber. Tubers collected from the field in autumn 1998 were stored under moist dark conditions at 5°C, and in spring 1999, the fresh weight of all the tubers was measured. Three series of 30 tubers from the tubers collected from the field (see previous section) with the following fresh weight (g) were selected for the experiment: 0.5, 0.6, 0.9, 1.0, 1.1, 1.5, 1.6, 1.9, 2.0, 2.1, 2.5, 2.6, 2.9, 3.0, 3.1, 3.5, 3.6, 3.9, 4.0, 4.1, 4.9, 5.0, 5.1, 5.9, 6.0, 6.1, 7.0, 7.1,

8.0, 10.0. The dry weight of the remaining 450 tubers was measured to establish the fresh-dry weight relationship ($freshweight = b \cdot dryweight + a$, where $b=0.01$ and $a=3.25$ $p<0.05$). On May 17, 1999 the three series of tubers were randomly allocated to one permanent water level treatment: shallow (15 cm), medium (45 cm) or deep (85 cm). Single tubers were planted at 2 cm depth in pots of diameter 21 cm, filled with a 1:2 compost-sand mixture. The pots were put outside into containers under the three permanent water levels above the soil surface. In Amsterdam from May-September 1999, key weather indices determining the growth environment of the tubers were: mean air temperature 16.5 degrees Celsius, mean humidity 76.2%, total precipitation 41.1 cm, and mean wind speed 16.2 km/h. In September 1999, the dry weight of every tuber produced by each planted tuber was recorded. For each planted tuber, the mean and standard deviation of its offspring tuber weights were calculated. Moreover, for those planted tubers with a sufficiently large number of offspring, the offspring size distribution was fit to several candidate functions using the statistical software package JMP (version 5.1 for Macintosh) and goodness-of-fit for the functions was assessed, in order to characterize the offspring size distribution of individual tubers. The size distribution of the pooled offspring tubers was also fitted in JMP for each water level, thus characterizing population-level distribution of offspring tuber sizes.

We treat the total biomass produced by an initial tuber as a proxy for the tuber's fitness. To quantify the relationship between fitness and offspring size, we fit the data from the experiments to a commonly used fitness function (e.g. Smith & Fretwell 1974): offspring fitness F_w in a given water level w is related to the size s of the offspring via

$$\boxed{\phantom{F_w = \frac{a \cdot s^b}{1 + c \cdot s^d}}} \quad (1)$$

where m_w is the minimum viable offspring size in water level w and α_w is a constant determining how quickly the fitness curve approaches its asymptotic value as s increases. In the special case where the environmental quality is constant over time, the optimal offspring size s^* can be obtained from equation 1 (Smith & Fretwell 1974):

(2)

We computed the best fit of the experimental results to equation 1 for each of the three environmental conditions using the nonlinear-fitting algorithm in JMP, and setting maximum observed biomass produced as the maximum fitness level. Hence, we obtained three sets of m_w and α_w values for each of the three experimental water levels.

MATHEMATICAL MODEL

We used the empirical data to parameterize a mathematical (difference equation) model of biomass production in a single genet of *S. maritimus* over multiple seasons. The goal was to compare fitness under the observed offspring size distribution to fitness under two hypothetical alternatives under several environmental scenarios, and thus to test the hypothesis that the observed variation in *S. maritimus* offspring tuber size is adaptive to a temporally varying environment. We chose the route of “simulation as experiment” because of the difficulty of testing this hypothesis empirically (Peck 2004).

We derived a discrete-time difference equation model of the temporal dynamics of total biomass production under the three strategies for some given temporal variation in water level. The total biomass produced in the current year depends in a simple way upon how many tubers were present in the genet at the beginning of the growth season (produced the year previous), their size distribution, and how much biomass a tuber of a given size can

produce as dependent on this year's average water level. Mathematically, the total biomass b_t produced in year t is related to the biomass b_{t-1} produced the year previous and the water levels $w(t)$ and $w(t-1)$ in years t and $t-1$, by the equation

$$\boxed{\phantom{b_t = b_{t-1} \left(\frac{w(t)}{w(t-1)} \right)^{\frac{1}{\phi_{w(t)}(s)}}}} \quad (3)$$

where $\boxed{}$ is the mean tuber size produced in year $t-1$, $\phi_{w(t)}(s)$ is the offspring size distribution, i.e., the probability of producing an offspring of size s when the average water level in year t is $w(t)$, and $F_{w(t)}(s)$ is the fitness function, equation 1 (see Supporting Information for derivation). *S. maritimus* ramets may die through excessive water depth. This source of mortality is represented in equation 1 since no biomass is produced in year t if all tubers produced in year $t-1$ are smaller than the minimal offspring size $m_{w(t)}$ for year t . This happens if there is a string of years with sufficiently high water levels. To account for other causes of mortality (such as herbivory, disease), we assumed a 1% probability of genet death each year from other causes.

Let $\boxed{}$ denote the ratio of biomass produced in year t to biomass produced in year $t-1$. This quantity is analogous to fecundity, in the sense that it must remain above one for the genet to experience net growth over multiple seasons. From equation 3, R_t is given by

$$\boxed{\phantom{R_t = \frac{b_t}{b_{t-1}} \left(\frac{w(t)}{w(t-1)} \right)^{\frac{1}{\phi_{w(t)}(s)}}}} \quad (4)$$

Then, we define fitness as the geometric mean of the values of R_t for $t = 1 \dots T$, where T is the lifespan of the genet in years. Thus

$$\boxed{\phantom{F = \left(\prod_{t=1}^T R_t \right)^{\frac{1}{T}}}} \quad (5)$$

The geometric mean is a good measure of fitness in situations where environmental conditions vary from year to year (McGinley et al 1987), because the geometric mean would

1 indicate zero fitness for a genet that died before time T , whereas the arithmetic mean would
2 indicate positive fitness in the same situation.

