**Accessories dominate the costs of producing seed**

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[general comment: these are all at some level costs of sex -- at face value, a selfing or apomictic species would not need to produce any surplus ovules, plus would not need showy flowers -- accessory costs would be strictly fruit and seed-coat structures for successfully-provisioned seeds]

# Abstract

Despite the obvious importance of quantifying energy allocation to reproduction, relatively few complete estimates of reproductive investment (RE) exist across multiple species in a community. RE includes energy directly invested in seeds, energy invested in required non-seed tissues (termed fixed reproductive costs; including petals, pedicels, seed pods, and dispersal tissues), and energy invested in plant parts that fail to develop into seeds. To quantify the size of these pools and how they shifted across co-occurring species, we collected detailed RE measurements for a year from 14 perennial species in a recurrent-fire coastal heath community in eastern Australia. Total accessory costs, the proportion of RE not directly invested in provisioning the seed, were enormous, varying from 92% to 99.8% across the study species. While failed tissue costs accounted for the largest proportion of RE for most species, fixed reproductive costs were not negligible. From this follows that studies using seed or fruit production as measures of reproductive investment vastly underestimate RE. In addition, among individuals within and across species, RE and seed production were only weakly correlated likely due to stochastic processes that affect seed set. A quite accurate and easy to measure estimate of RE was obtained from a composite variable “bud count\*flower mass”.

Merging the predictions of the seed size-number trade-off and the trade-off between investment in pollen attraction versus seed provisioning tissues (from the parental optimist-pessimist literature), we predicted coordinated shifts in floral construction costs, seedset and seed size, reflecting alternate strategies to maximize fitness. As predicted, large-seeded species had low seed set (were parental optimists) and had relatively low pollen-attraction costs (relative to seed provisioning costs) while small-seeded species displayed the alternate suite of traits. This coordination occurs, because larger-seeded species produce relatively fewer seeds, and are therefore predicted to be more selective about the genotypes of embryos they provision, leading to lower seedset. This selectivity requires a greater excess of ovules, in turn selecting for a reduction in per-ovule pollen-attraction costs. Incorporating tissue construction costs in the seed size-number trade-off extends our understanding of the relatives sizes of floral and fruiting structures observed across angiosperms.

# Introduction

Plants allocate a sizeable proportion of their photosynthetic energy to reproduction (Obeso 2004; Hirayama *et al.* 2008; Thomas 2011; Wenk & Falster 2015), into seeds and also into the many other tissues associated with reproduction, termed accessory costs. Accessory costs include energy required to form a successful seed (e.g. flower petals, seed pod, and dispersal tissues) and energy lost via aborted buds, flowers and fruit. Previous studies show that for perennial species anywhere from 15% – 99% of total reproductive investment may go into accessory costs (Haig & Westoby 1988; Ashman 1994; Henery & Westoby 2001; Lord & Westoby 2006; Chen, Felker & Sun 2010). Since fruit set and seed set are generally below 50% in perennial species (Stephenson 1981; Wiens 1984; Sutherland 1986; Knight *et al.* 2005; Rosenheim *et al.* 2014), the cost of aborted tissues may be a substantial proportion of total accessory costs. Yet, despite being a significant energy sink in ecosystems, little is known about the allocation of energy among different reproductive tissues across the plant kingdom.

While plant species demonstrate an extraordinary diversity of reproductive structures and strategies, reproductive investment can be divided into broad functional categories that are consistent across species (Figure 1a). Defining such categories is a prerequisite to determining if species vary in the size of these reproductive tissue pools and asking if underlying trade-offs in energy allocation explain the observed variation. The total energy investment per seed matured are the *total reproductive costs per seed,* which can be divided into the investment in required parts, termed the *success costs* and the energy expenditure on flowers, fruit, and seeds that never form mature propagules, so-called *discarded tissue costs*. Both are calculated on a *per seed matured* basis. *Success costs* can be further divided into structures required for *pollen-attraction* (e.g. petals) versus structures developed post-pollination (e.g. seed pod, seed), hereafter termed *provisioning costs*. The provisioning component can be further split into investment in the seed itself (*propagule costs,* i.e. seed size) versus the dispersal and packaging tissues. The *discarded tissue costs* likewise be divided into energy invested prior to versus after pollination, here termed *pre-provisioning discarded costs* and *post-pollination aborted costs. Accessory costs*, high-lighted in red in Figure 1, *are the sum of discarded tissue costs, pollen-attraction costs, and packaging and dispersal costs.* Throughout the manuscript the “costs” indicates investment per seed matured, while “investment” refers to total dry weight invested in a structure.

There are multiple reasons to expect that both success costs and discarded tissue costs will be substantial. Investment in the success cost components, pollen-attraction costs, packaging and dispersal costs, and propagule costs, is undeniably beneficial for the successful formation and dispersal of a seed. Without showy petals insects would not be attracted to the stamens and stigma, without sepals the developing bud would not be protected, without a seed coat a seed would not be protected during dispersal, and without an attractive fruit, many seeds would not be dispersed. High discarded tissue costs (due to low seedset) occur in perennial plants for a diversity of reasons, some due to conditions beyond the plant’s control and others by evolutionary design to increase an individual’s fitness. They include pollen-limitation, pollen-ovule incompatibility, parental embryo abortion, resource limitation and also as a bet-hedging strategy to capitalize on stochastic variation in pollen availability, pollen quality, and resource availability to mature fertilized ovules (Bierzychudek 1981; Stephenson 1981; Sutherland 1986; Burd 1994, 2008; Ramsey 1997; Obeso 2004; Ashman *et al.* 2004; Knight *et al.* 2005; Holland & Chamberlain 2007; Rosenheim, Schreiber & Williams 2015).

