Why do big plants make big seeds?

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Summary

1. The conventional explanations for large plant species producing larger seeds on average than small plant species have recently been challenged, and it has been suggested that the pattern is better explained by the theory developed by Charnov (1993). Here we use simple life-history theory to explore the logic underlying Charnov's models and show that under most reasonable conditions they predict no relationship between seed mass and size at maturity.

2. Using a simple general model incorporating size-specific growth and survival, we explore the joint evolution of seed mass and size at maturity, and argue that seed mass will be correlated with adult traits, such as the timing of reproduction and size at reproduction, only if seedling and adult growth and mortality rates are correlated. Evidence for such correlations is briefly explored.

3. It has also been suggested that the standard model for seed mass evolution (Smith & Fretwell 1974) has been misinterpreted, and that application of the model requires measurement of survivorship to reproductive maturity. Using a simple model incorporating size-specific growth and survival we show that this criticism is unfounded.

4. Our results differ from those of Moles and colleagues because they look at the effect of long juvenile period on survival to maturity, but do not recognize that this may be compensated by covarying life-history traits, such as plant size and reproductive lifespan. Also, they seem to argue that life-history evolution is constrained by cross-angiosperm correlations, such as that between seed mass and longevity, while the life-history models presented here seek selective causes of such correlations, rather than regarding them as constraints.

5. Models similar to those of Charnov (1993) only predict a positive relationship between seed size and plant size if unrealistic assumptions are made about the effects of seed mass on survival, such as the effect of seed mass on instantaneous survival persisting to adulthood.

Key-words: life-history theory, seed mass, size at maturity, Smith–Fretwell model, evolutionary stable strategy

Introduction

Global variation in seed mass of different plant species spans 10 orders of magnitude. Part of this variation is related to plant size; large species tend to produce larger seeds than small species, but at any one plant size there is enormous variation in the size of seeds produced (Thompson & Rabinowitz 1989; Rees 1996;

Moles *et al.* 2004; Grubb *et al.* 2005; Moles & Westoby 2006). The increase in seed mass with plant species size is thought to reflect differences in establishment conditions, the nature of competition, and/or physical or dispersal constraints (Salisbury 1974; Tilman 1988; Thompson & Rabinowitz 1989; Moles *et al.* 2004; Grubb *et al.* 2005; Moles *et al.* 2005a; Moles *et al.* 2005b; Moles & Westoby 2006). However, recent studies of seed mass evolution (Moles *et al.* 2004; Moles *et al.* 2005b, 2005c; Moles & Westoby 2006) have challenged this view, arguing that the positive relationship between plant species size and seed mass can be explained in

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terms of the life-history models developed by Charnov (1993). For example, Moles *et al.* (2004) suggested that 'species require a long juvenile period to become large adults, and to survive a long juvenile period requires high juvenile survivorship, which is associated with large seeds. Large plants would not be able to make small seeds, because seedling survivorship would be too low for sufficient seedlings to reach maturity' and that 'Charnov's theory predicts that larger adult body sizes will be associated with larger offspring mass at weaning because the long period of growth required for large adults to develop exposes individuals to a long period of juvenile mortality'. Here we explore the logical basis of this explanation, focusing on the life-history theory on which it is based.

In order to understand the theory underpinning these ideas we first discuss the idea that long juvenile periods impose a population dynamic constraint on seed mass, and then explore the evolution of plant size/age at reproduction, showing that for simple models, such as those developed by Charnov (1993), this is independent of seed and seedling traits. We then consider a slightly more general model for the evolution of seed mass and explore the conditions under which this is independent of adult size. The results of this model indicate when a positive correlation between seed mass and adult size is to be expected. The relationship between large-scale, cross-species patterns of trait variation and simple life-history models is then discussed. The basic life-history models were developed by Charnov (1993). These models, and those presented below, all assume that fecundity increases with size, mortality is size- or age-dependent, and density dependence acts primarily on new recruits. Thus, maximizing R_0, the total number of offspring produced by an individual over its lifetime, characterizes the evolutionarily stable strategy (ESS) (Mylius & Diekmann 1995). The links between various theoretical models, and between model predictions and existing data are explored.

Do long juvenile periods constrain seed mass?

The idea that large plant species have long juvenile periods, and that this prevents them from producing small seeds because seedling survivorship would be too low for sufficient seedlings to reach maturity, is intuitively appealing (Moles *et al.* 2004; Moles *et al.* 2005a; Moles *et al.* 2005b, 2005c; Moles & Westoby 2006; Moles *et al.* 2007). To make the ideas underlying this explicit, write $R_0 = S \times T$ where S is survival to reproductive maturity and T is lifetime seed production. T can be decomposed further, as $T = AR/s_w$, where A is adult life expectancy, R is the yearly mass allocated to producing seeds, and s_w is mean seed mass. For a population to persist we require $R_0 \geq 1$. For low survivorship through the juvenile period to prevent large species from producing small seeds it is necessary that larger species cannot compensate for lower survival to maturity in other ways. Using data from Moles *et al.* (2004) we

find that both reproductive life span (A) and plant height (a surrogate for R) increase with the duration of the juvenile period (Fig. 1a,b), and that tall plant species have higher mean seed production per year (Fig. 1c). Mean seed production per year increases with plant height and decreases with seed mass according to the following regression model:

$$\ln(\text{Seeds year}^{-1}) = 6.12(0.14) + 1.11(0.12) \times \ln(\text{Height}) - 0.67(0.07) \times \ln(\text{Seed mass})$$

where the figures in brackets are the standard errors ($n = 169$, $r^2 = 0.41$, $P < 0.0001$). So tall, small-seeded species produce more seeds per year than short, large-seeded species. This means that species with long juvenile periods could compensate for lower survival to maturity by having longer reproductive life spans, or by being taller/larger, or by producing *smaller* seeds, all of which increase lifetime seed production (T), or possibly by producing larger seeds (although this decreases T) it might increase survival to reproduction (S). Note that the lack of a significant relationship between seed mass and lifetime seed production (Moles *et al.* 2004) only holds if one averages over indirect effects operating through plant size. Re-analysing the data from Moles *et al.* (2004) shows that lifetime seed production is positively related to plant height and negatively related to seed mass, as expected

$$\ln(\text{Lifetime seed production}) = 7.18(0.28) + 2.28(0.29) \times \ln(\text{Height}) - 0.65(0.13) \times \ln(\text{Seed mass})$$

where the figures in brackets are the standard errors ($n = 37$, $r^2 = 0.65$, $P < 0.0001$).