3
4 We carried out four sets of simulation experiments to test the hypothesis that offspring tuber
5 size variation has adaptive value in *S. maritimus*, and to investigate the relationship between
6 our predictions and previous models that predict a single optimal offspring size (McGinley *et*
7 *al* 1997; Smith & Fretwell 1974). We compared geometric mean fitness and lifespan of
8 genets under the three offspring size distributions. For each given set of parameter values, a
9 large number of realizations were carried out (8,000 for experiments 1, 2 and 4 and 5,000 for
10 experiment 3), starting from the same initial conditions. The resulting geometric fitness over
11 350 years was averaged over the realizations. The simulation experiments are described in
12 greater detail in Results.

15 Results

17 FIELD DATA

18
19 The distribution of tuber sizes in the field appears to be qualitatively consistent with the
20 lognormal distribution (Fig. 1A). A quantity X is lognormally distributed if $\log(X)$ is normally
21 distributed (Limpert *et al* 2001). The lognormal distribution is given by

22 $\frac{1}{\sigma \sqrt{2\pi} X} \exp\left(-\frac{(\ln X - \mu)^2}{2\sigma^2}\right)$, where μ is the mean of $\ln(X)$ and σ is the variance of $\ln(X)$.

23 Though not found to be statistically significant, the best-fit parameters (Kolmogorov test:
24 $D=0.06$, $p=0.01$) for the tuber sizes from the field data were when $\mu=-0.636$ and $\sigma=0.821$
25 (corresponding to a mean tuber size of 0.529 g and a variance of 2.27). The frequency

distribution of the water level w from 1932 to 2003 (Fig. 2A) is well-described by a function of the form

$$\boxed{} \quad (7)$$

The best-fit ($r^2=0.937$, $p<0.001$) parameters were found to be $a=2.323$, $b=0.080$. This function provided a better fit than better-known distributions such as Gamma and lognormal.

EXPERIMENT

Water level had a significant effect on tuber survival. In the shallow treatment, all planted tubers survived and produced new tubers, while in medium and deep conditions all planted tubers smaller than 0.33 g and 0.79 g respectively produced a shoot that never reached the water surface, and died during the summer (Fig. 2B). The water level also affected the total biomass of newly produced tubers. Productivity was highest in shallow water and decreased successively under medium and deep water levels (Fig. 2B).

After fitting equation 1 to the experimental data, the following parameter values for shallow, medium and deep respectively were obtained: $m_{15}=0.05$ g, $m_{45}=0.31$ g, $m_{85}=0.77$ g, $\alpha_{15}=0.22$, $\alpha_{45}=0.17$, $\alpha_{85}=0.07$ ($p<0.01$). A least-squares regression between the three values of m_w and water level w fits the data very well ($r^2=0.99$, $p<0.01$),

$$\boxed{}, \quad (8)$$

and the fit between the three values of α_w and w is also significant ($r^2=0.98$, $p<0.05$),

$$\boxed{}. \quad (9)$$

Using the parameterized fitness functions, we can estimate the optimal offspring tuber size s^* from equation 2 for a clonal plant species in a hypothetical environment with unchanging

water level: $s^*=0.08$ g for shallow, $s^*=0.85$ g for medium, and $s^*=1.97$ g for deep water levels. For an unchanging water level of 25.5 cm, which is the average water level in the field as computed from equation 7, the optimal tuber size would be $s^*=0.332$ g. In absolute terms this is somewhat below the observed mean (0.533 g) and median (0.505 g) tuber size in the field, although it is not clear what relationship should be expected between offspring tuber sizes observed in field populations experiencing temporally-varying environmental quality and tuber sizes predicted from a model that assumes a constant environmental quality.

The offspring sizes of planted tubers were highly variable in all water level treatments (Supporting Information, Table A1). For each of the water treatment levels, we selected the three planted tubers that produced the largest number of offspring tubers (as long as they produced at least ten), and tested goodness-of-fit for lognormal, normal, and gamma distributions fitted to the data. The lognormal distribution fit the size distribution of tubers produced best for almost all individual ramets tested (Table 1). For the purposes of parameterizing the simulation model, we also pooled individual data to determine estimates of the parameters of the lognormal distribution. In the shallow treatment ($N=398$) appeared to follow a lognormal distribution, but it was not statistically significant ($\mu=-0.788$, $\sigma=0.837$, Kolmogorov $D=0.05$; $p<0.01$) (Fig. 1B). The distribution for the medium ($N=210$) and deep treatments ($N=94$) did statistically fit a lognormal distribution ($D=0.05$; $p=0.15$ and $D=0.07$; $p=0.15$, respectively) (Fig. 1C, D). Note that the variance σ in all three water levels is similar to that of the field population.

