**Accessories dominate the costs of producing seed**

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# Abstract

accessory costs are BIG

in failed or surplus ovules more so than in costs of success

one consequence is that seed output radically underestimates RE and is only weakly correlated

prodn of surplus ovules is tied up with overall strategy, and correlates with propagule size

[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]

# Introduction

Plants allocate a sizeable proportion of their photosynthetic energy to reproduction (refs? including Wenk & Falster, 2016), including to 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 (see Table 1 for summary of terms). Previous studies show that for perennial species anywhere from 15% – 99% of total reproductive investment may go into accessory costs (Haig & Westoby 1988; Henery & Westoby 2001; Lord & Westoby 2006). Since fruit set and seed set is generally below 50% in perennial species (Stephenson 1981; Sutherland 1986; Knight *et al.* 2005; Rosenheim *et al.* 2014), the cost of aborted tissues may be substantial proportion of total accessory costs. Yet, despite being a significant energy sink in ecosystems, with the exception of a few well-studied species (refs), 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 categories (Figure 1). The total energy investment in required parts (per seed matured) is termed the *seed costs*, and these can be further divided into structures required for attracting pollen (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 versus the dispersal and packaging tissues. On top of required seed costs per seed matured are the so-called *costs of failure*,the energy expenditure on flowers, fruit, and seeds that never form mature propagules, again calculated on a *per seed matured* basis. Low seed to ovule ratios (seedset), and concurrently high costs of failure, occur in perennial plants for a diversity of reasons, including pollen-limitation, pollen-ovule incompatibility, 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).

There are multiple reasons to expect that investments into these different types of accessory cost will not only be substantial, but also that the relative amounts might differ during ontogeny and among species. Evolutionary arguments would suggest plants evolve to optimize the amount of accessory costs per successful seed and indeed, across angiosperm species, total per seed accessory costs have been shown to scale approximately isometrically with seed size (Henery & Westoby 2001; Moles, Warton & Westoby 2003; Lord & Westoby 2006, 2012; Chen, Felker & Sun 2010). Some investment 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 a tasty fruit, many seeds would not be dispersed. At the same time, there are surely diminishing returns in the benefits accrued through greater investment in accessory costs, especially given that energy invested in accessory costs is energy not funnelled directly to seed production. There will therefore be an optimal level of accessory investment per seed. Moreover, this optimal investment is likely to differ among species, depending on their life history strategies and most specifically their interactions with pollinators and dispersal agents. This notion of an optimal investment in accessory tissues suggests some systematic variation in accessory costs among species, likely arising from differences in traits such as pollen-to-ovule ratio, seedset and seed size.

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 ovule 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 across multiple species.(Rosenheim *et al.* 2014, 2016; Burd 2016). These studies indicate that species with relatively low pollen-attraction costs should display parental optimism: an overproduction of 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 ovule number limiting seed production in many years (Mock & Forbes 1995; Burd 2008; Rosenheim *et al.* 2014). Generally, parental optimists will abort a large number of less costly flowers (i.e. have proportionally higher provisioning costs), while parental pessimists will abort a relatively smaller number of more costly flowers (i.e. have proportionally higher pollen attraction costs. Moreover, a tendency towards over- or under-production of ovules will be exacerbated by environmental stochasticity, because plants will invest more heavily in the cheaper of the tissue categories (Rosenheim *et al.* 2010, 2014). In addition, high individual variation in pollen receipt will cause increased investment in flowers (Burd 2008; Burd *et al.* 2009; Schreiber *et al.* 2015) and an increased number of ovules per flower (Burd 1994).

Extending these ideas around parental pessimists and optimists from Rosenheim et al (2014), leads us to hypothesize that across species differences in proportional investment in pollen attraction versus post-pollination provisioning costs will result in coordinated shifts in seedset and seed size (Fig. 1b). Since a parental optimist, by definition, aborts a large proportion of pollinated ovules (and has a low seedset), such plants will be selected to evolve relatively smaller flowers: producing a large number of excess flowers and also having those flowers individually costly is plainly a disadvantage. In turn, proportional provisioning costs, the complement to pollen-attraction costs, will be higher. Consider an important evolutionary driver for this strategy: if there is a large quantity of pollinated ovules, few of which will be provisioned, the parent plants can be choosy, selecting to provision only offspring with the most vigorous genotypes. In turn, the parent then benefits from greater provisioning investment, wanting to ensure the successful maturation of its carefully selected zygotes. A final strand links seed size to these traits: the species with proportionally higher provisioning costs are predicted to be big-seeded species, as an increase in seed size is associated with a disproportionate increase in the seed coat and other dispersal structures (Fenner 2000). s###.

