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Bird pollinators, seed storage and cockatoo granivores explain large woody fruits as best seed defense in Hakea

Lamont, BB

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Corresponding Author: Prof. Byron Lamont,

Corresponding Author's Institution: Curtin University

First Author: Byron Lamont

Order of Authors: Byron Lamont; Byron Lamont; Mick Hanley; Philip Groom

Abstract: Nutrient-impoverished soils with severe summer drought and frequent fire typify many Mediterranean-type regions of the world. Such conditions limit seed production and restrict opportunities for seedling recruitment making protection from granivores paramount. Our focus was on Hakea, a genus of shrubs widespread in southwestern Australia, whose nutritious seeds are targeted by strong-billed cockatoos. We assessed 56 Hakea species for cockatoo damage in 150 populations spread over 900 km in relation to traits expected to deter avian granivory: dense spiny foliage; large, woody fruits; fruit crypsis via leaf mimicry and shielding; low seed stores; and fruit clustering. We tested hypothesises centred on optimal seed defenses in relation to to a) pollination syndrome (bird vs insect), b) fire regeneration strategy (killed vs resprouting) and c) on-plant seed storage (transient vs prolonged). Twenty species in 50 populations showed substantial seed loss from cockatoo granivory. No subregional trends in granivore damage or protective traits were detected, though species in drier, hotter areas were spinier. Species lacking spiny foliage around the fruits (usually bird-pollinated) had much larger (4-5 times) fruits than those with spiny leaves and cryptic fruits (insect-pollinated). Species with woody fruits weighing >1 g were rarely attacked, unlike those with spiny foliage and small cryptic fruits. Fire-killed species were just as resistant to granivores as resprouters but with much greater seed stores. Strongly serotinous species with prolonged seed storage were rarely attacked, with an order of magnitude larger fruits but no difference in seed store compared with weakly/non-serotinous species. Overall, the five traits examined could be ranked in success at preventing seed loss from large woody fruits (most effective), fruit clustering, low seed stores, spinescence, to crypsis (least effective). We conclude that the evolution of large woody fruits is contingent on pollinator type (dictates flower/fruit location, thus apparency to granivores), level of serotiny (response to poor soils and fire that requires prolonged seed defense) and presence of a formidable granivore (that promotes strong defense).

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Perspectives in Plant Ecology, Evolution and Systematics

To Diethart Matthies
Editor in Charge
Perspectives in Plant Ecology, Evolution and Systematics

Dear Editor: attached is the revised manuscript as requested. We believe we have done everything as suggested by the reviewer and I have indicated our responses beneath each comment of the reviewer. We hope that you now consider the ms ready for publication.

Sincerely

(Distinguished Professor Emeritus) Byron Lamont

Reviewer #2: This is an interesting manuscript in which the authors studied the evolution of defence strategies against seed predation in the Hakea genus. In this MS the authors present a large data set to test 23 different hypotheses related to this topic.

This MS could be a nice contribution in the evolution of fruit traits and its correlation with other plant traits to avoid seed predation. However, I have some important concerns about the current version of this MS. I think that the data set is very valuable, but the authors should review significantly part of the statistical analyses and re-think how to tell the history to allow that non-specialist readers (like me) can understand the MS.

Main concerns:

- The main message is hidden under a complex structure of different interconnected hypotheses. I felt lost reading through the introduction. Every biological problem is complex and has many functional links between different mechanisms and traits. It is true that it is very hard to simplify some of these relationships. However, the authors should try to rewrite the introduction in a way where one general objective would be addressed rather than stating that 23 different hypothesis were tested. I guess that these hypotheses might be grouped in functional modules that could be explained in the introduction without having to explain all of them. The other option could be to select some hypotheses, for instance, the authors could give more importance to those hypotheses that can be more general and therefore more useful for other organisms different than Hakea.

Authors response: The first paragraph of the Introduction explains that seeds control species fitness so that they must be well protected. The second paragraph now begins: “Our focus here is on how species with nutritious seeds are best adapted to the presence of formidable avian granivores in a seed-limited environment”, then outlines the biology of the study group, *Hakea*. The third paragraph introduces the main granivore, the black cockatoo and concludes: ”Since seeds that are held longest on the plant are also contained within the largest and woodiest fruits (Groom and Lamont 1997), our overarching hypothesis was that these give the greatest protection against cockatoo granivores.” The fourth paragraph is a general introduction to the ways plants can defend their seeds against granivores, in association with the flow diagram, Fig. 1, highlighting the many options available to *Hakea*. The optimal defense hypothesis is now introduced and its predictions in relation to *Hakea* outlined. The hypotheses are no longer referred to specifically and we note: “Together, these adaptive traits can be related in a flow diagram (Fig. 3), each arrow representing a directional hypothesis (Table 1)” and that “our objective was to compare the relative abundance and effectiveness of these alternative strategies for deterring avian granivory.” The search for possible syndromes of (qualitative) traits is emphasised. The dilemma that species which have open inflorescences to allow access to large (bird) pollinators means that their subsequent fruits are exposed to large (bird) granivores is now described. “Consequently, we tested whether ‘highly accessible’ species develop larger, woodier fruits than those that defend fruits with spiny foliage, reflecting a pollinator–fruit defense trade-off.” Finally, the relevance of optimal defense theory to seed protection by species that either survive fire or are killed and those that store seeds on the plant until the next fire is outlined.

We invite the editor (as a “non-specialist reader”) to dip into any part of the Introduction and confirm that it is now clear, logical and relevant to the topic.

- I have some concerns about the statistical methods. Mainly three:
-- Categorization of continuous variables. The authors have discretized many variables from continuous data. This is a strange decision, which is not well justified in the MS. In general, the use of continuous variables has more advantages than disadvantages compared with discrete variables. For instance, continuous variables allow the use of more powerful statistical tools than contingency tables.

We defend our use of categorical data on the following grounds:

1) Much of the data is qualitative. In particular, populations are either attacked by cockatoos or they are not, leaves are spinescent or not, plants are killed by fire or survive, flowers are either insect or bird-pollinated etc.
2) As such, these data are not normally distributed and statistical errors occur when they are treated as if they are.
3) We are particularly interested in syndromes of traits and whether there are trade-offs between groups of categorical data – certainly it is only possible to map categorical data onto phylogenies as we have done (Fig. 5). We say in the Introduction: “As they appeared complementary solutions to the same problem, traits were placed in a hierarchy to see if any formed syndromes of effectiveness or were independent of each other due to trade-offs. These traits were further placed in the context of syndromes of pollinator-type (insect *vs* bird), disturbance-response-type (killed *vs* survives) and seed-storage-type (serotinous *vs* non-serotinous) to examine their relationship with levels of granivory and the testing of optimal defense theory.”
4) We overcame the statistical problems when we were interested in quantifying responses by dividing the question into two parts: a) was there an effect or not (presence/absence)? and b) if there was an effect, did it vary in size between groups? (See under Materials and Methods)
5) Where we divided data into classes, it is now couched in terms such as the following: “For qualitative comparisons, as the data were not normally distributed and to assist the search for syndromes, values were divided into no damage (≤0.05, class 1), mild damage (>0.05 to 2.5, class 2) and severe damage (>2.5, class 3) to give similar numbers of species per class.”

-- The phylogenetically adjusted analyses. The authors should use more advanced statistical analyses for controlling the phylogenetic relationships. The phylogenetic control used by the authors could be not enough. During the last years, a significant contribution on phylogenetic comparative methods has been done. Nowadays, we

have tools that allow for testing correlation between traits (including continuous and discrete ones) taking into account intraspecific variation, phylogenetic relationships and different models of trait evolution such as Brownian and Ornstein-Uhlenbeck models. Why don't use them? One of the many available options is "phylolm" R package: http://pages.stat.wisc.edu/~lamho/phylolm/
-- The authors used SEM analysis to test the potential causal links between different variables. However, they used comparative data from many different species and therefore they must account by the lack of independency between these data. ?I think that the authors could introduce the phylogenetic relationships by means of the variance-covariance matrix. This has been used in the next papers:
Santos & Cannatella (2011) Phenotypic integration emerges from aposematism and scale in poison frogs. PNAS 108: 6175-6180
http://www.pnas.org/content/108/15/6175.abstract
Gómez & Verdú (2012) Mutualism with Plants Drives Primate Diversification. Systematic Biology 61: 567-577
https://sysbio.oxfordjournals.org/content/61/4/567.abstract
In addition, there are several general introductory books explaining different methods and statistical packages:
Paradis E. 2011. Analysis of Phylogenetics and Evolution with R. London: Springer.
Nunn CL. 2011. The comparative approach in Evolutionary Anthropology and Biology. Chicago: The University of Chicago Press

Authors response: We have now undertaken more advanced statistical analyses for testing quantitative trait correlation that takes phylogenetic relationships into account. In the revised version, we have used a phylogenetic independent contrasts (PICs) method and carried out a phylogenetically corrected multivariate correlation analysis using the R package *phytools* that adopts a Brownian trait (random) evolutionary model.

The relevant section in the Materials and Methods reads: "Phylogenetic signal was quantified to evaluate species independence for each trait using Page's lambda and significance tests. All nine variables were compared by multiple phylogenetically corrected correlation analysis using a phylogenetic independent contrasts (PICs) method. Both phylogenetic signal quantification and PICs correlation analysis were conducted using the R package *phytools (*Revell, 2012). Phylogenetically generalised least square regression was used to explore the relationship between fruit size and seed size using R package *ape* (Paradis et al. 2004)."

As a consequence, both Table 1 (significance of hypotheses) and Table 5 (Correlation matrix for the SEM analysis) had to be changed to reflect the new results. It is true that the significance level of the correlations usually changed but the effect was minor.

Minor comments:

P3. L8. I am not sure if we should think in seeds as one plant organ. Seeds are embryos covered by maternal tissue not plant organs.

Authors response: Replaced organ by plant part

P5. L11. ODH should be explained the first time that appears in the text.

Authors response: Optimal defense hypothesis (ODH) is now spelled out on first mention in the Introduction

P8. L15-17. The authors stated here that they decided to study as many species as possible to capture the great variation in this genus rather than replicate within species. I partially agree with this statement. However, it is important to show that the variation found within species was smaller than the variation found between species. In this way, they can support this statement.

Authors response: while it is not possible to do a formal comparison of within and between species as each multiply assessed species would need to be considered individually, we make the following observations under M&M: "We reasoned it was better use of limited resources to sample as many species as possible to capture the great variation in this genus rather than replicate within species. In addition, we often inspected multiple populations but did not formally assess them when it was apparent that there was no granivory. Ten of the species with formally assessed multiple populations were constant (zero granivory) while 13 gave different results only 40% of the time that we considered were sufficient grounds for treating species responses as representative, especially as our focus was on whether fruits were attacked or not."

P8. L22. How it was the sampling? Was it random? or some individuals were preferentially chosen for any reason like small size, or having more (enough) fruits. Sampling should be better described.

Authors response: This has been expanded to read: "This involved walking in an approximate straight line from the edge of the population towards the centre and assessing each plant as it was encountered either side within 2 m of the line." We believe this resulted in an unbiased, representative sample.

P14. L10-22. I believe that this whole paragraph could be moved to material and methods.

Authors response: Done

P14. L25. This analysis should be done with phylogenetic general linear models.

Authors response: As suggested by the reviewer, we conducted a phylogenetic generalised least square regression analysis on the two traits, and report the new regression coefficient and probability. The M&M section now reads:
"Phylogenetic generalised least square regression was used to explore the relationship

between fruit size and seed size using the R package, *ape* (Paradis et al. 2004)" and the Results read: "Logging of mean fruit (F) and seed (S) weights for 55 species yielded the equation: S = 1.126F + 3.643, $r = 0.754$, $P < 0.001$, by phylogenetically-corrected, generalised least squares regression." As expected from other analyses, the effect of this correction was minor.

Table 3. Could the authors add here some measure of statistical dispersion and sample sizes? In addition, P values alone are uninformative and not useful for future meta-analyses. I suggest to add in all tables where is needed the sample size.

Authors response: Table 3 and Table 4 (that has the same format as Table 3) now have added to each value its sample size. Together with the *P* value this gives an idea of dispersion as noted by the reviewer (though dispersion has no meaning in Table 4 as these are total values).

***Highlights**

- We test five seed-defense traits among 56 species, addressing optimal defense/foraging theory. This is done in the context of important variables in ecology: geography, pollination, seed-storage and disturbance-response traits.
- We show for the first time that granivorous birds may have a profound effect on the evolution of large woody fruits among bird-pollinated species on poor soils that are fire-prone.

Bird pollinators,~~ on-plant~~ seed storage and cockatoo granivores explain large woody fruits as best seed defense in *Hakea*

Byron B. Lamont[a]*, Mick E. Hanley[a,b], Philip K. Groom[a], Tianhua He[a]

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[a]*Department of Environment and Agriculture, Curtin University, PO Box U1987, Perth, WA 6845, Australia; and* [b]*School of Biological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, United Kingdom*

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[*] Corresponding author. Department of Environment and Agriculture, Curtin University, PO Box U1987, Perth, WA 6845. *E-mail address*: B.Lamont@curtin.edu.au (Byron Lamont)

Short title: Seed defense traits and granivory

Abstract

Nutrient-impoverished soils with severe summer drought and frequent fire ~~as occur in~~typify many Mediterranean-type regions of the world. Such conditions ~~,~~limit seed production and restrict opportunities for seedling recruitment making ~~seed~~ ~~. P~~protection ~~of seeds~~ from granivores ~~is~~ paramount~~ in such an environment~~. Our focus was on ~~the shrub~~ *Hakea*, a genus of shrubs widespread in southwestern Australia, ~~and~~ whose nutritious seeds are targeted by strong-billed cockatoos~~ and is widespread in southwestern Australia~~. We assessed 56 *Hakea* species for cockatoo damage in 150 populations spread over 900 km in relation to traits expected to deter avian granivory: ~~(i.e.~~ ~~:~~ dense spiny foliage; large, woody fruits; fruit crypsis via leaf mimicry and shielding; low seed stores; and fruit clustering~~). to test~~ We tested ~~.~~ ~~We tested 23~~ hypothesises centered on ~~variation in fruit~~optimal seed defen~~se~~es ~~according~~in relation to to a) pollination syndrome (bird *vs*~~or~~ insect), ~~and~~ ~~species possessing open foliage that allows access to bird pollinators have large woody or clustered fruits for seed defense while insect-pollinated species deploy spinescence and crypsis;~~ b) fire regeneration strategy (~~-~~killed *v~~ersu~~s* resprouting~~ers~~) and c) on-plant seed storage (~~weak~~ transient *v~~ersu~~s* ~~strong serotinous~~prolonged). ~~species produce many fruits seeds that are well-protected from granivores; c) seeds with prolonged on-plant storage (serotiny) are well defended. Level of spinescence (fruit accessibility) was gauged directly by inserting dummy cockatoo heads into the foliage and noting extent of wounds.~~

Twenty species in 50 populations showed substantial seed loss from cockatoo granivory. No subregional trends in granivore damage or protective traits were detected, though species in drier, hotter areas were spinier. Species lacking spiny foliage around the fruits (usually bird-pollinated)~~) or leaves abscised)~~ had much larger (4~~–~~–5 times) fruits ~~(and seeds) 4–5 times larger~~ than those with spiny~~escent~~ leaves~~ce~~ and cryptic fruits (insect-pollinated). Species with woody fruits weighing >1 g were rarely attacked, unlike~~ while~~ those with spiny foliage and small cryptic fruits~~ often were~~. Fire-killed species were just as resistant to granivores as resprouters but with much ~~higher~~ greater seed stores. Strongly serotinous species with prolonged seed storage were rarely attacked, with an order

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Comment [MH1]: I think this can be simplified greatly to add clarity and impact - the detail is in the Introduction and methods section

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of magnitude larger fruits but no difference in seed store compared with weakly/non-serotinous ~~but while their seeds were over an order of magnitude larger with 11.5× larger fruits (and seeds) butthere was no difference in seed store size than displayed by non-serotinous~~ species. Overall, the five traits examined ~~traits~~ could be ranked in ~~importance of~~success at preventing~~ion of~~ ~~at~~seed loss ~~preventing seed loss~~ from large woody fruits~~-~~ (most effective), fruit clustering, low seed stores, spinescence, to crypsis (least effective). ~~Successful seed defense~~We conclude that t~~T~~he evolution of large woody fruits is contingent on pollinator type (~~[~~dictates flower/~~-~~fruit location, thus apparency to granivores)~~]~~, level of serotiny (response to poor soils and fire that requires prolonged seed defense) and presence of a formidable granivore (that ~~induces~~ promotes strong defense).

Comment [MH2]: Simplifying the 'hypothesis' bit might allow for a more wider so-what here? - for example, what does this study tell us about Hakea evolution?

Key words: Bird pollination; Black cockatoo; Crypsis; Fruit size; Granivory; Resprouter; Seed protection; Serotiny; Spinescence

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Introduction

Given the key role of seeds in accounting for species fitness, dispersal and adaptive potential, reproductive structures are more valuable to the species than any other plant ~~organ~~ part (McCall and Irwin 2006). In addition, they are energy~~-etically~~ and nutrient-demanding and represent a major drain on the plant's resources (Witkowski and Lamont, 1996; Cramer and Midgley, 2009). Yet, to be accessible to ~~vertebrate~~ large pollinators and seed dispersal agents, flowers and fruits need to be held away from protective foliage and thus ~~are~~ may be vulnerable to florivores and granivores. It is not surprising therefore that flowers ~~may~~ often contain chemical defenses (Twigg and Socha, 1996; Hanley et al., 2009) and fruits may protect their seeds via warning coloration, distasteful chemicals, woody ~~chambers~~ fruits or sharp appendages (Schaeffer and Ruxton, 2011).