Across species variation in the relative size of these energy pools should reflect underlying trade-offs, indicating different reproductive energy allocation strategies. The current data set allows us to take two established reproductive strategy trade-offs and expand upon their hypotheses. The first is the well-supported seed size-seed number trade-off and the second is the seed set-pollen-attraction cost trade-off described in the parental optimist-parental pessimist literature.

**Seed size – seed number trade-off:** Previous studies have shown that, to first order, plants, relative to their size, have a fixed amount of energy to invest in all reproductive materials (###). Moreover, they have a fixed energy budget to invest in seeds, materializing as the seed size - seed number trade-off: relative to their size, plants have a fixed amount of energy to invest in seeds. Plants can divide this pool of energy into many small seeds or fewer larger seeds, such that a log-log plot of seed size versus scaled seed count should have a slope of -1 (Figure 1b) (Smith & Fretwell 1974; Henery & Westoby 2001; Sadras 2007). Very small and very large seeds represent endpoints of a continuous life history strategy (Rees & Westoby 1997; Leishman 2001; Turnbull et al. 2004; Moles & Westoby 2006), with small-seeded species displaying superior colonization ability, while larger-seeded species have a greater likelihood of establishing and better competitive outcomes. In turn, since large-seeded species produce fewer seeds, they display a suite of traits to ensure that a greater proportion of their seeds successfully establish (Moles & Westoby 2006).

While well-supported by empirical data, the seed size-seed number trade-off does not account of investment in other *success costs* tissues, leading us to hypothesize two alternative trade-offs. First, we suggest plants, relative to their size, should invest a fixed amount of energy up to the point of pollination, depicted as a trade-off between pollen-attraction costs and the number of ovules that are displayed to pollinators (Figure 1b). Species with higher pollen-attraction costs will be able to produce fewer ovules. Second, we hypothesize that plants, again relative to their size, should display a trade-off between total success costs and seed count (Figure 1b). Both trade-offs should have a slope = -1, but the pollen-attraction costs – ovules at point of pollination trade-off should have a higher intercept, since seed set is <1.

**The pollen attraction-seed provisioning trade-off:** Haig & Westoby (1988) developed a conceptual model for the relative allocation of energy to different reproductive tissues, dividing the total energy investment per seed between the costs of attracting pollen versus the cost of provisioning pollinated ovules. Their simple model makes several predictions, including that plants 1) produce excess ovules and flowers to optimize seed production across a population and across time, 2) face a trade-off between pollen attraction and embryo provisioning, and 3) allocate just enough to pollen-attracting tissues to ensure pollination of the number of ovules they are able to provision *on average*. This initial model has since been extended to account for the proportion of energy invested in pollen attraction versus seed provisioning tissues to predict expected seed set across multiple species (Rosenheim *et al.* 2014, 2016; Burd 2016). These studies indicate that species with relatively low pollen-attraction costs (in their studies, defined as successful and discarded costs) should produce a greater excess of ovules, relative to what they are able to provision, epitomized as lower seedset.

This axis of variation accords with the parental optimist-parental pessimist strategy continuum (Mock & Forbes 1995; Burd 2008; Rosenheim *et al.* 2014). A parental optimist is defined as a species that overproduces pollinated ovules, relatively few of which mature in an average year due to limited resource supply. In contrast, species with proportionally higher pollen-attraction costs should display parental pessimism: an underproduction of ovules, with embryo number limiting seed production in many years, often as a result of pollen limitation.

Since parental optimists have lower seed production, logically they need to ensure that the seeds they mature are likely to germinate and establish. One mechanism to increase seed and seedling success is to ensure that the provisioned seeds are vigorous genotypes. One way plants can accomplish this outcome is by being selective about which pollen grains to use and which zygotes to provision, termed selective abortion and shown to be an important mechanism to increase plant fitness (Willson & Burley 1983; Sutherland 1986; Kozlowski & Stearns 1989; Guittian 1993; Melser & Klinkhamer 2001; Harder & Barrett 2006). A parent plant can of course only be selective about embryo provisioning if there are excess fertilized embryos – relative to the number the plant has energy to provision. The parent plant can exert stronger zygote selection if there is a larger pool of excess embryos. Indeed, we expect the ratio of ovules to seeds, defined here as *choosiness* (the inverse of *seedset*), to be highest in parental optimists, those species with relatively lower pollen-attraction costs (Figure 1c). A plant can invest more energy, relative to its size, in developing each ovule to maturity and be less selective about which ovules to provision to mature seeds or invest proportionally less in each ovule (and associated floral tissues), produce a larger number of ovules, and then display greater choosiness in which ovules to provision. (Note, that *choosiness* as defined here, encompasses a number of processes that occur between ovule maturation and the onset of zygote provisioning, including pollen-limitation, pollen-ovule incompatibility, and selective embryo abortion. It is illogical that pollen-limitation or pollen-ovule incompatibility – on a proportional basis – would be higher in plants with a relatively higher ovule count, such that selective embryo abortion is the most likely explanation for low seedset among parental optimists.)