The mean size of the produced tubers was also significantly affected by water level. The produced tubers were significantly larger in shallow ($\bar{x}=0.62$ g, S.E.=0.02) than in medium ($\bar{x}=0.46$ g, S.E.=0.03) or deep water ($\bar{x}=0.30$ g, S.E.=0.03) (one way ANOVA on log-

transformed data: $F=28.8$, $DF=2$, $p<0.001$). The three data points relating mean tuber size produced ($\square$) to water level (w) are well-fit by a linear regression ($r^2=0.99$, $p<0.01$):

$$\square = 0.001w + 0.0001 \quad (10)$$

MATHEMATICAL MODEL

We compared biomass production under the observed lognormal strategy to two hypothetical alternative strategies: the *single-size* distribution, in which all offspring are the same size, and the *uniform* distribution, in which the probability of producing tubers of a given size x is a constant, nonzero value over a given interval of sizes $[x_{\text{lower}}, x_{\text{upper}}]$, and is zero outside the interval (Supporting Information, Fig. A2 and equation A1). The single-size distribution corresponds to the “optimal offspring size” theory and thus should be optimal in an environment without temporal variation. The uniform distribution represents an intermediate strategy between the single-size and lognormal strategies. These alternative strategies act as theoretical controls for the lognormal strategy. The three distributions together represent a broad possible range of resource allocation strategies: (1) low variance, where all offspring have the same size (*single-size* strategy), (2) intermediate variance, where offspring of various sizes can be produced but only over a restricted interval of sizes (*uniform* strategy), and (3) high variance, where there is a nonzero probability of offspring of any size being produced (*lognormal* strategy).

Simulation experiment #1: fitness at empirical parameter values. In simulation experiment #1, we compared the fitness of the three strategies when the model parameters are set to match the empirically observed values, and where the water level varies from year to year according to patterns observed in the field. The water level $w(t)$ in a given year t was a random variate sampled from equation 7 at best-fit parameter values, normalized to yield a probability density

function. Then, α_w , m_w and σ for the sampled water level $w(t)$ were determined from equations 8-10. For $w < 12.01$ cm in equation 8, we set $m_w = 0$ since otherwise m_w is negative; likewise for $w > 114.91$ cm in equation 9 we set $\alpha_w = 0$ since otherwise α_w is negative. Thence, fitness $F_w(s)$ was determined from equation 1 and $\phi_w(s)$ from equation A1 (Supporting Information). Finally, total biomass b_t produced during the season was determined from equation 3.

For a given water level w , the three strategies produce the same mean tuber size $\bar{s}$ given by equation 10. Thus, the strategies differ only in the way that tuber offspring size is distributed about the mean, and any difference in strategy fitness arises from the variance σ of the offspring size distribution. For the single-size strategy, $\sigma = 0$ by definition. For the lognormal strategy, σ did not vary widely across the three experimental treatments and the field data, hence we used $\sigma = 0.821$ in the simulations, which is the field value and also very close to the average of the three values of σ (0.817) from the three experimental treatments. For the uniform strategy, σ is determined by s_{half} ; we used $s_{\text{half}} = 0.1$ and considered only $s \geq s_{\text{half}}$. The value $s_{\text{half}} = 0.1$ was chosen because it produces a distribution broad enough to be meaningfully different from the single-size distribution, yet narrow enough to allow a large range of mean tuber sizes to be tested (everything up to $\bar{s} = 0.1$). All baseline parameter values for this and subsequent simulation experiments are summarized in Table 2.

At the empirical parameter values, the lognormal strategy had the highest average fitness across all realizations (mean 663.6, SD 622.9), followed by the uniform strategy (mean 327.9, SD 362.7) and the single-size strategy (mean 229.6, SD 240.6). The lognormal strategy had the highest fitness in 56% of realizations, followed by the uniform strategy (24%) and the single-size strategy (18%). The distribution of mean geometric fitness K over all realizations

appears to be approximately exponential (Fig. 3A), which is why the mean approximately equals the standard deviation. Accordingly, lifespan tends to be distributed exponentially as well (Fig. 3B). Exponentiality arises from the assumption of a constant probability of death due to causes other than excessive water depth. Under the lognormal strategy, genets also had the longest mean lifespan (mean 89.6 years, SD 84.0), followed by the uniform (mean 36.6, SD 37.3) and single-size strategies (mean 23.6, SD 24.4).

Simulation experiment #2: fitness landscape. If the observed lognormal variation in offspring size is indeed adaptive to temporally-varying environmental conditions, then the fitness of the lognormal strategy at the empirical parameter values should be higher than the fitness at other hypothetical parameter values to which the organism is free to evolve toward. Therefore, in simulation experiment #2, we examined fitness of the three strategies across a range of parameter values in order to determine whether the empirical values fall near the global maximum of the fitness landscape. The lower bound for σ was zero. The upper bound for σ was chosen as the value above which discrete effects invalidate the use of the model (see Supporting Information). Accordingly, σ was varied in the range [0, 1.5] in increments of 0.1 to explore the fitness landscape. We also varied the slope of the linear relationship between mean tuber size produced and water level, equation 10. This corresponds to a tradeoff between producing many small tubers or a few large tubers. The water level at which no tubers are produced (the x-intercept of equation 10) was fixed at 137.7 cm. We assumed the inability to produce tubers beyond this depth to be an absolute constraint on the organism. Hence, we varied the slope of equation 10 by changing the y-intercept (y_{int}). High y_{int} means that fewer, but larger, tubers are produced. For all three strategies y_{int} was varied in the range [0, 2] in increments of 0.05. Beyond $y_{\text{int}} = 2$, fitness approaches zero monotonically and discrete effects may become important (see Supporting Information). As in simulation experiment #1, the water level was sampled from equation 7 and we used equations 3, 8-10 to

1 model biomass dynamics. Together, the parameters σ and y_{int} control the most important
2 degrees of freedom in an organism's offspring size strategy: σ controls the amount of
3 variability in offspring size and y_{int} controls whether few large tubers or many small tubers are
4 produced. Therefore, a fitness landscape with σ and y_{int} on two axes should indicate whether
5 selection is expected to occur with respect to those parameters.