Our focus here ~~i~~was on how species with nutritious seeds are best adapted to the presence of formidable avian granivores in a seed-limited environment. Our study group was the Australian genus, *Hakea* (Proteaceae), with >150 species, that possesses a remarkable array of plant life-history traits linked to survival in the presence of efficient herbivores, florivores and granivores (Hanley and Lamont, 2002; Groom and Lamont, 1997) coupled with strong ~~selective pressures associated with seedling herbivory (Hanley and Lamont, 2002), avian granivory (Groom and Lamont, 1997),~~ summer drought/heat (Lamont et al., 2002; Groom et al., 2004), nutrient-~~ uptake from~~ impoverished soils (Lamont, 2002), ~~presence of~~ disparate pollinators (Hanley et al., 2009) and ~~persistence in~~ fire-prone environments (Groom and Lamont, 1996a). Fruit and seed size, fecundity and levels of on-plant seed storage (serotiny) vary between species by orders of magnitude (Richards and Lamont, 1996; Groom and Lamont, 1997), leaves may be cylindrical or flat, fruits are cryptic among spinescent foliage or fully exposed to granivores, and produced singly or in clusters, species resprout or are fire-killed, and they are bird- or insect-pollinated (Barker et al., 1999; Groom and Lamont, 2015). In a Mediterranean-climate region where serotiny reaches its world peak (Lamont and Enright, 2002), most hakeas retain their seeds in woody fruits until the passage of fire triggers fruit dehiscence and seed release. However, long-term retention of seeds on the plant means that fruits are exposed to granivores for many years, even decades.

Given their high nutrient content (Groom and Lamont, 2010) and availability on the plant throughout the year (Groom and Lamont, 1997), hakea seeds are attractive to strong-billed black cockatoos (*Calyptorhynchus*, Cacatuidae) and ~~are represent~~comprise an important part of their diet (Saunders, 1980; Stock et al., 2013). Historically, the most widespread and abundant of the three extant species has been Carnaby's black cockatoo, *C. latirostris*, with European pioneers in the 19C reporting flocks "blackening the sky" (R. Johnstone, W.A. Museum, pers. comm.) and flocks of 6,000 birds were still observed in the 1940s (Perry, 1948). The evolutionary history of *Hakea* and *Calyptorhynchus* can both be traced to the Cenozoic, with the median stem of *Hakea* at 18 (root)–14 (crown) million years ago (Ma) (Sauquet et al., 2009; Lamont et al., 2016) and the median stem of *Calyptorhynchus* at 21.5–15 Ma (White et al., 2011). Hence, the scene was set for a classic Darwinian 'struggle' between a highly malleable plant genus and a formidable selective agent on

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reproductive traits key to its fitness in a nutrient-impoverished, drought- and fire-prone environment that severely limits seed production and seedling recruitment (Lamont, 1995; Lamont and Groom, 2013). Since seeds that are held longest on the plant are also contained within the largest and woodiest~~most lignified~~ fruits (Groom and Lamont 1997), our overarching hypothesis was that these give the greatest protection against cockatoo granivores.

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Types of seed defense

Many seed-protective mechanisms are available to hakeas that provide an ideal opportunity to test theories on optimal defense and foraging strategies, only chemical defense not being represented among the full range of possible options (Fig. 1). *Direct* defense strategies refer to where the target is apparent but protected: here the fruits are accessible to potential granivores but the seeds are embedded in a woody pericarp that cockatoos can only ~~penetrate~~ pierce with much effort (Fig. 2). The endocarp of most species can be placed in the “high~~-~~density wood” category (> 540 kg/m^3, Groom and Lamont, 1997), akin to that of major hardwood timbers (Commonwealth of Australia, 2012). Alternatively, woody fruits may be crowded into dense clusters that produce a barrier through self-protection (Fig. 2e). In addition, fruits may be inaccessible because they are held within sea-urchin-like clumps of dense, outwardly-pointing, spiny leaves, prolonged by retention of dead leaves in many species (Fig. 2; Hanley et al., 2009), under threat of severely wounding visitors or infecting them with pathogens (Cheville et al., 1988; pers. observ.). *Indirect* strategies refer to where the target is accessible but not apparent: fruit crypsis is achieved via mimicry of the subtending leaves ~~(Groom et al., 1994; Moore, 1994)~~ or stems (Groom et al., 1994; Moore, 1994), or shielding by the surrounding foliage (Fig. 2); or fruit production is so low or sporadic that it is ignored either because fruits are missed or they are not considered a worthwhile target (marginal return theorem of optimal foraging, Charnov, 1976). In addition, other (contingent or modifying) variables affect the intensity of the primary variables via secondary pathways. For *Hakea*, these comprise pollinator type, fire response and level of serotiny as detailed below.

In terms of granivory risk and fitness value to the plant, optimal defense hypothesis (ODH)~~ODH~~ predicts that large seeds will be better protected than small seeds and thus are less likely to be consumed by granivores (McKey, 1974; Stamp, 2003). For *Hakea*, this will be expressed through the heavier seeds being held within larger woodier~~y~~ fruits, cryptic through camouflage or shielding, and/or protection~~ed~~ by spiny leaves. S~~ince s~~erotiny provides time for the development of large seeds that must be well-protected during their long storage period and their seeds may be larger than non-serotinous species (Groom and Lamont, 2010). Thus, levels of granivory by cockatoos were compared against traits expected to deter them, involving ~~three ~~direct and ~~two ~~indirect defenses and ~~three ~~contingency factors interacting with the defense factors, that ~~with ~~involved ~~five ~~several primary pathways and ~~18 ~~numerous secondary (contingent) pathways.

Together, these adaptive traits can be related in a flow diagram (Fig. 3), each arrow representing a directional hypothesis (Table 1). We predicted that cockatoos would be deterred by a) dense spiny foliage~~ (Hypothesis 7, Table 1, Fig. 2)~~, b) fruit crypsis~~ (10)~~, c) large fruit size~~ (5)~~, d) fruit clustering ~~(19) ~~and/or e) small seed store as alternative defences available to hakeas~~(15)~~. Our objective was to compare the relative abundance and effectiveness of these alternative strategies for deterring avian granivory. As they appeared complementary solutions to the same problem, traits were placed in a hierarchy to see if any formed syndromes of effectiveness or were independent of each other ~~as a~~due to trade-offs. These traits were further placed in the context of syndromes of pollinator-type (insect *vs* bird), disturbance-response-type (killed *vs* survives) and seed-storage-type (~~level of ~~serotinous *vs* non-serotinous~~y~~) ~~for possible impact~~to examine their relationship with levels of granivory and the testing of optimal defense theory (McKey, 1974; Stamp, 2003).

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Pollinator attraction–seed protection dilemma

Hanley et al. (2009) demonstrated that hakeas with conspicuous and accessible, bird-pollinated inflorescences also possess flowers containing high levels of cyanoglycosides that c~~ould~~an deter florivory by non-pollinators, such as cockatoos. On the other hand, the inflorescences

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of insect-pollinated congenerics are small and protected ~~by~~ within dense, spiny~~escent~~ foliage that deters vertebrate florivores but allows access to invertebrate pollinators (~~Hypothesis 3,~~ Table 1, Fig. 2). However, variation in floral defense strategies presents an evolutionary dilemma for the plant: while insect-pollinated flowers (and thus fruits) are located within spiny~~escent plants possess~~ protective foliage, fruits produced by bird-pollinated taxa remain exposed, often for many years. The only defensive option for hakeas with exposed fruits then is ~~to produce~~for them to be large and woody~~ fruits~~ so~~that~~ preventing cockatoos from reaching their seeds (~~Hypothesis 4,~~ Fig. 2g,h, Groom and Lamont, 1997). Consequently, we tested whether ‘highly accessible’ species develop larger, woodier fruits than those that defend fruits with spiny foliage, reflecting a pollinator~~ion~~–fruit defense trade-off (~~Hypothesis 1,~~ Fig. 2).

Since seeds produced from bird-pollinated flowers will be exposed to granivores they will be protected by large fruits that ~~will enable~~allow them to grow larger than those from insect-pollinated flowers. ~~Since~~ As allometric relations ~~would~~ suggest that larger fruits support larger seeds (when the number is fixed, as here), we expected bird-pollinated species to possess larger seeds. We also predicted that fruit clustering is more common in these species as an alternative/supplementary mechanism for seed defense~~ (Hypothesis 2)~~. In contrast, the incidence of cryptic fruits associated with persistent foliage will be more common in insect-pollinated species, and there will be a close association between crypsis and dense foliage~~ (8)~~, especially as small fruits may mimic leaves or stems (Groom et al., 1994; Fig. 1), and have an inverse relationship with fruit weight~~ (9)~~. Since bird pollination appears to be the more-recently evolved syndrome over insect (Toon et al., 2014), we also postulated that bird-pollinated species have more effective traits for deterring granivores.

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Disturbance responses and seed defense

Although many species rely entirely on seeds for persistence in the postfire community, other hakeas are capable of resprouting from roots and lignotubers (Groom and Lamont, 1996a). ~~Presuming~~ Accepting that the value of ~~fruits~~ seeds to fire-killed nonsprouters (NS) is greater than it is for postfire resprouters (RS), since their fitness revolves around successful postfire recruitment, not only will NS produce more seeds ~~(Hypothesis 14)~~ but the optimal defense hypothesis (ODH) predicts that fruit defense in NS species will be higher than in RS species (~~Hypotheses 11–13,~~ Table 1, Fig. 2). We therefore compared fruit size, crypsis and spinescencs between NS and RS species. ~~Since fruit clustering requires high fruit production, this hypothesis (17) subsumes one stating that nonsprouters will have clustered fruits.~~

The impetus for the evolution of serotiny involves environments that restrict annual seed production but where conditions are sometimes optimal for seedling recruitment (essentially immediately postfire) favouring the on-plant accumulation of seeds between such events and their cued release in response to the fire (~~18,~~ Lamont et al., 1991). We predicted that species with long-term storage would invest more effort in seed defense as time alone would make them more vulnerable to granivores ~~(Hypotheses 6, 22, 23)~~ whereas poorly protected seeds can escape predispersal granivory through their release soon after reaching maturity (Groom and Lamont, 1997, 2010). Fruit clustering, offering mutual protection between fruits, can be viewed as an alternative defense to large woody fruits among serotinous species ~~(20, 21)~~. On-plant seed stores vary greatly among species, with RS possessing much lower levels than NS among hakeas (~~14,~~ Groom and Lamont, 1996a, El-ahmir et al., 2015). Independent of fire-response type, the ODH predicts that species with few seeds should provide greater protection for them ~~(16)~~. Taking fire-response type into account, fitness of nonsprouters is solely dependent on seeds, so it can be expected that they will be better protected. However, highly fecund plants will be more attractive (apparent) to granivores than those with scattered fruits, consistent with the optimal foraging hypothesis (Charnov 1976). Here, resource trade-offs and the quest for reduced apparency/rewards imply that nonsprouters will produce smaller seeds and fruits, so they might opt for other forms of protection such as fruit clustering ~~(17)~~, crypsis or spinescence.

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Materials and Methods

Study species and avian granivory

We studied fruit traits and the extent of pre-dispersal fruit damage for~~in~~ 56 *Hakea* species ~~from~~ in 150 populations. Authorities for names follow http://florabase.dpaw.wa.gov.au. Our survey area incorporated four of the five botanical districts in SW Australia (Irwin, Darling, Roe, Eyre) over a latitudinal range of 900 km. While essentially a Mediterranean-type climate, temperatures and summer drought are greater in the north while annual rainfall is higher in the more-coastal central district. One to nine populations per species were assessed for pre-dispersal parrot damage to fruits. Time and travel constraints meant that for 33 species only one population was examined, but a concerted effort was made to assess all hakeas growing in representative parts of the Irwin (centred on Eneabba, 300 km N of Perth), Darling (mainly the Darling Range, 20 km of Perth) and Eyre/Roe (centred on the Stirling Ranges, 350–500 km SE of Perth) botanical districts. We reasoned it was better use of limited resources to sample as many species as possible to capture the great variation in this genus rather than replicate within species. In addition, we often inspected multiple populations but did not formally assess them when it was apparent that there was no granivory. Ten of the species with formally assessed multiple populations were constant (zero granivory) while 13 gave different results only 40% of the time that we considered were sufficient grounds for treating species responses as representative, especially as our focus was on whether fruits were attacked or not. Each of the three subregions was visited in mid-late 2012 and 2013 and resulted in data for 30, 15 and 26 species respectively.

The extent of pre-dispersal parrot attack on fruits was gauged by inspecting 20 plants per population (where populations were small we examined as few as 10 plants, Appendix, Table A). This involved walking in an approximate straight line from the edge of the population towards the centre and assessing each plant as it was encountered either side within 2 m of the line. Cockatoo granivory was recognized where fruits were torn open and their seeds missing, categorized as: zero damage; 1–10% of fruits damaged; 11–50% damaged; >50% damaged. Insect-attack was indicated

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by small holes in the fruits that remained on the plant but were rare and difficult to identify so were included in the total fruit count. Fruit damage was quantified by assigning the values 0, 1, 2 and 3 to each category respectively, multiplied by the number of plants in that category, divided by total plants, to give a range of 0–3. For ~~purposes of statistical analysis~~qualitative comparisons, as the data were not normally distributed and to assist the search for syndromes, values were divided into no damage (≤0.05, ~~(~~class 1), mild damage (>0.05 to 2.5, class ~~(~~2) and severe damage (>2.5, class ~~(~~3) to give similar numbers of species per class. Granivory was still considered zero where the *most heavily attacked* population of a given species was ≤5% of plants with ≤10% of their seeds removed by cockatoos (i.e. value ≤0.05), on grounds that it was *ad hoc* and biologically insignificant. We used the population with greatest fruit damage as indicating the lowest level of protection against cockatoos that the species could offer but accept that this may be ~~be a function of~~affected by the number of populations examined. This was not such an issue for the qualitative analyses use in the binary comparisons but may have been with the quantitative pathway analysis. There was no evidence of intact seeds remaining in discarded fruits nor of being carried any distance from the parent plant so that these birds have no role in seed dispersal.

Geographic considerations

Overall, 50 populations spread among 20 species showed signs of fruit damage consistent with visits by black cockatoos (Appendix, Table A). For five species, at least two-thirds of plants had >50% of their seeds removed. There was no phylogenetic signal in the distribution of species attacked through the three subregions (Table 2A). There was no geographic gradient or difference between districts in the incidence of fruit damage. Proportionately more species in the hotter/drier Irwin were strongly spinescent than the southern districts and spiny species there caused more wounding of the dummy cockatoo heads (Table 2B). There were no differences in incidence of camouflage, or distribution of fruit size or seed store classes, between districts (Table 2C–E) but mean fruit weight was twice as high in the Irwin and Eyre/Roe than the Darling district (Table 2D). Overall, there were no significant differences in levels of granivory, spinescence, camouflage, fruit

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size or seed store between subregions, justifying combining all data and considering any trends independently of location.

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Fruit traits and accessibility

Fruit accessibility (spinescence) was determined by inserting dummy heads of Carnaby's black cockatoo into the foliage of each of 56 *Hakea* species until the bird's beak touched a fruit. The purpose was to determine how effective *in situ* spiny leaves were ~~in~~ at deterring granivory, accepting that behavioural modification by the birds might overcome such defenses. Note that some species have spiny leaves but that foliage is lost by the time flowers are produced on that part of the stem (cauliflory) or by the time fruits are mature so that they are left exposed (caulifrugy) – all these were bird-pollinated. Dummies were prepared by removing feathers, skin and flesh from heads severed from preserved bodies of two mature birds. Feathers only were removed from one head to act as a model for building up the 'flesh' with polyclay (Eberhard Faber GmbH, 92318 Neumarkt, Germany) on the skull of the other. The eye sockets were filled with different-coloured clay. A stake was inserted into the skull to enable it to be pushed into foliage. Later, the polyclay was replaced with 'Fun Dough' Bright (EL0700, Elephant Learning Co, Victoria 3165, Australia).

Cockatoo heads were positioned on the plant as if the bird was perched and pushed into the foliage until the beak touched the fruit target. On withdrawal, the number of indentations and scratches due to spinescent leaves on the neck, eyes and rest of head were noted. 'Wounds' were smoothed over after each retraction. This procedure was conducted on ten plants per population. The level of spinescence (inverse of accessibility) was gauged as the mean number of wounds per insertion, with neck and eye wounds weighted by a factor of two (because of the greater injury to the bird these would cause). For ~~purposes of analysis~~qualitative comparisons, as the data were not normally distributed and to assist the search for syndromes, ~~the data~~results were grouped into no spinescence, moderate spinescence (0.1–1.9) and strong spinescence (≥2) to give equal-sized classes.

Fruit camouflage (crypsis) was based on the extent to which they appeared to mimic, or were shielded by, the surrounding leaves. Fruits that remained green at maturity (they usually turn brown then grey with age) and possessed serrations or prickles similar to the sclerified margins of the surrounding leaves, or turned dark and appeared to mimic the subtending branchlets or persistent dead foliage, and/or were difficult to distinguish because the surrounding foliage was dense, were categorized as camouflaged (Fig. 1). Such assignment has a subjective element but similar self-mimicry and shielding is an effective granivore deterrent in *Hakea trifurcata* (Groom et al., 1994) and it is a testable hypothesis.

Fruit size was based on oven-dry weight of 20 fruits per species as used in Groom and Lamont (1997). For qualitative comparisons, as the data were not normally distributed and to assist the search for syndromes, t~~T~~hey were divided into three categories to give similar numbers of species in each category: small (<0.7 g), medium (0.7–3.0 g), large (>3.0 g). We also assessed seed size as the ultimate target (reward) by weighing 20 air-dry seeds per species. There were always two seeds per fruit (Fig. 2g). Seed store was initially assessed in the field according to six categories of on-plant fruit (×2 = seed) numbers reduced to three, to ensure sufficient numbers for nonparametric comparisons, by merging each successive pair: <10, 10–100 and >100 seeds/plant for populations >15 years since fire and mature plants in the case of resprouters (having passed through several fire cycles). Clustering was quantified by counting the number of fruits per node at ten nodes on each of six plants in 1–4 populations. Species were classed as clustered where more than 50% of nodes contained grouped fruits. Resprouting ability followed Groom and Lamont (1996a) or our own field observations. Overall, we assumed that plant traits were diagnostic for the species and did not vary ~~in multiple~~between populations; thus~~—~~ traits were only assessed on one population.

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Hakea phylogeny

We assembled a *Hakea* phylogeny using published DNA sequences (50 species, El-ahmir et al., 2015; Mast et al., 2012) and morphological studies (6 species, Barker et al., 1999). Eight DNA sequences from the nuclear ribosomal internal transcribed spacers (ITS) and plastid matK, rbcL, trnL intron, and trnL-trnF intergenic spacer, atpB, atpB-rbcL intergenic spacer, and rpl16 intron were obtained from NCBI Genbank (accession numbers in Appendix Table B). The sequences were aligned and edited using the computer software MUSCLE (Edgar 2004). BEAST v2.1.0 (Drummond and Rambaut, 2007) was used to estimate phylogeny and branch length (divergence time) under a relaxed clock model. A secondary calibration point ~~with~~ at 16.2 million years and a normal distribution prior was applied at the divergence of *Hakea* with *Grevillea/Finschia* following Sauquet et al. (2009). We used a Yule prior for rates of cladogenesis and ran analyses of 10 million generations, sampling every 2000 generations, with a one million generation burn-in. TreeAnnotator v1.6.1 (Drummond and Rambaut 2007) was used to generate a maximum credibility tree (MC tree) based on this analysis. The six species without DNA sequences available were grafted onto the molecular phylogeny (MC tree) based on their morphological classification (Barker et al., 1999).