In addition to the species-level shifts in total accessory costs and investment in specific accessory tissues, individuals within a species may shift their investment patterns as they grow and age. If accessory costs shift with reproductive effort (RE), plant size or plant age, then individuals should be selected to shift their timing of reproduction to minimize accessory costs and to increase propagule production from a given energy investment. Kelly (1994) lists as one potential explanation for masting the reduction in accessory costs, indicating that if accessory costs were lower in individuals of a species with higher RE, plants would be selected to have fewer, larger reproductive episodes. We do know that RE increases with plant size (or age) (Obeso 2002; Weiner *et al.* 2009; Wenk & Falster 2015), but not how the balance between seed versus accessory costs shifts.

A detailed look at investment in reproductive tissues within and among species is therefore warranted. In this study, we ask the following questions:

1. How much do species invest in different reproductive tissues and does this differ among species?
2. Does total reproductive investment scale isometrically with seed size, as has been previously suggested?
3. Across species, does proportional investment in seed provisioning (versus pollen attraction) increase with seed size, and decrease with seedset, as hypothesised?
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*, *Grevillea speciosa*, *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 fruit 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 “seed costs” (see Appendix B for a list of parts). Seed 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 seed 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 methods

For 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 costs of failure (the weight of all aborted parts, including mature flowers that fail to set seed) versus costs of success (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 greater investment in successful tissues than in failed tissues. 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 (Supplementary Material). Note that fruit that abort after pollination but before provisioning are recorded as shed flowers, such that the pollen-attraction (pre-provisioning) category includes ovules that are aborted both due to lack of pollination and due to early maternal selection.

Total seed costs are further divided into mass of parts formed up to the point of pollination (on a per ovule basis; terms 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 seedcosts, while 5 species had pollen-attraction costs that were less than 10% of total seedcosts (Table 1). 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). Importantly, the maximum any species invested in seeds was less than 10% of total reproductive energy expenditure.

## 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 much shallower than -1 (slope=-0.673±0.074, pslope ≠ -1 =<0.0001). However, larger-seeded species also aborted a disproportionately large number of buds and the slope of the regression between scaled seed count versus seed size is somewhat steeper than -1 (slope=-1.190±0.097, pslope ≠ -1 =0.0002). 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 seed costs and failed tissue costs, all increased isometrically with species’ mean seed size (Table 2). However, the two components of total seed costs did not scale 1:1 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 (Table 2, Figure 2d). The two components of failed tissue costs, failed pollen-attraction costs and failed provisioning costs, both scaled 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 all individuals 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 (seedcosts\*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 are 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 for the 14 perennial species included in this study, with just 1-8% of reproductive energy going to seeds versus other reproductive tissues (Table 1). Even the individual with the lowest accessory costs invested just 15% of its reproductive energy into the seed itself.

Second, 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. Using the established *parental optimist* vs *parental pessimist* as a starting axis, we confirmed the previously reported trend (Rosenheim *et al.* 2014) that species on the *optimist* end of the spectrum had proportionally costlier provisioning tissues relative to pollen attraction tissues, as expected of species with low seedset. The data also showed that the *parental optimists* were, as predicted, the large-seeded species: seed size increased in tandem with both proportional investment into provisioning tissues and decreased seedset.

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 reproductive investment (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; 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 (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 calculation of RE must tabulate all pools accessory costs. Indeed, across the species studied, both failed tissue costs and all seed costs (see Figure 1 for definitions) contributed to the high accessory costs.