6
7 Fig. 4A, B shows the fitness landscape of the lognormal distribution for range of y_{int} and σ
8 values described above. The fitness landscape has a single peak in the lower-right quadrant of
9 the parameter plane (dark red region): the maximum geometric mean fitness of 723.5 occurs
10 at $y_{\text{int}}=0.5$, $\sigma=0.8$. The empirical parameter values ($y_{\text{int}}=0.671$, $\sigma=0.821$) fall near this peak.
11 (This fitness at the peak is also higher than those obtained for the single-size and uniform
12 strategies.) The proximity of the empirical parameter values to the hypothetical values where
13 fitness is maximized is consistent with an adaptive response to temporal variation in water
14 level. The fitness changes more dramatically with changes in y_{int} than with changes in σ ; this
15 suggests that selection upon the size-number strategy is stronger than selection on the degree
16 of variability in offspring size, although it is difficult to know how absolute changes in fitness
17 for changing σ maps to absolute strength of selection on variance in natural populations.

18
19 Simulation experiment #3: fitness under a discrete number of possible environmental states.

20 Several studies have modeled temporal variability by assuming that environmental quality is
21 sampled from a discrete number of possible environmental states (McGinley et al. 1987,
22 Kalisz & McPeck 1993). For instance, McGinley et al model fitness using equation 1 but
23 only allow for two possible environmental states—"good" and "bad" each with corresponding
24 values for m in the fitness function—together with three possible offspring sizes—"small",
25 "medium", and "large". To compare our results to those of McGinley et al., we performed a

simulation experiment that allows only two possible water levels--“good” and “bad”--that occur with probabilities p_G and $p_B = 1 - p_G$ respectively. McGinley et al. computed the geometric fitness of strategies for various values of p_G and various possible differences in quality between good and bad environments (k in their notation) and found that a variable-size strategy was favored only for sufficiently large k (large difference in environment quality) and sufficiently large p_G . In our model, we choose the “good” and “bad” environments based on results from the experiments. We chose the “good” environment to be $w=16.9$ cm, yielding $m=0.60$ and $\alpha=0.22$ (equivalent to $k=1$ in the notation of McGinley *et al.*). For “bad” environments we looked at $w=21.8, 31.5, 41.2, 50.9, 60.6$, and 70.4 cm (equivalent to $k=2, 4, 6, 8, 10, 12$ in the notation of McGinley *et al.*) with corresponding values for m_w and α_w from equations 8 and 9.

When we allow environmental quality to be either “good” or “bad” in this way, the single-size strategy wins more often (Fig. 5), which is consistent with what McGinley *et al.* found. This suggests that the success of the lognormal strategy derives from the fact that real-world environmental conditions are continuously distributed such that there is a nonzero probability of a year with arbitrarily poor conditions. When environmental conditions are distributed as a continuous random variate with nonzero probability for all possible environmental conditions, then for any given tuber size, there must eventually occur a year in which water levels are too deep for the organism to survive. Hence a genet adopting a single-size strategy would eventually die due to a rare but unfavorable year in which water levels were excessive. By comparison, for a genet adopting a lognormal strategy, there is a greater probability of a few large tubers being produced that can survive arbitrarily deep water levels.

As in McGinley *et al* (1987), the single-size strategy wins when k is small but the variable-size strategies win more often as k increases (Fig. 5). The main difference between our results and those of McGinley *et al.* is that the variable-size strategy does better when p_G is larger in their model but when p_G is smaller in our model. When k is small (such that the difference between “bad” and “good” years is small) or when p_G is large (such that “bad” years are rare), the lognormal strategy does worse than the single-size strategy because it needlessly invests resources in large tubers. Such a strategy would work well when k is large or when p_G is small, but when “bad” years are rare, it is more efficient to invest resources in producing large numbers of small tubers that are guaranteed to succeed. The lognormal distribution is more successful than the single size distribution for larger k and smaller p_G because the water levels are too deep for any but the largest tubers to survive.

Simulation experiment #4: fitness in an unchanging environment. The purpose of this experiment was to examine the performance of the lognormal strategy in an environment where the average water level does not change from year to year. For a fixed environmental quality, an optimal tuber size s^* can be obtained from equation 2. At the average water level of 25.5 cm observed from field conditions (equation 7) equation 2, 8 and 9 yield $s^*=0.332$ g. For simulations where the water level w is fixed at 25 cm, we plotted the fitness of the lognormal strategy with mean tuber size $\bar{\mu}=s^*=0.332$ g, for various values of σ . For $\sigma=0$ the lognormal distribution reduces to a single-size strategy. We repeat this with mean tuber size $\bar{\mu}=0.565$ g as computed from equation 10. The results for both comparisons are given in Fig. A3 (Supporting Information). As expected, the geometric mean fitness K decreases with increasing σ in both cases, since there is no advantage to a variable-size strategy when environmental conditions are constant. The global maximum fitness is 885.6 and is achieved by the single-size strategy with mean tuber size $\bar{\mu}=0.565$ g. We note that this is higher than the optimal tuber size of $s^*=0.332$ g predicted from equation 2.