Phylogenetically adjusted and unadjusted analyses

~~Current phylogenetic co mparative methods can only handle quantitative data using covariance techniques, so that nonlinearity is a problem (Quader et al., 2004). Nonlinearity was exacerbated here as our focus was on “presence-absence” traits and “effect–no effect” responses such that our data were dominated by zeros and unsuitable for covariance-type analyses. To adjust for phylogenetic 'distances' between qualitative data, all nodes were allocated a number commencing from the crown of the *Hakea* clade (1) to the node subtending each species (up to 9 nodes). From the species pair with the highest node, numbers of nodes between all other species were counted then square rooted to give euclidean distances between the species and reference species. Exploration with this approach showed that starting position affected the phylogenetic~~

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~~distances between species but using the ultimate (most distant from the crown) species as reference maximized their range. Distances were standardized by dividing by their mean so that the grand total equalled the number of species assessed (56) before contingency table analysis. Since each species was now given a weighted fraction relative to its relationship with all other species in the phylogeny, the independent fractions were summed for contingency analysis that accepts non-integer totals (Preacher, 2001). Simulations showed that if traits were concentrated in one part of the phylogeny (i.e. high and low weightings not spread through the phylogeny) then the *P* level would change markedly. Statistical analyses (χ^2 contingency table, t-tests, see below) were conducted on 17 phylogenetically weighted data by multiplying the observed values by their weighted fractions from the above (vassarstats.net 2014). Comparisons between the raw and phylogenetically adjusted data (Appendix, Table C) showed that *P* values differed at most in the second decimal place, with no effect on significance levels at* P *= 0.05. Weighted data analyses were therefore considered redundant and omitted from the final tables.~~

Phylogenetic signal among the continuous form of the data was quantified ~~to evaluate species independence for each trait~~ using Page's lambda and significance tests in order to evaluate species independence for each trait. ~~–~~All nine variables were compared by multiple, phylogenetically-corrected correlation analysis using~~using~~ a phylogenetically independent contrasts (PICs) method. Both phylogenetic signal quantification and PICs correlation analysis were conducted ~~out~~ using the R package, *phytools* (Revell, 2012)~~Pearson's correlation coefficients for quantitative variables and Spearman's rank coefficients for binary and ranked data using SPSS 22.0 (SPSS Inc., Chicago, IL)~~. Phylogenetic generalised least square regression was used to explore the relationship between fruit size and seed size using the R package, *ape* (Paradis et al. 2004). Granivory was treated as a quantitative variable even though it was often zero. Structural equation modelling (SEM) was ~~then~~ used to reveal direct interactions between traits and to test the specific hypotheses proposed. SEM extends the basic correlation approach to path analysis by testing the goodness of fit of various

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models to the data, calculates new correlation coefficients (standardized by variance) and separates total effects into direct (primary pathways) and indirect (secondary pathways) effects. The modelling process in SEM analysis is guided by *a priori* and theoretical knowledge and begins with a consideration of expected relationships based on the mechanisms thought to operate in the system (Mitchell, 1992; Grace et al., 2010). We began by building a conceptual SEM model (Fig. 3) of the expected multivariate relationships based on logic and current evidence and theories of the interactions between functional traits and levels of cockatoo granivory (Table 1). The conceptual model was tested and then refined by deleting uncorrelated pathways (Amos 22.0, SPSS Inc., Chicago, IL). The deletion of pathways from the model was guided by improvement in goodness of fit, as measured by χ^{2}-test of the model fit, root mean square error of approximation (RMSEA < 0.08), and comparative fit index (CFI > 0.95) (Steiger, 2007). A final model with highest goodness of fit and all pathways significant is reported here. Goodness of fit was accepted at $P < 0.05$.

Current phylogenetic comparative methods can only handle quantitative data using covariance techniques, so that nonlinearity is a problem (Quader et al., 2004). Nonlinearity was exacerbated here as our focus was on the identification of syndromes, especially traits associated with presence/absence of granivory, such that our data were dominated by zeros and did not satisfy the requirements for covariance-type analyses. To adjust for phylogenetic 'distances' between qualitative data, all nodes were allocated a number commencing from the crown of the *Hakea* clade (1) to the node subtending each species (up to 9 nodes). From the species pair with the highest node, numbers of nodes between all other species were counted then square rooted to give euclidean distances between the species and reference species. Exploration with this approach showed that starting position affected the phylogenetic distances between species but using the ultimate (most distant from the crown) species as reference maximized their range. Distances were standardized by dividing by their mean so that the grand total equalled the number of species assessed (56) before contingency table analysis. Since each species was now given a weighted fraction relative to its relationship with all other species in the phylogeny, the independent fractions were summed for contingency analysis that accepts non-integer totals (Preacher, 2001). Simulations showed that if traits were concentrated in one part of the phylogeny (i.e. high and low weightings not spread through the phylogeny) then the *P* level would change markedly. Statistical analyses (χ^2 contingency table, t-tests, see below) were conducted on 17 phylogenetically weighted data by multiplying the observed values by their weighted fractions from the above (vassarstats.net 2014). Comparisons between the raw and phylogenetically adjusted data (Appendix, Table C) showed that *P* values differed at most in the second decimal place, with no effect on significance levels at $P = 0.05$. Weighted data analyses were therefore considered redundant and omitted from the final tables.

For individual binary comparisons, we first asked: was the trait present or absent when the paired trait was in a given condition? Contingency tables for number of species in each category were compared by χ^2-test. Where the original (directional) hypothesis was supported numerically, 1-tailed tests were applied; where the results were in the opposite direction to that predicted, 2-tailed '*ad hoc*' tests were applied. Where quantitative values were available, the second question was: if the trait was present, did it vary in value between the categories? These were compared by Tukey's test. Natural logs were taken to normalize the data as required and equality of variances confirmed. Each set of hypotheses was regarded as independent of the others as the objective was to identify the most significant comparisons and few results were close to $P = 0.05$ anyway (Moran, 2003; O'Keefe, 2003).

The relative effectiveness of each of the five traits (accessibility, camouflage, fruit size and clustering, seed store) were compared by dividing the proportion of species with the hypothesised deterrent but not attacked, by the proportion lacking the hypothesised deterrent but not attacked. Where there were three classes, the two with closest % values were combined. They were then ranked from most to least effective at deterring (preventing) fruit damage. Each species was also placed into one of 54 possible hierarchical combinations of ± spinescence, ± camouflage, three classes of fruit size and three classes of seed storage in an attempt to identify seed-defense syndromes of traits. The dominant three syndromes recognized by this process accounted for 55 of the 56 species and were added to the phylogeny and assessed for the level of phylogenetic signal as above. Evolutionary histories of the three syndromes were re-constructed using the likelihood method in Mesquite V2.0 (Maddison and Maddison, 2007). In the search for pollination/seed-defense syndromes, the species data (with additional information from Hanley et al., 2009) were searched for insect vs bird pollination, with small or medium/large/clustered fruits, level of serotiny, and absence or presence of spiny leaves/camouflage (crypsis), noting in addition if leaves were missing when in flower (cauliflory) or once fruits were mature (caulifrugy). Three syndromes emerged: the percentage of species in each, the fraction of species that escaped cockatoo granivory, and the maximum extent of granivory of those species that were attacked, were noted and analysed statistically using 2-tailed tests (χ^2 and Tukey's).

Results

~~*Geographic considerations*~~

~~Overall, 50 populations spread among 20 species showed signs of fruit damage consistent with visits by black cockatoos (Appendix, Table A). For five species, at least two-thirds of plants had >50% of their seeds removed. There was no phylogenetic signal in the distribution of species attacked through the three subregions (Table 2A). There was no geographic gradient or difference between districts in the incidence of fruit damage. Proportionately more species in the hotter/drier Irwin were strongly spinescent than the southern districts and spiny species there caused more wounding of the dummy cockatoo heads (Table 2B). There were no differences in incidence of camouflage, or distribution of fruit size or seed store classes, between districts (Table 2C–E) but mean fruit weight was twice as high in the Irwin and Eyre/Roe than the Darling district (Table 2D). Overall, there were no significant differences in levels of granivory, spinescence, camouflage, fruit size or seed store between subregions, justifying combining all data and considering any trends independently of location.~~

Seed size vs fruit size

Logging of mean fruit (F) and seed (S) weights for 55 species yielded the equation: $\ln S$ = 1.126$\ln F$ + 3.643, ~~, phylogenetic generalised least square regression~~ r = 0.754~~15~~, P < 0.00~~0~~1, by phylogenetically-corrected, generalised least squares regression. Thus, larger fruits protect larger seeds in an exponential manner (slope > 1). The seeds consumed by cockatoos were smaller than those not consumed (Tables 3,4). The main source of this protection were large woody fruits since seeds in fruits > 1 g were on average 4× the size of those in fruits < 1 g (Table 3) or, alternatively, such fruits possessed 2.7× as many of the available large seeds (> 21.5 mg, the median size among 55 species) as of the small seeds (< 21.5 mg) (Table 4). Mean seed:fruit ratio of species attacked was 2.7× greater than seed:fruit ratio of species not attacked (P = 0.001, 1-tailed t-test, unequal variances). Seed size was not affected by the presence or absence of crypsis or spinescence (Table 3) nor did the fraction of large or small seeds associated with these differ (Table 4). Seed size did not differ between fire-killed and resprouting species (Table 3) but more than twice as many of the available small seeds were present among fire-killed species than of the resprouters (Table 4). There was a tendency for serotinous species to have larger seeds (Table 3) but the same fractions of small and large seeds were in serotinous fruits (Table 4). Bird-pollinated species did not have larger seeds (Table 3) nor was a greater fraction of the large seeds allocated to them (Table 4). Overall, cockatoos attacked species with smaller seeds as these were not as well protected by large fruits as those with larger seeds, while crypsis, spinescence, fire-response type, level of serotiny and pollinator-type were usually unrelated to seed size.

Multivariate (quantitative) comparisons

~~Among the tested~~For the 56 *Hakea* species, cockatoo granivory wa~~i~~s statistically independent of~~to~~ species~~'~~ phylogenetic relationships (Page's lambda = 0.011, P = 0.949), while other traits show various degrees of phylogenetic dependence. Of 36 simultaneous pairwise comparisons made via multiple correlation analysis after phylogenetic correction using PICs methods, ~~12 eight~~ nine were significant at P = 0.05 (Table 5). Cockatoo granivory was positively associated with ~~spiny foliage~~

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~~and~~ fruit camouflage and inversely with fruit weight. ~~Spiny foliage was associated with insect pollination.~~ Camouflaged fruits tended to be weakly serotinous while serotinous fruits were large such that camouflaged fruits were small. Resprouters have low seed stores. Fruit clustering was associated ~~with large seed stores~~, with bird pollination and nonsprouters. SEM analysis yielded 18 pairs of variables with significant standardized coefficients ~~(Table 5)~~, 13 of which were related to fruit weight and cockatoo granivory. The seven most significant variables contributed to the best-fit pathway through the data set (Fig. 4). Dense spiny foliage was associated causally with fruit camouflage and pollinator type (insects), camouflaged fruits being smaller and bird pollinators being associated with larger fruits. Resprouters produced smaller seed stores that were less likely to possess clustered but larger fruits. Of the five direct defense options, only fruit weight, controlled by three significant factors, was related (negatively) to the extent of cockatoo granivory.

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Bivariate (qualitative) comparisons

Fruits of species lacking spinescence were 10× less likely to be attacked by avian granivores than those protected by spiny foliage (Table 7A). Non-camouflaged fruits were 4× less likely to be attacked than camouflaged and seed loss was 3× less when attacked (Table 7B). Small fruits were 3× more likely to be attacked than medium-sized fruits that were 4× more likely than large fruits. Small fruits suffered 7× more seed loss than the one large-fruited species attacked (Table 7C). Granivory did not vary significantly with size of seed store (Table 7D). >50% of the spinescent species had small fruits whereas >50% of non-spinescent species had large fruits (Table 7E). The fruits of non-spinescent species weighed 4× that of spinescent species (Table 7F). Non-camouflaged fruits were 5× heavier than camouflaged fruits (Table 7G). Fruit weight of high-seed-storage species was not significantly less than low/moderate-seed-storage species (Table 7H).

Fruit-trait hypotheses

The fraction of bird-pollinated species attacked by cockatoos was significantly less than for insect-pollinated species (Table 8A) though they were less likely to be spinescent or camouflaged (Table 8B,C). Bird species had 2.5× larger fruits that were 3.5× more likely to be clustered than insect species (Table 8D,E). Neither fruit damage, spinescence nor fruit size varied significantly between nonsprouters and resprouters (Table 9A,B,D). However, there was a tendency ($P = 0.058$) for resprouter fruits to be better camouflaged than nonsprouters (Table 9C). Over 50% of resprouters were in the low seed store class but all nonsprouters were in the medium-high categories (Table 9E). Ten of the 11 species with clustered fruits were nonsprouters (Table 9F).

Strongly serotinous species were rarely attacked whereas non/weakly serotinous species often were (Table 10A), even though all/most weakly serotinous species were spinescent/camouflaged (Table 10C). When strongly serotinous species were spinescent, they caused 3× as many wounds as weakly serotinous (Table 10B). Most fruits of strongly serotinous species weighed >0.7 g while most weakly serotinous species weighed <0.7 g, and the overall difference in fruit weight between strongly and weakly serotinous species was 11.5× (Table 10D). There was no significant difference in seed store size between the two serotinous types (Table 10E). Species with isolated fruits were 2.3× more likely to be attacked than clustered fruits, and those with non-attacked clusters had over twice the number of fruits/cluster as the attacked clusters (Table 11A). Only 45% of species with clustered fruits were spinescent while 71% with isolated fruits were, accepting $P = 0.057$ as significant (Table 11B). Isolated species were 5× more likely to be camouflaged than clustered species (Table 11C). Although there was no difference in fruit size between clustered and unclustered species (Table 11D), all species with clustered fruits, and 60% with isolated fruits, had medium-high seed stores (Table 11E).

Relative effectiveness of traits and defense syndromes

The most effective of the five morphological traits at deterring (preventing) granivory were medium/large fruits; these were 1.7× more effective than clustered fruits, 3.7× more effective than medium/low seed stores, 4.3× more effective than moderate/strong spinescence, and 5× more effective than camouflaged fruits (Table 12). The number of species not attacked declined from 29 out of 34 (85%) with medium/large fruits to 8 out of 20 (40%) with camouflaged fruits. When attacked, relative seed loss tended to increase in the same order, except that seed loss among the two affected clustered species was much less than expected possibly biased by the small sample size of only 2 species. Of 54 possible combinations of spinescence, camouflage, fruit size and seed store, 24 were represented among the 56 species, with seven combinations containing ≥ 2 species (Table 13). Three defense syndromes could be recognized, each accounting for about one-third of species. Among the spinescent ± camouflaged species with small fruits, 63% were attacked by cockatoos, among the spinescent ± camouflaged species with large fruits, 35% were attacked, while no non-spinescent, non-camouflaged species with large or clustered fruits was attacked. Placing these three defense syndromes on the *Hakea* phylogeny showed no phylogenetic signal in their distribution (P = 0.432, χ^2 contingency table) such that all three subclades were capable of producing all three defense syndromes (Fig. 5).

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The 56 species were then assigned to these three syndromes modified on the basis of pollinator-type (Table 14). Initially, they were grouped according to their foliage: whether dense and spiny current season's growth or open and non-spinescent or lacking surrounding foliage (cauliflorous). The former group could be divided into insect-pollinated species with 1) small, submerged, pale/dark flowers, sometimes cyanogenic or 2) bird-pollinated species with large, partly-submerged, usually pale flowers that were sometimes cyanogenic. The last group (3) contained large, prominently-displayed, bright-red flowers that were typically cyanogenic. Among the insect-pollinated species (70% of all species), the majority (77%) could be assigned to the two syndromes with camouflaged fruits due to retention of leaves even if dead: 41% could be allocated to syndrome 1, with small, cryptic fruits sometimes weakly serotinous; 36% to syndrome 2 with large, cryptic, strongly-serotinous fruits; and the remainder (23%) to syndrome 3 with large/clustered, strongly-serotinous fruits on naked stems (caulifrugy) due to abscission of the leaves that once surrounded the flowers. Among the bird-pollinated species (30% of all species), 12% could be allocated to syndrome 1, 29% to syndrome 2 and the majority (59%) to syndrome 3. Syndrome 1 was the most vulnerable to cockatoo granivory (61% of species attacked) and syndrome 3 the least (21%). Attacked species in the former sustained ten times greater seed loss than the latter.

Discussion

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The primary seed defense and defense-modifying (contingency) factors examined together here were pollinator type, spinescence, crypsis, fruit size and clustering, seed store, fire-response type and serotiny. It is rare for so many defense-related traits to be present in the same genus (*Hakea*) and essentially directed at the same class of highly efficient granivores (cockatoos). This provided a unique opportunity to test their relative effectiveness unfettered by irrelevant confounding variables. Overall, the lack of a consistent geographical gradient in granivory levels (Table 2) justified pooling the data for all 56 species assessed. Nevertheless, spinescence in the much drier/hotter northern part of SW Australia (Irwin district) was over twice that in the milder southern part (Eyre/Roe). This is consistent with the observed climatic gradient in sclerophylly among hakeas in the same region (Lamont et al., 2002) and concentration of needle-leaved *Banksia* species in the north of their range (Lamont and Connell, 1996). A structural relationship between spinescence and sclerophylly is expected, each relying on highly cellulosic/lignified tissues, and both are exceptionally high in SW Australia on a world scale (Lamont, 1995; Cowling et al., 1996; Read et al., 2005; Lamont et al., 2015). Even so, the lack of a corresponding (inverse) relationship with granivory at the regional scale underscores the minor role that needle leaves play in deterring granivory in *Hakea* (in contrast to their anti-herbivory role, Hanley et al., 2007).