These two trade-offs embody different reproductive tissue measures, but both represent the same reproductive strategy continuum: a species with low seed count and high ovule count, relative to plant size, is a large-seeded species that is choosy (has low seedset) and expends relatively less energy maturing each ovule (pollen-attraction cost). Two previous studies have indeed observed that big-seeded species should have lower seedset, attributed by the authors to these species displaying greater selectivity since they are investing more energy in each offspring and maturing fewer seeds (Lord & Westoby 2012). Incorporating energy allocation into pollen-attraction versus provisioning tissues, we furthermore predict that larger seeded species will spend a decreasing proportion of their success costs on pollen-attraction costs, as they are expected to produce a large number of inexpensive ovules (Figure 1d). In addition, in large-seeded species total pre-provisioning investment will be predominately into discarded tissues, as most of the ovules produced will be shed or aborted before the onset of provisioning (Figure 1e). In contrast, it is predicted that once large-seeded species begin provisioning a zygote they are more likely to successfully create a viable seed, such that the proportion of total provisioning investment allocated to successful tissues (provisioning costs) versus discarded tissues should be higher in large-seeded species (Figure 1e). These outcomes also ### themselves ###

In particular, we address the following questions:

1. How much do individual plants invest in different reproductive tissues and does this differ among species?
2. Do the hypothesized pollen attraction costs-ovules available for pollination and success costs-seed count trade-offs exist?
3. Is there a trade-off between choosiness and pollen-attraction costs?
4. Within a species, do total accessory costs or particular accessory cost components shift with plant size, age, or reproductive investment?

The dataset we use to address these questions is, to our knowledge, the most complete dataset that simultaneously measured plant size, vegetative investment, reproductive investment, seed investment, seed count, and seed mass across multiple species at different size and ages in a native community. In a recurrent-fire coastal heath community, we studied fourteen species differing in seed size, lifespan, and maximum height. Individuals were sampled at different ages across a fire-created chronosequence, from 3 months to 30 years. We assessed total reproductive investment every 3 weeks for a year, to determine total investment both in tissues that developed into mature seeds and in tissues that were aborted during the developmental trajectory. This detailed accounting allows us to investigate correlates of reproductive investment across and within species.

Finally, given the complexity of measuring all the components of reproductive investment, we assess how well different surrogate measures potentially predict total reproductive investment? For this purpose we consider total seed weight, total fruit weight, and total investment to the point of pollination.

# Methods

## Study system

The study was carried out in Kuring’gai National Park, just to the northeast of Sydney, Australia. The sandstone ridges throughout the park host a coast heath community, whose dynamics have been governed by fire for at least 6000 years (Kodela & Dodson 1988). Fire regimes under traditional aboriginal management are unknown, but current New South Wales National Parks and Wildlife Service (NSW NPWS) management practises seek to achieve an average interval between 7-30 years to maintain the current floristic diversity (NSW Office of the Environment 2006). The community includes perennial species that re-sprout following fire and also obligate seeders, species that are killed by fire and re-establish from seed. The obligate seeders included in this study germinate within a year of the fire and often after the next rain. Since the fire history of the park is well documented, the age of obligate seeders at a site can be estimated. In total, we selected 14 obligate-seeder, woody perennials that are common in the community, with asymptotic heights ranging from 0.5 m – 5 m. They were *Banksia ericifolia* (Proteaceae), *Boronia ledifolia* (Rutaceae), *Conospermum ericifolium* (Proteaceae), *Epacris microphylla* (Ericaceae), *Grevillea buxifolia* (Proteaceae), *Grevillea speciosa* (Proteaceae), *Hakea teretifolia* (Proteaceae), *Hemigenia purpurea* (Lamiaceae), *Leucopogon esquamatus* (Ericaceae), *Persoonia lanceolata* (Proteaceae), *Petrophile pulchella* (Proteaceae), *Phyllota phylicoides* (Fabaceae), *Pimelea linifolia* (Thymelaeaceae), *Pultenaea tuberculata* (Fabaceae). The family Myrtaceae is well represented in the community, but absent from the study, as all common species in this family re-sprout following fire. All sites were chosen to have minimal *Eucalyptus* cover, such that *Banksia ericifolia*, *Hakea teretifolia*, and *Allocasuarina distyla* (not included in our study because it is dioecious) would be the dominant canopy species late in succession, at heights of 3-5 m.

## Field measurements

The study was conducted over a single year, with the initial plant measurements and subsequent harvest conducted during the late autumn and early winter, the period of minimal vegetative growth in this plant community, and repeat visits made throughout the year to record reproductive activity. Individuals were sampled at different ages across a fire-created chronosequence, from 3 months to 30 years. Site ages were estimated from fire records maintained by NSW NPWS. At the conclusion of the study, the approximate ages of the individuals on the six sites were: 1.4, 2.4, 5, 7, 9 and 31 years. Plants were tagged during May-June 2012 and harvested during May-June 2013, with a given individual tagged and harvested within 2 weeks of the same calendar date. Only one species, *Persoonia lanceolata*, displayed any shoot extension during these months. These months are similarly a period of minimal reproductive activity – only *Banksia ericifolia*, *Grevillea speciosa,* and (occasionally) *Hemigenia purpurea* flowered during this period – although a number of species had immature fruit from the previous year (*Persoonia lanceolata*) or small buds that would open in the subsequent year (*Boronia ledifolia*, *Conospermum ericifolium*, *Epacris microphylla*, *Grevillea buxifolia*, *Leucopogon esquamatus*).

Seven healthy individuals of each species were selected at each site (and thus age). At the beginning of the study year, the basal diameter was recorded approximately 10 mm above the base to avoid the basal swelling. At the end of the study year, the diameter was remeasured at the same location. The plants were then harvested at ground level and oven dried at 60ºC for at least 1 week. Leaves and stems were separated and weighed.