Discussion

A model by Smith and Fretwell (1974) predicted that, in an unchanging environment, the optimal strategy is to produce propagules of a single size. Subsequently, modeling analyses (some using empirical data to parameterize model) have investigated whether strategies such as dormancy and the production of variably sized offspring might represent adaptive responses to temporally varying environments (see Introduction for references). Most modeling analyses of offspring size distribution strategies have found that producing variably size offspring confers higher fitness than a single-size strategy in variable environments under many scenarios. Here, we presented and analyzed experimental data from the clonal macrophyte species *Scirpus maritimus* showing that the distribution of offspring tuber sizes is highly variable and best described by a lognormal distribution. The experiments also showed that the distribution was lognormal even under fixed experimental conditions, suggesting that production of variably sized offspring is a developmentally programmed syndrome. We then used a mathematical model parameterized with empirical data to illustrate how production of variably sized offspring tubers can lead to higher fitness than a single-size strategy, by acting as a buffer against temporal environmental variability. This was illustrated using four simulation experiments. The first experiment showed that, at the empirical parameter values controlling the investment strategy in offspring sizes, the fitness under the lognormal strategy was higher than the fitness under the other two strategies. The second experiment showed how the empirical parameter values lie near the global maximum in the fitness landscape of a genet adopting a lognormal strategy. The third experiment showed that a single-size strategy can outperform the lognormal strategy when environmental quality is sampled from a small, restricted set of possible states, but not when it is sampled from a continuous distribution of

possible states where there is a nonzero probability of arbitrarily poor environmental states. The fourth experiment confirmed that the single-size strategy does best when environmental quality does not change over time.

The success of the lognormal strategy over the other two strategies relies upon classic within-generation bet hedging (Hopper 2003) and the reasons for its success can be understood *a posteriori* by considering the model equations. Under the single-size strategy, for a given tuber size s , there is a 100% probability that a water level sufficiently deep to preclude any biomass production eventually occurs, i.e. $s < m_w$ in equation 1. This is because $f(w) > 0$ for all w in equation 7 and so any given water level w will eventually occur if enough time passes. Hence, for any given offspring tuber size under a single-size strategy, there will eventually occur a water level sufficiently deep to kill the genet. We speculate that dormancy will mitigate this effect but may not remove it altogether: a string of sufficiently bad years also occurs eventually with 100% probability, and hence a dormant tuber may not be able to emerge in a favorable year before becoming unviable or being removed through other processes. Hence, in this model system, single-size strategies are prone to extinction. By comparison, for a large genet adopting a lognormal strategy, for any given water level w , there is a nonzero probability of having offspring tubers large enough to survive a year of arbitrarily poor quality ($s > m_w$), since $\frac{1}{s} > \frac{1}{m_w}$ for all values of w and s . This effect does not occur when environmental states are sampled from a small, discrete set (see Simulation Set #3 Results).

The observation of a lognormal distribution in tuber sizes, as opposed to some other common statistical distribution with nonzero variance, is not unexpected. Lognormal distributions are common and have been documented in such diverse phenomena as the critical dose of a drug,

1 incubation periods of diseases, time to recovery from illness, time to failure of electronic and
2 mechanical devices, times to marriage, divorce, and death, cloud sizes, the abundance of
3 biological species, velocities in air, time required to solve a research problem, and the lengths
4 of telephone calls (Crow & Shimizu 1988, Haley and Inchausti 2002). It has been shown
5 (Crow and Shimizu 1988, Limpert et. al. 2001) that lognormal distributions should be
6 expected in phenomena that are the result of a multiplicative product of various factors,
7 because the distribution of such outcomes is governed by the multiplicative central-limit
8 theorem. Tuber production in *S. maritimus* appears to be a multiplicative process rather than
9 an additive one, as the size of new tubers produced along a rhizome in a given season is a
10 function of tubers previously produced along that rhizome in that season as well as previous
11 seasons. Furthermore, if the change in a variate obeys the law of proportionate effect (the
12 change at any step in the process is a random proportion of the previous value), then the
13 variate will tend to be lognormally distributed. This is also true of *S. maritimus* tuber
14 production. These factors may explain why *S. maritimus* tuber size is lognormally distributed
15 rather than according to some other continuous probability distribution with nonzero
16 variance. If a lognormal distribution may be the product of a complex set of processes not
17 directly relating to fitness, a lognormal distribution *per se* cannot be called adaptive.
18 However, it is adaptive in the sense that the species may exploit the fact that a lognormal
19 distribution entails production of variably sized offspring. Moreover, it may be possible for a
20 species to evolve with respect to some of the processes that determine the variance of the
21 lognormal distribution. Hence, the variance of the distribution may evolve until the optimal
22 value $\sigma \approx 0.8$ is reached.

23
24 As with any theoretical model, there are several limitations to the present model. For
25 instance, the model does not take into account the possibility that tubers may remain dormant

1 for several years before sprouting. Dormancy and density dependence were not incorporated
2 due to lack of empirical data on those aspects of *S. maritimus* growth. As noted above,
3 dormancy should mitigate the effects of temporal variability in the environment since a
4 portion of tubers can remain dormant during bad years. This should change the quantitative
5 results. However, we speculate that this would not change the relative fitness of the
6 strategies, since dormancy would benefit all strategies to a similar extent. (Just as the
7 probability of an arbitrarily bad year eventually occurring is 100%, so is the probability of a
8 string of arbitrarily bad years, and therefore a single-size strategy remains more prone to
9 failure than a variable-size strategy.) Nonetheless, incorporating dormancy into this model
10 system should be an important priority for future work. Other model limitations include the
11 lack of density dependence in growth dynamics (again, this should change quantitative but not
12 qualitative outcomes) and the use of a continuous model instead of an individual-based model.
13 An individual-based (agent-based) model would allow us to account for discrete effects and
14 thus may be a topic of future research.