Of the 36 possible pairwise interactions, 23 were considered relevant here (Table 1, Fig. 3) and ~~11~~ nine were shown to be significant by phylogenetically-adjusted, multiple correlation analysis (Table 5). Of 26 individual qualitative binary comparisons assessed, 19 were significant; of 16 quantitative binary comparisons, seven were significant (Tables 7–11). Among these, t~~T~~he standout results for the ~~possible~~ control of cockatoo granivory were its negative relationship with fruit size/weight and its positive relationship with spiny foliage and fruit crypsis. The apparent paradox of higher levels of granivory with increasing spinescence and camouflage is readily explained by the smaller size of the woody fruits with increasing spinescence and camouflage, and their associated greater seed:fruit weight ratios (optimal foraging theory). Thus, large woody fruits more than compensate in effectiveness for their increased exposure to granivores due to lack of spinescence or camouflage. In fact, the best-fit SEM pathway analysis showed that the only effective defense against cockatoos are large woody fruits and that three pathways involving six other variables contribute to fruit size, including pollinator type (Fig. 4). Thus, dense, spiny foliage promotes self-mimicry and shielding of small fruits on the one hand (Fig. 2), and insect pollination with small, concealed inflorescences followed by small, cryptic fruits on the other (Table 15, Hanley et al., 2009, Groom and Lamont, 2015). From the other direction, fire-killed species have large seed stores (Lamont and Wiens, 2003) that promote fruit clustering which is associated with small fruits (Judd and Ashton, 1991). Conversely, large fruits are associated with open, non-spinescent foliage, bird pollination and small seed stores. This analysis ~~did~~ does not recognize the highly significant relationship between level of serotiny and fruit size (Tables 5,10) as an additional pathway, that we consider the ultimate driver of large fruits (see below), ~~possibly~~ because serotiny was correlated qualitatively (Table 10) but not quantitatively with granivory in the SEM analysis (Table 6) possibly associated with the non-linearity of the data due to the high incidence of zero granivory.

Camouflaged fruits often remain green and closely mimic the shape of surrounding leaves (Fig. 2; Groom et al., 1994; Groom and Lamont, 2015). They provided one of the strongest binary relationships (Tables 3,5,6,8): cryptic fruits are associated with insect pollination, they weigh on average only 20% of the non-cryptic, and are weakly serotinous. Yet they are generally ineffective against cockatoos. Small fruit size implies thin walls (high seed:fruit weight ratios, as demonstrated) and it is possible that crypsis is more directed at beetle and moth granivores, with poor eyesight/night activity, when young fruits are most vulnerable to invasion by insect larvae (Groom et al., 1994; Gordon and Fourie, 2011). Thus crypsis can be viewed as a form of neoteny, where paedomorphism in the form of small, green but mature fruits is adaptive for short-lived fruits associated with new season's foliage when they are most prone to insect granivores, while serotiny favours the production of large, woody fruits that outlive the surrounding leaves and defense is now directed against cockatoos. It is possible that crypsis involving dense foliage, insect pollination, small fruits, and weak serotiny preceded bird pollination, strong serotiny and large fruits in evolutionary time but this awaits the type of trait assignment analysis undertaken on other groups (e.g. He et al., 2011).

Pollination syndromes

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Greater fruit exposure is essentially a legacy of the need to allow bird pollinators access to the inflorescences, so that ultimately large fruits may also be a response to bird pollination, along with cyanide-bearing flowers that deter florivory by non-pollinators such as cockatoos (Hanley et al., 2009, Table 14). Ready access to large granivores results from possessing open, non-spinescent foliage or producing flowers on old stems (cauliflory) that no longer bear leaves. In addition, the high level of serotiny in this genus (Groom and Lamont, 1997) means that fruits often outlive their subtending leaves so exposure to granivores occurs following leaf dehiscence (16 of the 56 species studied here), though some insect-pollinated species retain their dead leaves and this can add to the cryptic effect of the grey/brown fruits. Thus, with a few notable exceptions, our hypothesis that bird-pollinated species would have large and/or clustered fruits but lack spinescence and camouflage, while insect-pollinated would have the reverse, was supported (Tables 6,8,14). Differences in fruit size and levels of granivory in the presence/absence of spinescence–camouflage was even more striking when pollinator-type was ignored, as the exceptions were taken into account (Table 12). The ancillary hypothesis that bird-pollinated species should be more resistant to avian granivory (if bird pollination is the derived state, Hanley et al., 2009) was also supported, essentially due to their possessing much larger fruits (Table 8).

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Fire responses

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There was little evidence to support our hypothesis that resprouters would relax their resistance to granivores (as a trade-off between longevity and fecundity): resprouters are just as spinescent and exhibit the same distribution of fruit sizes (Tables 5,9). Lamont et al. (1991) also concluded that there was just as much selective pressure on resprouters to protect their (few) seeds as for nonsprouters. Instead, by far the largest differences were for seed stores, with over half of resprouters having low seed stores but all nonsprouters having medium/large seed stores. Since both disturbance-response types showed little difference in susceptibility to attack, any lack of 'apparency' due to low seed stores (optimal foraging hypothesis, Charnov, 1976) might have been mitigated by the tendency for nonsprouters to have granivore-resistant clustered fruits. ~~However,~~ ~~t~~The more likely reason~~,~~ however, is that the distribution of fruit sizes between the disturbance types was identical (Table 9D). Major differences in seed stores without an associated difference in fruit weights also suggest no trade-off between fecundity and defense (thus not supporting the optimal defense hypothesis). Low seed storage unaccompanied by greater fruit size is not an effective defense against granivory.

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Serotiny

There was strong support for our hypothesis that highly serotinous species would resist granivory much better than weakly serotinous species (Tables ~~5,~~10). Again, this was essentially due to differences in fruit size (11.5×), despite the fact that the weakly serotinous species were almost universally spinescent with cryptic fruits. With the difference in fruit weight ratio between strong and weak serotiny greater than any other trait dichotomy in our study, it is reasonable to interpret large woody fruits in essence as the optimal adaptive solution to the need to protect seeds against powerful granivores for an extended time until their release in response to fire. This interpretation has been suggested before (Stock et al., 1991) but this is the first time that there has been direct empirical evidence in its favour. This view overrides the interpretation of woody infructescences as essentially protection against the heat of fires, for even the smallest fruits examined in our study (20 mg, *H. sulcata*: nonsprouter) must be able to withstand crown fires to ensure seedling establishment in the postfire community. Alternatively, weak serotiny can be considered a resource-conserving way of avoiding predispersal granivory and fire (Groom and Lamont, 2010) akin to that by certain pines that become non-serotinous in the presence of large populations of tree squirrels (Talluto and Benkman, 2014). On the other hand, this has a much greater risk of failure as interfire recruitment is rarely successful here (Lamont and Groom, 1998).

Implications for o~~O~~ptimal defense theory

There can be no doubt that seeds are the most 'precious' resource for plants in a nutrient/water limited environment and ~~will be~~are the key to long-term fitness, even among resprouters. In addition, the seeds are enriched in mobile nutrients that facilitate recruitment following germination (Lamont and Groom, 2013). That the worldwide peak for the occurrence of serotiny lies in SW Australia is understandable where seed production is curtailed by harsh growing conditions yet it may take up to 200 seeds when droughts are severe to replace a 15-year-old plant killed by fire (Enright et al. 1996). The selection pressure has not just been in terms of the production of seeds with a high chance of recruitment success but also the presence of a formidable granivore throughout its evolutionary history. Thus, seeds are the focus of defense efforts and *Hakea* has experimented with a wide array of defense mechanisms. Though much of optimal defense theory has revolved around the use of chemical and inducible defenses (Stamp, 2003), *Hakea* has been constrained by possession of dry dehiscent fruits that at least can become woody, and/or clustered, highly sclerophyllous, isobilateral leaves that can become spinescent, and great plasticity in leaf and fruit form that lend themselves to morphogenetic shielding and mimicry, all non-chemical and constitutive (non-inducible). Since up to 50% of total above-ground phosphorus and 25% nitrogen may reside in the seeds (which account for only 0.5% of total biomass, Witkowski and Lamont, 1996), it is understandable that they be protected

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by non-chemically demanding means in the interests of nutrient conservation.

However, while the defense effectiveness of the various trait solutions can readily be assessed (as here), their relative cost, as a key component of the ODH, is less obvious. It is difficult to relate fruit size to the ODH for it is not clear what are the costs of large fruits relative to spinescent leaves (direct defense), or release of seeds at maturity or soil storage (indirect defense) as viable alternatives. It is not even clear that there is a common currency between traits for determining the cost of defense – is it carbon, phosphorus, nitrogen or water (Cramer and Midgley, 2009)? Perhaps there is merit in viewing cost/benefits in terms of seeds sacrificed or preserved (Lamont and Enright, 2000)? But then it returns to the complex issue of the resource costs of seeds. As an adaptation to minimize water loss (Groom et al., 1994), long-lived needle leaves are a source of carbon and nutrients to the developing fruits and seeds (Stock et al., 1991), with minimal costs relative to benefits. But cockatoos can learn to overcome the most intricate arrangement of spiny leaves to access the detected fruits [e.g. the highly spinescent *H. auriculata* (Fig. 2A) may on occasions be severely attacked].

Likewise, woody fruits are multifunctional, producing carbon compounds when green with little water loss (Cramer and Midgley, 2009), acting as a source of nutrients during seed-filling (Groom and Lamont, 2010), and protecting the seeds against fire heat and granivores, so that their net cost is not obvious. In addition, seeds of more serotinous fruits have a higher phosphorus content and the consequent fitness advantages for recruitment may be critical in a nutrient and water-constrained environment (Lamont and Groom, 2013). In a seed-limited environment, where seedling recruitment is most likely after fire, the benefits of serotiny/pyriscence are clear (Lamont et al., 1991; He et al., 2011, Causley et al., 2016) and our study shows that seeds are best protected by large woody fruits for maximizing seed stores. This defense is so successful that strongly serotinous species (low annual production) store just as many seeds on the plant at any time as weakly serotinous (high annual production).

Consistent with the ODH, larger seeds are protected by larger fruits and decreasingly likely to be attacked. This was not at the expense of the number of seeds stored however (resource trade-offs), partly because growth form varies greatly between species (and hence their ability to support fruits) and the confounding caused by different fire responses (resprouters produce few fruits independent of seed size) and levels of serotiny (seed stores are not necessarily a function of annual production). So, while the traits with maximum benefits are clear their relative costs are not, such that some aspects of the ODH could not be addressed here. However the benefits versus costs of large woody fruits are measured, they clearly outweigh those of any other seed defense trait under the selection pressures of fire-prone, resource-limited environments (that promote serotiny), efficient bird pollinators [~~(~~that promote flower (hence fruit) apparency]~~)~~ and formidable avian granivores (that promote strong defense).

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Implications for a general understanding of seed defense

The five traits could be ranked from most to least effective in deterring granivory in the following order: large fruits (85% of medium/large-fruited species with no granivory), fruit clustering, low seed store, spinescence and camouflage (40% of camouflaged species with no granivory) with the first five times more effective at preventing seed loss than the last (Table 12). As a result, the best combinations for deterring granivory were medium/large fruits lacking spinescence or camouflage independent of seed store size (30% of species in five combinations), i.e. essentially due to large fruit size (Table 13). There was no support for the optimal foraging view that predators favour plants with a few, larger seeds over many, smaller seeds (contrast Blate et al., 1998) because the former are so well-defended by woody tissues. Besides, smaller seeds have higher seed:fruit weight ratios making them more rewarding to open (if detected) per unit effort. Our initial hypothesis of a dominant syndrome having moderate/strong spinescence and camouflage with medium/large fruits and low/medium seed stores received no support, only accounting for 14% of species in eight combinations.

There are limited parallels with other plant groups. Self-mimicry occurs among certain *Lambertia* (Proteaceae) species: contrast the echinate fruits and spinescent leaves of *L. echinata* and

L. ilicifolia with the orbicular leaves and fruits (that remain green) of *L. orbifolia* (Hnatiuk, 1996; B. Lamont, pers. observ.). *Lambertia* is bird-pollinated and the single, exposed, serotinous fruits are vulnerable to granivory by parrots (L. Sage and B. Lamont, unpubl. report). However, the fruits are never woody like hakeas. Some other grevilleoid Proteaceae possess woody fruits equivalent to those of *Hakea*: *Banksia*, *Cardwellia*, *Strangea* and (especially) *Xylomelum* (Lamont and Groom, 1998). However, none of these displays spinescence or camouflage. The leaves of *Xylomelum* may be cyanogenic but they are never wrapped around the fruits and granivory on their huge woody fruits, similar to *H. platysperma* (Fig. 2h) in weight, is unknown (B. Lamont, pers. observ.). *Banksia* and *Dryandra* usually possess clustered fruits partly buried among velvety bracts to form a cone. These provide a ready target for cockatoos but are most vulnerable when the follicles split open to expose the seeds after fire (Cowling and Lamont, 1987; Merwin et al., 2012). Clustering of serotinous fruits among leptospermoid Myrtaceae has been shown to reduce heat damage from fire (Judd and Ashton, 1991) but this is the first time that clustered fruits have been implicated in deterring granivores.

The most obvious parallels are with some conifers (Table 15): the red crossbill (*Loxia curvirostra*) is a finch adept at prising apart the scales of serotinous pine cones and extracting the seeds (Benkman et al., 2003). Just as strongly serotinous fruits have thicker, woodier tissues and are thus better protected from fire heat and granivores, so too strongly serotinous conifer cones have thicker, woodier scales (and in some species, spinier as well) more resistant to heat, crossbills, squirrels and moth borers (Elliott, 1974; Linhart, 1978; Lamont et al., 1991; Benkman et al., 2003). When serotinous pines were introduced to Western Australia, black cockatoos quickly adapted to their presence, destroying the cones in their search for seeds and carrying removed cones for some kilometres (He et al., 2004, Stock et al., 2013). Clearly, cockatoos are a much more formidable selective agent than crossbills and hakeas have responded accordingly. On the other hand, squirrels may be so effective at gathering new cones in some areas that *Pinus contorta* subsp. *latifolia* has become non-serotinous (Talluto and Benkman, 2014). This is not an option for hakeas where cockatoos only remove a fraction of the seeds and interfire recruitment is rarely successful (Lamont and Groom, 1998). Interestingly, cockatoo granivory is unknown among grevilleas, ~~sister genus~~paraphyletic to *Hakea* (Table 15): here, seeds are released at maturity (non-serotinous) perhaps giving cockatoos inadequate or unreliable timespans to search for seeds (fruits are always present on serotinous hakeas so are a reliable source of seeds and we noted that some populations were visited continually over successive years).

By far the most intriguing finding is the link between pollination and seed-defense syndromes (Table 14). It is not unusual for the same group of animals to affect two components of the reproductive biology of a plant. Granivorous animals are typically seed dispersers as well, especially rodents and birds (Table 15). However, in the case of *Hakea*, cockatoos are adept at harvesting seeds while perched on the plant, whereas seeds are strictly wind-dispersed. There are specialized cases of animals that pollinate flowers as well as disperse seeds, such as mistletoe birds (*Dicaeum* spp.), with both flowers and fruits adapted to the same visitor without granivory. In many tropical species, bats (pteropodids) may be pollinators a well as non-granivorous, seed dispersers but a range of animals is used for both by any one species, and some of these may be granivorous (Table 15, Hodgkison, 2003).

It has been suggested that the flowers of the baobab (*Adansonia* spp.), sausage (*Kigelia africana*) and (possibly) cannonball (*Couroupita guianensis*) trees, suspended on hanging, naked stems (penduliflory), ensure access to aerial pollinators but deter large frugivores (e.g. monkeys) from reaching the unripe fruits (Marshall, 1983). This multipurpose mechanism is opposite to that in hakeas where (later) adaptation to bird pollinators increased their vulnerability to florivory and granivory by cockatoos and stimulated the evolution of an additional suite of resistance traits: cyanogenic, red (aposematic) flowers (Hanley et al., 2009); spinescence/crypsis; and, especially, woody, sometimes clustered, fruits (Table 14). The only other example of a plant group subject to the same florivore and granivore species that we could find was *Solanum carolinense* where beetles (*Leptinotarsa juncta*) feed on both its flowers and fruits. This species responds proximally, rather than ultimately – in contrast to *Hakea*, by altering its flower sex ratio, reducing production of male flowers as beetle activity increases (Wise and Hébert, 2010).

If large fruits are such an effective granivore deterrent, why do only 50% of the species we examined have fruits weighing in excess of 1 g? Certainly, phylogenetic constraints have little role as there is only a weak phylogenetic signal in the data (Appendix, Table C) and all fruits are essentially woody; thus any part of the clade is capable of forming large woody fruits (this is true of all traits we examined, Fig. 5). One reason is that they are resource-expensive to produce (Groom and Lamont, 2010): the fruits themselves are a major sink for mineral nutrients in a nutrient-limited environment despite the fact that major nutrients are remobilized efficiently into the seeds with time. Another is that a stout stem is required to support them – only shrubs > 2 m tall or resprouters that develop long-lived major stems, often coupled with the capacity for cauliflory, are suitable. Another is that they may take several years to reach their final size and woodiness and they may be vulnerable to attack in the meantime. Clustering seems one way to achieve mechanical protection without the constraints on large fruit size noted here but is rare by comparison, clustered fruits were often just as large as unclustered, and it appears to be phylogenetically constrained (the *H. francisiana* and *scoparia* groups).

If acicular, vertically-oriented leaves are essentially a water-conserving device (Groom et al., 1994; Lamont et al., 2002) then there is little resource cost in adding a sharp tip to their apices and making them protective as well. In view of their inefficiency at deterring granivores, they may be more directed at protecting new (axillary) foliage from herbivores, or flowers from avian florivores (Hanley et al., 2009). As with spinescence, camouflage can be considered an alternative defense to large fruits in many species but is rarely successful against cockatoos. It is difficult to view self-crypsis as other than a granivore deterrent, and it is highly effective in *H. trifurcata* (Groom et al., 1994), but, as noted above, it may be more directed at invertebrate granivores that favour young fruits. Otherwise, black cockatoos seem one step ahead of the plants though it is probably a learned response rather than genetic (they quickly adapted to pine cones once they became available).

Perhaps overcoming the defenses of spinescence and crypsis is a more recent learned response (associated with declining natural vegetation?) and the evolution of the more effective large fruits, that more than meet the match of these birds, is just a matter of time.

