

FORUM

The scaling of seed size

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Summary

1. Rees & Venable (2007; *Journal of Ecology*, **95**, 926–936) critically evaluated ideas of Moles *et al.* to explain the cross-species positive correlation between offspring size and adult size, arguing that they had misinterpreted the theoretical literature, and used cross-species patterns to constrain the evolution of life-histories.
2. In a reply to Rees & Venable, Westoby *et al.* (2009; *Journal of Ecology*, **97**, 23–26) claimed we had misrepresented their views. Here we try to clarify the arguments indicating points of agreement and disagreement.
3. Using simple models we then extend the current theory to allow (i) the time during which seedling survival is influenced by seed mass to scale with the duration of the juvenile period and (ii) the intensity of stress experienced by seedlings to scale with adult size. These new models predict that species with long juvenile periods or large adult size will have larger seeds.
4. We synthesize the new theoretical ideas with our current understanding of the evolution of seed mass, and suggest that much of the observed increase in seed mass with adult body size may be due to constraints correlated with adult body size.

Key-words: adult body size, juvenile period, life-history theory, scaling, seed size.

Introduction

In a series of papers Moles *et al.* (e.g. 2004, 2005) argued, contrary to previous work (Shipley *et al.* 1989; Leishman & Westoby 1992; Grime 2002), that to understand the evolution of seed mass we need to consider the entire plant life cycle. We agree with this view (Rees 1993, 1994, 1996). The problem then is to understand how established plant traits (length of juvenile period, canopy area, reproductive life span) influence the evolution of seed traits.

To summarize the debate and highlight the critical points of discussion, we first present some of the points of disagreement between Rees & Venable (2007) (R&V) and Moles *et al.*, and ask if we can reconcile our views with those of Westoby *et al.* (2009). We then extend current theory on the evolution of seed mass to allow (i) the time during which seedling survival is influenced by seed mass to scale with the duration of the juvenile period and (ii) the intensity of stress experienced by seedlings to scale with adult size. Finally we attempt to synthesize the theoretical ideas with our current understanding of the evolution of seed mass.

Points of agreement and disagreement

Some intuitive but unlikely interpretations

The idea that large plants cannot produce small seeds, because not enough would survive the longer juvenile periods to maturity, seems intuitively appealing, but does not take into account the fact that larger plants could produce small seeds and compensate for lower seedling survival to maturity in other ways, for example, by making more seeds due to large canopies and greater reproductive life span. Westoby *et al.* (2009) stated that they cannot understand us saying that they did not recognize the possibility of compensation by covarying traits. Our point was that they failed to reconcile the possibility of compensation with their argument that large plants cannot produce small seeds because too few would survive (e.g. Moles *et al.* 2004, 2005; Falster *et al.* 2008).

The idea that a model like that of Charnov (1993) would provide a new framework to explain the correlation of adult and offspring size

Despite assertions to the contrary (Westoby *et al.* 2009), when explaining the positive relationship between seed mass and adult size Moles *et al.* usually referred to Charnov's

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model in ways like this: ‘However, Charnov’s theory is well supported by the data we do have, and provides a coherent explanation for the positive associations between seed mass, plant size and plant life span, as well as suggesting a way to reconcile previous demonstrations of a positive correlation between seed mass and rates of seedling survival with the present finding of no relationship between seed mass and lifetime seed production’ Moles *et al.* (2004). Indeed Westoby *et al.* (2009) and Falster *et al.* (2008) still claim that Charnov’s (1993) life-history theory predicts an isometric relationship between offspring size and adult size. However, Charnov (1993) does not present a specific model predicting offspring/adult size relations. The model merely states that if a set of species had the same functional relationship between survival to reproduction and offspring/adult size ratio (δ), then δ would be invariant with adult size. This function would describe a Smith–Fretwell curve with δ substituted for offspring size. Yet no such function is given. The same logic could show that a set of species with the same functional relationship between offspring survival and offspring size (i.e. the same Smith–Fretwell offspring size/fitness curve) would have invariant offspring size with changes in adult size (as we already know). Likewise, a set of species with the same functional relationship between offspring survival and offspring size divided by adult size raised to 0.6 would have an ESS relationship between offspring size and adult size with an allometric constant of 0.6. Thus, rather than predicting an isometric relationship between offspring and adult size, Charnov (1993) states the conditions required for this to be true. It is up to others to provide realistic models that either predicts this or something different, such as no relationship, or the observed interspecific allometry. Both we and Falster *et al.* (2008) attempt to do this.