Moreover, the idea that long juvenile periods constrain seed size in large, long-lived species assumes that the various components of R_0 are species-specific constants, whereas in reality one or more of the components of R_0 are likely to be density dependent. Assuming that populations are at approximate demographic equilibrium, as a result of density dependence, means that $R_0 = S \times T \approx 1$. Therefore $S \approx 1/T$, implying that species with large lifetime seed production will automatically have low survival to maturity, thus making the measurement of S, as recommended by Moles & Westoby (2006), less informative than they suggest.

Therefore, unless unrealistic assumptions are made (e.g. that duration of the juvenile period is not related to adult reproductive life span or size and that there is no density dependence), it is not possible to make any firm prediction about how seed mass should vary in relation to the juvenile period based on demographic constraints. All these arguments take current patterns of cross-species trait variation and attempt to derive constraints on trait covariation from population dynamic principles ($R_0 \geq 1$ or $R_0 \approx 1$). An alternative approach is to model how evolution shapes life histories, and ask, What are the expected patterns of trait covariation?
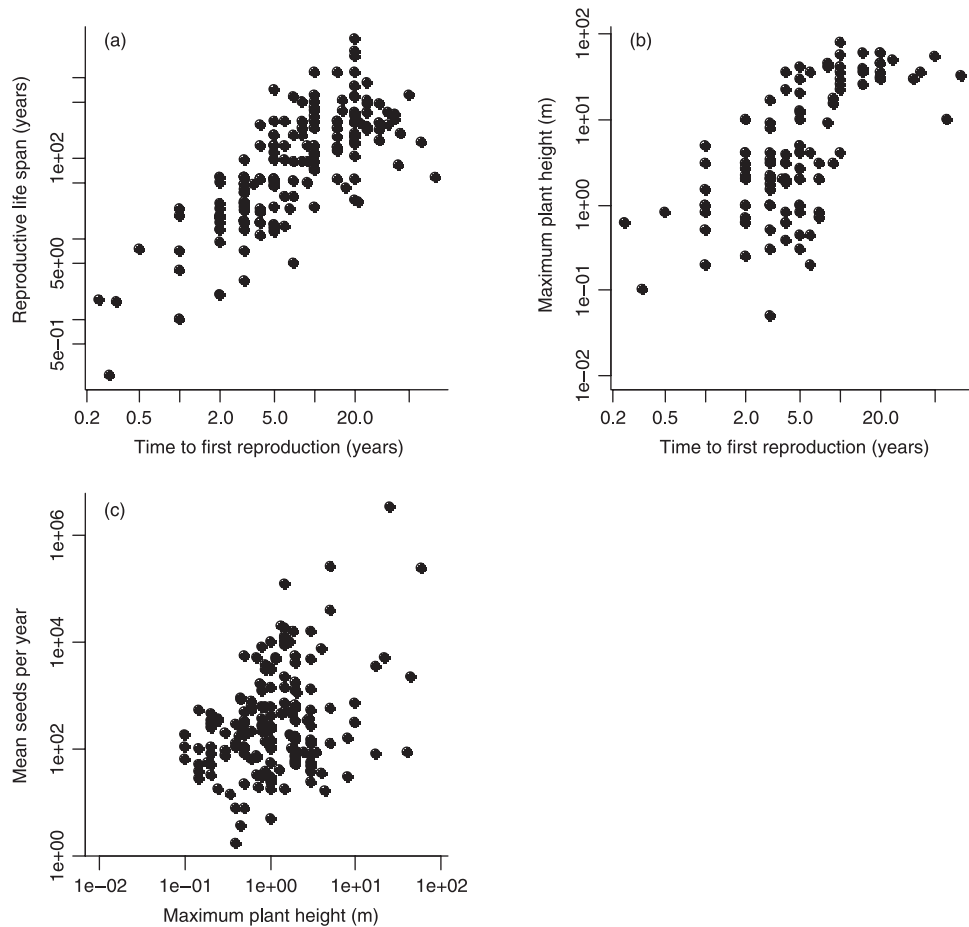
Fig. 1 Relationships between (a) time to first reproduction and reproductive life span ($R^2 = 0.59$), $P < 0.0001$), (b) time to first reproduction and maximum plant height ($R^2 = 0.46$, $P < 0.0001$), and (c) maximum plant height and mean seed production per year ($R^2 = 0.20$, $P < 0.0001$). Data from Moles *et al.* (2004).