15
16 Though we have focused primarily on temporal heterogeneity in water level fluctuations as
17 the source of diversifying selection, *S. maritimus* tubers are obviously subject to many other
18 different selective pressures that could interact to produce a diversity of tuber sizes in the
19 population. For example, it is well known, that *S. maritimus* tubers are predated upon by
20 diving ducks (Desnouhes et al. 2007). These predators may selectively remove larger tubers
21 from the population, influencing the size distribution. Our results obviously do not preclude
22 the possibility that the observed tuber size distribution in *S. maritimus* could arise from other
23 explanations and a multitude of mechanisms. However, it is striking that the lognormal
24 distribution appears both in the field data, which is likely to be the result of many years of
25 selective pressure on more than one genet, and also clearly within a genet in one season (from

the experiments), strongly suggesting a genetic component to this variation. Hangebroek and Santamaria (2004) have studied *Potamogeton pectinatus*, another aquatic macrophyte which reproduce via tubers and displays considerable size variation (though they do not explicitly discuss the size distribution and nature of variability). They suggest that the size variation is maintained through the interaction of maternal and genetic effects. They find that maternal effects play a major role in determining the size of tubers produced and note that these effects can result in an amplification of within-clone variation in tubers size across generations. As explained previously, this amplification effect is a well-known mechanism for producing lognormally distributed offspring. Hangebroek and Santamaria claim that this effect alone is sufficient to maintain variation in the population and reduce selection pressure towards an optimal tuber size, however, they do not discuss the link between these effects and the offspring size distribution.

In summary, this study supports the hypothesis that production of variably sized offspring in species like *S. maritimus* can increase fitness by acting as a buffer or bet-hedge against unpredictable temporal variation in an organism's environmental quality, and hence may be adaptive. This work illustrates the benefits of integrating mathematical modeling and empirical approaches in the same investigative framework.

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- 8
- 9

1 **Table 1.** Fit of test distributions to individual ramet data in shallow, medium, and deep water
2 levels*

		Distribution Fitted Statistical Test Used			
		Lognormal KSL	Lognormal Shapiro-Wilks	Normal Shapiro-Wilks	Gamma Cramer v. Mises
Shallow (15 cm)	N = 29	REJECT	REJECT	REJECT	REJECT
		D=0.179	W=0.908	W=0.919	No Convergence
		$p>D=0.03$	$p<W=0.03$	$p<W=0.02$	
		$\mu=-0.716$	$\mu=-0.716$	$\mu=0.626$	
	N = 25	$\sigma=0.741$	$\sigma=0.741$	$\sigma=0.418$	
		ACCEPT	ACCEPT	REJECT	REJECT
		D=0.128	W=0.944	W=0.877	No Convergence
		$p>D=0.15$	$p<W=0.182$	$p<W=0.006$	
	N = 22	$\mu=-0.776$	$\mu=-0.776$	$\mu=0.679$	
		$\sigma=0.955$	$\sigma=0.955$	$\sigma=0.574$	
		ACCEPT	ACCEPT	BORDERLINE	REJECT
		D=0.104	W=0.942	ACCEPT	No Convergence
	All N=398	$p>D=0.15$	$p<W=0.221$	W=0.913	
		$\mu=-0.708$	$\mu=-0.708$	$p<W=0.053$	
		$\sigma=0.777$	$\sigma=0.795$	$\mu=0.645$	
				$\sigma=0.447$	
Medium (45 cm)	N = 14	REJECT	REJECT	REJECT	REJECT
		D=0.05	W=0.988		No Convergence
		$p>D=0.012$	$p<W=0.002$		
		$\mu=-0.788$	$\mu=-0.788$		
	N = 16	$\sigma=0.837$	$\sigma=0.837$		
		ACCEPT	ACCEPT	BORDERLINE	REJECT
		D=0.200	W=0.912	ACCEPT	No Convergence
		$p>D=0.128$	$p<W=0.167$	W=0.897	
	N = 13	$\mu=-1.17$	$\mu=-1.17$	$p<W=0.101$	
		$\sigma=0.906$	$\sigma=0.940$	$\mu=0.624$	
				$\sigma=0.495$	
		ACCEPT	ACCEPT	REJECT	REJECT
	All N=210	D=0.143	W=0.949	W=0.867	No Convergence
		$p>D=0.15$	$p<W=0.467$	$p<W=0.03$	
		$\mu=-0.769$	$\mu=-0.769$	$\mu=0.435$	
		$\sigma=0.805$	$\sigma=0.831$	$\sigma=0.312$	
	All N=210	ACCEPT	ACCEPT	REJECT	REJECT
		D=0.102	W=0.914	W=0.853	No Convergence
		$p>D=0.15$	$p<W=0.206$	$p<W=0.03$	
		$\mu=-1.00$	$\mu=-0.126$	$\mu=0.428$	
	All N=210	$\sigma=0.538$	$\sigma=0.787$	$\sigma=0.263$	
		ACCEPT	ACCEPT	REJECT	REJECT
		D=0.05	W=0.989	W=0.870	No Convergence