A blurring of the distinctions between trade-offs that constrain within-species evolution and cross-Angiosperm correlations

Moles *et al.* (2004) state that, ‘Our previous understanding of seed mass as a spectrum from production of many small seeds, each with low establishment probability, to a few large seeds, each with higher establishment probability, was missing some important elements.’ Critical among these was a cross-species relationship showing that ‘Seed mass was not significantly related to the total number of seeds produced by an individual plant throughout its lifetime.’ But the ‘previous understanding’ was about within-species size-number trade-offs for a given amount of resources. The ‘new understanding’ is about cross-species correlations. This suggests that cross-species correlations constrain within-species evolution.

A technical point about graphing methods

Westoby *et al.* (2009) state ‘We do not agree that it is more desirable to graph (δ = offspring size/adult size) vs. adult size, as Rees and Venable recommend. Using y -variables that have been divided by the x -variable causes correlation of measure-

ment error, with distorting effects on hypothesis tests and line-fitting.’ We agree with Westoby *et al.* (2009) that the determination of the allometric slope of seed size vs. adult size relationship is best done on a log–log scale. However, our point was that such analyses tell us very little about *how variable the pattern is* (see Nee *et al.* 2005, 2006), for a detailed explanation of why R^2 , the proportion of the variance in offspring size explained by adult size, increases with the range of adult size considered on the x -axis in these multi-order of magnitude log–log regressions). For example, on log–log axes, offspring size vs. adult size of mammals has a very high R^2 , suggesting that offspring size is tightly linked to adult size (R&V, fig. 4a). Yet a graph of δ vs. body size (R&V, fig. 4b) reveals that mammals of most sizes exhibit the full range of δ from 0 to 1. We did not use Fig. 4b to test a statistical hypothesis or fit a line, so we need not fear ‘the distorting effects on hypothesis tests and line-fitting.’ If one is uncomfortable with this type of visualization, another approach would be to describe the range, or 95% distributional limits for the residual variance of offspring size for the log–log relation. For the Moles *et al.* (2004) data set this shows that, *at any given plant size*, seed size varies among species by about 400–650-fold depending on the details of the calculation.

Linking adult and juvenile traits

In R&V we presented models suggesting 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. We also stated that the positive relationship between plant size and seed mass can only be explained by models similar to those developed by Charnov (1993) that vary the juvenile period if unrealistic assumptions are made, such as seed mass survival effects persisting to adulthood. To explore this further, we extend the models of R&V so that the period of offspring survival dependence on seed size *scales* with the length of juvenile period aJ^α ; the chance that an individual survives to maturity is then:

$$f(s_w) = \exp\left(-\frac{d}{s_w} aJ^\alpha - \int_{aJ^\alpha}^J \mu(t) dt\right)$$

Here, s_w is seed mass, J is the length of the juvenile period and d is the instantaneous mortality rate during the period when it is sensitive to seed size. In this case, seedling survivorship only has a transient dependence on seed size, the first term inside the brackets, and $\exp\left(-\int_{aJ^\alpha}^J \mu(t) dt\right)$ is the chance that an established seedling survives to maturity, $\mu(t)$ being some arbitrary age-dependent mortality rate. In this case the ESS seed mass is daJ^α which seems to reconcile the models with the observed allometric scaling of seed size. However, we have developed this thinking by assuming that the sensitive period scales with the juvenile period (following the logic of Moles *et al.*). Most treatments of the allometric scaling of seed size use adult body size. What do the empirical data say about the scaling of seed size with the length of the juvenile period?

Using the Moles *et al.* (2004) data we find that seed size scales across species in an *accelerating* fashion with length of the juvenile period (allometric slope > 1 , least squares regression $s_w \propto J^{1.49}$, reduced major axis $s_w \propto J^{2.95}$). This relationship is so steep because juvenile period varies over many fewer orders of magnitude than seed size (or adult body size). An increase of 20% in juvenile period would require an increase of 30–60% in the sensitive period for our model to explain these data. This seems unrealistic, so we can probably reject scaling of sensitive period with juvenile period as a model explaining why big plants make big seeds.

An alternative approach is to allow $f(s_w)$ to scale with adult body size directly and not to operate through the juvenile period as emphasized by Moles *et al.* If large adults tend to deplete light or other resources more severely than small adults, or to occur in habitats with closed canopies, then the resources available to seedlings will be reduced (Salisbury 1942). This could translate into a scaling of the intensity of seedling mortality with adult body size. In keeping with this, we allow the initial transient effect of seed size on seedling survival to scale with adult mass (s_m), so that the probability of survival to maturity is

$$f(s_w) = \exp\left(-\frac{bs_m^\beta}{s_w} aJ^\alpha - \int_{aJ^\alpha}^J \mu(t) dt\right).$$

In this case the ESS seed mass is $bs_m^\beta \cdot aJ^\alpha$. So the model predicts the observed allometric relationship between adult body size and seed size, and is potentially testable in the field. Notice that this formulation leaves the possibility of a supplementary effect due to the length of the juvenile period.

