

SHORT COMMUNICATION

Selection for increased allocation to offspring number under environmental unpredictability

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*Department of Biology, Carleton University, Ottawa, ON, Canada***Keywords:**

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Abstract

According to life-history theory, the evolution of offspring size is constrained by the trade-off between allocation of resources to individual offspring and the number of offspring produced. Existing models explore the ecological consequences of offspring size, whereas number is invariably treated simply as an outcome of the trade-off with size. Here I ask whether there is a direct evolutionary advantage of increased allocation to offspring number under environmental unpredictability. Variable environments are expected to select for diversification in the timing of egg hatch and seed germination, yet the dependence of the expression of diversification strategies, and thus parental fitness, on offspring number has not previously been recognized. I begin by showing that well-established sampling theory predicts that a target bet-hedging diversification strategy is more reliably achieved as offspring number increases. I then use a simulation model to demonstrate that higher offspring number leads to greater geometric mean fitness under environmental uncertainty. Natural selection is thus expected to act directly to increase offspring number under assumptions of environmental unpredictability in season quality.

Introduction

Allocation of finite resources to offspring or propagule production is considered to result in a balance between offspring number and size (Smith & Fretwell, 1974). The evolution of ever increasing propagule number is kept in check by the corresponding decrease in the probability of survival of individual propagules, with the optimal balance depending on the particular ecological context. The original model (Smith & Fretwell, 1974) has provided an invaluable starting point for further refinements, and has been cited over 1000 times in the primary literature to date. Propagule size is in fact variable within and among species (e.g. Westoby *et al.*, 1992; Wolfe, 1995; Simons & Johnston, 2000; Imbert, 2002; Koops *et al.*, 2003; Halpern, 2005), and models attempt to explain this variation by considering the shape of the fitness function associated with propagule size.

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Whereas the ecological relevance of propagule size has been the focus of attention, that of propagule number has been ignored. Number is normally treated simply as a multiplier: a parent's reproductive success is given by offspring size and performance associated with offspring size, multiplied by the number of propagules of each size. Here I show that propagule number has a direct effect on parental reproductive success – independent of the relationship between propagule size and fitness – through its effect on the expression of diversification strategies.

So-called 'bet-hedging' (Slatkin, 1974) strategies are expected to evolve under environmental unpredictability (Seeger & Brockmann, 1987; Simons, 2002). Parents, by producing propagules that hatch or germinate over an extended time period, for example, reduce the variance in fitness (Gillespie, 1977) associated with variably detrimental conditions over time or may reduce density-dependent selection among siblings (Geritz, 1995). Seed germination has become the model diversification trait following the publication of Cohen's (1966) classic paper on the optimal timing of germination under

environmental unpredictability. I begin by asking how diversification is affected by offspring number, given that diversification bet-hedging is a plausible explanation for the sometimes extreme variation observed in the timing of seed germination and egg hatch both within and among seasons. I then model the effect of diversification on parental genotype fitness as influenced directly by offspring number.

Offspring number and diversification bet hedging

Diversification, by definition, requires the production of multiple phenotypes. The effect of propagule number on the expression of diversification is based on the simple principle that the variance, s^2 , within samples of size n drawn at random from a population approaches the population variance as n increases (Zar, 1984). Because sampling variance approaches population variance with sample size, the realized expression of a diversification strategy is expected to improve with the number of phenotypes produced. Thus, species characterized by high propagule number should more reliably produce a given diversification strategy, all else being equal.

The relationship between propagule number and variance depends on the mechanism whereby diversification is generated. The simplest assumption is that the timing of germination/hatch of a propagule is drawn randomly from a fixed diversification strategy (Simons & Johnston, 1997) wherein diversification may be generated randomly by a process such as microplasticity (Simons & Johnston, 2006). However, it is also possible to envision a variance strategy generated through the production of propagules whose timing of hatch/germination has somehow been specified at an early developmental stage. Assuming that a parental genotype has a characteristic diversification strategy of which each propagule is a random sample, the expression of the diversification strategy approaches the true strategy with the number of propagules produced.

The dependence of diversification on propagule number has a straightforward analytical solution. Given an optimal 'true' diversification strategy, σ^2 , the distribution of sample variances for samples of size n – i.e. realized diversification expressed by n offspring – given by the normalized sum of squares, s^2n/σ^2 , has a chi-square distribution:

$$\chi_n^2 = \frac{ns^2}{\sigma^2}.$$

Thus, the dependence of the reliable expression of diversification on offspring number can be obtained by calculating the confidence interval (CI) that has a $1 - \alpha$ chance of including the true diversification variance strategy. Assuming an α of 0.05, the upper and lower critical values of the chi-square distribution that bound the 95% CI for sample variances of sample size n , are:

$$\chi_{0.975,n}^2 \leq \frac{ns^2}{\sigma^2} \leq \chi_{0.025,n}^2$$

and, rearranging, the 95% CI, which are asymmetrical, are given by:

$$\frac{ns^2}{\chi_{0.975,n}^2} \geq \sigma^2 \geq \frac{ns^2}{\chi_{0.025,n}^2}.$$