Models for the evolution of seed mass and size at maturity

To explore how seed mass influences the evolution of the timing of reproduction, and hence the duration of the juvenile period and adult plant size, we will consider monocarpic (semelparous) species, and use the discrete time formulation for R_0 developed by de Jong & Klinkhamer (2005). Analogous calculations can be done for iteroparous species (Charnov 1993). Assume that seedling survival is C_j, the survival of g year old plants is C_g and their seed production S_g. A further delay in flowering is unfavourable when $R_0(g + 1) < R_0(g)$. This can be written as

$$C_j C_1 C_2 C_3 \ldots C_g S_{g+1} < C_j C_1 C_2 C_3 \ldots C_{g-1} S_g$$

$$C_g S_{g+1} < S_g$$

It follows that an individual should delay reproduction until its expected seed production next year, $C_g S_{g+1}$, falls below current seed production, S_g. Writing seed production at age g as $S_g = R_g/S_w$, where R_g is the reproductive mass of a plant of age g and s_w its seed

mass, allows the condition for flowering at age g to be written as

$$C_g \frac{R_{g+1}}{s_w} < \frac{R_g}{s_w}$$

$$C_g R_{g+1} < R_g,$$

from which we conclude that the ESS age/size at reproduction is independent of seed mass and seedling survival. Thus, varying seed mass has no direct effect on the optimal or ESS age at maturity or adult size; species with very different seed masses can have identical sizes/ ages at maturity providing their adult age-specific survival and reproductive masses are the same, and conversely, species with very different sizes/ages at reproduction can have similar seed masses. Therefore there is no necessary link between seed mass and the timing of reproduction.

This result holds for a wide range of more realistic models incorporating size and age-dependent demography, and variation in growth between individuals (Rees *et al.* 2000; Rose *et al.* 2002; Childs *et al.* 2003). To illustrate these more realistic models we modified the integral projection model for *Oenothera glazioviana*
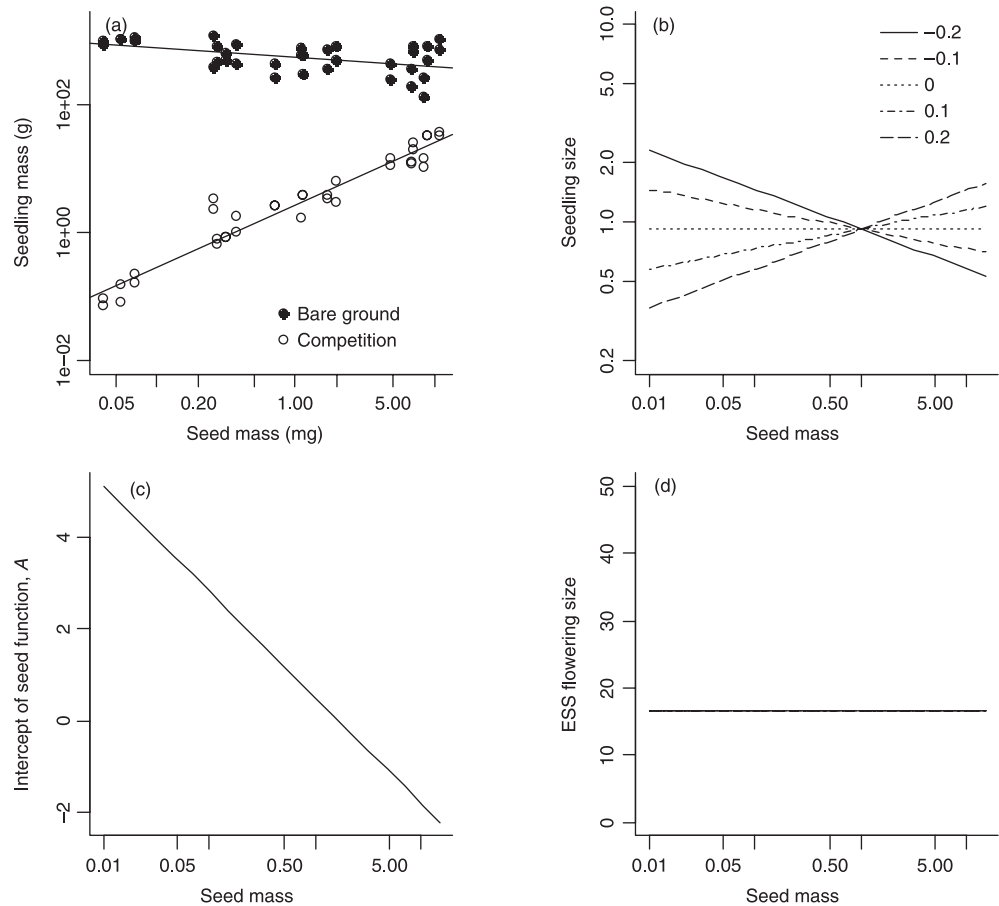
Fig. 2 (a) Relationship between seed mass and seedling mass. The data are from six species of monocarpic perennial (see Table 4 in Gross (1984) for details). To simplify presentation, the effects of litter were ignored. In both treatments (bare ground and competition) the slopes are significantly different from zero (bare ground, $P < 0.002$, competition $P < 1e^{-10}$). The relationships between seed mass and (b) seedling mass and (c) the seed production intercept (A) used in the simulation. (d) The ESS flowering sizes calculated using the mean seedling masses and A values from (b) and (c). The box in (b) refers to the slopes, b_{sd}, used to generate the lines in (b).

developed by Rees & Rose (2002). In this model plant size is a continuous variable (log rosette diameter), growth, survival, the probability of flowering and seed production are all functions of plant size, and seedling size is drawn from a normal distribution with specified mean and variance. To incorporate the effects of seed mass we made mean seedling size and seed production functions of seed mass. Specifically, using data from Gross (1984), we assumed that mean seedling size on a log scale, $\ln(\mu_{sd})$, was a linear function of seed mass on a log scale so that $\ln(\mu_{sd}) = a_{sd} + b_{sd}\ln(s_w)$ (Fig. 2a). We also modified the size-dependent seed production function, Seeds $= \exp(A + BL)$, where L is log-transformed rosette diameter, and A and B are the intercept and slope, respectively, so that $A = -\ln(s_w)$. In this way, increasing seed mass results in: (i) seedling size either increasing or decreasing (Fig. 2b) and (ii) a decrease in the size-specific seed production (Fig. 2c). Using the methods described in Rees & Rose (2002), we then calculated the ESS flowering size for a wide range of seed mass. Again, this shows that despite seed mass varying by more than 1500 fold, there is no change in the ESS flowering size (Fig. 2d). Therefore, both in

simple models and more complex ones incorporating realistic patterns of size-dependent demography, we see that the ESS size at maturity is independent of seed mass and seedling traits such as size and survival.

