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Canopy seed storage is associated with sexual dimorphism in the woody dioecious genus *Leucadendron*

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Summary

1. Species of the dioecious South African plant genus *Leucadendron* vary strikingly in their degree of sexual dimorphism, with males of dimorphic species typically possessing more and thinner branches and smaller leaves than the corresponding females.

2. Many *Leucadendron* species are serotinous, with females of serotinous species maintaining seeds in transpiring cones for a number of years. Since cones must be kept alive, serotinous females presumably incur higher costs in terms of water loss than non-serotinous females and, particularly, males. Given that branching architecture is known to affect water conductance, with less resistance in less highly branched plants, we predicted a positive correlation between the degree of serotiny in a species and sexual dimorphism in branching.

3. We tested the effect of serotiny and several other factors on the degree of sexual dimorphism in *Leucadendron* by conducting a comparative analysis of variation across 49 species using phylogenetic regression.

4. There was a strong positive association between the degree of serotiny and sexual dimorphism. This association is consistent with the idea that the costs of maintaining cones may select females to be less highly branched than males.

5. *Synthesis*. Serotiny is a strategy of maternal care that contributes to offspring survival after seed maturation. We found that, in *Leucadendron*, the evolution of increased serotiny corresponds with the evolution of more marked sexual dimorphism. This study exposes a hitherto unidentified association between sexual dimorphism and maternal care in plants and points to a possible additional reproductive burden carried by serotinous plants compared with those that release their seeds at maturity.

Key-words: branching, comparative analysis, pollination mode, ramification, resource, serotiny, water conductivity

Introduction

Sexual dimorphism has evolved in many dioecious plants (Darwin 1877; Lloyd & Webb 1977; Geber, Dawson & Delph 1999), with males and females differing in the number, size and morphology of flowers and inflorescences (Eckhart 1999); rates of growth, timing of reproduction and timing of senescence (Delph 1999); physiological traits, such as rates of photosynthesis, transpiration and water uptake (Dawson & Geber 1999); and rates of herbivory and infection by pathogens (Ågren *et al*. 1999). Whereas sexual selection is the most likely cause of sexual dimorphism in animal species (Andersson 1994), morphological differences between male and female plants are often likely to be due to differences in their resource use. In dioecious plants, females typically allocate a greater proportion of their resources to reproduction than males, resulting in larger reductions in vegetative growth and longevity (Darwin 1877; Antos & Allen 1990; Delph 1999; Obeso 2002), although in some species males may bear the greater reproductive burden (Harris & Pannell, 2008). Either way, we should expect differential resource requirements for reproduction by the two sexes to give rise to selection for divergent resource acquisition traits (Dawson & Ehleringer 1993; Delph & Meagher 1995; Dawson & Geber 1999), particularly in resource-limiting environments where sexual dimorphism would be expected to be greater (Lloyd & Webb 1977; Gehring & Linhart 1993; Dawson & Geber 1999). In the dioecious shrub *Simmondsia chinensis*, for instance, sexual dimorphism

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appears to be greater in desert populations than in more mesic environments, with females at drier sites possessing a less highly branched morphology and larger, thicker leaves (Wallace & Rundel 1979; Kohorn 1994).

The cost of reproduction in female plants, while often high, is limited by the fact that progeny tend to be dispersed as soon as fruits are mature. Thus, although plants typically demonstrate a certain degree of maternal care, it tends to be limited to a relatively short period after fertilization. In some plant species, however, seeds are retained in protective structures for extended periods. This strategy of 'serotiny' is particularly common in plants growing in fire-prone vegetation, where seeds are protected in woody cones, fruits or infructescences (compound fruits), often for many years, and are dispersed after fire (Cowling 1992; Enright *et al.* 1998). Given that serotiny almost certainly implies the additional reproductive burden of maternal care, if sexual dimorphism is the result of differences in the reproductive burden of females versus males, we might expect dioecious serotinous species to display greater sexual dimorphism than their less serotinous counterparts. In this sense, the extent of sexual dimorphism among dioecious taxa that vary in their degree of serotiny may provide an indirect indicator of the cost of maternal care.