The dependence of the expression of a diversification strategy on offspring number is thus given by the change in sampling distribution of variances with sample size (Fig. 1). The decreasing width of the 95% CI around sample variance with sample size demonstrates that the realized diversification of individual parental genotypes more reliably approaches the ideal diversification strategy as offspring number increases. It should be noted that this does not imply that selection for diversification is expected to result in an ever-increasing number of offspring; the balance between size and number depends concurrently on advantages of offspring size covered in traditional treatments of the topic. Nonetheless, to the extent that diversification is an adaptive response to fluctuating selection, this result suggests that natural selection will act directly on offspring number.

Offspring number and fitness

The demonstration that offspring number is expected to influence diversification independently of offspring size is the main result of the paper, and leads to the qualitative result that optimal offspring size is overestimated given that diversification strategies have evolved. Taking the additional step to estimate the strength of the effect of offspring number on parental geometric mean fitness is

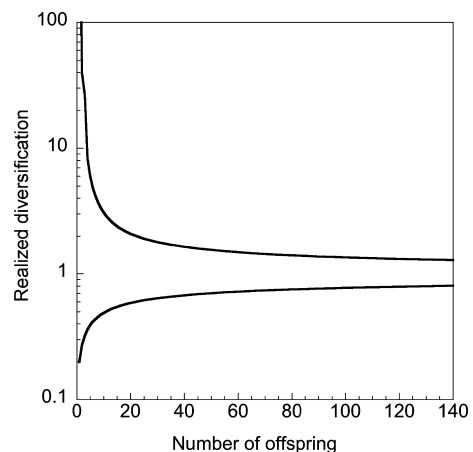


Fig. 1 The effect of offspring number on the realized expression of diversified bet-hedging strategies. The curves are the upper and lower bounds of the 95% confidence interval for variances of samples for a range of sample sizes. Realized diversification represents the proportion of the optimal diversification strategy ($\sigma^2 = 1$) that is expressed, and is thus shown on a logarithmic scale.

more difficult because this depends jointly on the magnitude of environmental variance and diversification; both notoriously difficult to derive empirically (Simons & Johnston, 2003, 2006). The effect of offspring number on a parental genotype's geometric mean fitness is thus best illustrated through a simulation model using a range of parameter values.

The simulation model asks how, in principle, allocation to offspring number affects the geometric mean fitness associated with various diversification strategies in a temporally variable environment. The example diversification strategy used here to illustrate is variation in the timing of seed germination in the monocarpic perennial, *Lobelia inflata* (L.), although the results apply equally to other diversification strategies. The timing of germination of seeds produced within a single capsule in this species may occur over several seasons, and over a range of 50 or more days within a season under growth chamber conditions (Simons & Johnston, 2000, 2006).

Random timing of germination – determined by the particular diversification strategy under study – is simulated within a randomly fluctuating environment. Fluctuation in effective length of growing seasons with an average length of 100 days is modelled as random normal variation in the date of the last killing frost in the spring (mean = 0; $\sigma = 6$). The choice of this particular parameter value is based on earlier simulations (Simons & Johnston, 1997) showing that empirically observed variation in seed germination timing ($\sigma = 12.8$ days) in *Lobelia inflata* (Simons & Johnston, 2006) would result from stabilizing selection under this level of environmental variation. In the present simulation, parents are generated that produce offspring numbers from 1 to 100. The effect of offspring number is simulated for parents characterized by four different diversification strategies (strategies 1–4: SD = 0, 4, 8, 12 days, respectively) in the timing of germination, where dates of germination are drawn from a normal distribution centred on day 0. A seed that germinates prior to a spring killing frost does not survive, whereas a seed germinating after this unpredictable date survives, but its contribution to parental fitness still depends on the timing of germination because an early germinating seed has more time in which to establish itself and accrue biomass and is thus at an advantage. Therefore, fitness of a seed germinating after the final spring frost is weighted linearly in proportion to the length of time remaining in the growing season. Parental fitness in one generation is given by the average fitness of each of its offspring rather than by the total fitness of all offspring. This step avoids confounding the obvious incremental advantage of producing additional offspring with the direct advantage gained through the potential for increased diversification. In other words, we are interested in comparing geometric mean fitness among different *evolved* strategies that lie along the size vs. number trade-off line and thus do not differ in expected (arithmetic mean) fitness. The parental

geometric mean fitness is then calculated over 30 unpredictable growing seasons. The geometric mean fitness is estimated as an average of 100 independent runs of the 30-generation model for each combination of offspring number and diversification strategy (Fig. 2).