To explore how the evolution of seed mass depends on adult plant size, consider the model of Kiflawi (2006) which assumes that mortality and growth are size-specific. Here we provide a very brief description of the model; a more detailed derivation is given in Kiflawi (2006). Specifically, let $u(s)$ be a function describing how mortality varies with plant size (the mass-specific instantaneous per capita mortality rate), and $g(s)$ be a function describing how relative growth rate (RGR) varies with plant size (the mass-specific relative growth rate). Without specifying the exact forms of these functions we can then calculate the probability that an individual seed of mass s_w survives to mature at size s_m. This is given by

$$S = \exp\left(-\int_{s_w}^{s_m} \frac{u(s)}{sg(s)}ds\right). \qquad \text{eqn 1}$$

If plants of size s_m allocate some fraction ρ of their biomass to seed production, then we can write R_0 as

$$R_0 = \exp\left(-\int_{s_w}^{s_m} \frac{u(s)}{sg(s)}ds\right)\frac{\rho s_m}{s_w}. \qquad \text{eqn 2}$$

In this formulation, as in Charnov's (1993), producing larger seeds is advantageous because (i) it increases survival, S, by reducing the time taken to reach maturity, and (ii) it reduces exposure to high mortality rates, assuming that small plants have high mortality rates. However, these advantages come at a cost in terms of reduced seed production ($\rho s_m/s_w$). The ESS seed mass, calculated by solving $\partial R_0/\partial s_w = 0$, is obtained by solving the equation $g(s_w) = u(s_w)$, which means that as long as the seedling growth rate, $g(s_w)$, or seedling mortality rate, $u(s_w)$, is independent of size at maturity (s_m), the ESS seed mass is also independent of size at maturity (Kiflawi 2006). The ESS size at maturity, calculated by solving $\partial R_0/\partial s_w = 0$, is the solution of $g(s_m) = u(s_m)$, which, in agreement with the simple theory discussed earlier, shows that size at maturity is determined by the growth and survival of mature plants, rather than by seed or seedling traits.

The classic model (Smith & Fretwell 1974) for the evolution of seed mass assumes that offspring quality increases (at a decreasing rate) with maternal investment. Offspring quality is typically measured as survival over some fixed time period, and as expected, many studies have shown that this is positively correlated with seed mass (Leishman *et al.* 2000). Recently however, the validity of this approach has been challenged by Moles & Westoby (2006), who state 'the requirement of the Smith–Fretwell model is for a positive relationship between seed mass and survival through to reproductive maturity, not just per unit time', and 'This oversight has allowed the Smith–Fretwell (1974) model, the foundation of most evolutionary theory on the evolution of seed size, to pass for almost three decades without an appropriate test of its assumptions'. Following Moles and Westoby's suggestion we can equate S, survival from seed to adulthood (equation 1), with offspring quality and calculate the optimal seed mass; according to the Smith–Fretwell model this is characterized by the condition,

$$\frac{dS}{ds_w} = \frac{S}{s_w}.$$

Making the calculation shows that, as in the ESS calculation described above, the Smith–Fretwell optimal seed mass is obtained by solving $g(s_w) = u(s_w)$. The important point here is that the Smith–Fretwell solution is characterized by the growth and mortality rates of seedlings. If it were true that one has to measure survival to reproductive maturity, as argued by Moles & Westoby (2006), then changing the size at maturity,

s_m, would change the ESS/Smith–Fretwell seed mass, which it does not. To understand why varying the time to reach adulthood has no direct effect on the relative fitnesses of seeds of different sizes, and hence on the ESS/Smith–Fretwell optimal seed mass, consider the model of Kiflawi (2006) described above. If we want to compare the success of small (s_w(small)) and large (s_w(large)) seeds we calculate R_0 for each; small seeds will be favoured if $R_0(s_w(\text{small})) > R_0(s_w(\text{large}))$, which, using equation 2, gives the condition,

$$\exp\left(-\int_{s_w(\text{small})}^{s_w(\text{large})} \frac{u(s)}{sg(s)}ds\right)\frac{1}{s_w(\text{small})} > \frac{1}{s_w(\text{large})},$$

which is independent of all growth and survival rates after attaining mass s_w(large) because all individuals, whether they are derived from small or large seeds, have the *same* mass-specific mortality and growth rates after they have grown past mass s_w(large). Therefore, for testing the assumptions of the Smith–Fretwell model, it is perfectly reasonable to estimate survival over a fixed time period, as many have done in the past.

In summary, the idea that large offspring are necessary to offset the low survivorship to maturity that is a consequence of large adult size is unlikely to account for the positive relationship between seed mass and plant size, either as a population dynamic constraint or as an evolutionary prediction based on simple life history theory. So why do our theoretical conclusions diverge from those of Moles and colleagues? There are two contexts in which the ideas of Moles and colleagues might be construed as 'going beyond' this modelling framework. We will examine each in turn, explaining why we do not find either approach satisfactory.

Cross-species correlations or within-species constraints?