Flowering parts on all individuals were recorded during repeat censuses, every four weeks during cooler months and every three weeks during spring and summer. At each census, all flowering parts were counted, including buds (by size class), flowers, young fruit, and mature fruit. For some species the size of immature and mature fruit and cones was also measured, as the final size of the structures was quite variable. The exact flowering parts considered varied considerably by species due to their diverse floral structures. Flowcharts detailing what flower parts were included for each species are provided in the Supplementary Material. The Supplementary Material also includes a table that indicates how each flowering part was measured for each species. Each of the flower parts was independently collected from multiple untagged individuals in the community to determine its dry weight.

## Calculating total reproductive effort

Total reproductive effort (RE) is the sum of investment in all the different flowering parts during the year, tabulated on a weight basis. Seed counts record the total number of propagules produced during the year. Per seed energy expenditure is calculated by dividing RE by seed count, designated as a “cost” throughout the manuscript and presented as mg dry weight per seed matured. For each species, the sum of the weights of all reproductive parts required for the successful creation and provisioning of a single propagule is termed the “fixed reproductive costs” (see Appendix B for a list of parts). Fixed reproductive costs were divided into pollen attraction costs, seed provisioning costs, and the weight of the endosperm and embryo itself. We chose to designate the endosperm and embryo as the primary reproductive unit, for it provides a consistent comparison of tissue weights across species. It is hereafter referred to as “seed weight”. In contrast, the propagule includes the seed coat and additional dispersal tissues in some species, but not others. In addition to the fixed reproductive costs, were the “costs of failure”, the weight of reproductive material that was aborted before progressing to a mature seed, expressed on a per seed matured basis. All calculations were made on an individual basis, although the weights of many plant parts are based on species level measurements.

Mention that the species included are all recorded [?] as producing a consistent number of ovules per flower.

Details: A document, for the supplementary materials, describing the methods should be out next priority.

Statistical methodsFor slope tests, are you using regression or SMATR? Should be the latter. All using SMART, sma, method=”OLS”

# Results

## Accessory costs and accessory cost components

Of the 599 plants included in this study, 223 individuals produced at least one seed during the year. Across these individuals, on average 91% of reproductive investment went to accessory tissues rather than to propagules, rising to 96% if only embryo and endosperm were treated as direct investment in offspring, with seed coats and dispersal structures attributed to accessory costs. Hereafter, all results report results for the “embryo and endosperm” component, designating them as “seed size” or “seed weight”. Across species, accessory costs (versus seed weight) ranged from a low of 91.9% for *Pimelea linifolia* to a high of 99.8% for *Hakea teretifolia* (Table 1).

Total accessory costs can be divided broadly into failed tissue costs (the weight of all aborted parts, including mature flowers that fail to set seed) versus fixed reproductive costs (seed weight plus the total per ovule cost of required floral parts, both pre- and post-pollination). Only the two cone-bearing species, *Banksia ericifolia* and *Petrophile pulchella* had fixed reproductive costs that were higher than failed tissue costs (Table 1). Three species, *Hakea teretifolia*, *Phyllota phylicoides*, and *Pultenaea tuberculata* spent more than 90% of their reproductive investment on failed tissues (Table 1). For most species, these failed tissues were predominantly pre-provisioning, with aborted seeds and fruit a minor component of failed tissue costs (Supplementary Material). Note that fruit that abort after pollination but before provisioning are recorded as shed flowers, such that pollen-attraction costs (pre-provisioning) includes the costs associated with ovules that are aborted both due to lack of pollination and due to early maternal selection.

Total fixed reproductive costs are divided into mass of parts formed up to the point of pollination (on a per ovule basis; termed pollen-attraction costs) and the mass of the seed, packaging, and dispersal structures (on a per seed basis; termed provisioning costs). The relative costs of these components shifted markedly across species (Table 1). Four species, *Epacris microphylla, Hemigenia pupurea, Pimelea linifolia, and Pultanaea tuberculata* had pollen-attraction costs that were greater than 50% of total fixed reproductive costs, while 5 species had pollen-attraction costs that were less than 10% of total fixed reproductive costs (Table 1). The remaining species fall out in-between. The proportion of energy invested in provisioning tissues (including the seed itself) ranged from a low of 0.36 (for both *Epacris microphylla and Pimelea linifolia*) to a high of 0.99 (*Banksia ericifolia*) (Table 1). The maximum proportions of RE any species invested directly in seeds were *Pimelea linifolia* (6.88%) and *Hemigenia pupurea* (4.21%).

## Correlations between seed size and seed set

Figure 2a shows bud and seed counts, scaled to the plant’s leaf area, plotted against seed size. Larger-seeded species produced disproportionately many buds, such that the slope of the relationship between number of buds versus seed size was close to -1 (slope=-0.971±0.071, pslope ≠ -1 =0.4491). However, because larger-seeded species aborted a disproportionately large number of buds and the slope of the regression between scaled seed count versus seed size is much steeper than -1 (slope=-1.397±0.094, pslope ≠ -1 <0.00001). The outcome of this pattern is that seed size was also significantly correlated with seedset: species with larger seeds had lower seedset (Figure 2b, r2=0.56, p=0.0022). There was also a significant negative correlation between pollen-attraction costs and seedset (r2=0.41, p=0.013).