The Cape fynbos genus *Leucadendron* (Proteaceae) comprises over seventy species that are exclusively dioecious and that vary considerably in both the extent of sexual dimorphism they display and their degree of serotiny. In sexually dimorphic species, males are typically more highly branched and have thinner branches and smaller leaves than females (Williams 1972; Rebelo 2001), whereas other species show little or no evidence of secondary sexual dimorphism. Similarly, while many species of *Leucadendron* release their seeds from their 'cones' when they are mature, many others are strongly serotinous and maintain their seed bank in cones for several years before their release (Williams 1972). The causes of the often extreme sexual dimorphism displayed by some *Leucadendron* species has attracted a good deal of attention (Bond & Midgley 1988; Bond & Maze 1999; Hemborg & Bond 2005), but the possibility of an association between sexual dimorphism and serotiny, and its potential implications, has never been investigated.

Because *Leucadendron* cones must transpire to remain closed (Midgley 2000), we might expect females in serotinous species to have evolved greater efficiency in water conductance and use than females in less serotinous species (just as females of *Simmondsia chinensis*, cited above, have traits associated with reduced water loss). If so, we would indeed expect an association between sexual dimorphism and the degree of serotiny among species. There are in fact good reasons to expect variation in serotiny among *Leucadendron* to be associated with sexual dimorphism in branching architecture, in particular. In several species of plant, including *Leucadendron* spp., it has been shown that thicker branches are more efficient at conducting water, per cross-sectional area, than thinner ones (Tyree & Zimmerman 2002; Slingsby 2004). This suggests that the high water demand of producing and maintaining cones may select for thicker branches and thus reduced ramification, and that selection on females might give rise to stronger sexual dimorphism in serotinous versus non-serotinous species.

Here, we use a comparative analysis of sexual dimorphism in *Leucadendron* to test these ideas. Specifically, we used phylogenetically independent contrasts (PICs) to test the hypotheses that (i) the degree of serotiny should be positively associated with the degree of sexual dimorphism and (ii) the degree of sexual dimorphism should be negatively associated with indices of water availability. Because variation in sexual dimorphism among species may also be due to variation in selection on traits that increase pollen dispersal by males (Niklas 1985; Charlesworth 1993; Bond & Maze 1999; Eckhart 1999), we also tested the hypothesis (iii) that sexual dimorphism should vary with the mode of pollination. Although little is known about the details of pollination in *Leucadendron*, some species are wind-pollinated, while others are pollinated by insects (Rebelo 2001). Bond & Maze (1999) and Hemborg & Bond (2005) showed that pollinator visitation increased with ramification in males of *L. xanthoconus*, putatively because highly ramified males had more showy inflorescence displays (Bond & Midgley 1988). If selection on traits that influence siring success has contributed to the evolution of sexual dimorphism in *Leucadendron*, as these studies suggest, then one might expect an association between dimorphism and the pollination mode. Finally, we included in our analyses the age (i.e. time since fire) of each of the populations sampled, whether the population was able to resprout after fire or not, an estimate of the cone mass, and the altitude, longitude and latitude of the study populations in our analysis. We were particularly interested in testing our key hypothesis after possible associations with these other factors had been accounted for.

Materials and methods

SAMPLING AND MEASUREMENTS

Leucadendron is endemic to the Western Cape of South Africa and includes over 70 dioecious species exhibiting variation in the degree of sexual dimorphism and an array of life-history traits, such as the ability to resprout after a fire (Williams 1972; Rebelo 2001). We sampled one population for each of 49 of these species across habitats that covered the full geographical range of the genus. These species represented 13 of the 15 subsections recognized by Williams (1972) and Rebelo (2001); the remaining two subsections each included only two highly inaccessible species. In each population, we selected 20 individuals of each sex along linear transects. To prevent morphological biases because of possible spatial heterogeneity of the sexes, we sampled males and females in an alternating fashion along the transect. For instance, following sampling of a male, we ignored all subsequent males along our transect until we could sample a female.

The branching habit of *Leucadendron* allows a straightforward quantification of both ramification and a plant's age. During the spring of each year, an inflorescence is produced at the tip of each branch. Upon flowering, the main axis of the branch terminates in an inflorescence that subtends a whorl of side branches that produce the new internodes destined to flower the following spring. Each internode therefore represents a single year of growth. The total number of branch terminals, and thus stem diameters (Corner 1949), in any given year is ultimately determined by the mean number of branches arising from each node, i.e. the ramification.