Moles and colleagues appear to suggest that cross-species patterns of covariation of seed mass and plant size should be considered as constraints in life-history models of intraspecific evolution such as the Smith–Fretwell model. They explicitly criticize the Smith–Fretwell model (which predicts intraspecific evolution of seed mass) for not taking cross-angiosperm correlations into account as constraints ('The tacit assumption that survival per unit time would be correlated with survival to maturity *other things being equal* turns out to be wrong *at the cross species level* because other things are not equal, and especially, because large-seeded species need more time to reach adulthood', Moles & Westoby 2006; emphasis added). True or not across angiosperms, this is not the same as saying that a larger-seeded genetic variant within a population will have an age at first reproduction that is delayed relative to the resident phenotype by an amount predictable from the cross-angiosperm pattern. The discussion of

seed mass evolution by these authors frequently seems to conflate cross-angiosperm patterns with constraints on intraspecific evolution like those modelled by Smith and Fretwell. In one case they criticize this framework by arguing, 'Although large-seeded species do make fewer seeds per square metre of canopy outline per year, they also tend to have larger canopies and longer reproductive lifespans than do small-seeded species' (Moles & Westoby 2006). This will be a constraint on evolution only if the genes causing larger seed mass also cause (or are linked to genes that cause) larger canopies and longer reproductive lifespans. It seems more likely that patterns across broad swaths of angiosperms might involve coadaptation of seed mass, canopy size and longevity in response to correlated selective pressures in species inhabiting dramatically different habitats. In another example, again in the context of criticizing the Smith–Fretwell model, Moles & Westoby (2004) argue that the survival advantage of large seeds is inadequate to balance the numerical advantage per unit canopy per year. Yet the relationship between seed mass and survival was an interspecific comparison across angiosperms. It seems unlikely that a seed-size/survival curve extrapolated across many species and orders of magnitude of seed mass would adequately represent the within-species Smith–Fretwell seed-size survival curves.

The models we present above vary one trait at a time and look for, but do not find, general reasons why changes in size or age at maturity will select for different seed mass (or vice versa). However, if one insisted that the models force changes in size or age at maturity as a consequence of changing seed mass, a Smith–Fretwell type model would give a different answer. For example, such a model might include a direct effect of seed mass on offspring survival operating through standard mechanisms involving the amount of parental resources available to the seed. But it would also include an indirect effect operating though the forcing of age at reproduction (that they suggest must occur with any change in seed mass) in combination with the effect that age at reproduction has on offspring survival. Moles *et al*. (2004) found that total lifetime fecundity was independent of seed mass across species (due to covariation with plant size) and Moles & Westoby (2006) conclude that the relationship between seed mass and survival from seed dispersal to reproductive maturity is most likely to be moderately positive, allowing everything to covary across angiosperms. If within-species evolution were constrained by these cross-angiosperms correlations, the ESS seed mass (for all angiosperms?) would be to produce one very big seed (or seed mass might be nearly neutral if the survival increase with seed mass is small enough).

Before building observed cross-angiosperm correlations into models of seed mass evolution it should be shown that their pattern and magnitude is reflected in within-population genetic correlations, or at least correlations among similar species in a common

environment. When smaller segments of this large scale variation are magnified, the patterns seem weak, so that the likelihood of this being so seems low. Indeed, Charnov (1993) does not seem to want to build this type of direct dependency into life-history models. On page 107 he states 'adult body size (and M) is independent of size at weaning', and goes on to build this assumption into his model (M is the adult instantaneous mortality rate). We argue that there is nothing wrong with Smith and Fretwell as a model of intraspecific evolution unless the cross-angiosperm correlations constrain microevolution, which we find implausible.

Do Smith–Fretwell curves scale with body size or juvenile period?

There is another context in which it could be construed from the arguments of Moles and colleagues that something is missing from the Smith–Fretwell framework for understanding large scale cross-angiosperm variation in seed mass. What if the shape of the Smith–Fretwell seed mass-survival curve varies systematically with the length of the juvenile period or size at maturity? Might this not create a large-scale interspecific pattern of seed mass that scales with body size as shown in the comparative studies of Moles and colleagues? In what follows we argue that the answer to this question is 'possibly' in theory, but most likely 'no' in practice. First, we present the general condition for changes in juvenile period/age at reproduction to influence the evolution of seed mass, and then explore what this means in terms of models of seed mass dependent survival. We use a result from Venable (1992) which emphasizes that the ESS for offspring size-number models can be obtained by equalizing the proportional marginal advantages of offspring size and number. This means $\partial \ln(f(n))/\partial \ln(n) = \partial \ln(f(s_w))/\partial \ln(s_w)$, where $f(n)$ describes the effect of offspring number on fitness and $f(s_w)$ describes the effect of offspring size on fitness. So, for example, the Smith–Fretwell model has $R_0 = f(s_w) \times n$ where $f(s_w)$ gives the well-known Smith–Fretwell seed mass fitness curve and $f(n)$ just equals n. Because, the effect of seed number on fitness is linear in n, $\partial \ln(f(n))/\partial \ln(n) = 1$, and so the equal marginal advantage solution (ESS) is given by $\partial \ln(f(s_w))/\partial \ln(s_w) = 1$. This can be rewritten as $\partial f(s_w)/\partial s_w = f(s_w)/s_w$ which is the standard way of expressing the Smith–Fretwell solution.

In order for juvenile period (J) to influence the ESS seed mass, $\partial \ln (f(s_w))/\partial \ln(s_w)$ must be a function of the juvenile period (mathematically, this is the requirement that $f(s_w)$ be 'non-homogeneous in J'). To see what this means biologically, consider the following simple but very general survival model, where the chance that an individual survives to age J is

$$f(s_w) = \exp\left(\rho(s_w) - \int_0^J \mu(t)dt \right), \qquad \text{eqn 3}$$

where $\exp(\rho(s_w))$ describes the initial, transitory effect of seed mass on seedling survival, and

$$\exp\left(-\int_0^J \mu(t)dt\right)$$

is the chance that an established seedling survives to maturity, $\mu(t)$ being some arbitrary age-dependent mortality rate. Calculating the partial derivative we find

$$\frac{\partial \ln(f(s_w))}{\partial \ln(s_w)} = \frac{\partial \rho(s_w)}{\partial \ln(s_w)},$$

which is independent of J. Thus, any change in the duration of the juvenile period will have no effect on the ESS seed mass. Equation 3 is very general and simply captures the idea that sequential mortality factors act in a multiplicative fashion.