## Correlations between seed size and accessory costs

Both total accessory costs and all accessory cost components were strongly correlated with seed size, but the slopes of the relationships were notably different (Table 2). Total accessory costs per seed, and the two main divisions of total accessory costs, total fixed reproductive costs and failed tissue costs, all increased slightly steeper than isometrically with species’ mean seed size (Table 2). However, the two components of total fixed reproductive costs deviated much further from 1:1 scaling with seed size. Pollen-attraction costs had a slope significantly < 1, indicating that larger-seeded species invested proportionally less in pollen-attraction tissues (Table 2, Figure 2c). In contrast, provisioning costs increased more rapidly than seed size, with a slope significantly > 1 – and also significantly more steeply than fixed reproductive costs (Table 2, Figure 2d). The two components of failed tissue costs, failed pollen-attraction costs and failed provisioning costs, both scaled slightly steeper than isometrically with seed size (Table 2).

## Shifts in accessory costs with plant size, age, or reproductive effort

None of these species demonstrated a decrease in per seed accessory costs with increasing plant size or RE, and only 3 species showed a decrease in per seed accessory costs with age. With only 3/42 tests significant (Supplementary Material), these may represent little more than chance.

## Correlates with total reproductive investment

Of the 599 plants included in this study, 357 individuals produced buds and 223 individuals produced mature seeds. Even among the individuals that produced seeds, propagule investment was only rather loosely correlated with total reproductive investment, both within and across species (Tables 3, Supplementary Material respectively). All but one species showed a significant correlation between the two metrics, but only two species displayed an r2 above 0.80 and only half the species had an r2 above 0.70. Furthermore, the slopes and intercepts of the relationship differed across species with the result that the correlation between reproductive investment and propagule investment across individuals of all species had an r2 of just 0.52 (Figure 3a, Table 3).

To assess what approximation of reproductive investment was the best alternative to measuring total reproductive investment, we regressed additional investment categories against total reproductive investment. Measures that included only investment in tissues associated with the production of mature seeds, were inferior predictors of total reproductive investment compared to measures that included investment in failed tissues (Table 3). In particular, note that the correlation between investment in all failed tissues versus all reproductive tissues was 0.94, while the correlation between investment in all successful tissues (fixed reproductive costs\*seed count) versus all reproductive tissues was just 0.71. Investment in failed tissues is a better predictor for two reasons. First, because failed tissues accounted for 81% of total reproductive investment; and second, because energy investment into buds and flowers was more predictable, while further filtering processes occur before buds become mature seeds. A composite metric, the count of buds initiated \* average flower mass, when regressed against total reproductive investment, had an r2 of 0.93, making it nearly as strong a predictor of total reproductive investment as failed tissue investment. This composite metric has the merits that it would be relatively easy to measure on large numbers of plants and that it effectively combines both the within and across species variation (Figure 3b, Table 3, Supplementary Material).

# Discussion

There were three key outcomes from this study. First, these long-lived perennial plants expended an astounding proportion of reproductive energy on accessory costs. Investment in seed dry mass represented a quite modest proportion of total reproductive investment (RE) for the 14 perennial species included in this study, with just 1-8% of RE going to seeds versus other reproductive tissues (Table 1). Even the individual with the lowest accessory costs invested just 15% of its RE into the seed itself. Second, larger-seeded species had lower seedset, as expected of species dependent on having a higher proportion of seeds successfully establish. We also confirmed the previously reported trend (Rosenheim *et al.* 2014) that species with lower seedset, those on the *parental* *optimist* end of the optimist-pessimist spectrum, had proportionally costlier provisioning tissues relative to pollen attraction tissues. Combining these two lines of theory, we can show that the *parental optimists* were, as predicted, the large-seeded species: part of the big seed-size, low seedset strategy is to invest proportionally less in flower construction to the point of pollination and proportionally more in provisioning tissues. The third major result from these data was that for perennial species with low seedset, total reproductive investment was best predicted by energy expenditure in buds and flowers, not by investment in seeds or fruit.

## Accessory costs are large

All species in this study allocated an enormous proportion of RE to accessory costs, both required accessory costs and failed tissues (Table 1). Many estimates of plant energy investment in reproduction do not account for total accessory costs, leading to potentially misleading results (reviewed in Obeso 2002; Lord & Westoby 2006; Rosenheim et al. 2014; Wenk & Falster 2015). For example, studies seeking to estimate the cost of reproduction, may reach erroneous conclusions if they record only shifts in seed production year upon year, ignoring investment in accessory tissues (Obeso 2002). Reproductive allocation, the proportion of energy spent on reproduction, instead of on growing and replacing vegetative tissue (Ashman 1994; Bazzaz, Ackerly & Reekie 2000; Wenk & Falster 2015), will also be substantially underestimated, leading to overestimates of the proportion of energy (and absolute amount of energy) available for vegetative growth. The current study indicates accurate calculations of RE must tabulate all pools of accessory tissues. Indeed, across the species studied, both failed tissue costs and various seed cost components (see Figure 1 for definitions) contributed to the high accessory costs.