Deep (85 cm)	N = 10	$p>D=0.15$	$p<W=0.1$	$p<W=0.001$	REJECT No Convergence
		$\mu=-1.06$	$\mu=-1.06$	$\mu=0.459$	
		$\sigma=0.786$	$\sigma=0.787$	$\sigma=0.347$	
		ACCEPT	ACCEPT	BORDERLINE	
		$D=0.73$	$W=0.924$	ACCEPT	
		$p>D=0.15$	$p<W=0.392$	$W=0.85$	
	N = 10	$\mu=-1.39$	$\mu=-1.39$	$p<W=0.057$	REJECT No Convergence
		$\sigma=0.973$	$\sigma=1.02$	$\mu=0.387$	
				$\sigma=0.366$	
		ACCEPT	ACCEPT	ACCEPT	
		$D=0.128$	$W=0.936$	$W=0.956$	
		$p>D=0.15$	$p<W=0.51$	$p<W=0.7428$	
	All N=94	$\mu=-1.44$	$\mu=-1.44$	$\mu=0.302$	REJECT No Convergence
		$\sigma=0.775$	$\sigma=0.817$	$\sigma=0.194$	
		ACCEPT	ACCEPT	REJECT	
		$D=0.07$	$W=0.984$	$W=0.720$	
		$p>D=0.15$	$p<W=0.327$	$p<W=0.001$	
		$\mu=-1.58$	$\mu=-1.58$	$\mu=0.295$	
	$\sigma=0.824$	$\sigma=0.828$	$\sigma=0.296$		

* Lognormal fitting used two different methods in order to be able to compare p-values directly with the method commonly used for fitting the normal distribution. In most cases (marked in bold type), the lognormal fit the data tested best. In the few cases where the data was fit by the normal distribution, the lognormal fit was better. None of the data were fit by the gamma distribution. Note that the null hypothesis tested in each case is different, however for ease of presentation ACCEPT/REJECT refers to the null hypothesis that the data belong to the distribution labelled in the respective column.

1 **Table 2.** Parameter values used in simulations for simulation experiments 1 through 4

Parameter/Function	Definition	Values
<div></div> equation 7	Probability distribution function for fluctuations in water level w from year to year	Simulation set #1: $a=4.646$, $b=-$ 0.080 Simulation set #2: $a=4.646$, $b=-$ 0.080 Simulation set #3: n/a (used only two possible water levels) Simulation set #4: n/a (used a constant water level of 25 cm)
σ	Variance (of $\log(S)$ for a lognormally distributed tuber size S).	Sets #1, 3: 0.821 Sets #2, 4: varies on [0,1.5]
<div></div> equation 8	Minimum viable offspring size as a function of water level w	$c=0.010$, $d=-0.124$ g for all sets
<div></div> equation 9	Shape parameter for fitness function as a function of water level w	$e=-0.022$, $f=0.258$ for all sets
<div></div> equation 10	Mean tuber size produced as a function of water level w	Sets #1, 3, 4: $y_{\text{int}}=0.680$ g Set #2: y_{int} varies on [0 g, 2 g]
s_{half}	Width parameter for uniform distribution	0.1 g for all sets
T	Duration of simulation runs	350 years per simulation run for all sets
R	Number of realizations per set	Sets #1, 2, 4: 8,000 Set #3: 5,000

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Fig. 1. Distribution of tuber sizes (A) collected from the field ($N=455$) and lognormal fit (Kolmogorov D-test, $\mu=-0.636$, $\sigma=0.821$, $D=0.06$, $p=0.01$); (B) produced in shallow water level ($N=398$) and lognormal fit (Kolmogorov D-test, $\mu=-0.788$, $\sigma=0.837$, $D=0.05$, $p=0.01$); (C) produced in medium water level ($N=210$) and lognormal fit (Kolmogorov D-test, $\mu=-1.06$, $\sigma=0.786$, $D=0.05$, $p=0.15$); (D) produced in deep water level ($N=94$) and lognormal fit (Kolmogorov D-test, $\mu=-1.58$, $\sigma=0.824$, $D=0.07$, $p=0.15$).

Fig. 2. (A) Frequency distribution of water level at the end of March over the period 1932-2003 ($n = 71$) and fitted water level distribution function, equation 7 (B) Relationship between the total biomass of produced tubers and the size of planted tubers, with fitted fitness functions, equation 1, for the three experimental water levels: shallow (15 cm), medium (45 cm) and deep (85 cm). (B).

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7 **Fig. 3.** Frequency distributions of (A) fitness and (B) lifespan for simulation experiment #1.

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Fig. 4. Fitness landscape for simulation experiment #2, (C) top view and (D) three-dimensional view. For comparison, note that $\sigma=0.821$ and $y_{\text{int}}=0.680$ at empirical values.

Probability of a Good Year (p_G)	Difference in environmental quality (k)						
	k=1	k=2	k=4	k=6	k=8	k=10	k=12
$p_G=0$	0.85	0.78	0.68	0.71	1.60	80.4	1496.9
	0.85	0.78	0.69	0.73	1.51	422.0	207.1
$p_G=0.1$	0.85	0.78	0.70	0.72	1.40	41.8	189.8
	0.85	0.78	0.70	0.73	1.34	120.0	63.7
$p_G=0.2$	0.85	0.79	0.71	0.86	1.24	27.6	90.6
	0.85	0.79	0.71	0.74	1.20	41.4	37.3
$p_G=0.3$	0.85	0.79	0.73	0.74	1.12	21.3	59.8
	0.85	0.79	0.73	0.75	1.09	16.7	27.8
$p_G=0.4$	0.85	0.80	0.75	0.75	1.03	16.3	40.8
	0.85	0.80	0.75	0.76	1.01	7.7	20.9
$p_G=0.5$	0.85	0.81	0.76	0.76	0.96	12.8	29.9
	0.85	0.81	0.76	0.77	0.95	4.0	16.4
$p_G=0.6$	0.85	0.82	0.78	0.78	0.91	9.3	19.1
	0.85	0.82	0.78	0.78	0.90	2.3	11.6
$p_G=0.7$	0.85	0.83	0.79	0.79	0.87	6.3	11.6
	0.85	0.83	0.79	0.79	0.87	1.5	7.7
$p_G=0.8$	0.85	0.83	0.81	0.81	0.85	3.7	5.9
	0.85	0.83	0.81	0.81	0.85	1.1	4.3
$p_G=0.9$	0.85	0.84	0.83	0.83	0.84	1.60	2.1
	0.85	0.84	0.83	0.83	0.84	0.92	1.8
$p_G=1.0$	0.85	0.85	0.85	0.85	0.85	0.85	0.85
	0.85	0.85	0.85	0.85	0.85	0.85	0.85