This need not always be the case. For example if $\exp(-d/s_w)$ describes the initial, transitory effect of seed mass on seedling survival, *and* this remains constant throughout the juvenile period, then

$$f(s_w) = \exp(-dJ/s_w).$$

In this case the ESS seed mass is dJ, which increases with the length of the juvenile period; s_w/J would be a type A life-history invariant with respect to changes in juvenile period. A type A invariant occurs when one trait does not vary systematically with another; a type B invariant occurs when a trait exhibits a unimodal central tendency and varies over a limited range (Savage *et al.* 2006). We believe this may be the kind of new interspecific perspective that Moles and colleagues have been looking for to replace the ostensibly flawed Smith–Fretwell approach. However, notice that we used the Smith–Fretwell model to get this result. Also, for this model to be appropriate requires the effects of seed mass to be constant throughout the juvenile period. This seems extremely unlikely, given that the effects of seed mass on survival are typically transitory (Moles & Westoby 2004), and mortality rates are often size and/or age dependent (Metcalf *et al.* 2003). So, while this approach can provide a theory for the kind of life-history invariant for seed mass that Moles and colleagues appear to be looking for, it is ultimately unsatisfactory due to the lack of realism of the required assumptions.

Moles and colleagues frequently refer to 'a theory lineage developed by Charnov (1993)' as a conceptual justification for their ideas (Moles *et al.* 2004; Moles & Westoby 2006). Any such model must satisfy the 'non-homogeneity in J' requirement, but we can find no such model for offspring size in Charnov (1993). Charnov (1993) seems to suggest that offspring size/adult size ratio, which he calls δ, might be a life-history invariant with respect to changes in adult size (cf. his Fig. 5.4),

and outlines a model of the evolution of δ (Charnov 1993; pp. 107–108). Yet little biology is built into the offspring size fitness equation for this model other than scaling constants and the density dependence required for offspring mortality to compensate for reproduction to give $R_0 = 1$. When we build this logic into the above framework, the offspring size is selectively neutral, and thus the ESS size does not depend on the juvenile period, J (or body size). So the ideas in Charnov (1993) do not seem to provide theoretical support for the assertions of Moles and colleagues about the correlation between body size and seed mass.

Correlation between seedling and adult growth and mortality rates

Under what conditions does the theory developed in this paper suggest that correlations between seed mass and adult size should evolve? They are predicted to evolve when seed traits (weight, growth and mortality rates) are correlated with established plant demographic rates (i.e. growth or survival). We briefly review the evidence for this. Metcalf *et al.* (2006) present data for seven monocarpic perennial species which allows the correlation between seed mass and established plant growth rate to be estimated. They characterized between-year growth using linear regression, namely $L(t + 1) = a_g + b_g L(t)$, where $L(t)$ is the logarithm of longest leaf length in year t, and a_g and b_g are the estimated intercept and slope, respectively. Analysis of covariance suggested species-specific intercepts, a_g, and a common slope b_g. Regressing a_g against log-transformed seed mass suggests a marginally significant positive relationship (Fig. 3, $F_{1,5} = 4.85$, $P < 0.08$), with perhaps a single outlier (*Digitalis purpurea*, exclusion of which increases r^2 from 0.49 to 0.89, and the significance level changes from $P < 0.08$ to $P < 0.006$;
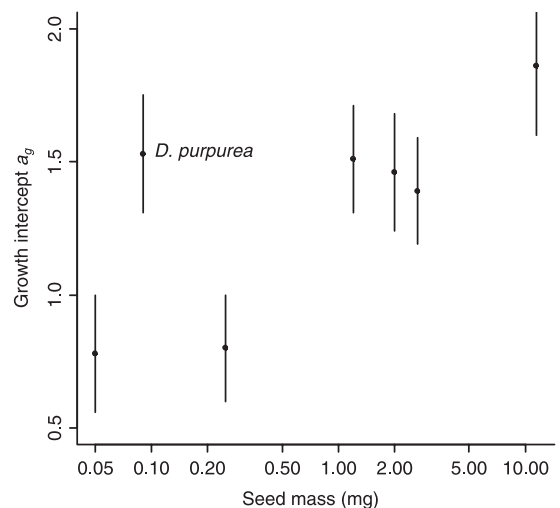
Fig. 3 Relationship between the intercept of the linear growth function, a_g, and seed mass. Data from Metcalf *et al.* (2006). Vertical lines indicate 95% confidence intervals.

D. purpurea grows fast and is small-seeded). Relative growth rate (RGR) is given by RGR = $a_g + (b_g - 1) \times L(t)$, so species with large a_g grow faster at all sizes. Note that this positive relationship is the opposite of the usual negative relationship between seed mass and seedling RGR (Maranon & Grubb 1993). The difference is probably a consequence of studying established plants rather than seedlings, the fact that RGR was estimated in the field over one year rather than under favourable conditions in the glasshouse over a few weeks, and allowing for the size dependence of RGR. Small individuals typically grow faster than large ones (Metcalf *et al.* 2003) so that comparisons of growth rates must correct for size (Sack *et al.* 2003; MacFarlane & Kobe 2006).

Incorporating a positive relationship between seed mass and a_g results in a positive relationship between seed mass and adult size (results not presented). This is a consequence of large-seeded species growing faster and having larger asymptotic sizes, which increases the payoff from delayed reproduction, and hence flowering at a large size (Rees & Rose 2002; Rose *et al.* 2002; de Jong & Klinkhamer 2005). However, even in this small data set of species with similar life histories from similar environments, the relationship between seed mass and adult growth is weak, and species like *D. purpurea* are small-seeded, fast growing, and flower at relatively large sizes. In Aarssen & Jordan's (2001) study of monocarpic perennials, the two species with the largest masses at flowering, namely *Arctium minus* and *Verbascum thapsus*, had, respectively, the largest and smallest seed masses of the 15 species studied. Interestingly, in Metcalf *et al.*'s (2006) study large plants all had high survival and so the size at maturity was largely determined by variation in growth rates, whereas in seedlings there is substantial variation in both growth (Maranon & Grubb 1993) and survival (Leishman *et al.* 2000). If this pattern is generally true, this suggests that, even in cases where seed traits and adult growth are correlated, the correlation between seed mass and size at flowering will be weak as a result of variation in seedling survival being weakly correlated with adult survival.