For each plant, we measured ramification as the rate that stems become progressively thicker from the crown to the base of the plant. Specifically, at the mid-point of each consecutive internode, n, in series, from the tip of the highest branch to the base of the plant, we measured: (i) the cross-sectional area of the stem, A_n and (ii) the relative distance to this point from the crown of the plant, B_n. For each plant, we then plotted the logarithm of each stem cross-sectional area against the relative distance from the crown (Fig. 1). We used the slope of the linear regression as an estimate of ramification for each plant (Fig. 1). This method is based on the observation that the sum cross-sectional area of all the internodes branching from any one node will approximately equal that of the supporting internode (Leonardo's notes 394, 395, Richter 1970; Tyree & Zimmerman 2002). As a consequence, the cross-sectional area of any given internode, relative to its supporting internode, is, on average, a direct reciprocal of the number of branches at that node. Therefore, the rate that stems become thicker from the crown to the base of the plant is directly related to ramification, with a greater rate of stem thickening in more highly branching plants.

We calculated an index for the degree of sexual dimorphism in ramification for each species as

$$\mathrm{SD} = 2\frac{X_\mathrm{m} - X_\mathrm{f}}{X_\mathrm{m} + X_\mathrm{f}},$$

where X_m and X_f are the mean degrees of ramification for males and females, respectively, for the given species. Since this index for the degree of sexual dimorphism is essentially the absolute difference in ramification between the sexes divided by the mean ramification, it controls for any allometric relationship between sexual dimorphism and mean ramification. We also measured sexual dimorphism for a number of other traits, including stem cross-sectional area, leaf surface area, plant volume and plant height : diameter ratio. However, since these traits were strongly correlated with our index for ramification, we report here only on the analyses on ramification as this was a good all-encompassing measurement of morphology.

We characterized each female plant in terms of its degree of serotiny by estimating the age of the oldest cone encountered by descending the internodes, in series, from the highest branch tip on the plant. We also estimated the dry mass of the highest cone on the plant and estimated the plant's age by counting the number of internodes, in series, from the crown to the base.

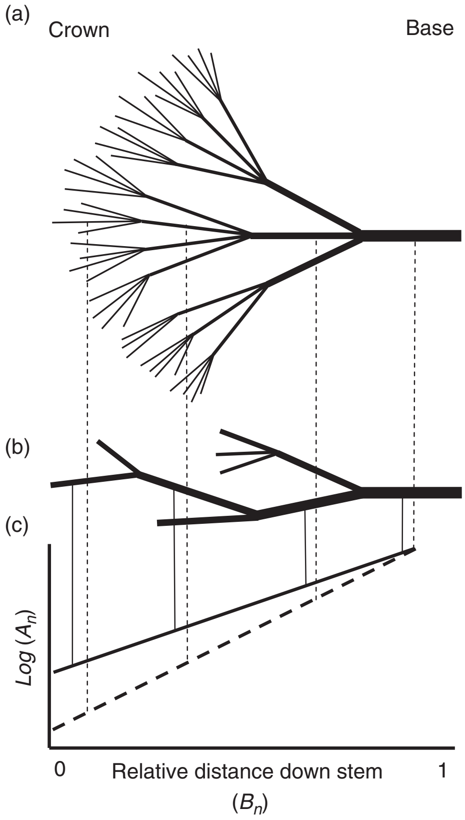

Fig. 1. Schematic diagrams of (a) a highly ramified plant and (b) a sparsely ramified plant, related to (c) our measure of branching. Notice that base diameter, internode number and internode length are the same in both cases. The essential difference between (a) and (b) is the number and evenness of branches arising from each node. When log(stem cross-sectional area) is plotted against relative distance down the stem, as in (c), the gradient of the line of best fit is greater for more ramified plants (dashed line) than less ramified plants (solid line).

ANALYSES

We tested the effect of each of several different variables on the degree of sexual dimorphism, calculated for ramification (presented here) and other traits (presented in Supporting Information), using independent contrasts in the phylogenetic regression (Grafen 1989); this method essentially takes an approach based on general linear models. The variables were: degree of serotiny, calculated as an average across 20 females in each population; cone mass (averaged for a single cone sampled from each of 20 females); mean plant age (averaged across all 40 plants sampled); pollination mode (i.e. insect versus wind), following Williams (1972); regeneration strategy (i.e. resprouter versus non-resprouter); altitude; latitude; longitude and mean annual precipitation. We first analysed our data using a full model with all terms. Where the full model was significant, we incrementally eliminated the most non-significant terms until only variables significant at $P = 0.05$ remained.