Fig. 5. Results for simulation experiment #3. Each cell shows the ratio of lognormal strategy fitness to single-size strategy fitness (top entry in each cell) and lognormal fitness to uniform strategy fitness (bottom entry in each cell), for various values of p_G and k . Clear cells (resp. light grey and dark grey cells) denote cases where the single-size strategy (resp. uniform and lognormal) obtained the highest fitness.

Supporting Information

Equations for strategies

The three probability density functions for offspring size distributions (single-sized, lognormal, and uniform) are given by

$$\begin{aligned}\phi_w^{\text{single}}(s) &= \delta(\hat{s}_w - s) \\ \phi_w^{\text{log}}(s) &= \frac{1}{s\sqrt{2\pi\sigma}} \exp\left[-\frac{1}{2\sigma^2}(\ln(s) - \ln(\hat{s}_w) - \sigma/2)^2\right] \\ \phi_w^{\text{uni}}(s) &= \begin{cases} 1/(2s_{\text{half}}) & s > \hat{s}_w - s_{\text{half}} \text{ and } s < \hat{s}_w + s_{\text{half}} \\ 0 & \text{otherwise} \end{cases}\end{aligned}\tag{A1}$$

where $\hat{s}_w$ is the mean offspring size in water level w , σ is the variance of the lognormal distribution, and s_{half} controls the width of the uniform distribution. The integral of these distributions from $s=0$ to $s=\infty$ is 1.

Derivation of model equation 3

We first assume that tubers come in discrete sizes $s_1 = \Delta s$, $s_2 = 2\Delta s$, $s_3 = 3\Delta s$, ... where Δs is a small, fixed value (later we will relax this assumption). The total biomass b_t produced in year t depends upon the sizes of tubers produced in year $t-1$, when the water level was $w(t-1)$, and the total biomass produced by these tubers in year t , when the water level is $w(t)$, according to the equation

The number of size s_k tubers produced in year $t-1$ is equal to the total number of tubers (of all sizes) produced in year $t-1$ (i.e., total biomass b_{t-1} produced divided by mean tuber size of tubers produced in year $t-1$), times the fraction that are size s_k . The biomass produced per size s_k tuber in year t is equal to the fitness function corresponding to the water level in year t . Hence,

$$\text{[Empty box for equation]}$$

Taking the limit as , one finally obtains

$$\text{[Empty box for equation]}$$

which governs the time evolution of total biomass produced from one season to the next.

Discrete effects

This model assumes that tuber offspring sizes are distributed according to a continuous function. However, real populations are discrete in nature, consisting of a finite number of distinct individuals. Because of this there exist parameter values for which the assumption of continuity does not hold, and discrete effects become significant. For example, in some years when the water level is unusually deep, it may happen that a tuber fails to produce enough total biomass to make even a single daughter tuber at the sizes required by the mean tuber size vs. water level regression (equation 3). Although this does not occur very often at empirically realistic parameter values, it can occur more frequently at certain extremes in parameter values and at these points the model becomes inapplicable.

Hence we restrict our analysis to parameter values such that these violations are rare. Let denote the mean tuber size produced in year t . Then, a violation of the continuity assumption

is considered to occur if the total biomass produced by a tuber of size $\square$ in year t is less than $\square$ plus two standard deviations of the lognormal distribution. That is, a violation occurs when tubers with mean required size from the previous year cannot produce even a single tuber, at the mean required size in the present year, in 2.3% of the cases (since two standard deviations covers 97.7% of the distribution of produced tuber sizes). It can be shown that this translates into the condition

$$\square$$

Note that, since the lognormal distribution has the largest variance, it is sufficient to apply this criterion to the lognormal strategy only: if one of the other strategies experiences a violation event, then the lognormal strategy must also (although the converse is not true). A particularly deep water level in year $t-1$, or year t , or both, tends to produce a violation. We restrict all analysis to parameter values such that years with a violation event constitute no more than 5% of the years of a given simulation run.

Table A1. Tuber production at the individual level, for the shallow, medium and deep treatment*

* For each treatment, the dry weight (g) of the planted tuber, the total number of produced tubers (N), the dry weight (g) of the smallest (min) and biggest (max) produced tuber, the median (M), mean and standard deviation (S.D) are presented

Fig. A1. Relationship between rainfall and water level for the period 1995-2003.

Fig. A2. Illustration of the three offspring size distribution strategies: lognormal, uniform, and single-size.

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5 **Fig. A3.** Results for simulation experiment #4: fitness in an unchanging environment for
6 various values of σ .