It seems likely that shifts in physiology are common, resulting in seedling and adult demographic rates being weakly correlated, especially for long-lived, large species. For example, in tropical forests species that are shade-tolerant and slow-growing when small can be either fast- or slow-growing as adults (Clark & Clark 1992, 1999; Condit *et al.* 1996; Svenning 2000). In a meta-analysis of multi-species growth studies of tropical trees, Poorter & Rose (2005) found that the correlation between seed mass and growth parameters declines over time and disappears after 1–4 years. For other examples of shifts in physiology/morphology/ habitat during ontogeny see Comita *et al.* (2007), Kneeshaw *et al.* (2006), Lusk (2004), Metcalf *et al.* (2003), Niinemets (2006). A weak correlation between seedling and adult demography means that this body of theory predicts a weak positive relationship between

seed mass and adult plant size, in agreement with numerous published studies (Rees 1996; Aarssen & Jordan 2001; Aarssen 2005; Moles *et al.* 2005a; Moles & Westoby 2006).

When measuring the strength of the correlation between seedling and adult traits it is essential to understand how seedling and adult demography are influenced by the environment. Independent environmental sensitivities of juvenile and adult traits should further weaken their correlation and consequently the coevolution of seed mass and adult size. In monocarpic perennials seedling RGR is negatively related to seed mass in favourable environments, and unrelated to seed mass in competitive conditions (Gross 1984) (Fig. 2a). Likewise, seedling RGR in high nutrient treatments is not correlated with seedling RGR in low nutrient treatments (Shipley & Keddy 1988). This lack of correlation was a result of species with high RGRs being much more sensitive than slow-growing species to nutrient shortage. This sensitivity of fast-growing species to shortage of resources is also mirrored in their susceptibility to defoliation, both in terms of seedling survival and the growth of survivors (Armstrong & Westoby 1993).

Comparative data revisited

As Charnov's ideas were developed for mammals it is instructive to compare the patterns of offspring mass at independence between mammals and plants. Recently it has been suggested that mammals and plants differ fundamentally in the way that offspring size scales with adult size, with mammals showing a proportional increase in offspring size with adult size whereas in plants the increase is less than proportional (Aarssen 2005). Here we show that this difference is a consequence of the way in which the data are analysed. This is typically done by plotting log offspring mass against log maternal mass (Charnov 1993; Moles *et al.* 2004; Aarssen 2005; Moles & Westoby 2006). Such plots are difficult to interpret when the variable plotted on the *y*-axis is a fraction of that on the *x*-axis, and the variable on the *x*-axis ranges over several orders of magnitude (Nee *et al.* 2005). Under these conditions, even if offspring mass is some random fraction of maternal mass, the double log regression of weaning mass against maternal mass will have a slope ≈ 1 and a high (> 0.9) coefficient of determination. This is indeed the case for mammals (Charnov 1993; Moles *et al.* 2005c; Fig. 4(a)). This seems to suggest that in mammals, offspring are weaned at some constant fraction of adult mass (Charnov 1993; Savage *et al.* 2006). However, if we plot δ (= weaning or seed mass divided by maternal mass) against maternal mass (Fig. 4b), we see that for mammals δ is far from constant, and in fact varies over almost the entire possible range [0.03, 1] and decreases significantly with maternal size ($r = -0.36$, $P < 1e^{-10}$, in agreement with the log-log analysis, Fig. 4a). So the seemingly trivial deviation from 1 of the slope of the
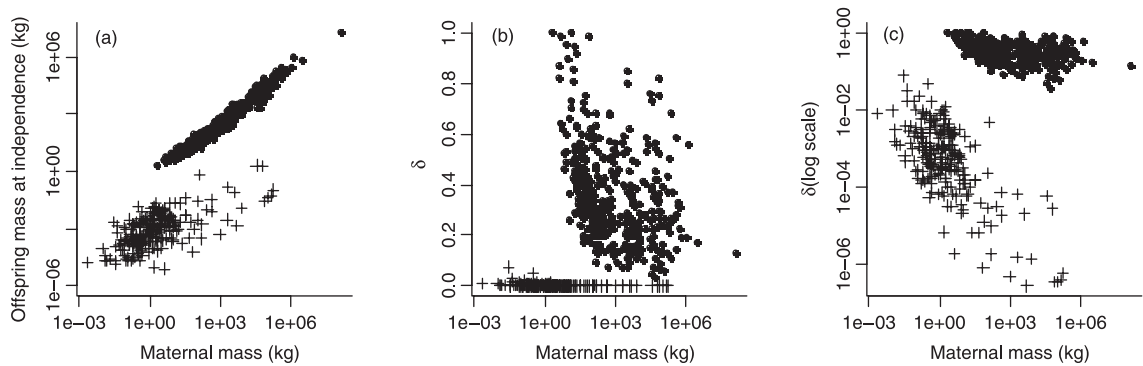
Fig. 4 Relationship between maternal mass and offspring mass at independence plotted as (a) a double log plot. Note that the slopes of both relationships are significantly less than 1 for both least squares (LS) and reduced major axis (RMA) regressions. For mammals the slopes were 0.93 ± 0.008 (LS) and 0.95 ± 0.008 (RMA). For plants the slopes were 0.47 ± 0.04 (LS) and 0.71 ± 0.04 (RMA) (b) δ (offspring mass at independence/maternal mass) against log maternal mass, and (c) log(δ) against log maternal mass. Data for plants (crosses) from Moles *et al.* (2004) and for mammals (filled circles) from Ernest (2003).

mammal data in Fig. 4(a) (the estimated slope is 0.93 or 0.95 depending on the type of regression used) is actually consistent with an enormous variation in δ, which is also size-dependent. While offspring mass does increase with adult size, δ is neither a type A nor type B life-history invariant with body size in mammals.