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Appendices

Tables A, B, C

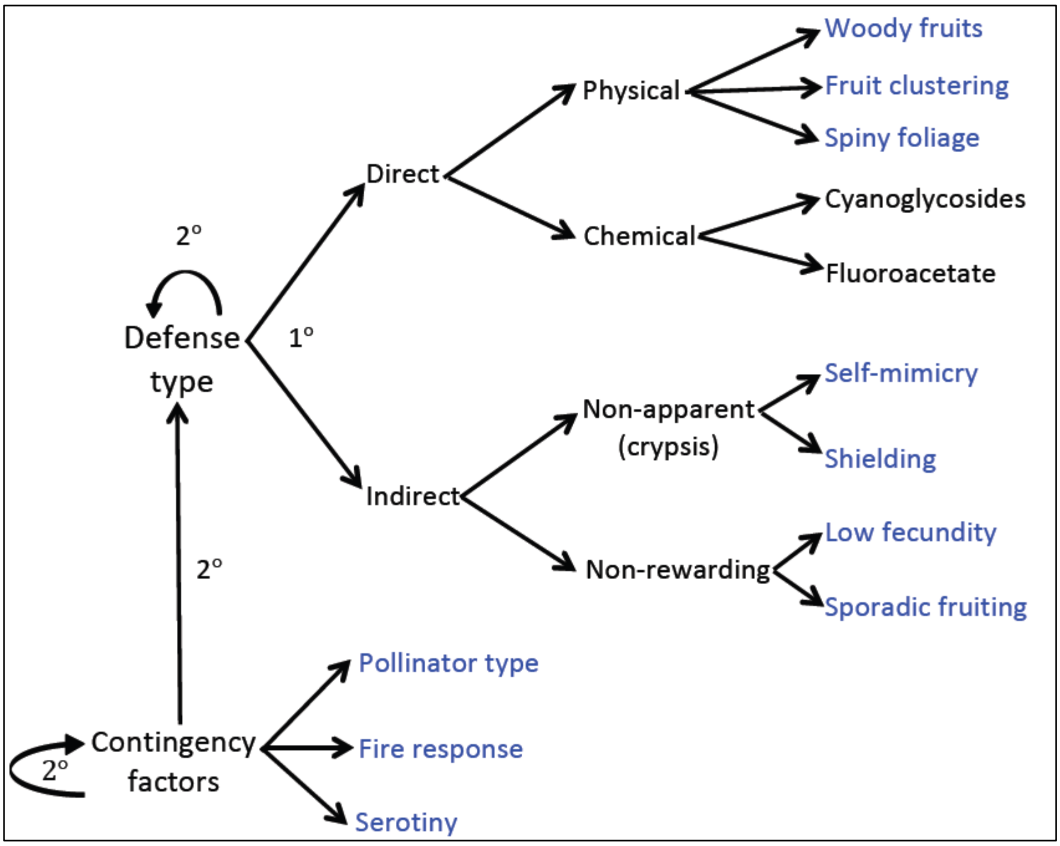

Fig. 1. Scheme showing relationships between the various possible seed-defense types and factors that modify their intensity through evolutionary time. For example, bird pollination promotes open foliage via a secondary (2°) pathway that favours production of large woody fruits, which protect seeds directly through the primary (1°) pathway. Thus, fruit size is (partly) contingent on pollinator type. Note that both contingency and defense factors can affect the intensity of others via 2° pathways (see Fig. 2). Factors relevant to this study are highlighted in blue. Note also that fire regime is the ultimate driver of fire responses and level of serotiny among hakeas.

Fig. 2. Selection of *Hakea* species showing various putative seed-defense traits against cockatoos. a. Echinate fruits of *H. auriculata* surrounded by extremely spinesent leaves (that caused more wounding of dummy cockatoo heads than any other species in this study); b. *H. polyanthema* with needle leaves projecting beyond young fruits with other fruits deeper in the retained dead foliage not visible; c. Dummy head of black cockatoo showing punctures, scratches and embedded spiny leaf that abscised during withdrawal from *H. polyanthema* foliage. d. *H. cristata* with green barbed fruit not unlike the surrounding toothed leaves in appearance. e. *H. spathulata* with brown warty fruit hidden among dead persistent leaves and stems of similar shape and colour; f. mature fruit of *H. stenocarpa* apparently mimicking short stems, even bearing dormant 'buds'; g. Open fruits of four *Hakea* species showing the two woody valves and impressions left by the two winged seeds they contained before dehiscence; h. Cricket-ball-~~-~~shaped *H. platysperma* fruit showing beak score marks from failed attempts by black cockatoo to open it; i. *H. orthorrhyncha* with clusters of smooth, woody fruits from flowers produced on old stems devoid of leaves (cauliflory). Scales also serve to identify the fruits. (photos by M.E. Hanley, B.B. Lamont and T. He)

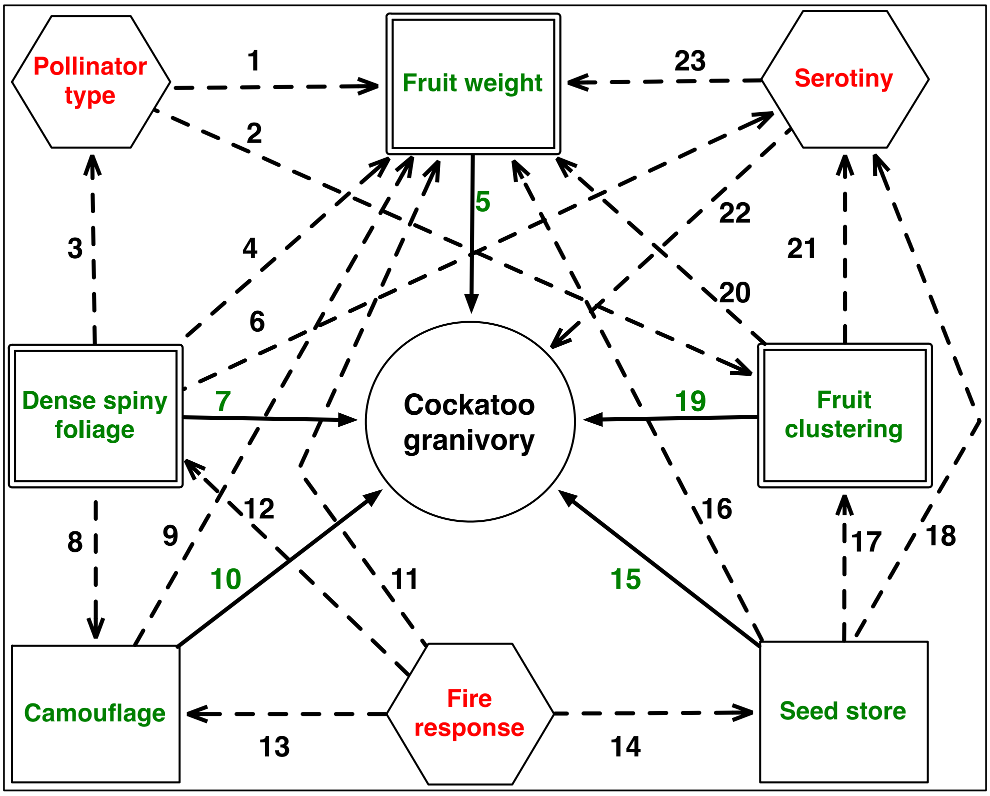

Fig. 3. Variables expected to affect the presence and level of cockatoo granivory (circled) and tested for their significance and relationship via SEM analysis (Table 1). Variables expected to defend seeds directly via large woody fruits, fruit clustering or dense spiny foliage are framed by double squares while those acting indirectly (camouflage, low seed store) are framed by single squares. Hexagons frame variables expected to have a contingency effect on granivory by modifying (through evolutionary time) properties of the variables having a primary effect. Primary pathways are indicated by solid arrows while secondary pathways are given by broken arrows. Numbers correspond to the hypotheses outlined in Table 1.

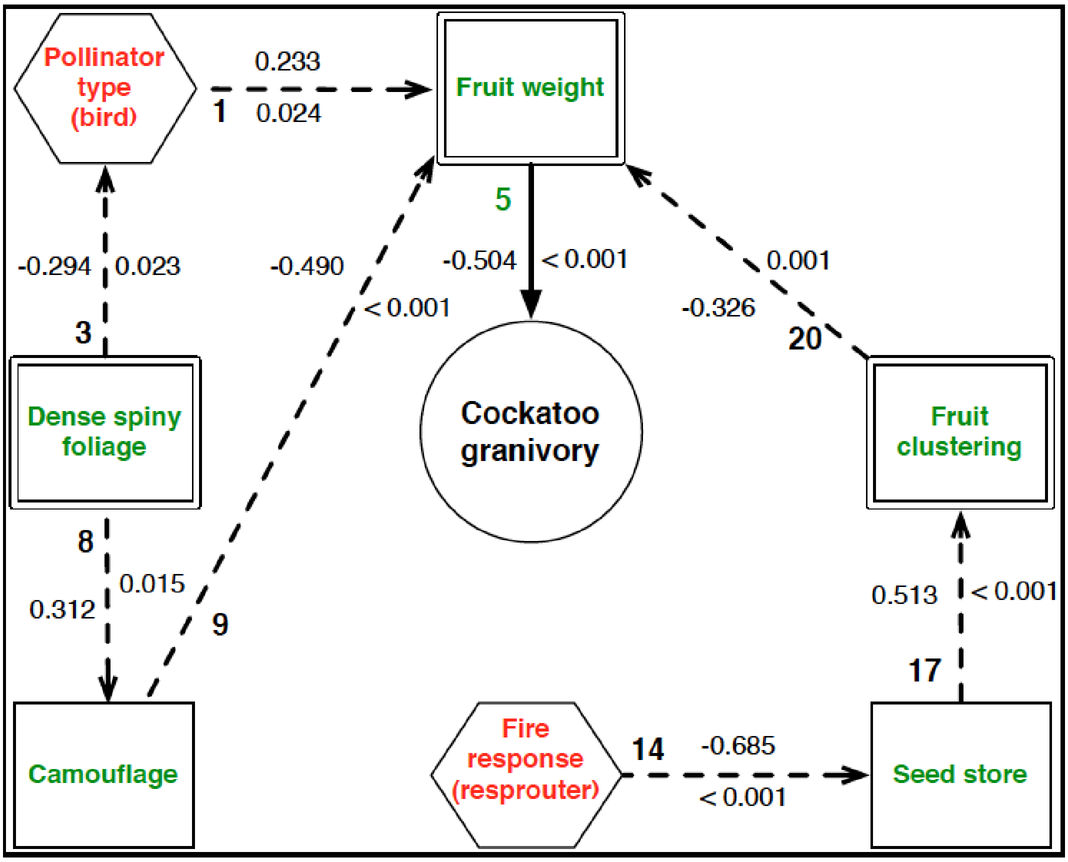

Fig. 4. Best-fit model showing the causal pathways affecting the presence and level of cockatoo granivory (model fit: $\chi^2 = 25.0$, df =20, *P* =0.20; RMSEA = 0.06; CFI = 0.95). Numbers at the base of the arrows refer to the hypotheses specified in Table 1. Numbers within the arrows are values of the most significant standardized direct effects followed by their *P* values.

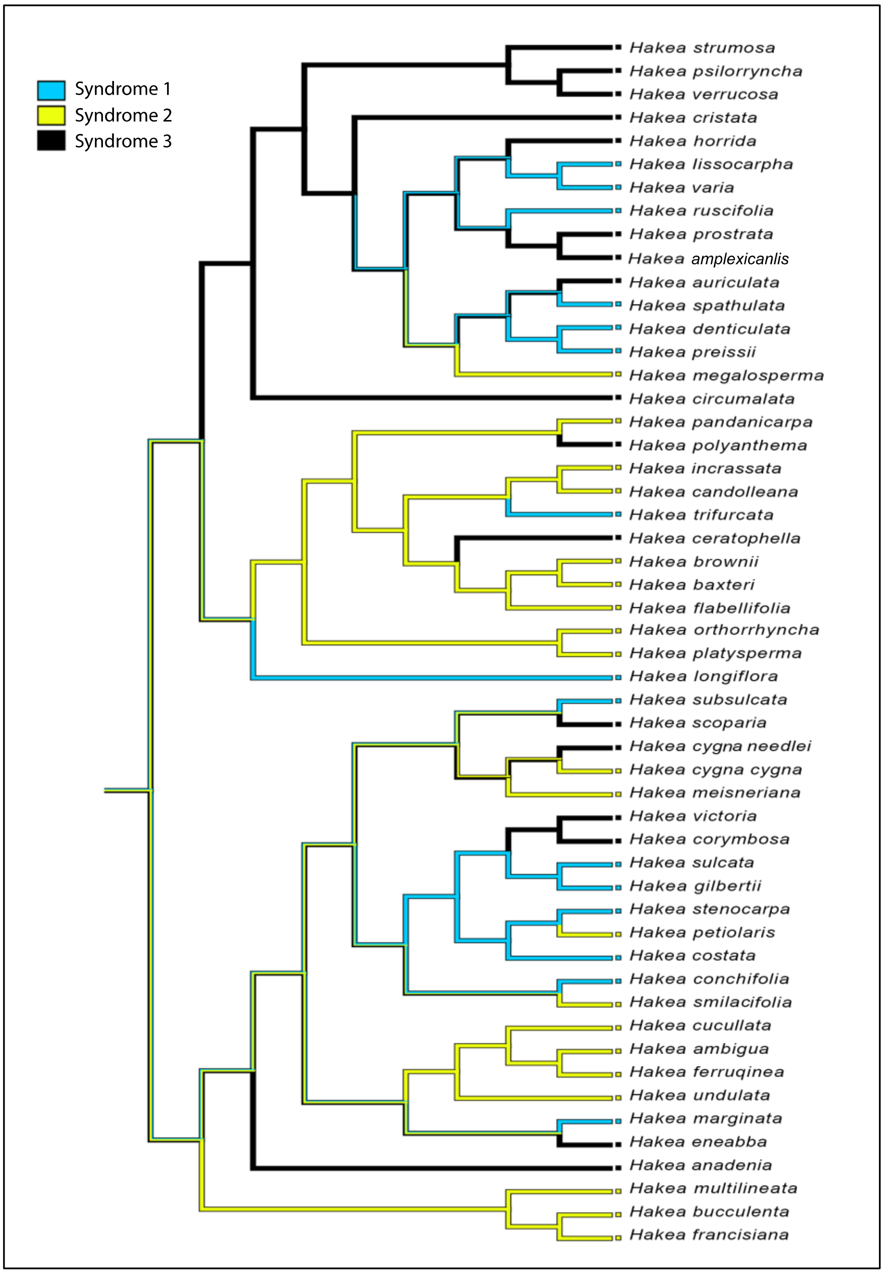

Fig. 5. Molecular phylogeny for 52 *Hakea* species in southwestern Australia to which three seed-defense syndromes (based on fruit size and clustering, presence of spiny foliage and fruit camouflage) have been added (see Table 12). Trait syndromes~~s~~ ~~have been~~were assigned to all lineages, according to MCMC procedures, with the ~~trait~~ syndrome having highest probability indicated in blue, yellow or black. Where assignment is ambiguous, lines are multi-colored, green indicating equal probability of blue and yellow.

Table 1. Outlines of 23 directional hypotheses analysed individually and collectively via contingency table, multiple correlation and SEM analyses with current support added. The associated opposing hypothesis is not always stated. Hypotheses shown to be significant by contingency-table analysis (Tables 7~~5~~–11~~9~~) are given in *italics* and~~,~~ phylogenetically-corrected partial correlation analysis (Table 5~~7~~) in green, while pathways shown to be significant by SEM analysis (Table 6~~7~~) are in **bold**.

#	Hypothesis	Support
1	***Bird-pollinated flowers favour seed defense by large woody fruits***	Groom and Lamont 1997
2	*Bird-pollinated flowers favour seed defense by clustered fruits*	Judd and Ashton 1991
3	***Dense, spiny foliage favours insect pollination while open, non-spiny foliage and cauliflory favour bird pollination***	Hanley et al. 2009
4	*Dense, spiny foliage favours small (cryptic) fruits while open, non-spiny foliage and cauliflory favour large (exposed) fruits*	Groom et al. 1994, Groom and Lamont 1997
5	***Large woody fruits deter cockatoo granivores directly***	Groom and Lamont 1997
6	Dense, spiny foliage deters cockatoo granivory and favours evolution of serotinous fruits*	Hanley et al. 2009, logic
7	Dense, spiny foliage deters cockatoo granivory directly*	Hanley et al. 2009
8	***Dense, spiny foliage promotes fruit camouflage (crypsis)***	Groom et al. 1994
9	***Poorly camouflaged fruits are large***	Groom and Lamont 1997
10	Well-camouflaged fruits deter cockatoo granivory indirectly*	Groom et al. 1994
11	Resprouters maximize defense of their few fruits by ~~their~~ being large and woody	Optimal defense theory (contrast optimal foraging theory)
12	Resprouters maximize defense of their few fruits via dense, spiny foliage	Optimal defense theory (contrast optimal foraging theory)
13	*Resprouters maximize defense of their few fruits via crypsis*$^{\#}$	Optimal defense theory (contrast optimal foraging theory)
14	***Resprouters have low seed stores (and no fruit clustering, #17)***	Lamont and Wiens 2003
15	Species with large seed stores are more likely to be attacked by cockatoos	Optimal foraging theory (contrast optimal defense theory)
16	Large seed stores have small fruits	Resource trade-off theory, optimal defense theory
17	***Species with large seed stores are more likely to have clustered fruits (requires high seed set)***	Logic, personal observations
18	Seeds with low seed stores are more likely to be serotinous	Optimal defense theory, Lamont et al. 1991
19	*Clustering of fruits increases resistance to cockatoos directly*	Judd and Ashton 1991 (less heat damage)
20	**Clustered fruits are smaller than non-clustered**	Resource trade-off theory
21	Fruit clustering deters cockatoo granivory and favours evolution of serotinous fruits	Judd and Ashton 1991 (less heat damage), Lamont et al. 1991
22	*Strongly serotinous fruits are well defended against cockatoos*	Groom and Lamont 1997
23	*Serotinous fruits are larger than non-serotinous*	Groom and Lamont 1997

*results the reverse of those predicted

$^{\#}$*P* = 0.058 (Table 9)

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Table 2. Distribution of (A) granivory, (B) spinescence, (C) camouflage, (D) fruit size and (E) seed store among all *Hakea* species in each of three districts (subregions) along a 900 km climatic gradient. Values are % (number of species) within districts. (F) Mean level of seed loss through granivory among species in common in the three districts (*as a % of the maximum possible by class). (1)/(2) 1/2-tailed test depending on conformity to initial hypothesis (see Methods). For Tukey’s test, categories with different letters differ at $P \leq 0.05$. $^{\#}P$ for 1-way ANOVA of standardised phylogenetic distances (SPD).