We conducted PICs, using three different phylogenetic hypotheses. First, we based our PIC analyses on the taxonomy of Williams (1972), (Table S1 in Supporting Information). Because this taxonomy is based partly on fruit and seed traits, it would appear to be potentially confounded with the characters focused on in our analysis. However, it is important to note that such confounding, should it occur, would only weaken the power of our analysis by reducing the effective number of contrasts available in the tree, making our tests conservative. Second, we used a strict consensus (Fig. 2a) of all the most parsimonious trees derived from reanalysis of the ITS sequence data of Barker *et al.* (2004) using Winclada (Nixon 2001). And third, we used a strict consensus (Fig. 2b) of the most likely trees derived from reanalysis of the ITS sequence data by Bayesian analysis (Huelsenbeck & Ronquist 2001). As ITS sequence data were only available for 37 of the 49 species for which we had morphological data, the analyses involving the molecular phylogenies were based on fewer species. For the purpose of comparison, we also conducted a 'tips' analysis on trait variation, i.e. treating each species as independent and found very similar results. There was no need to adjust P-values with a Bonferroni correction because each model was a separate analysis of the same data using a different phylogenetic hypothesis.

We performed PIC analyses using Grafen's (1989, 1992) phylogenetic regression. This method uses, as each independent data point, a

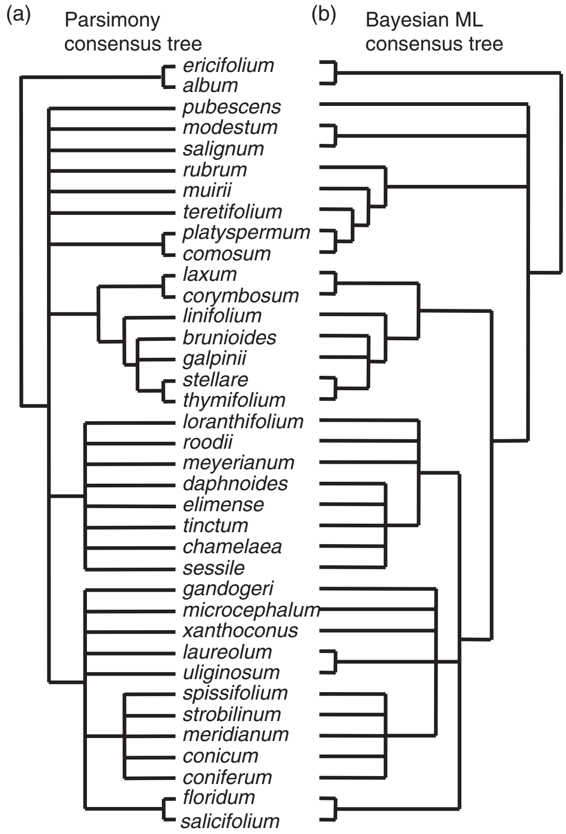

Fig. 2. Consensus phylogenies based on (a) parsimony analysis and (b) Bayesian analysis of 37 *Leucadendron* species derived from reanalysis of Barker *et al.*'s (2004) ITS sequence alignment.

linear contrast of trait associations amongst the immediate descendents of each node. A number of features ensure that this is a robust method for phylogenetic correction when the given tree is not fully resolved. Unlike other methods that account for uncertainty in the topology of the phylogeny (see Garland *et al.* 1993; Pagel 1997, 1999), the phylogenetic regression does not assume that unresolved nodes represent true polytomies. It therefore abstracts information only from the resolved aspects of the phylogeny (Grafen 1989). In particular, employing this method on a less than fully resolved phylogeny merely reduces the power of the analysis rather than its logical validity. Given these strengths, Grafen's (1989) phylogenetic regression has been widely adopted for phylogenetic correction in comparative analyses where only poorly resolved phylogenies are available (e.g. Belshaw, Grafen & Quicke 2003; Murray & Lepschi 2004; Hamilton *et al.* 2005; Figuerola & Green 2006; Sheil *et al.* 2006). We assigned segment lengths for the phylogenies using the 'Fig. 2' method in the phylogenetic regression (Grafen 1989).

We also attempted to analyse our data with a method for inferring correlated evolution using Bayesian analysis (Pagel & Meade 2006). The advantage of this method is that it accounts for uncertainty in the phylogeny by repeating the analysis using several likely phylogenetic hypotheses. However, the high degree of variation between the phylogenetic trees derived from Bayesian analysis and the low level of resolution of our consensus trees meant that the program was unable to function properly (A. Meade, personal communication). All our results are therefore based on Grafen's (1989) phylogenetic regression method, which seems to be the most robust method to use when only a poor phylogeny is available.

Results

The parsimony and Bayesian consensus trees were largely consistent with one another, except that the Bayesian tree was more highly resolved, containing eight more internal nodes than the parsimony tree (Fig. 2).