For 12 of the 14 study species, more than 60% of RE was invested in failed tissues, those tissues that are aborted without contributing directly to the formation of successful seeds (Table 1). Only in *Banksia ericifolia* and *Petrophile pulchella,* the two species with a high energy investment in woody cones,was a smaller proportion of RE attributable to failed tissues. The majority of failed tissue costs was due to buds and flowers that were aborted before seed provisioning became substantial (Supplementary Material). In this study, seed set ranged from <1% for *Hakea teretifolia* to 22% for *Hemigenia* purpurea, within the range of perennials worldwide, and importantly, showing that these plants produced a vast number of ovules they subsequently aborted. Indeed, a large energy investment in failed tissues is true for all species that display low seed or fruit sets (Stephenson 1981; Sutherland 1986; Ramirez & Berry 1997; Knight *et al.* 2005) and in this study as well there was a strong negative correlation between species average seedset and failed tissue costs (r2=0.64, p = 0.0010 when excluding the species producing the largest cones, *Banksia ericifolia*). Explanations for the abortion of a large number of ovules include environmental stochasticity, pollen-limitation, poor pollen-tube growth, pollen incompatibility, selective abortion, and resource limitation (Ashman *et al.* 2004; Knight *et al.* 2005; Ruane, Rotzin & Congleton 2014).

The complement to the failed tissue costs, the success-associated costs, termed fixed reproductive costs, are those required for the formation of a seed, and include pollen attraction costs and seed provisioning costs, the latter category including both packaging and dispersal costs, and the seed itself (Figure 1, Table 1). Across the study species, the proportion of RE attributable to the seed ranged from a low of 0.2% of RE for *Hakea teretifolia* to a high of 6.9% of RE for *Pimelea linifolia*. For all species, energy invested in other fixed reproductive costs components represented a higher proportion of RE and included tissues such as showy petals, a fleshy fruit, a tall pedicel, or a large fire-resistant cone. These are tissues that must be produced to mature each seed and their exact structures have presumably evolved to optimize seed production, but these data show their cost to plants is not negligible.

The study species have quite diverse floral and fruiting structures, resulting in disparate tissues accounting for most of the seed cost expenditure. For three species (*Epacris microphylla, Hemigenia purpurea,* and *Pimelea linifolia*), the costs of producing pollen-attraction tissues (on flowers that form mature seeds) was 15-20% of total RE, while for other species it was substantially less (Table 1). The two cone-producing species, *Banksia ericifolia* and *Petrophile pulchella,* had the costliest packaging and dispersal tissues, spending 61.2% and 36.6% of total RE, respectively. Other species also had high packaging and dispersal expenditure due to structures including sturdy fruiting stalks (*Conospermum ericifolium*), fleshy fruit (*Persoonia lanceolata*), and woody seedpods (*Grevillea* species). In the following section we explore whether the relative investment in different accessory cost pools shifted predictably with two species’ traits, seed size and seed set.

## Seed size shifts across the parental optimist-parental pessimist axis

In the introduction we identified a collection of reproductive traits that are expected to show coordinated shifts, representing alternate strategies to optimize seed production, and hence fitness (Figures 1b-1d). Parental optimists, those species that produce an overabundance of ovules relative to their ability to provision them (manifested as low seedset) were, as hypothesized, the bigger-seeded species and also the species that invested a great proportion of their fixed reproductive costs in seed provisioning (versus pollen attraction) (Figure 2).

Across angiosperms, total costs per seed and accessory costs scale isometrically with seed size (Henery & Westoby 2001; Moles *et al.* 2003; Lord & Westoby 2006, 2012; Chen *et al.* 2010), a trend nearly observed in this data set (Table 2). Indeed, given the enormous diversity of floral forms and the known adaptive function of many floral parts (Harder & Barrett 2006; Harder & Johnson 2009), it is an excellent affirmation of theories on optimal energy allocation that the total costs scale approximately 1:1 with seed size (Rosenheim *et al.* 2010; Mironchenko & Kozłowski 2014). If they did not, there should be strong selection against seed sizes with higher accessory costs.

The complement to accessory costs is direct investment in the seed, and the near-isometric relationship between accessory costs and seed size, mean that relative to plant size, plants also have a fixed amount of energy to invest in seeds. This can be visualized as the seed size-seed number trade-off: Plants can invest this energy pool into many small seeds or proportionally fewer heavier ones (Smith & Fretwell 1974; Rees & Westoby 1997; Moles & Westoby 2006). Since large-seeded species have lower seed output, they are under stronger selection to produce seeds that will successfully establish (Lord & Westoby 2006). Simply being larger is part of their strategy (Moles & Westoby 2006), but ensuring their seeds have vigorous genotypes is another strategy dimension and one achieved through greater choosiness of the most vigorous embryos shortly after pollination (Willson & Burley 1983; Sutherland 1986; Guittian 1993). Choosiness can only occur is there is a surplus of ovules and so we predicted that larger-seeded species would have a proportionally larger number of surplus ovules (Figure 1b, c) and hence a lower seedset. This trend was indeed borne out by the data (Figure 2).

Species with low seed set are also termed parental optimists: they produce excess pollinated ovules, relative to the seeds they can provision in an average year, because they are always optimistic that the year will be better than average. Due to the large number of ovules they produce, they are selected to reduce their pollen-attraction costs (Figure 1a) (Haig & Westoby 1988; Schreiber *et al.* 2015; Rosenheim *et al.* 2015). Indeed, in this data set, there exists an ovule count-pollen attraction costs trade-off: Relative to plant size, all species invest the same amount of energy in pollen-attraction costs (Table 2). This energy can be divided into more lower-cost ovules or fewer costlier ovules (r2=0.86, slope= -1.137, pslope ≠ -1 =0.3432). The large-seeded species still have, in absolute terms, higher pollen attraction costs and lower ovule counts, but relative to the seed count-seed size trade-off, they produce relatively more, cheaper ovules (Supplementary Material). For the parental-optimists, the benefits of having excess ovules pollinated is that they can be more selective in terms of pollen receipt (Zimmerman & Pyke 1988) and which zygotes to provision (Willson & Burley 1983; Sutherland 1986; Guittian 1993).