A. Granivory	Not attacked	Attacked	SPD	Seed loss when attacked*	Tukey's test
Irwin District	70 (21)	30 (9)	0.997	36	a
Darling District	53 (8)	47 (7)	0.991	25	a
Eyre/Roe Districts	77 (20)	23 (6)	1.005	23	a
P χ2 test (2)		0.287	0.942$^{\#}$		
B. Spinescence	Nil	Moderate	Strong	Head wounds from spiny foliage	
Irwin	27 (8)	30 (9)	43 (13)	4.88	a
Darling	20 (3)	47 (7)	33 (5)	2.52	b
Eyre/Roe	31 (8)	46 (12)	23 (6)	2.18	b
P χ2 test (1)		0.256			
C. Camouflage	Nil	Camouflaged		Non-camouflaged fruit wt (mg)	
Irwin	67 (20)	33 (10)		6116	a
Darling	40 (6)	60 (9)		3885	a
Eyre/Roe	69 (18)	31 (8)		5282	a
P χ2 test (2)		0.140			
D. Fruit size	Small	Medium	Large	Fruit weight (mg)	
Irwin	40 (12)	30 (9)	30 (9)	4348	a
Darling	47 (7)	20 (3)	33 (5)	2174	b
Eyre/Roe	35 (9)	38 (10)	27 (7)	3810	a
P χ2 test (2)		0.817			
E. Seed store	Low	Medium	High		
Irwin	37 (11)	50 (15)	13 (4)		
Darling	53 (8)	40 (6)	7 (1)		
Eyre/Roe	27 (7)	65 (17)	8 (2)		
P χ2 test (2)		0.445			

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Table 3. Mean seed weights (mg) under given conditions/traits (true) versus their opposing conditions/traits (not true) compared by t-tests with unequal variances and 1-tailed if numerically supporting the hypothesis (optimal defense theory) and 2-tailed if not supporting the hypothesis (see text). ~~Need sample sizes~~Number of species in each category given in parentheses

Condition/trait	**True**	**Not true**	***P* (t-test)**
Consumed by cockatoos	20.9 (20)	55.2 (36)	0.0173 (1)
Fruits large (> 1 g)	62.9 (31)	15.2 (25)	0.0033 (1)
Fruits cryptic	32.0 (20)	48.4 (36)	0.3204 (2)
Leaves spinescent	29.0 (36)	63.3 (20)	0.1745 (2)
Burnt plants killed	39.0 (32)	46.1 (24)	0.1741 (1)
Fruits serotinous	46.4 (45)	26.1 (11)	0.0596 (1)
Bird-pollinated	59.1 (17)	36.6 (39)	0.2287 (1)

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Table 4. Fractions of small (< 21.5 mg, median size for all species) and large (≥ 21.5 mg) seeds under given conditions/traits compared by Fisher's exact probability test and 1-tailed if numerically supporting the hypothesis (optimal defense theory) and 2-tailed if not supporting the hypothesis (see text).

Condition/trait	**Small seeds (%, *n* = 27 ~~total~~)**	**Large seeds (%~~-~~, *n* = 28~~total~~)**	***P* (χ^2-test)**
Consumed by cockatoos	51.9	25.0	0.0377 (1)
Fruits large (> 1 g)	29.6	78.6	< 0.0001 (1)
Fruits cryptic	33.3	39.3	0.4295 (1)
Leaves spinescent	66.7	57.1	0.5815 (2)
Burnt plants killed	77.8	35.7	0.0018 (1)

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Fruits serotinous	77.8	85.7	0.3401 (1)
Bird-pollinated	37.0	25.0	0.3911 (2)

Table 5. Phylogenetically corrected ~~Pairwise~~ correlation between all traits that may be related to granivory. Lower triangle contains partial correlation coefficient values and upper triangle has their *P* values. Significant values ($P \leq 0.05$) highlighted in red, while ~~significant~~ pairs used in the best-fit SEM pathway (Fig. 4) have grey backgrounds. –ve and +ve represent the direction of the correlation.

Attribute	Cockatoo granivory	Spiny foliage	Camouflage	Fruit weight	~~Fire response~~ Resprouter	Serotiny	Insect p~~P~~ollinator ~~type~~	Seed store	Fruit clustering
Cockatoo granivory	-	0.698	0.032 (–ve)	0.022 (–ve)	0.357	0.083	0.864	0.234	0.606
Spiny foliage	0.055	-	0.233	0.124	0.729	0.040 (–ve)	0.254 (+ve)	0.381	0.522
Camouflage	0.298	0.167	-	0.017 (–ve)	0.088	0.034 (–ve)	0.281	0.346	0.386
Fruit weight	–0.305	–0.219	–0.332	-	0.662	0.050 (+ve)~~6~~	0.014 (–ve)	0.486	0.662 (–ve)

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Fire response (resprouter)	0.138	0.044	0.189	0.032	-	0.086	0.915	<0.001 (–ve)	0.043 (–ve)
Serotiny	–0.242	–0.279	–0.279	0.258	0.240	-	0.795	0.750	0.525
Pollinator type (insect)	0.063	0.161	0.151	–0.339	0.044	–0.037	-	0.951	0.053 (–ve)
Seed store	0.044	–0.118	–0.130	–0.094	–0.590	0.045	–0.027	-	0.249 (+ve)
Fruit clustering	–0.067	–0.089	–0.122	–0.063	–0.494	0.089	–0.250	0.162	-

Table 6. Standardised total effects from SEM analysis on attributes relevant to the presence and level of cockatoo granivory. Pairwise traits used in the best-fit model have grey backgrounds.

Attribute	**~~Fire response~~ Resprouter**	**Seed store**	**Spiny foliage**	**Camouflage**	**Fruit clustering**	**Insect p~~P~~ollinator~~ type~~**	**Fruit weight**
Seed store	–0.685	-	0	0	0	0	0
Camouflage	0	0	~~-~~0.312	-	0	0	0
Fruit clustering	–0.351	0.513	0	0	-	0	0
Insect p~~P~~ollinator ~~type~~	0	0	~~-~~0.294	0	0	-	0
Fruit weight	0.115	–0.167	–0.2~~2~~1	–0.490	–0.326	–0.233	-
Granivory~~Cockatoo granivory~~	–0.058	0.085	~~-~~0.113	0.250	0.166	0.119	–0.504

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Table 7. Distribution of granivory among 56 *Hakea* species relative to level of (A) spinescence, (B) camouflage, (C) fruit size and (D) seed store, and relationship between (E) spinescence and fruit size, (F) fruit weight and spinescence, (G) fruit weight and camouflage, and (H) fruit weight and seed store. Values in A—E are % (# species) across rows. * % of maximum possible (by class). (1), (2) = 1, 2-tailed test depending on conformity to initial hypothesis (see Methods). For Tukey's test, categories with different letters significantly different at $P \leq 0.05$. Pale grey background: significant in multiple correlation analysis (Table 5), medium grey background: component of best-fit SEM model (Fig. 4).

A. Spinescence	**No granivory**	**Granivory**	**Seed loss when attacked***
Nil	95 (18)	5 (1)	17
Moderate	45 (9)	55 (10)	30
Strong	56 (10)	44 (8)	34
		0.004	
B. Camouflage			
Nil	81 (29)	19 (7)	13
Camouflaged	40 (8)	60 (12)	37
P χ2 test (2)		0.002	
C. Fruit size			
Small	38 (8)	62 (13)	36
Medium	67 (12)	22 (6)	24
Large	94 (16)	6 (1)	5
P χ2 test (1)		0.001	
Fruit weight (mg)	5216	1323	*P* <0.001 (1)
D. Seed store			
Low	79 (11)	21 (3)	48
Medium	64 (21)	36 (12)	34
High	88 (7)	12 (1)	□
P χ2 test (2)		0.255	
E. Spinescence vs fruit size			
	Small	Medium	Large
Nil	15 (3)	30 (5)	55 (11)
Moderate/strong	53 (19)	33 (13)	14 (5)
P χ2 test (1)		0.001	
F. Fruit weight (mg) vs spinescence			
	Nil	Moderate	Strong
	8180	1882	1965
Tukey's test	a	b	b
G. Fruit weight (mg) vs camouflage			
	Nil	Camouflaged	
	5578	1124	
P t-test (1)		<0.001	
H. Fruit weight (mg) vs seed store			
	Low	Moderate	High
	4035	4602	2412
Tukey's test	a	a	a

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Table 8. Distribution of 56 *Hakea* species with bird or insect pollination classified according to their levels of (A) granivory, (B) spinescence, (C) camouflage, (D) fruit size and (E) fruit clustering. Values are % (# species). * % of maximum possible (by class). (1)/(2) 1/2-tailed test depending on conformity to initial hypothesis (see Methods). [@] *P* t-test. Pale grey background: significant in multiple correlation analysis (Table 7), medium grey background: component of best-fit SEM model (Fig. 4).

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~~**Table 8.** Distribution of 56 *Hakea* species with bird or insect pollination classified according to their levels of (A) granivory, (B) spinescence, (C) camouflage, (D) fruit size and (E) fruit clustering. Values are % (# species). * % of maximum possible (by class). (1)/(2) 1/2-tailed test depending on conformity to initial hypothesis (see Methods). $^{@}$ *P* t-test. Pale grey background: significant in multiple correlation analysis (Table 7), medium grey background: component of best-fit SEM model (Fig. 4).~~

A. Granivory	Not attacked	Attacked	Seed loss when attacked*
Bird pollination	84 (15)	16 (2)	37
Insect pollination	58 (22)	42 (17)	30
P χ2 test (1)		0.010	>0.500 (2$^{@}$)
B. Spinescence	Nil	Mod/strong	Head wounds from spiny foliage
Bird	56 (10)	44 (7)	1.88
Insect	23 (9)	77 (30)	4.11
P χ2 test (1)		0.005	0.235 (1$^{@}$)
C. Camouflage	Nil	Camouflaged	
Bird	78 (14)	22 (3)	
Insect	58 (22)	42 (17)	
P χ2 test (1)		0.031	
D. Fruit size	Small	Medium/large	Fruit weight (mg)
Bird	18 (3)	82 (14)	7214
Insect	44 (17)	56 (22)	2861
P χ2 test (1)		0.031	0.020 (1$^{@}$)
E. Clustering	No	Yes	
Bird	61 (10)	39 (7)	
Insect	95 (37)	5 (2)	
P χ2 test (1)		<0.001	

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Table 9. Distribution of 56 *Hakea* species that resprout or are killed by severe disturbance classified according to their levels of (A) granivory, (B) spinescence, (C) camouflage, (D) fruit size and (E) seed store. Values are % (# species). *% of the maximum possible by class. (1)/(2) 1/2-tailed test depending on conformity to initial hypothesis (see Methods). $^{@}$ *P* t-test. Pale grey background: significant in multiple correlation analysis (Table 7), medium grey background: component of best-fit SEM model (Fig. 4).

A. Granivory	Not attacked	Attacked	Seed loss when attacked*
Resprouter	57 (13)	43 (10)	31
Nonsprouter	73 (24)	27 (9)	30
P χ2 test (1)		0.104 (0.160)	0.262 (1$^{@}$)
B. Spinescence	Nil	Mod/strong	Head wounds from spiny foliage
Resprouter	26 (6)	74 (17)	4.20
Nonsprouter	39 (13)	61 (20)	3.26
P χ2 test (2)		0.155	0.374 (1$^{@}$)
C. Camouflage	Nil	Camouflaged	
Resprouter	48 (11)	52 (12)	
Nonsprouter	73 (24)	27 (9)	
P χ2 test (2)		0.058	
D. Fruit size	Small	Medium/large	Fruit weight (mg)
Resprouter	39 (9)	61 (14)	3847
Nonsprouter	39 (13)	61 (20)	4372
P χ2 test (2)		0.984	0.299 (1$^{@}$)
E. Seed store	Low	Moderate	High
Resprouter	52 (12)	31 (7)	17 (4)
Nonsprouter	0 (0)	73 (24)	27 (9)
P χ2 test (1)		<0.001	
F. Clustering	Isolated	Clustered	
Resprouter	96 (22)	4 (1)	
Nonsprouter	70 (23)	30 (10)	
P χ2 test (1)		0.008	

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Table 10. Distribution of 56 *Hakea* species with weak or strong serotiny classified according to their levels of (A) granivory, (B) spinescence, (C) camouflage, (D) fruit size and (E) seed store. Values are % (# species). * % maximum possible (by class). (1)/(2) 1/2-tailed test depending on conformity to initial hypothesis (see Methods). $^{@}$ *P* t-test. Pale grey background: significant in multiple correlation analysis (Table 7).

A. Granivory	Not attacked	Attacked	Seed loss when attacked*
Strong serotiny	76 (35)	24 (11)	32.6
Weak serotiny	20 (2)	80 (8)	27.8
P χ2 test (1)		<0.001	>0.500 (2$^{@}$)
B. Spinescence	Nil	Mod/strong	Head wounds from spiny foliage
Strong serotiny	41 (19)	59 (27)	4.47
Weak serotiny	0 (0)	100 (10)	1.59
P χ2 test (2)		0.012	0.035 (1$^{@}$)
C. Camouflage	Nil	Camouflaged	
Strong serotiny	78 (36)	22 (10)	
Weak serotiny	10 (1)	90 (9)	
P χ2 test (2)		<0.001	
D. Fruit size	Small	Medium/large	Fruit weight (mg)
Strong serotiny	28 (13)	72 (33)	4966
Weak serotiny	80 (8)	20 (2)	430
P χ2 test (1)		0.001	<0.001 (1$^{@}$)
E. Seed store	Low	Medium/high	
Strong serotiny	26 (12)	74 (34)	
Weak serotiny	50 (5)	50 (5)	
P χ2 test (2)		0.136	

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Table 11. Distribution of 56 *Hakea* species with clustered or isolated fruits classified according to their levels of (A) granivory, (B) spinescence, (C) camouflage, (D) fruit size and (E) seed store. Values are % (# species). ^sample size too small for statistical test. (1)/(2) 1/2-tailed test depending on conformity to initial hypothesis (see Methods). $^{@}$ *P* t-test. Medium grey background: component of best-fit SEM model (Fig. 4).

A. Granivory	Not attacked	Attacked	Seed loss when attacked*
Isolated	62 (28)	38 (17)	34
Clustered	82 (9)	18 (2)	3
Fruits/cluster	4.50	2.10^	
P χ2 test (1)		0.109	<0.001 (1$^{@}$)
B. Spinescence	Nil	Mod/strong	Head wounds from spiny foliage
Isolated	29 (13)	71 (32)	3.59
Clustered	55 (6)	45 (5)	4.20
P χ2 test (1)		0.053	>0.500 (2$^{@}$)
C. Camouflage			
	Nil	Camouflaged	
Isolated	56 (25)	44 (20)	
Clustered	91 (10)	9 (1)	
P χ2 test (1)		0.015	
D. Fruit size			Fruit weight (mg)
	Small	Medium/large	
Isolated	47 (21)	53 (24)	4723
Clustered	45 (5)	55 (6)	1839
P χ2 test (1)		0.471	0.394 (1$^{@}$)
E. Seed store			
	Low	Medium/high	
Isolated	40 (18)	60 (27)	
Clustered	0 (0)	100 (11)	
P χ2 test (1)		0.005	

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Table 12. Five morphological attributes ranked according to their Effectiveness at deterring avian granivores (black cockatoos) among 56 *Hakea* species in SW Australia, calculated as % of species supporting the proposed hypothesis divided by % not supporting that hypothesis. x/y is number of species conforming to the hypothesis (ie no granivory) compared with the total possessing that trait. Seed loss when attacked is presented as % of maximum possible.

Attribute	**Values used**	**No. of species**	**Effectiveness**	**Seed loss when attacked**
1. Fruit size	(large + medium)/small	29/34	2.39	23
2. Clustering	clustered/isolated	9/11	1.41	3*
3. Seed store	(medium + low)/high	26/38	0.64	32
4. Spinescence	(strong + moderate)/nil	18/36	0.56	32
5. Camouflage	camouflaged/nil	8/20	0.48	37

*only 2 species attacked

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Table 13. Hierarchical classification of 56 *Hakea* species in southwestern Australia based on their level of spinescence (injury to dummy black cockatoo heads) and three fruit attributes, plus presence of fruit clustering, ability to resprout after disturbance, and whether fruits are attacked by black cockatoos. Colour scheme: blue = - spinescence, - camouflage, medium/large/clustered fruits, pink = + spinescence, ± camouflage, small fruits, green = + spinescence, ± camouflage, medium/large fruits.