We found that sexual dimorphism in ramification was significantly associated with the degree of serotiny and cone mass, but not with annual precipitation or pollination mode. Highly serotinous species were more sexually dimorphic than less serotinous species, both in the tips analysis ($P \leq 0.010$, Fig. 3, Table 1) as well as in PIC analyses that indicate a tendency for sexual dimorphism to evolve in association with serotiny (in all PIC analyses, $P \leq 0.010$, Table 1). A tendency for species with large cones to be more sexually dimorphic than those with small cones was revealed by both a positive association between sexual dimorphism and cone mass in the tips analysis as well as in phylogenetic contrasts using the molecular-based phylogenies (Table 1). We found no significant association

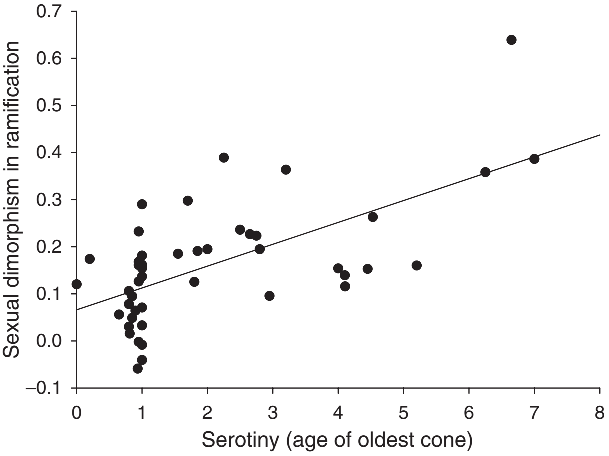

Fig. 3. Sexual dimorphism in ramification plotted against serotiny amongst 46 *Leucadendron* species. The line of best fit is significant following phylogenetic correction ($P < 0.05$), irrespective of the method of phylogenetic correction.

Table 1. Significant terms in multiple regression analyses on sexual dimorphism in *Leucadendron* species based on a TIPS analysis and on comparative analyses using phylogenies produced from the taxonomic framework of Williams (1972), a Bayesian analysis and a parsimony analysis (see text for details). Models were simplified by stepwise regression until only significant terms remained

Phylogenetic control	Variable	Estimate	*F*-ratio	d.f.	*P*-value
TIPS	Serotiny	0.030	9.46	1	0.005
	Cone mass	0.017	13.3	1	0.001
Taxonomy	Serotiny	0.041	12.6	1	0.004
Bayesian	Serotiny	0.030	10.6	1	0.006
	Cone mass	0.017	12.7	1	0.003
Parsimony	Serotiny	0.028	11.2	1	0.010
	Cone mass	0.017	10.3	1	0.012

between sexual dimorphism in ramification and either the pollination mode or the annual precipitation inferred for the population localities (Tables S1 and S2) and these factors were excluded from the final model.

Discussion

The degree of sexual dimorphism in ramification in *Leucadendron* was highest in species with the greatest level of serotiny: retention of seeds in the canopy-stored seed bank for longer periods of time was thus associated with increased divergence between male and female branching patterns. Three non-mutually exclusive hypotheses may explain this association. First, females of serotinous species may experience selection for thicker branches and thus reduced ramification because of developmental allometry. However, although the more dimorphic species tended to have larger cones, the observed association between dimorphism and serotiny remained significant after the effect of cone size was accounted for. Thus, while allometry may account for some of the pattern observed, the degree of serotiny would seem to be important in itself.

Second, it is possible that the observed association between serotiny and sexual dimorphism is a result of the evolution of branching patterns as a correlated response to selection on serotiny. Midgley (2000) suggested that the benefits of serotiny in species such as *Leucadendron* should decline with increased ramification, because the relative contribution of seeds by highly ramified individuals in any one year makes contributions from previous years negligible (Midgley 2000); as a consequence, selection on branching architecture might cause a correlated response in the degree of serotiny. However, although this hypothesis predicts an association between the degree of ramification of a species and the degree of serotiny, it cannot explain why males and females should differ in their degree of ramification.

Third, the association between serotiny and sexual dimorphism in ramification could be driven by selection on the costs and benefits of resource utilization. Females selected to sustain a canopy-stored seed bank for extended periods will pay a cost of cone maintenance additional to that paid by females that disperse their seeds soon after they are set. Because serotinous cones must continue to transpire as long as they remain closed (Midgley 2000), they probably represent a substantial resource cost in water use that is not paid by species that shed their seeds as soon as they are mature, particularly during the dry summers that are typical of the Cape mediterranean climate.