For plants we see a similar pattern, with δ much smaller but still size-dependent and highly variable (over five orders of magnitude; Fig. 4c). Note that this data set does not include large species. For example, *Sequoia sempervirens* which can weigh over 900 000 kg and has a seed mass of 0.0037 g, would have a $\delta < 1e^{-11}$. Its inclusion would result in δ varying over nine orders of magnitude. Thus the relationship between seed mass and adult size is weak, and neither a type A nor B invariant with plant size, as predicted by the theory presented here.

Discussion

Moles and colleagues have contributed greatly to our understanding of the ecology and evolution of seed mass by compiling large scale data sets on seed mass-related traits and analysing the various relationships in a modern phylogenetic context (Moles *et al.* 2005a; Moles *et al.* 2005b). These patterns have lead them to propose a conceptual framework for understanding seed mass evolution that challenges the traditional view (Moles *et al.* 2004; Moles *et al.* 2005b, 2005c; Moles & Westoby 2006). We have examined this new framework and found it problematical from both empirical and theoretical perspectives. The available comparative data are inadequate to confirm the assertion that, because large plants have long juvenile periods, they are unable to produce small seeds because seedling survivorship would be too low for sufficient seedlings to reach maturity. Furthermore such calculations suffer from treating demographic rates as constants rather than as plastic and density dependent. The comparative data show that seed mass-body size ratio

is neither a type A nor type B life-history invariant, but rather that it decreases with plant size and is highly variable at any particular plant size.

The positive relationship between plant size and seed mass can only be explained by life-history models similar to those developed by Charnov (1993) if un-realistic assumptions are made, such as seed mass survival effects persisting to adulthood. Alternatively, cross-angiosperm correlations could be incorporated as constraints on intraspecific evolution (e.g. by assuming that a mutation in seed mass forces a change in longevity). This seems unreasonable *a priori* and leads to unlikely predictions such as selective neutrality, or unbounded increase of seed mass (i.e. all angiosperms should produce one large seed). A range of more realistic models presented here suggests that seed mass and the length of the juvenile period should evolve independently and only be correlated when seed and seedling vital rates are correlated with adult vital rates. The model of Kiflawi (2006) is particularly informative in this respect, as the ESS seed mass and size at maturity are both functions of the size-dependent growth and mortality functions ($g(s)$, $u(s)$). However, the ESS seed mass is determined by growth and mortality rates of seedlings, whereas the ESS size at maturity is determined by the growth and mortality of established plants. This means that understanding the extent to which the growth and survival of seedling and adults is correlated is essential if we want to apply simple life history theory to the problem of why large plants produce large seeds. A review of available empirical information suggests that weak correlations may be the norm, which is consistent with the weak pattern of seed mass/body size correlation reported in the literature.

For the life-history models discussed above, and those of Charnov (1993), it is assumed that density dependence acts primarily on recruitment. This is a reasonable assumption for rare species (Rees *et al.* 1999; Rees *et al.* 2000; Rose *et al.* 2002; Rees *et al.* 2006), although unlikely to be true for abundant species, for

which competition between established plants will be common. When considering the evolution of seed mass, this implies that seedlings compete, but that the outcome of competition will be independent of seed mass, in agreement with some recent field-based studies (Eriksson 2005; Turnbull *et al.* 2005. See also Turnbull *et al.* (2004), where seed mass was unrelated to competitive ability in one year and positively related in another). If competition between seedlings is size-dependent however, a different modelling framework is required (Geritz 1995; Rees & Westoby 1997). A better understanding of the nature of seedling interactions is clearly important, and in particular we need to understand how variation in physical environment mediates seedling-seedling competition. For a discussion of a range of different niche models in relation to seed mass, see Levine & Rees (2002) and Turnbull *et al.* (2005).

The theory developed here ignores other complicating factors as well. In addition to assuming that density dependence acts on recruitment, it assumes that the environment does not vary either in time or space. Models incorporating the effects of spatial and temporal variation in the environment have demonstrated that this can substantially alter the timing of reproduction in monocarpic perennials (Rees *et al.* 1999; Rose *et al.* 2002; Childs *et al.* 2004; Rees *et al.* 2004), and extending the current theory for the evolution of seed mass to include this complication will undoubtedly lead to a fuller understanding of why big plants make big seeds.

The simple life-history models in this paper suggest that an important way forward in the search for explanations of the noisy cross-angiosperm seed mass/ body size correlation is examination of the pattern of correlation between seedling growth and survival rates and adult growth and survival rates. The requirement of correlation between seedling and adult rates is consistent with a number of previous ideas explaining seed mass-plant size correlations. For example, it is widely thought that the advantage of large plant size is related to competition for light and the resulting need to overtop other plants to pre-empt canopy space (Tilman 1988; Grime 2002). Growing large in turn requires time. Plants growing in competitive environments may also require larger seed mass, creating a correlation between seedling and adult growth and survival rates. Yet some large plants of competitive environments require gaps to establish, which may create a premium on small seeds to increase dispersal and seed number, thus weakening the correlation between juvenile and adult survival and growth rates. Additional factors not identified by these models may come into play in the creation of noisy seed mass/plant size correlations (Thompson & Rabinowitz 1989; Venable 1992; Rees 1996; Grubb *et al.* 2005). For example, larger seeds may require larger plants for support and dispersal and may require more time to mature, which in turn sets lower limits on longevity. Clearly, much remains to be understood about seed mass evolution and its relationship with adult plant size.

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