In most species, a majority of reproductive energy is invested in failed tissue costs, those tissues that are aborted without contributing directly to the formation of successful seeds. For 12 of the 14 study species, more than 60% of RE was invested in failed tissues (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). In this study, there was a strong negative correlation between 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, are those required for the formation of a seed, and include pollen attraction costs, packaging and dispersal costs, and the seed itself (Figure 1, Table 1). For all species, the proportion of RE attributable to the seed itself is much less than the costs of the other components of seed costs, ranging from 0.2% of RE for *Hakea teretifolia* to 6.9% of RE for *Pimelea linifolia*. The remaining energy is expended on tissues such as showy petals, a fleshy fruit, a tall pedicel, or a fire-resistant larger cone. These are tissues that must be produced to mature each seed and their exact structures have presumably evolved to optimize seed production, but their cost to plants is not negligible. The species included in the structure have quite diverse floral and fruiting structures, resulting in disparate expenditure patterns. For three species (*Epacris microphylla, Hemigenia purpurea,* and *Pimelea linifolia*), the costs of producing pollen-attraction tissues on flowers that form mature seeds is 15-20% of total RE (Table 1). The two cone-producing species, *Banksia ericifolia* and *Petrophile pulchella,* have the costliest packaging and dispersal tissues spending 61.2% and 36.6%, respectively. However, other species also have 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 sections we explore whether the relative investment in different accessory cost pools shifts predictably with two species’ traits, seed size and seed set.

Vagary

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

Species’ relative investment in pollen-attraction versus seed provisioning costs shift in tandem with seedset and seed size as predicted (Figure 1b). Parental optimists are defined as species that produce an overabundance of ovules relative to their ability to provision them, in effect species with low seedset. Across the study species, parental optimists, invested a great proportion of their seed costs in seed provisioning (versus pollen attraction) and were the bigger-seeded species. A positive correlation between low seedset and the cost of each ovule (pollen attraction cost) is expected, due to a trade-off: in order to produce so many ovules parental optimists are selected to reduce their pollen-attraction costs relative to their seed provisioning costs, (Schreiber *et al.* 2015; Rosenheim *et al.* 2015) (Figure 1b). A second trade-off links seedset with seed size, in that a species with low seedset, must have higher seed germination and seedling survival, achieved through larger seed size.

They then have only sufficient resources to provision a modest number of seeds and will abort all but a few ovules, pollinated or un-pollinated. Consider Figure 2a, showingthat the species that make disproportionately many flowers, invest proportionately less per flower.

: the slope of the regression between bud count (scaled to plant size) and seed size is shallower than -1, while the regression between seed count and seed size is indistinguishable from -1. Their seed production, indicating their fitness, scales isometrically to their seed size, while flower production, an intermediate step, does not. The final investment in seeds then matches theoretical expectations – species either make many small seeds or proportionally fewer heavier ones (Moles & Westoby 2006).

Haig & Westoby’s (1988) model has been extended to model how the trade-off curves shifts in stochastic environments and with different levels of individual variation in pollen receipt (Burd 2008; Burd *et al.* 2009; Rosenheim *et al.* 2014, 2015). Among their conclusions, species in stochastic environments will generally over invest in the tissue type that is relatively cheaper. For the parental optimists, with less costly pollen-attraction materials, this means that an overabundance of ovules is produced – and usually aborted – but there are additional ovules that can be matured when sufficient resources are available (Andrade *et al.* 2005; Sadras 2007; Burd *et al.* 2009; Schreiber *et al.* 2015; Rosenheim *et al.* 2015). For these species, an additional benefit of having excess ovules pollinated is that they can be more selective in terms of pollen receipt (Zimmerman & Pyke 1988). Not only is an increase in per-flower ovule number a mechanism to reduce total accessory costs (Haig & Westoby 1988), but an oversupply of ovules slightly lessens overall pollen limitation, by increasing the proportion of pollen grains that are used (Rosenheim *et al.* 2015, but see Burd 2008). This effect is slightly larger than the decrease in the proportion of ovules fertilized due to the increase in ovule number. Although the authors of these models have reached different conclusions regarding the frequency of pollen-limitation in natural ecosystems, they have both established that species with greater pollen-attraction costs produce relatively fewer more expensive flowers and have a greater probability of being pollen-limited while species with greater post-pollination costs will display the opposite set of trait values.

attributed to attracting the animal dispersers and protecting their seeds during dispersal (Lord & Westoby 2006, 2012). This is in agreement with a strong correlation between seed size and biotic dispersal agents both in the fossil record (Moles *et al.* 2005; Eriksson 2008) and modern floras (Hughes *et al.* 1994). Worldwide, there is an observed decrease in seed set with increasing seed size (Moles & Westoby 2006).

While seed size, seedset, and the relative investment in pollen attraction versus provisioning costs are strongly correlated, neither total accessory costs nor failed tissue costs are correlated with seed size.