We speculate that increased costs in terms of water may select for thicker branches in serotinous females, and thus reduced ramification, compared with males, because thick branches are able to conduct water more efficiently. It is known for a number of species (Tyree & Zimmerman 2002), including *Leucadendron laureolum* (Slingsby 2004), that water conductance per cross-sectional area (i.e. specific conductivity) should be greater through thicker stems. As noted by Leonardo da Vinci (Leonardo's notes 394, 395, Richter 1970), stem diameter and the degree of ramification are negatively correlated in woody plants (Corner 1949; Tyree & Zimmerman 2002). Less ramified plants should therefore have greater overall specific conductivity than more ramified individuals. In a separate study on three *Leucadendron* species, we found that more highly ramified plants had more negative xylem pressure potentials than less ramified conspecifics growing in similar environments, suggesting that more highly ramified plants have thinner xylem vessels and thus greater hydraulic resistance than less ramified plants (M.S. Harris and J.R. Pannell, unpublished data). If so, it would seem that the increased cost of cone maintenance in serotinous females of *Leucadendron* and the corresponding selection for reduced ramification compared with males might provide a plausible explanation for the association between serotiny and sexual dimorphism. To our knowledge, this is the first time an association has been found between sexual dimorphism and parental care in plants, and similar studies on other dioecious groups displaying serotiny, such as *Allocasuarina* and *Casuarina*, would be worthwhile.

We predicted that if sexual dimorphism has evolved in response to differential resource trade-offs between males and females, then sexual dimorphism should be more marked in areas of greater resource limitation, particularly water (Lloyd & Webb 1977; Gehring & Linhart 1993; Dawson & Geber 1999). However, we found no significant association between sexual dimorphism and mean annual precipitation. Given that sexual dimorphism seems to be related to the degree of serotiny in *Leucadendron* and serotiny probably imposes greater water costs, this negative result might seem surprising. However, we are aware of only one study in which sexual dimorphism has been found to change with resource availability (Wallace & Rundel 1979), whereas several other studies, like ours, have failed to find the predicted association (Gehring & Linhart 1993; Marion & Houle 1996; Dorken & Barrett 2004; Sakai, Sasa & Sakai 2006). It is possible, of course, that our failure to detect a significant association between mean annual precipitation and dimorphism is caused by insufficient statistical power. However, it is also possible that mean annual precipitation is a poor indicator of water availability locally or indeed that the patterns in sexual dimorphism and serotiny in *Leucadendron* are being driven by some other factor. Experimental studies would be worthwhile.

Bond & Midgley (1988) and Bond & Maze (1999) have argued that sexual dimorphism in *Leucadendron* has been shaped to some extent by selection acting on males to increase their siring success by increasing the number of their inflorescences and thus their degree of branching. We found no significant association between sexual dimorphism and pollination mode in *Leucadendron*, and this study thus throws no further light onto this hypothesis. Our sample included only six wind-pollinated species and our categorization of pollination was coarse and may thus have missed important effects of different types of insect pollinators; our failure to detect any association between pollination and dimorphism is thus perhaps not too surprising. It would be worthwhile to incorporate more detailed data on the pollination biology of *Leucadendron* species and a more exhaustive sample of taxa in future comparative analyses of the genus. It certainly remains plausible that sexual dimorphism in *Leucadendron* is the result of both differential selection on male and female traits that influence resource use (this study), as well as of selection on male traits that influence siring success (Bond & Midgley 1988; Bond & Maze 1999).

In conclusion, this study complements those of Bond & Midgley (1988) and Bond & Maze (1999) by highlighting the potential importance of selection not only on males but also on females in shaping sexually dimorphic traits. The idea that sexual dimorphism results from divergent selection on males as well as females is implicit in theories of sexual dimorphism, but there has been a tendency to focus on the outcome of selection acting predominantly on males only, or, in plants, predominantly on females (Lloyd & Webb 1977; Wallace & Rundel 1979; Cipollini & Whigham 1994). This study suggests that, in *Leucadendron*, sexual dimorphism may be partly a result of selection on males to maximize siring success (Bond & Maze 1999; Eckhart 1999), but also on females that have evolved a strategy of maternal care through serotiny.

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Supporting information

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

Table S1. Species of *Leucadendron* sampled.

Table S2. Summary of significant terms in the multiple regression analysis.

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