So we have come full circle in concluding that juvenile period alone is unlikely to drive the noisy empirical seed size/body size correlation. Rather, the traditional idea, that large plants have seedlings that are more likely to gain significant seedling survival advantages by having large seeds, seems more likely to generate the observed empirical pattern. This would be because they live in environments with greater depletion of resources or because they provide a fitness advantage in more competitive situations. These ideas were implicit in the early life-history work of Salisbury (1942).

Alternative approaches and mechanisms

This is not the only approach predicting scaling of seed size with adult size. Venable (1992) provided a model predicting larger seed size with increasing plant size driven by increased sib competition, since larger plants make more seeds. This results in an adaptive reallocation from seed number to seed size as plant size, and hence resources available for reproduction, increase. In this model and the ones considered above, adult traits are assumed to be fixed, and to correlate with, or scale with seedling survival. Only seed size is allowed to evolve. In R&V we considered a very general model where both seed and adult sizes were allowed to evolve, and argued that correlations between seed and adult size required demographic rates to be correlated across the life cycle.

Recently Falster *et al.* (2008) have produced an interesting new model for the coordination of offspring and adult size. The model assumes that larger seeds have an initial establishment advantage, and that this initial size difference persists during growth such that plants derived from larger seeds have a competitive advantage later in life. In the derivation of the model, Falster *et al.* (2008) consider a single cohort of individuals and derive the critical plant weight W_T at which competition begins. While the introduction to this paper still perpetuates some of the ideas we have objected to in the italicized points above, the actual model does not rely on them. Also, it moves away from the idea that juvenile period is driving the correlation between seed size and adult size. The model is novel in that seed size fitness advantage is influenced by the plant weight at which competition begins, and this weight is influenced by various factors that depend on adult size, generating a mechanism for an evolutionary coordination of adult size and seed size. These adult-size dependent factors (reproductive investment and adult mortality) typically drop out of simpler ESS analyses, making seed size independent of adult size.

A similar result was given by Rees & Westoby (1997) who assumed that seed size provides a competitive advantage in a density-dependent model. In both this model and the more detailed Falster *et al.* model, increases in reproductive allocation (associated with plant size) increase density, which favours competitively superior larger seeds. In both models an allometric relationship between reproductive allocation and body size influences the predicted allometry of seed size with adult size. Both models can explain the different allometric slope for plants and mammals (see Supplementary Appendix S1). Larger plants are increasingly composed of dead wood. If reproductive allocation is related to living biomass, the allometric constant for reproductive allocation with total plant mass should be shallower than that of mammals. Also, both models predict a difference between interspecific and intraspecific seed size/adult size allometries, and, as predicted, seed size in nature varies less with plant size within- than among-species (see Supplementary Appendix S1).

The more detailed Falster *et al.* model incorporates a number of assumptions which may limit its applicability. It assumes that self thinning occurs in monospecific, even-aged cohorts that establish in gaps created by adult mortality. For annuals with synchronous germination it is straightforward to calculate W_T . While perennials may sometimes recruit in monospecific even-aged cohorts, their populations often have multiple-aged plants interacting during regeneration. For these it is not clear how to calculate W_T or indeed whether it can be done. For example, a new recruit entering a population which has already entered the competitive phase will experience competition immediately, even though it is at a size where there is supposed to be no competition. Multiple species also create problems for calculating W_T , even in single-age stands. The model also assumes that initial size differences persist through to maturity. This might occur, but given the enormous differences in growth between similar sized individuals, it is hard to see that small initial differences in seed size will influence

the competitive ability of individuals many months or years after recruitment occurs. Finally, many of the model's novel predictions arise as a consequence of assuming that W_T , and hence the duration of competition, are determined by the way in which increases in adult reproductive investment increase the density of competitors. This can be justified in a single-species setting, but in a more realistic multi-species setting this is unlikely to be true. Conventional models, such as those discussed above, may be more robust in this respect as they do not assume a direct link between reproductive investment and the duration of competition. Nevertheless, the model is an exciting development with a novel mechanism for linking the sizes of adults to that of their offspring, and its assumptions and predictions merit careful exploration.