Since direct investment in seed dry mass represents a modest component of total reproductive investment, shifts in the relative allocation of energy to seeds versus accessory tissues with seed size would be a potentially important trade-off across species. However, confirming the results of previous studies (Henery & Westoby 2001; Moles *et al.* 2003; Lord & Westoby 2006, 2012; Chen *et al.* 2010), accessory costs increased isometrically with seed size (Figure 2, Table 2). That is, the relative investment in seeds versus accessory costs did not shift with seed size and did not represent a variable that differentiates species from one another. 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 reproductive investment was uncorrelated with seed size (Rosenheim *et al.* 2010; Mironchenko & Kozłowski 2014).

Dividing total accessory costs into the specific accessory tissue types outlined in Figure 1, allowed us to test for the existence of additional trade-offs, as the division into these smaller energy pools reflects further branch-points in plant energy allocation. For instance, relative investment in pre- versus post-pollination accessory cost components predicts where a plant lies along the pollen-limitation to resource-limitation spectrum (Haig & Westoby 1988; Burd 2008; Rosenheim *et al.* 2014, 2016) and we hypothesized this would also be correlated with seed size and seedset. To determine if the three accessory tissue pools identified in Figure 1 shifted across species, we regressed each against seed size. The results show that larger-seeded species invested disproportionately in seed provisioning (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).

Previous studies (Lord & Westoby 2006, 2012) defined a single pool of pollen-attraction tissues and found that total pollen-attraction costs scale isometrically with seed size. We instead divided these tissues into those associated with seeds that matured (required pollen-attraction tissues, a component of total seedcosts) versus the costs of failed buds and flowers (failed pollen-attraction tissues). This allowed us to show that the cost of failed buds and flowers scaled isometrically with seed size, while required pollen-attraction costs scaled with a slope significantly <1 (Table 2, Figure 2). Since all but one species had failed pollen-attraction costs that were at least twice as large as required pollen-attraction costs and for some species one hundred times as large as required pollen-attraction costs, failed pre-pollen costs would dominate the “all pre-pollen costs pool” and the regression between all pre-pollen costs and seed size, concealing the relationship between required pollen-attraction costs and seed size. The cost of failed fruits and seeds also scaled isometrically with seed size (Table 2), but represents a much more modest energy expenditure (Table 1).

This collection of results emphasizes that there is a trade-off between investment in required pollen-attraction tissues and provisioning tissues, similar to that proposed by Haig & Westoby (1988), and this trade-off correlates with seed size. (Note that, we are explicitly comparing investment just in seedcosts, while the Haig & Westoby model considers all pollen-attraction and seed provisioning tissues.) The less-than-isometric slope between required pollen-attraction tissues and seed size indicates 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 provisioning tissues require proportionally greater reproductive investment in larger-seeded species (Table 2). Moreover, in both previous studies (Moles & Westoby 2006) and the current data set, species with larger seed size are observed to have lower seed set, adding an additional variable that correlates with the pollen-attraction vs. post-pollination provisioning gradient.

Overall, larger-seeded species are

In summary, the correlations observed in our study indicate that seed size, bud production, and the magnitude of specific accessory cost components are coordinated across species. Understanding how plants allocate their pool of available reproductive energy to different accessory tissues and the seeds themselves is very relevant to understanding a plant’s energy allocation. Accessory costs constitute an enormous proportion of plant reproductive investment and plants must evolve to ensure these resources are invested to maximize their fitness.

## 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 reproductive investment (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 RA in older plants. Decreasing accessory costs, and hence more efficient seed production, with increasing reproductive allocation 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 (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. 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 (###refs), while demographic models maybe need estimates of seed production for a given RE (###refs). 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 made for this study 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 accessory costs 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* is omitted). Total plant weight was equally 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 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, investment in failed tissues, primarily representing investment in aborted flowers and buds, and our artificial composite measure, “total bud count \* average flower weight at the time of pollination”, provided excellent estimates of total RE across all individuals (r2=0.94 and r2=0.93 respectively; 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 is 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 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 in the population and across species (###). 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) (###). 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 (###). 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 (###)? 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 *Gevillea* 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). Notably, *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

[ideally Discussions would end with some sort of tidy wind-up, referring back to the single most important conclusion]

[It's good that in this draft you've tried to be comprehensive about thoughts and reading. But generally my feeling is that a submitted version should be shorter, and cut down to the most positive points that you really want to make]

NOTES….