Spinescence	**Fruit camouflaged**	**Fruit size**	**Seed store**	**Σ Species**	**Clustered**	**Resprouting**	**% not attacked***
nil	no	small	low	0	–	–	–
nil	no	small	medium	1	1	0	100
nil	no	small	high	1	1	0	100
nil	no	medium	low	0	–	–	–
nil	no	medium	medium	2	0	0	100
nil	no	medium	high	4	2	0	100
nil	no	large	low	5	0	3	100
nil	no	large	medium	4	1	0	100
nil	no	large	high	2	1	1	100
nil	yes	small	low	0	–	–	–
nil	yes	small	medium	1	0	1	0
nil	yes	small	high	0	–	–	–
nil	yes	medium	low	0	–	–	–
nil	yes	medium	medium	0	–	–	–
nil	yes	medium	high	0	–	–	–
nil	yes	large	low	0	–	–	–
nil	yes	large	medium	0	–	–	–
nil	yes	large	high	0	–	–	–
moderate	no	small	low	2	0	2	100
moderate	no	small	medium	2	1	0	50
moderate	no	small	high	1	1	0	0
moderate	no	medium	low	0	–	–	–

moderate	no	medium	medium	3	0	1	67
moderate	no	medium	high	0	–	–	–
moderate	no	large	low	1	0	1	100
moderate	no	large	medium	1	0	1	0
moderate	no	large	high	0	–	–	–
moderate	yes	small	low	4	0	4	50
moderate	yes	small	medium	4	0	0	25
moderate	yes	small	high	0	–	–	–
moderate	yes	medium	low	2	0	2	0
moderate	yes	medium	medium	0	–	–	–
moderate	yes	medium	high	0	–	–	–
moderate	yes	large	low	0	–	–	–
moderate	yes	large	medium	0	–	–	–
moderate	yes	large	high	0	–	–	–
strong	no	small	low	0	–	–	–
strong	no	small	medium	2	1	1	0
strong	no	small	high	0	–	–	–
strong	no	medium	low	0	–	–	–
strong	no	medium	medium	3	1	1	100
strong	no	medium	high	0	–	–	–
strong	no	large	low	0	–	–	–
strong	no	large	medium	1	0	0	100
strong	no	large	high	0	–	–	–
strong	yes	small	low	1	0	1	0
strong	yes	small	medium	3	0	0	67
strong	yes	small	high	0	–	–	–
strong	yes	medium	low	2	0	2	50

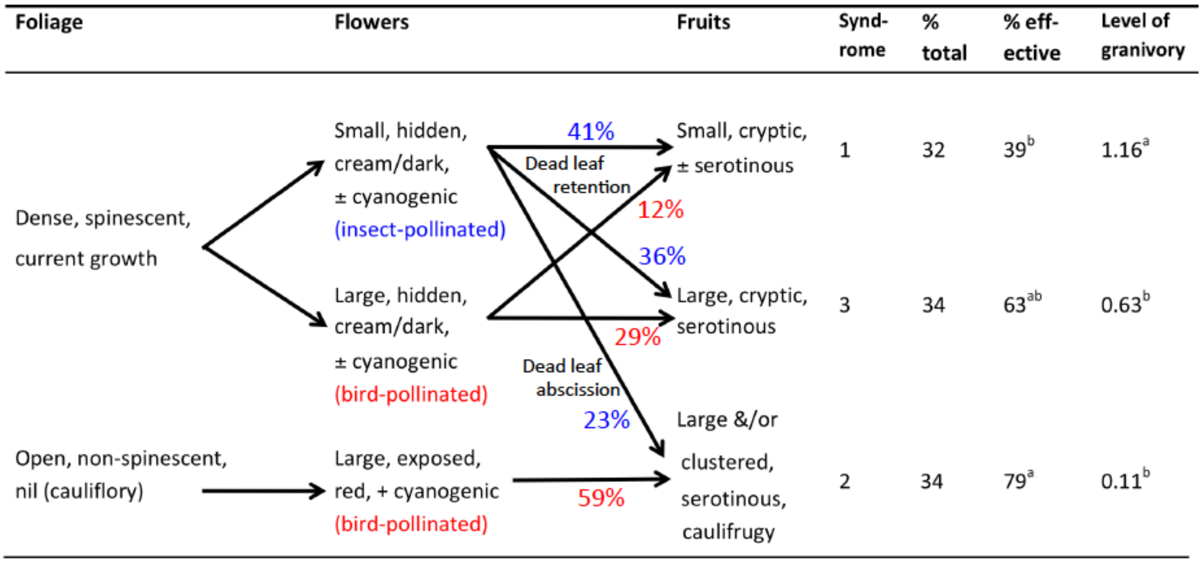
strong	yes	medium	medium	2	1	1	50
strong	yes	medium	high	0	–	–	–
strong	yes	large	low	0	–	–	–
strong	yes	large	medium	2	0	1	100
strong	yes	large	high	0	–	–	–

*Zero granivory (35 spp) up to the *most heavily attacked* population with ≤5% of plants with ≤10% of their seeds removed by cockatoos (i.e. granivory considered *ad hoc* and negligible) (4 spp)

Overall:

Syndrome	**Spinescence/camouflage**	**Fruit size**	**# spp (% total)**	**Granivory (%)**
1 (pink)	+ spinescence/± camouflage	Small ± clustered	19 (34)	12^{b} (63)
2 (green)	+ spinescence/± camouflage	Medium-large ± clustered	17 (30.5)	6^{b} (35)
3 (blue)	- spinescence/- camouflage	Medium-large or clustered	19 (34)	0^{a} (0)
			Fisher's test:	P < 0.0001

Table 14. Relationship between pollination and seed-defense syndromes among hakeas. The seed defense syndrome numbers correspond to those given for individual species in Appendix Table A from which the stated % contributions of the 56 species were obtained. Note that strongly serotinous fruits are not in themselves a granivore defense but weak (–) serotiny (granivore avoidance) and large woody fruits (direct defense) may be. % effective refers to % of species in each defense syndrome that was not attacked by cockatoos while level of granivory refers to the extent of seed removal when species were attacked. Values with different superscript letters are significantly different at $P < 0.05$. ± = condition may or may not apply.



Foliage	Flowers	Fruits	Synd-rome	% total	% eff-ective	Level of granivory
Dense, spinescent, current growth	Small, hidden, cream/dark, ± cyanogenic (insect-pollinated)	Small, cryptic, ± serotinous	1	32	39^{b}	1.16^{a}
	Large, hidden, cream/dark, ± cyanogenic (bird-pollinated)	Large, cryptic, serotinous	3	34	63^{ab}	0.63^{b}
Open, non-spinescent, nil (cauliflory)	Large, exposed, red, + cyanogenic (bird-pollinated)	Large &/or clustered, serotinous, caulifrugy	2	34	79^{a}	0.11^{b}

Table 15. Plant genera and the animal groups associated with their reproductive biology (pollination, florivory, seed dispersal, predispersal granivory). Agents that participate in two of these processes on the same plant are given in bold.

Plant group	Pollinators	Florivores	Granivores (predispersal)	Seed dispersers/ frugivores	References
Hakea	Bees, beetles, flies, honeyeater birds	**Cockatoos,** emus	**Cockatoos**, insect borers	Wind	Hanley et al 2009, this study
Grevillea	Bees, beetles, flies, honeyeater birds	Cockatoos, emus	Insect borers (rare)	Wind, ants (especially)	B. Lamont, pers. observ.
Solanum	Bees	**Beetles**	**Beetles**, flies	Birds	Bowers 1975, Wise and Hébert 2010
Pinus	**Wind**	–	**Crossbills, squirrels**, moths	**Crossbills, squirrels, wind**	Benkman et al. 2004, Talluto and Benkman 2014
***Adansonia* (Baobab)**	**Bats**, bushbaby, lemurs	–	**Rodents, extinct lemurs** (seeds in fruit)	**Bats**, **rodents**, tortoise, **extinct lemurs**	Hodgkison et al. 20 Andriantsaralaza et 2014, various
***Couroupita* (Cannonball)**	**Bats**	**Bats**	**Peccary, rodents, fowl**	**Peccary, rodents, fowl**	Various
Mistletoes	**Mistletoe birds,** humming birds, lycaenid butterflies, **honeyeaters**	Moths (rare)	Insects (rare)	**Mistletoe birds, honeyeater birds**	Calder and Bernha 1983, Kelly et al. 2008
***Lophocereus* (cactus)**	**Moths, flying foxes,** bees	–	**Moth larvae, doves**	**Flying foxes, doves**	Holland and Fleming 1999

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Appendix

Table A. Species, study sites, traits and levels of granivory used in this analysis.

NP = National Park, NR = Nature Reserve. (can only be viewed in its entirety using Outline)

Hakea species	Sampling details				Minimum fruits assessed per plant	Number of plants sampled	Damage category				Overall damage (granivory)	Maximum granivory	Spinescence
	Botanical district (subregion)	Location	Lat:Long	Date			0 (0% fruit loss)	1 (1-10% fruit loss)	2 (11-50% fruit loss)	3 (>50% fruit loss)			
H. ambigua	Eyre	Mt Trio, Stirlings	34^{o}19'25.65"S : 118^{o}03'57.04"E	28/11/2012	5	20	20				0	0	0
H. amplexicaulis	Darling	Korung NP	32^{o}00'58.85"S : 116^{o}02'25.30"E	19/11/2012	5	10	8	2			0.2		
		Lesmurdie Falls NP	31^{o}59'29.25"S : 116^{o}02'04.08"E	30/11/2013	5	13	13				0		
		Paulls Valley	31^{o}58'24.54"S : 116^{o}06'00.68"E	24/11/2013	5	13	13				0		
		Margaret River	33^{o}56'51.13"S : 115^{o}05'12.04"E	22/11/2013	5	12	8	1		3	0.83		

		Augusta	34^{o}19'40.17"S : 115^{o}09'44.89"E	22/11/2013	5	15	15				0	0.83	1.6
H. anadenia	Irwin	Coomallo Creek	30^{o}13'16.3"S : 115^{o}24'21.7"E	6/07/2012	10	20	20				0	0	3.3
H. auriculata	Irwin	Trig Point	29^{o}33'04.37" S : 115^{o}16'45.21" E	7/07/2012	5	18	18				0		
		coomallo creek - ridge to north	30^{o}12'24.49"S : 115^{o}23'44.05"E	6/07/2012	5	6	6				0		
		Wotto NR, Eneabba	29^{o}44'09.31' S : 115^{o}24'36.44' E	8/07/2012	5	16	2	0	7	7	2.19		
		Marchagee Rd, Coomallo	30^{o}13'15.58" S : 115^{o}26'26.88" E	28/11/2013	5	22	3	7	6	6	1.68	2.19	15.2
H. baxterii	Eyre	Mt Trio, Stirlings	34^{o}19'25.65"S : 118^{o}03'57.04"E	28/11/2012	5	20	20				0	0	0
H. brownii	Irwin	Marchagee Rd, Coomallo	30^{o}12'44.69" S : 115^{o}27'23.57" E	27/11/2013	5	10	10				0	0	0
H. bucculenta	Irwin	Ding Road, Eneabba	29^{o}38'04.11' S : 115^{o}17'41.54' E	8/07/2012	100	15	14	1			0.07*	0.07*	0
H. candolleana	Irwin	Western Flora	29^{o}37'33.82"S : 115^{o}12'59.29"E	8/07/2012	5	10	10				0	0	0
H. ceratophylla	Eyre	Chester Pass Rd/Stirling Range Rd	34.39148° S : 118.11147° E	4/12/2013	5	20	19	1			0.05		
		Toolbrunup Road, Stirlings	34.39777° S: 118.09240° E	4/12/2013	5	20	20				0		

		Salt River Road (Park edge)	34.30852° S: 117.68410° E	5/12/2013	5	10	10				0		
		Red Gum Pass Rd, Stirlings	34.4357° S: 117.7276° E	3/12/2013	5	14	10	1	2	1	0.57	0.57	2
H. circumulata	Irwin	Robb Road to Trig Point	29^{o}33'52.9" S : 115^{o}17'13.6" E	7/07/2012	10	20	20				0	0	9.2
H. conchifolia	Irwin	North Cataby	30^{o}41'25.5``S : 115$^{o}$29`10.8``E	6/07/2012	5	12	12				0		
		South Eneabba NR	29^{o}52'01.17"S : 115^{o}14'58.86"E	29/11/2013	5	11	11				0	0	1.6
H. corymbosa	Eyre	Chester Pass, Stirlings	34.23761° S : 118.06480° E	28/11/2012	5	20	20				0	0	3.5
H. costata	Irwin	Marchagee Rd, Coomallo	30^{o}12'44.69" S : 115^{o}27'23.57" E	27/11/2013	10	10	10				0	0	2.9
H. cristata	Darling	Gooseberry Hill NP	31^{o}56'25.87"S : 116^{o}03'14.44"E	24/11/2013	5	17	17				0		
		John Forrest NP	31^{o}53'01.31"S : 116^{o}05'36.31"E	23/11/2013	5	20	20				0	0	3.7
H. cucullata	Eyre	Mt Trio, Stirlings	34^{o}19'25.65"S : 118^{o}03'57.04"E	28/11/2012	5	20	20				0		
		Red Gum Pass Rd, Stirlings	34.38926° S: 117.77228° E	3/12/2013	5	20	20				0		
		Stirling Range Drive, Stirlings	34.39713° S: 117.85440° E	3/12/2013	5	20	20				0		
		Stirling Range Drive,	34.41516° S:	3/12/2013	10	20	20				0	0	0

		Stirlings	117.92757° E										
H cyclocarpa	Darling	JFNP		23/11/2013							0	0	0
H. cygna cygna	Irwin	Robb Road to Trig Point	29^{o}33'52.9" S : 115^{o}17'13.6" E	7/07/2012	5	11	11				0	0	0
H. cygna needlei	Roe	Lake King	31.14201° S : 119° 43.969 E	27/11/2012	5	20	20				0	0	1
H. denticulata	Eyre	Chester Pass, Stirlings	34.23761° S : 118.06480° E	28/11/2012	5	20	20				0	0	0.1
H. eneabba	Irwin	Warradarge	29.44254° S: 115.24521° E	6/07/2012	5	10	10				0	0	1.1
H. erinacea	Darling	Korung NP	32^{o}00'43.89"S : 116^{o}02'00.14"E	19/11/2012	10	20	20				0		
		John Forrest NP	31^{o}53'00.10"S : 116^{o}05'44.09"E	23/11/2013	5	20	20				0		
		Gooseberry Hill NP	31^{o}56'25.87"S : 116^{o}03'14.44"E	24/11/2013	10	25	16	3	4	2	0.68		
		Lesmurdie Falls NP	31^{o}59'44.23"S : 116^{o}01'57.02"E	30/11/2013	10	20	20				0		
		Brixton St Reserve	31^{o}59'01.11"S : 115^{o}59'17.38"E	30/11/2013	10	20	20				0	0.68	1.8
H. ferruginea	Eyre	Chester Pass, Stirlings	34.23761° S : 118.06480° E	28/11/2012	5	20	20				0	0	0
H. flabellifolia	Irwin	North Cataby	30.01072° S : 115.119383° E	6/07/2012	2	2	2				0	0	0

H. francisiana	Irwin	Ding Road, Eneabba	29^{o}38'04.11' S : 115^{o}17'41.54' E	8/07/2012	100	10	9	1			0.1	0.1	0
H. gilbertii	Irwin	Wotto NR, Eneabba	29^{o}44'09.31' S : 115^{o}24'36.44' E	8/07/2012	10	20	19	0	1	0	0.1	0.1	11
H. horrida	Roe	Frank Hann NP	33.05587° S : 119.23084° E	27/11/2012	5	20	17	1	1	1	0.3	0.3	7.4
H. incrassata	Irwin	Coomallo Creek	30^{o}13`18.71``S : 115$^{o}$23`54.35``E	6/07/2012	5	20	20				0		
		Eneabba	29^{o}43'04.10" S : 115^{o}12'44.17" E	28/11/2013	5	10	10				0		
		Correy Road	29^{o}35'33.44" S : 115^{o}15'27.10" E	28/11/2013	5	20	20				0		
		Marchagee Rd, Coomallo	30^{o}13'15.58" S : 115^{o}26'26.88" E	27/11/2013	5	20	20				0		
	Darling	Gooseberry Hill NP	31^{o}56'25.87"S : 116^{o}03'14.44"E	24/11/2013	5	19	19				0		
		Lesmurdie Falls NP	31^{o}59'38.50"S : 116^{o}01'57.49"E	30/11/2013	5	14	14				0		
		Korung NP	31^{o}01'01.92"S : 116^{o}01'57.76"E	19/11/2012	5	20	20				0	0	0.8
H. lissocarpha	Irwin	Coomallo Creek	30^{o}13`18.71``S : 115$^{o}$23`54.35``E	6/07/2012	10	20	20				0		
		Eneabba	29.38813° S : 115.08626° E	8/07/2012	10	20	0	0	2	18	2.9		
		Correy Road	29^{o}35'33.44" S : 115^{o}15'27.10" E	28/11/2013	10	20	20				0		

	Eyre	Sundalara Road, Eneabba	29^{o}31'54.53" S : 115^{o}19'45.15" E	28/11/2013	10	20	20				0		
		Stirling Range	34.18861° S : 118.11455° E	29/11/2012	10	15	4	5	2	4	1.4		
	Darling	John Forrest NP	31^{o}53'00.10"S : 116^{o}05'44.09"E	23/11/2013	5	14	12	2			0.14		
		Gooseberry Hill NP	31^{o}56'25.87"S : 116^{o}03'14.44"E	24/11/2013	10	20	20				0		
		Lesmurdie Falls NP	31^{o}59'44.23"S : 116^{o}01'57.02"E	30/11/2013	5	20	20				0		
		Margaret River	33^{o}56'51.13"S : 115^{o}05'12.04"E	22/11/2013	5	20	17	0	3	0	0.15	2.9	10.2
H. lissocarpha (grey form) - unnamed sp	Darling	Gooseberry Hill NP	31^{o}56'25.87"S : 116^{o}03'14.44"E	24/11/2013	5	16	16				0		
		Lesmurdie Falls NP	31^{o}59'38.50"S : 116^{o}01'57.49"E	23/11/2013	5	15	15				0		
	Eyre	Red Gum Pass Rd, Stirlings	34.40212° S: 117.75342° E	3/12/2013	10	20	20				0		
		Stirling Range Drive, Stirlings	34.40068° S: 117.98213° E	3/12/2013	5	13	13				0		
		Bluff Knoll Rd, Stirlings	34.332108° S: 118.19511° E	4/12/2013	5	16	16				0		
		Yetemerup/Salt River Rd	34.47867° S: 118.17374° E	4/12/2013	5	20	20				0	0	2.4

H. longiflora	Irwin	Coomallo Creek	30^{o}13`09.71``S : 115$^{o}$24`12.35``E	6/07/2012	10	4	4				0	0	1.55
H. marginata	Irwin	Coomallo Creek	30^{o}13`18.71``S : 115$^{o}$23`54.35``E	6/07/2012	10	10	10				0	0	1
H. megalosperma	Irwin	Mullering Road, Cataby	29.38813° S : 115.08626° E	9/07/2012	10	14	14				0	0	0
H. meisneriana	Irwin	Wilson NR, Eneabba	29.33239° S : 115.25781° E	8/07/2012	10	20	19	1			0.05*	0.05*	0
H. multilineata	Avon	Corrigin Rd NR	32.19952° S : 117.51264° E	28/11/2012	10	20	20				0	0	0
H. orthorrhyncha	Irwin	Western Flora	29^{o}37'27.34" S : 115^{o}13'29.39" E	7/07/2012	20	8	8				0	0	0
H. pandanicarpa	Eyre	Red Gum Pass Rd, Stirlings	34.38926° S: 117.77228° E	3/12/2013	5	20	20				0	0	0
H. petiolaris	Darling	John Forrest NP	31^{o}53'00.10"S : 116^{o}05'44.09"E	23/11/2013	5	14	14				0		
		Gooseberry Hill NP	31^{o}56'25.87"S : 116^{o}03'14.44"E	24/11/2013	10	11	11				0		
		Lesmurdie Falls NP	31^{o}59'38.50"S : 116^{o}01'57.49"E	23/11/2013	5	20	20				0		
		Sillivan's Rock	32.37858° S: 116.25192° E	5/12/2013	5	20	19	1			0.05*	0.05*	0
H. platysperma	Irwin	Wilson NR, Eneabba	29^{o}32`35.16``S : 115$^{o}$26`54.28``E	8/07/2012	20	20	20				0	0	0