This trade-off is also summarized by the less-than-isometric slope between required pollen-attraction tissues and seed size, indicating that, pollen-attraction tissues are cheaper for larger-seeded species to construct. In contrast, the greater-than-isometric slope between provisioning costs and seed size indicates that larger-seeded species invest disproportionately in provisioning tissues (Table 2, Figure 2), in agreement with Lord & Westoby’s results (2006, 2012, but see Chen *et al.* 2010). This is expected, since larger seeds tend to have biotic dispersal agents, and animal-dispersed species allocate a greater proportion of their reproductive energy to packaging and dispersal materials (Hughes *et al.* 1994; Moles *et al.* 2005; Eriksson 2008).

Not addressed by this dataset, are other known factors that undoubtedly also contribute to low seedset in this system, including pollen-limitation (Burd 2008, 2016) and environmental stochasticity. Insufficient pollen receipt may certainly be contributing to the patterns observed in this community, but given recent theoretical treatments that suggest pollen-limitation should be more severe among parental-pessimists (Rosenheim *et al.* 2014, 2016), it is unlikely the observed trend of lower seedset among the parental-optimists is primarily attributable to pollen-limitation. Environmental stochasticity, both in terms of pollen receipt and resources to provision embryos, also select for overproduction of embryos in parental optimists (Haig & Westoby 1988; Rosenheim *et al.* 2014). Indeed the tendency towards over- (or under-) production of ovules among parental optimists (or pessimists) will be exacerbated by environmental stochasticity, because plants will invest more heavily in the cheaper of the tissue categories (Rosenheim *et al.* 2010, 2014). Indeed, it is from the environmental stochasticity in resource supply that “parental optimists” have their name: They over-produce ovules because they are optimistic about resource supply and the number of ovules they will be able to mature and therefore have additional ovules that can be matured when sufficient resources are available (Mock & Forbes 1995; Burd *et al.* 2009; Schreiber *et al.* 2015; Rosenheim *et al.* 2015).

## Shifts in accessory costs with plant size and age

An additional motivation for this study was to determine if accessory costs shifted with plant age, size or RE. The theoretical literature suggests that for plants to increase their allocation to reproduction (versus growth) as they grow and age, plants must realize some compounding benefit (Myers & Doyle 1983; Sibly, Calow & Nichols 1985; Reekie & Bazzaz 1987a; Kozlowski 1992). Increasing mortality with age and concurrent decreases in future reproductive value, is one mechanism that can increase reproductive allocation (RA) in older plants. Decreasing accessory costs, and hence more efficient seed production, with increasing RA is another obvious compounding benefit. If, for instance, accessory costs declined with RE, plants should be selected to have fewer, larger reproductive episodes (Kelly 1994; Kelly & Sork 2002) or delay reproduction until they are larger and can invest more energy in reproduction (Cole 1954; Wenk & Falster 2015). This pattern was not observed in this dataset. Across individuals within a species, total accessory costs and accessory cost components did not shift consistently with plant size, age, or total reproductive investment (Supplementary Material). The consistent lack of shift in per seed accessory costs (or seedset, data not shown) with RE (or bud count, data not shown) is notable. There is a large literature on expected and observed trends in pollination and seedset with the size of the floral display, with quite disparate patterns, but we had not anticipated a flat relationship for 13 of 14 species (Supplementary Material). In conclusion, for many species, the sample sizes of the current data set are large and for most species we sampled across their entire age range, such that if a shift in accessory costs (or accessory cost components) existed with plant size, age, or RE it should have been detected in this data.

## Estimating reproductive effort

Realistic estimates of RE are essential for many research questions: plant functional growth models require estimates of the proportion of photosynthetic energy that is allocated to growth versus reproduction (Fisher *et al.* 2010; Falster *et al.* 2011; Scheiter, Langan & Higgins 2013), while demographic models may need estimates of seed production for a given RE (Garcia & Ehrlen 2002; Miller *et al.* 2012). The current study – and others – have shown that plants are allocating energy to many different reproductive tissues, with a notably small proportion going to seeds. However, the detailed measurements required to account for all reproductive energy expenditure are not practical for many research projects and pointing researchers to the best rapidly-obtainable estimates of total RE would be beneficial to many.

Total RE scaled isometrically with seed size, indicating that total RE, *on a species level*, could be broadly estimated by knowing seed size (r2 = 0.52 (*p = 0.0035*), increasing to r2 = 0.67 (*p = 0.0007*) if *Epacris microphylla*, with very small seeds,is omitted). Total plant weight was similarly strongly correlated with seed size *on a species level* (r2 = 0.57, *p = 0.0017*). These relationships simply show that larger-seeded species were bigger and therefore had more energy going to reproduction. However, seed size cannot provide an estimate of RE for individual plants in a population

At the individual level, total seed investment (seed count \* seed mass) and fruit investment (seed count \* fruit mass) were poor predictors of RE (Table 3), with r2=0.52 and r2=0.36, respectively, for regressions across individuals of all species. Even within species, knowing seed investment provided only a mediocre total RE, with only 8 of the 14 species having an r2>0.70 and one species not even displaying a significant correlation across individuals (Supplementary Material). In contrast, all investment in failed tissues, primarily representing investment in aborted flowers and buds, and our artificial composite measure, “total bud count \* average flower mass at the time of pollination”, provided excellent estimates of total RE (r2=0.94 and r2=0.93 respectively for regressions across all individuals; Table 3). While total failed tissue investment is not a “quick measure”, requiring repeat visits to the field and tedious accounting, the composite measure would work well for species where most of their buds are visible at a single point in time. Doing a single bud count and determining flower weight for the species would be a manageable prospect. These results conversely demonstrate that if your research question requires seed investment or seed count as an output, estimates of RE will not accurately predict seed production. Instead, and in contrast to many herbaceous species (Shipley & Dion 1992), this is a measure that must be measured at the individual level for perennial species with relatively low seedset.