Discussion and conclusions

The main result (Fig. 1) suggests that offspring number is expected to influence the expression of diversification. Furthermore, the geometric mean fitness increases with increasing allocation to offspring number for a range of diversification strategies. It should be noted that the simulation results are meant only as a qualitative demonstration of the effect of offspring number on geometric mean fitness; input parameters – such as environmental variance in the field – are necessarily arbitrary.

This optimality approach is a first step towards an understanding of the selective advantage of increased offspring number, and does not pretend to detail its evolutionary dynamics. For example, the rate of evolution towards the optimal balance between offspring number and size will depend not only on the magnitude of fluctuating selection, but also on the quantitative genetic basis of diversification and demographic properties of the population. Diversification must be manifested at the individual level to confer a bet-hedging advantage to a genotype, and this is most obvious for small populations, or in cases where population size fluctuates widely among generations. Under such situations, in which a genotype is represented by only one or a few

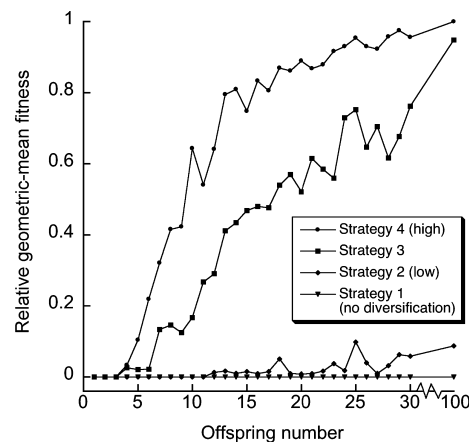


Fig. 2 An illustration of the direct effect of offspring number on geometric mean fitness. Geometric mean fitness for 2–100 offspring is simulated for four different diversification strategies (strategies 1–4: SD = 0, 4, 8, 12 days, respectively) in the timing of seed germination or egg hatch. The quality of the environment within a season is assumed to vary randomly. Results for each diversification strategy and offspring number are averages of 100 estimates of geometric mean fitness calculated over 30 growing seasons (see text for details).

individuals, the possibility that diversification can be expressed collectively among individuals of the same genotype is reduced.

To avoid misunderstanding, though, it is worth pointing out that selection acts on the germination distribution of individual parents even if multiple parents of the same genotype exist in the population. Of course, collectively, multiple parents produce a germination distribution that is determined by all of their offspring. However, it is the genotype that has produced the optimal offspring distribution *among* generations, not *within* generations, that has maximized geometric mean fitness and is thus best represented in the present population. For example, consider two asexual lineages of the same genotype that, separately, produce a suboptimal long-term germination distribution within each generation, but collectively produce an apparently optimal long-term distribution within each generation. There is nothing optimal about diversification within a given generation: synchronous germination at the appropriate moment, if it were possible, would always be the fittest phenotype. Because selection acts on the distribution only over generations of fluctuating selection, *both* asexual lineages will suffer a low geometric mean fitness, and thus be selected against despite their apparently optimal joint distribution within any generation. A mutant genotype characterized by individuals that consistently produce the long-term optimal distribution will thus invade.

It would be tempting to conclude from these results that the benefit of producing additional offspring declines rapidly from, say, 2–30 offspring, until the improvement in diversification becomes negligible. However, it should be noted that these offspring numbers may be meaningless in an absolute sense; instead, they should be viewed as the ecologically relevant surviving fraction after accounting for mortality from all sources. For example, a single *Lobelia inflata* individual may produce > 10 000 seeds, but it would be unreasonable to assume that more than a tiny proportion of these would survive to express the diversification strategy.

It is believed that the joint evolution of offspring number and size is constrained by the existence of finite resources available for allocation to reproduction (Smith & Fretwell, 1974). Allocation to offspring size and number is a particularly straightforward example of a life-history trade-off in that, unlike other life-history trade-offs involving multiple traits, allocation to this single structure is not confounded by problems of multiple resource constraints (Venable & Lloyd, 2004). The model results illustrate that a well-known statistical phenomenon can have important life-history consequences: diminishing standard error with sample size is of consequence to a diversity of biological phenomena (Simons, 2004), and here implies that diversification strategies improve with offspring number.

The relationship between propagule number and variance offers an additional explanation for the evolu-

tion of plentiful, small seeds that typify annual and monocarpic perennial plants whose long-term survival is expected to rely heavily on variance strategies such as a persistent seed bank (Rees, 1997). Given that much otherwise unexplained variation exists in the timing of egg hatch and seed germination in insect and herbaceous plant species, the influence of the evolution of diversification strategies on the optimal balance between propagule size and number deserves consideration. Optimal propagule size is overestimated, and optimal propagule number underestimated, when diversification strategies have evolved.

A large body of literature explores the adaptive significance of diversification strategies, and an empirical test of adaptive diversification is beyond the purpose of this paper. However, to the extent that diversification is selected for, selection also favours an increase in allocation to number of propagules. This must be true in principle; a parent producing only one propagule cannot express diversification. The degree to which fluctuating selection influences the evolution of propagule number, however, provides fertile ground for future study.

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