H. polyanthema	Irwin	Robb Road to Trig Point	29°33'52.9" S : 115°17'13.6" E	7/07/2012	20	20	20				0	0	10.8
H. preissii	Irwin	Beekeepers Reserve	29.38813° S : 115.08626° E	8/07/2012	100	5					2	2	1.2
H. pritzelii	Eyre	Stirling Range - corner track and rd to cranbrook		28/11/2012	5	20	20	0	0	1	0.15	0.15	0.6
H. prostrata	Eyre	Branson Road, Stirlings	34.47867° S: 118.17374° E	4/12/2013	5	20	18	0	1	1	0.25		
		Yetemerup/Salt River Rd	34.32914° S: 117.91692° E	4/12/2013	5	15	13	2			0.13		
		Salt River Road	34.47867° S: 118.17374° E	5/12/2013	5	20	20				0		
		Salt River Road (Park edge)	34.30852° S: 117.68410° E	5/12/2013	5	10	10				0		
	Darling	North Bannister	32.57965° S: 116.44418° E	5/12/2013	5	20	20				0		
	Irwin	Ding Road, Eneabba	29°38'04.11' S : 115°17'41.54' E	8/07/2012	5	10	9	1			0.1		
		Robinson/Sundalara intersection	29°31'01.52"S : 115°21'14.98"E	28/11/2013	5	10	10				0		
		Marchagee Rd, Coomallo	30°13'03.03"S : 115°26'50.30"E	27/11/2013	5	11	11				0		
		Three Springs Road	29°45'22.47"S : 115°25'33.87"E	28/11/2013	5	20	20				0	0.25	4

H. psilorrhyncha	Irwin	North Cataby	30.01072° S : 115.119383° E	6/07/2012	10	20	20				0		
		Eneabba[1]	29.38813° S : 115.08626° E	8/07/2012	10	20	20				0		
		Wotto NR, Eneabba	29°43'05.49"S : 115°24'41.02"E	28/11/2013	10	20	20				0		
		Marchagee Rd, Coomallo	30°13'03.03" S : 115°26'50.30" E	27/11/2013	10	20	20				0	0	6.7
H. ruscifolia	Eyre	Stirling Range Drive, Stirlings	34.39713° S: 117.85440° E	3/12/2013	5	10	10				0		
		Stirling Range Drive, Stirlings	34.39683° S: 117.89056° E	3/12/2013	5	20	20				0		
		Stirling Range Drive, Stirlings	34.41516° S: 117.92757° E	3/12/2013	5	13	13				0		
		Stirling Range Drive, Stirlings	34.40068° S: 117.98213° E	3/12/2013	5	20	20				0		
	Darling	Margaret River	33°56'51.13"S : 115°05'12.04"E	22/11/2013	5	20	15	3		2	0.45		
		Augusta	34°19'40.17"S : 115°09'44.89"E	22/11/2013	5	16	16				0		
		John Forrest NP	31°53'26.43"S : 116°05'57.49"E	23/11/2013	5	11	11				0	0.45	0.3
H. scoparia	Irwin	Western Flora	29°37'27.34" S : 115°13'29.39" E	7/07/2012	50	10	10				0		
		Wilson NR,	29°33'04.61" S : 115°25'55.03" E	8/07/2012	50	10	9	1			0.1	0.1	0.3

		Eneabba[2]											
H. smilacifolia	Irwin	North Cataby	30.01072° S : 115.119383° E	6/07/2012	20	20	4	11	5		1.05		
		Wotto NR, Eneabba	29°44'09.31' S : 115°24'36.44' E	8/07/2012	20	10	1	4	3	2	1.6		
		South Eneabba NR	29°51'49.56"S : 115°15'09.35"E	9/07/2012	20	20	6	0	0	14	2.1		
		Three Springs Road	29°45'22.47"S : 115°25'33.87"E	28/11/2013	5	20	20				0	2.1	1
H. spathulata	Irwin	Correy Road	29°35'33.44" S : 115°15'27.10" E	28/11/2013	5	20	20				0		
		Western Flora	29°37'27.34" S : 115°13'29.39" E	28/11/2013	5	20	20				0		
		Three Springs Road	29°45'22.47"S : 115°25'33.87"E	28/11/2013	5	14	14				0	0	15
H. stenocarpa	Darling	John Forrest NP	31°53'00.10"S : 116°05'44.09"E	23/11/2013	5	20	17	2	1		0.25		
		Lesmurdie Falls NP	31°59'29.25"S : 116°02'04.08"E	23/11/2013	10	20	13	4	3		0.5		
		Korung NP	32°02'29.83"S : 116°02'54.19"E	1/12/2013	5	20	20				0		
		Korung NP	32°00'58.85"S : 116°02'25.30"E	19/11/2012	5	20	16	2	2		0.1	0.5	0
H. strumosa	Roe	Lake King	33.05397° S : 119.32525° E	26/11/2012	5	20	17	1	1	1	0.15	0.15	0.69

H. subsulcata		Corrigin Rd	32.20221° S : 117.50612° E	28/11/2012	5	20	20				0	0	1.9
H. sulcata	Darling	Brixton St Reserve	31^{o}59'01.11"S : 115^{o}59'17.38"E	30/11/2013	20	20	1	5	11	3	1.8		
		Yule Brook Reserve	32^{o}01'40.95"S : 115^{o}58'21.97"E	30/11/2013	30	20	1	12	7	1	1.45		
	Eyre	Red Gum Pass Rd, Stirlings	34.4357° S: 117.7276° E	3/12/2013	40	20	3	5	9	3	1.6		
		Red Gum Pass Rd, Stirlings	34.38926° S: 117.77228° E	3/12/2013	20	20	2	0	3	15	2.55		
		Toolbrunup Road, Stirlings	34.39777° S: 118.09240° E	4/12/2013	10	20	9	3	4	4	1.15		
		Chester Pass Rd/Stirling Range Rd	34.39148° S : 118.11147° E	4/12/2013	5	20	7	3	10	0	1.15	2.55	0.4
H. trifurcata	Irwin	Ding Road, Eneabba	29^{o}38'04.11' S : 115^{o}17'41.54' E	8/07/2012	20	10	10				0		
		Wotto NR, Eneabba	29^{o}44'09.31' S : 115^{o}24'36.44' E	8/07/2012	10	10	8	2			0.2		
		Sundalara Road, Eneabba	29^{o}31'54.53" S : 115^{o}19'45.15" E	28/11/2013	10	20	20				0		
		Marchagee Rd, Coomallo	30^{o}13'03.03" S : 115^{o}26'50.30" E	27/11/2013	10	18	18				0		
	Eyre	Stirling Range Drive, Stirlings	34.39713° S: 117.85440° E	3/12/2013	5	20	20				0		
		Stirling Range Drive,	34.41516° S: 117.92757° E	3/12/2013	10	20	20				0		

	Darling	Stirlings											
		Stirling Range Drive, Stirlings	34.40068° S: 117.98213° E	3/12/2013	5	20	19	1			0.05		
		Toolbrunup Road, Stirlings	34.398155° S: 118.09660° E	4/12/2013	5	20	20				0		
		Korung NP	32^{o}00'43.89"S : 116^{o}02'00.14"E	19/11/2012	10	20	20				0		
		John Forrest NP	31^{o}53'00.10"S : 116^{o}05'44.09"E	23/11/2013	20	20	20				0		
		Lesmurdie Falls NP	31^{o}59'38.50"S : 116^{o}01'57.49"E	23/11/2013	20	20	20				0		
		Gooseberry Hill NP	31^{o}56'25.87"S : 116^{o}03'14.44"E	24/11/2013	20	20	20				0	0.2	3.8
H. undulata	Darling	John Forrest NP	31^{o}53'00.10"S : 116^{o}05'44.09"E	23/11/2013	5	20	20				0		
		Gooseberry Hill NP	31^{o}56'25.87"S : 116^{o}03'14.44"E	24/11/2013	10	14	12		2		0.29		
		Lesmurdie Falls NP	31^{o}59'44.23"S : 116^{o}01'57.02"E	30/11/2013	30	20	18		1	1	0.25		
		Korung NP	32^{o}00'43.89"S : 116^{o}02'00.14"E	19/11/2012	25	20	15	5			0.25	0.29	0.1 (treat as 0)
H. varia	Darling	Roe/Tonkin intersection	31^{o}59'01.11"S : 115^{o}59'17.38"E	30/11/2013	5	20	20				0		
		Yule Brook Reserve	32^{o}01'43.93"S : 115^{o}58'37.41"E	30/11/2013	20	30	29	1			0.03		

	Eyre	Red Gum Pass Rd, Stirlings	34.4357° S: 117.7276° E	3/12/2013	10	20	19	1			0.05		
		Stirling Range Drive, Stirlings	34.3973° S: 117.84641° E	3/12/2013	10	20	20				0		
		Stirling Range Drive, Stirlings	34.40068° S: 117.98213° E	3/12/2013	10	20	20				0		
		Toolbrunup Road, Stirlings	34.39811° S: 118.10098° E	4/12/2013	10	20	19	1			0.05		
	Irwin	Wilson NR, Eneabba	29.35\`28.99\`\`S : 115.26\`54.90\`\`E	8/07/2012	10	10	3	4	2	1	1.1	1.1	2.8
H. verrucosa		Fitzgerald River NP		28/11/2012	5	20	20				0	0	1.4
H. victoria	Eyre	Fitzgerald River NP		28/11/2012	5	20	20				0	0	4.3

$ 1 = <5 fruits/plant, 2 = 5-50, 3 = >50+

*treated as 0

1 = spinescent and/or camouflage, small fruits, 2 = large and/or clustered fruits, 3 = spinescent and/or camouflage, large fruits

Table B. GenBank accession numbers of eight DNA fragments used in *Hakea* genus phylogenetic reconstruction

	atpB	**atpB-rbcL**	**ITS**	**matK**	**rbcL**	**rpl6**	**trnL**	**trnL-trnF**
Hakea ambigua	JQ257292.1	-	-	JQ257223.1	-	JQ257420.1	-	-
Hakea amplexicaulis	JQ257297.1	-	-	JQ257228.1	-	JQ257425.1	-	-
Hakea auriculata	JQ257280.1	KJ872975.1	KJ872942.1	JQ257211.1	KJ872899.1	JQ257408.1	KJ873015	KJ873000.1
Hakea baxterii	JQ257286.1	-	-	JQ257217.1	-	JQ257414.1	-	-
Hakea brownii	KJ872875.1	KJ872969.1	KJ872932.1	KJ872879.1	KJ872894.1	KJ872923	KJ873030	KJ873011.1
Hakea bucculenta	JQ257275.1	KJ872955.1	KJ872931.1	KJ872882.1	KJ872896.1	JQ257403.1	KJ873033	KJ872992.1
Hakea candolleana	KJ872869.1	KJ872971.1	KJ872938.1	-	KJ872895.1	KJ872922	-	KJ873012.1
Hakea ceratophylla	KJ872868.1	KJ872972.1	-	-	KJ872901.1	KJ872921	KJ873027	KJ873010.1
Hakea circumulata	KJ872873.1	KJ872978.1	KJ872939.1	KJ872881.1	KJ872897.1	KJ872919	KJ873014	KJ872982.1
Hakea conchifolia	JQ257291.1	-	-	JQ257222.1	-	JQ257419.1	-	-
Hakea corymbosa	JQ257272.1	-	-	JQ257203.1	-	JQ257400.1	-	-
Hakea cristata	JQ257255.1	-	-	JQ257186.1	-	JQ257383.1	-	-
Hakea cucullata	JQ257271.1	-	-	JQ257202.1	KJ872886.1	JQ257399.1	KJ873026	KJ872991.1
Hakea cygna cygna	KJ872863.1	KJ872964.1	-	KJ872883.1	KJ872902.1	KJ872917	KJ873035	KJ872994.1
Hakea cygna needlei	KJ872862.1	KJ872960.1	-	-	KJ872903.1	KJ872911	KJ873038	KJ872989.1
Hakea denticulata	-	-	KJ872941.1	-	-	-	-	KJ872999.1
Hakea eneabba	KJ872860.1	-	KJ872948.1	-	-	-	-	KJ872996.1
Hakea ferruginea	KJ872861.1	KJ872962.1	-	-	-	KJ872916	KJ873024	KJ872985.1
Hakea flabellifolia	KJ872876.1	KJ872973.1	KJ872937.1	KJ872880.1	-	KJ872924	KJ873031	KJ872984.1
Hakea francisiana	KJ872856.1	KJ872956.1	-	-	KJ872889.1	KJ872925	KJ873034	KJ872997.1
Hakea gilbertii	KJ872866.1	KJ872958.1	KJ872953.1	KJ872885.1	-	-	-	-
Hakea horrida	JQ257288.1	-	KJ872944.1	JQ257219.1	-	JQ257416.1	-	-
Hakea incrassata	JQ257257.1	KJ872970.1	-	JQ257188.1	KJ872892.1	JQ257385.1	KJ873029	KJ873008.1
Hakea lissocarpha	-	-	-	-	KJ872890.1	-	KJ873018	KJ873006.1
Hakea longiflora	-	KJ872968.1	-	-	-	-	KJ873022	KJ872980.1
Hakea marginata	KJ872864.1	KJ872959.1	KJ872949.1	-	KJ872906.1	KJ872913	-	-
Hakea meglosperma	JQ257248.1	-	-	JQ257179.1	-	JQ257376.1	-	-

Hakea meisneriana	KJ872859.1	KJ872967.1	KJ872930.1	KJ872884.1	KJ872908.1	KJ872912	KJ873028	KJ873009.1
Hakea multilineata	JQ257270.1	-	-	JQ257201.1	-	JQ257398.1	KJ873032	KJ872995.1
Hakea orthorrhyncha	JQ257266.1	-	-	JQ257197.1	-	JQ257394.1	-	-
Hakea pandanicarpa	JQ257267.1	-	KJ872933.1	JQ257198.1	-	JQ257395.1	-	-
Hakea petiolaris	JQ257269.1	-	-	JQ257200.1	-	JQ257397.1	-	-
Hakea platysperma	JQ257287.1	-	-	JQ257218.1	-	JQ257415.1	-	-
Hakea polyanthema	JQ257252.1	-	-	JQ257183.1	-	JQ257380.1	-	-
Hakea preissii	-	-	KJ872940.1	-	-	-	KJ873020	KJ872998.1
Hakea pritzellii	JQ257281.1	-	-	JQ257212.1	-	JQ257409.1	-	-
Hakea prostrata	JQ257254.1	-	-	JQ257185.1	-	JQ257382.1	-	-
Hakea psilorrhyncha	KJ872874.1	-	KJ872935.1	-	KJ872905.1	KJ872918	KJ873013	KJ873007.1
Hakea ruscifolia	JQ257295.1	-	-	JQ257226.1	-	JQ257423.1	KJ873019	-
Hakea scoparia	KJ872865.1	KJ872966.1	KJ872952.1	-	KJ872898.1	KJ872914	KJ873039	KJ872987.1
Hakea smilacifolia	KJ872857.1	KJ872965.1	KJ872951.1	-	KJ872907.1	KJ872910	KJ873036	KJ872981.1
Hakea spathulata	-	KJ872974.1	KJ872943.1	-	KJ872891.1	KJ872926	-	KJ872983.1
Hakea stenocarpa	JQ257283.1	-	-	JQ257214.1	-	JQ257411.1	-	-
Hakea strumosa	JQ257259.1	KJ872979.1	KJ872947.1	JQ257190.1	KJ872893.1	JQ257387.1	KJ873021	KJ873004.1
Hakea subsulcata	JQ257299.1	-	-	JQ257230.1	-	JQ257427.1	KJ873037	KJ872993.1
Hakea sulcata	-	KJ872957.1	KJ872950.1	-	KJ872909.1	-	-	KJ872986.1
Hakea trifurcata	JQ257260.1	-	-	JQ257191.1	-	JQ257388.1	-	-
Hakea varia	KJ872870.1	KJ872954.1	KJ872945.1	-	KJ872888.1	KJ872920	-	KJ873003.1
Hakea verrucosa	JQ257253.1	-	-	JQ257184.1	-	JQ257381.1	-	-
Hakea victoria	-	-	KJ872929.1	-	-	-	-	-
Buckinghamia celsissima	JQ257247.1	AF060747.1	FJ468589.1	JQ257178.1	DQ875862.1	JQ257375.1	-	FJ626569.1
Finschia chloroxantha	JQ257245.1	AF060742.1	DQ499133.1	JQ257176.1	DQ875861.1	JQ257373.1	AF482145.1	AF482190.1
Grevillea juncifolia	AY837794.1	AF060731.1	DQ499129.1	AY823169.1	HM849807.1	JQ765093.1	AY23210.1	AY823215.1

Table 3. *P* values for χ^2 and t-tests on raw and phylogenetically corrected data for 17 trait-pair comparisons (to take into account any phylogenetic signal).

Comparison	*P* for raw data	*P* for phylogenetically corrected data
Fruit size class vs ± granivory	0.001	0.005
± Spinescence vs ± granivory	0.002	0.006
± Camouflage vs ± granivory	0.002	0.002
Fruit weight vs ± granivory	<0.001	<0.001
Seed store vs ± granivory	0.255	0.271
± Spinescence vs fruit size class	0.001	0.001
Pollinator type vs ± granivory	0.010	0.013
Pollinator type vs ± spinescence	0.005	0.007
Pollinator type vs head wounds	0.235	0.307
Pollinator type vs ± camouflage	0.031	0.039
Pollinator type vs fruit size class	0.031	0.024

Pollinator type vs fruit weight	0.020	0.024
Pollinator type vs ± clustering	<0.001	0.005
Fire-response type vs ± granivory	0.104	0.160
Serotiny level vs ± spinescence	0.012	0.011
Serotiny level vs head wounds	0.035	0.032
± Clustering vs ± spinescence	0.053	0.057