The explanation for the poor correlation between seed investment and RE is clear: most of these species have relatively low seedset (Table 1) and moreover, seed set is quite variable across individuals at a single site and across species (Figure 3). Therefore, although the number of initiated buds is well-predicted by plant size (for most species) and is in turn tightly correlated with total reproductive investment (for all species), the unpredictability of seedset and overall low seedset means that investment in seeds, at the individual level, cannot be predicted by any easy-to-measure metrics. Many stochastic processes, from pollinator activity to pollen compatibility to resource availability lie between bud production and seed production (Herrera *et al.* 1998; Wesselingh 2007; Gómez 2008). These processes lead to both individual and inter-annual variation in seed production (Copland & Whelan 1989; Mitchell 1997; Herrera *et al.* 1998).

## Considerations

To reach meaningful conclusions about the strength of trade-offs between total accessory costs or particular accessory cost pools and seed size, seed set or any other trait, accurate measurements of total reproductive investment is essential. Our accounting scheme is very good, but of course imperfect. The largest source of error is that we have not measured nectar production, despite knowing that several of the species (in particular *Banksia ericifolia*, *Hakea teretifolia* andboth *Grevillea* species) produce abundant nectar (Pyke 1983; Pyke, O’Connor & Recher 1993; Lloyd, Ayre & Whelan 2002). Very rough back of the envelope calculations, based on studies of closely related species in nearby communities, indicate nectar production increases total reproductive investment by ~20% for *Grevillea speciosa*, 10% for *Hakea teretifolia*, and well under 5% for the other two species, increasing pollen-attraction costs relative to provisioning costs. These seemingly large energy expenditures, segue to our next consideration: Is dry weight the best measure of energy expenditure, especially in a community growing on soils known to be very low in P (Beadle 1968)? Previous studies indicate that nutrient concentrations may better estimate energy allocation choices (Reekie & Bazzaz 1987b; Ashman 1994; Rosenheim *et al.* 2014), but also that all currencies yield similar results. It is however, possible that in a P-limited community, it is less “costly” to produce copious quantities of nectar, for carbon is not limiting. This is a direction for future investigations. A final consideration, is how to choose which tissues to include as “reproductive tissues”, since some green reproductive tissues are known to photosynthesize (Cohen 1976; Reekie & Bazzaz 1987a; Wesselingh 2007). Since the net photosynthetic benefit of green reproductive tissues was unknown in this study and likely varied enormously across species, tissues and time, we adopted the parsimonious approach of considering all plant parts produced solely for the benefit of reproduction as components of reproductive investment.

The coastal heath community in eastern Australia has been well studied, both as a focal point for data collection on trait ecology and because of a general interest in the family Proteaceae, a dominant in this and many nearby communities. Indeed, 7 of the 14 species in this study are in Proteaceae, a family known to have particularly low fruit set (Hermanutz *et al.* 1998) (###) and to produce large woody fruits designed to allow seeds to withstand the frequent fires and then germinate following fire. Five species of *Grevillea* studied in communities nearby had fruit set between 1.5-9.6% (Hermanutz *et al.* 1998), similar to the seedset of the two species growing at our study site (Table 1). *Grevillea* species tend not to be self-incompatible, with the low fruit set attributed to pollen limitation and flower and fruit predation. *Banksia ericifolia*, *Hakea teretifolia*, and *Petrophile pulchella* all have fire-resistant fruits, and *Banksia* and *Hakea* have the largest seeds and greatest packaging and dispersal investment among the species in this study. Also of interest, although none of the species included in the study are explicitly masting species, the two cone-producing species, *Banksia* and *Petrophile*, do not form seeds each year (pers. obs.). This is shown at the population level by the large number of reproductively mature individuals that do not produce any seeds – or sometimes even any buds – in a given year. As has been shown in other species of *Banksia* (Copland & Whelan 1989), the inter-annual variability in seed production for these species may be due to resource limitation in the year following seed production.

## Conclusions

In summary, the correlations observed in our study indicate that seed size, ovule production versus seed production, and the magnitude of specific accessory cost components are coordinated across species. While a plant’s accessory costs may be startlingly large at first glance, one must assume their allocation of energy to different tissues represents an evolved strategy to maximize fitness. Identifying trade-offs between specific energy allocation choices – and then determining that energy allocation within this community matches the predicted patterns – provides a framework for understanding coordinated responses for seed size, seedset, and allocation to pollen-attraction versus seed provisioning tissues. Just as species have long been shown to follow a seed size-seed number trade-off, so do all species have the same amount of energy (relative to their leaf area) to invest in ovules, leading to a trade-off between the cost pollen-attraction tissues and ovule count. Large-seeded, low seedset species have proportionally less costly pollen-attraction tissues and produce a proportionally larger excess of ovules relative to, on average, the seeds they are able to provision.

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