* Is it possible that seed set decreases for some species at oldest sites, because fewer individuals of a species remain in the area – greater pollen limitation? (Haig &Westoby 1991 propose that species with lower accessory costs do better when rare than do species with higher accessory costs; termed lower cost of rarity); PHPH and PUTU certainly become rarer, but weak correlation for PUTU, none for PHPH with age

References not in manuscript

* Recent papers, especially in the horticultural literature, have shown a variety of mechanisms whereby hormonal changes will limit flower production or additional fruit maturation. For instance, abscisic acid production was reduced in the year following a big fruit yield and in trees where fruits are removed (Shalom *et al.* 2014).
* Several recent reviews have identified a diverse pollinator community as increasing seedset (Albrecht *et al.* 2012; Garibaldi *et al.* 2015).
* Zhang et al. (Zhang *et al.* 2015) observed that bumble bees are superior pollinators of peach trees, relative to honey bees because …
* Németh MB, Smith-Huerta NL (2006) Effects of pollen load size and maternal plant on pollen performance and seedling vigor in Clarkia unguiculata (Onagraceae). International Journal of Botany 2: 83–
* (Saa & Brown 2014)- reduced photosynthesis in fruit-bearing branches
* (Thompson & Stewart 1981) – call RA measure of greatest importance as well
* (Primack 1987)
* (Goulson *et al.* 1998; Harder *et al.* 2004),
* (Ackerman 2000) – book chapter worth reading on pollination
* (Cruden 2000) – book chapter on pollen grain – ovule ratios for different pollination syndromes
* Mehlman 1993,Obeso 2004 – within species, larger seeds, more seed/fruit = lower disp costs
* (Lázaro, Jakobsson & Totland 2013) Good references for seedset on page 888, including: “At the within-species level, several studies have shown that the total number of visits to a plant increases with its flower number (Eckhart 1991; Makino et al. 2007), but in a decelerating manner (Robertson and Macnair 1995; Ohashi and Yahara 2002; Mitchell et al. 2004). One reason for such a pattern may be that insects attempt to avoid revisiting previously visited, and thus less rewarding, flowers (Dreisig 1995). As a consequence, visitation rate and seed set per flower may be independent of (Robertson and Macnair 1995; Goulson et al. 1998; Mitchell et al. 2004), or even decrease with, flower number (Klinkhamer and de Jong 1990; Grindeland et al. 2005).”
* pollen limitation is higher in species with larger floral displays (Lázaro *et al.* 2013).
* (Gómez 2008) – article showing that different factors drive selection at different stages in seed (and seedling) development. In particular, pollinators drive # flowers and # seeds initiated, resource controls # seeds initiated and pre-disp seed predors = # final seeds
  + Pollinator preference for large flowers is common to many other plant species (Conner et al. 1996b; Lloyd and Barrett 1996; Shykoff et al. 1997
* (Knight *et al.* 2005)
  + Larger flowered species have less pollen limitation – Momose 2004
* (Harder & Johnson 2009): “This review has revealed somewhat contrasting views of floral and inflorescence adaptation. On one hand, the survey of phenotypic selection studies indicates that selection on individual traits acts sporadically within populations and inconsistently among populations. On the other hand, experimental studies of pollination function usually demonstrate the adaptive nature of floral and inflorescence traits in prevailing pollination environments and phylogenetic studies reveal patterns consistent with a key role for adaptation of pollination systems in floral diversification.”
* (Burd *et al.* 2009) more ovules per flowers in species with greater variation in pollen receipt
* We now show that the opposite is the case, namely, that whole-plant pollen receipt (the parameter used by our model) is more predictable than pollen receipt by individual flowers and that by deploying larger numbers of flowers, plants lessen their uncertainty in pollen receipt. (Rosenheim 2016)
* . High RE due to masting would increase seedset through seed predator satiation and reduced pollen limitation in wind-pollinated species, thereby reducing accessory costs (Kelly 1994; Kelly & Sork 2002). While “masting” implies synchronous reproduction peaks across a population of plants, higher RE could also reduce accessory costs at the individual level, if, for instance, a larger floral display reduced pollen-limitation by an insect, avian, or mammalian pollinator.

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