The article by Nee *et al.* (2005) showed that apparent life-history invariants may arise as statistical artefacts. But it also provides the basis of a null model in which selection takes a back seat to constraint in explaining scaling. Start with the assumption that offspring size is selectively neutral. Then constrain offspring size to be greater than zero and less than, or equal to, adult size. Assigning offspring size randomly within this range (since offspring size is selectively neutral) results in an isometric relationship with adult size (a log–log slope of 1), mean offspring : adult size ratio of $1/2$ and high R^2 if the range of adult size is large. While offspring size is unlikely to be selectively neutral, it is edifying to explore how well such a null model reproduces observed offspring–adult size relations. The null model reproduces the observed pattern of mammalian offspring : adult ratio satisfactorily, although the observed exponent is slightly lower than 1 (in the 0.93–0.95 range, R&V) and, while offspring : adult ratios span the full range between 0 and 1, the distribution is not uniform (Savage *et al.* 2006). Plants seem to deviate from this model in at least three important ways. First, offspring size is seldom more than 0.01 as large as adult size, the allometric constant is much less than 1 (*c.* 0.5–0.7), and the distribution of δ is unimodal rather than uniform. Several aspects of plant biology may explain these deviations.

The low maximum seed size and allometric slope may be caused by the structural limitation of supporting large seeds on the twigs of the open branching network characteristic of most plants (Grubb *et al.* 2005). This argument depends on a relationship between seed size and twig size and a relationship between twig size and plant size. Increase of adult plant size across species is accomplished more by an increase in the number of modules (hence in the number of twigs and leaves) than by increasing the size of modules. Nonetheless, Cornelissen (1999) shows that there is a relationship ($R^2 = 0.76$) between maximum plant height and mean adult leaf area (leaf size) for Angiosperms which appears to have a strong upper boundary preventing large leaves from occurring on smaller plants. Corner's rules (Brouat *et al.* 1998) show an even stronger relationship between leaf area and the cross-sectional area of subtending twigs. Plant size and leaf function therefore can be inferred to set a limit on twig size. But since increasing plant size is associated with an increase in twig number as well as twig size, the twig size/plant size relationship is allometric

(size and number allometries add to one if size and number are subject to a common resource constraint, see Supplementary Appendix S1). Cornelissen goes on to show a triangular relationship between leaf size (which through Corner's rules we can use as a surrogate for twig size) and seed size: large leaf (twig) plants can produce small seeds, but small leaf (twig) plants cannot produce large seeds. This suggests a limit on seed size in small plants operating through the inability to produce large seeds on small twigs. It also suggests a way to derive the allometric constant for seed size vs. body size. Aarssen (2005) discusses twig size constraints as a reason (among others) for the less than isometric slope of seed size vs. plant size.

A synthetic view

So why do large plants have large seeds? First, they do not necessarily have them (e.g. *Sequoia sempervirens* has a seed mass of 0.0037 g). The pattern is a weak one. While very small plants never produce seeds as large as those of big seeded trees, plants of any size have seeds that vary approximately 400–650-fold between species. In terms of the fitness consequences of seed size, this is a huge interspecific range, independent of adult size. A strictly constraint approach to seed size evolution assumes selective neutrality of seed size, but boundary conditions on seed size determined by correlates of adult plant size, such as the size of twigs subtending seeds and fruits. Since there are known biological effects of seed size which are probably under selection, selection presumably modifies the position of species within any constraint envelope such that species are not uniformly distributed. For example, it might turn out that, while twig size/plant size relations set a triangular envelope within which seed size evolves, larger plants might tend to have more stressed seedlings, perhaps due to density effects, resulting in a portion of the triangle being more thinly populated.

We hope this exchange has enriched our understanding of the scaling of seed size both by cautioning against some misconceptions in the literature and by providing, along with Falster *et al.* (2008) a solid theoretical framework for considering the coordination of offspring and adult size.

Acknowledgements

Authors thank Lindsay Turnbull, Jessica Metcalf, Brad Murray, Ken Thompson, Peter Grubb, Gordon Fox, Amy Angert and Kathy Gerst for helpful discussions. Research support was provided by NERC grant NER/A/S/2002/00940 (MR) and NSF grants DEB 0717466, 0817121 (LTREB), DEB 0453781 and DEB 0717380 (DLV).

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Received 12 June 2008; accepted 10 October 2008

Handling Editor: Michael Hutchings

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Can the models explain the differences between intra- vs. interspecific allometry and plant vs. mammal allometry?

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