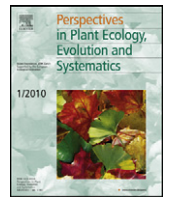




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Bird pollinators, seed storage and cockatoo granivores explain large woody fruits as best seed defense in *Hakea*

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ABSTRACT

Nutrient-impooverished 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 hypotheses centred on optimal seed defenses in relation 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 spiner. 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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1. 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 part (McCall and Irwin 2006). In addition, they are energy- 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 large pollinators and seed dispersal agents, flowers and fruits need to be held away from protective foliage and thus may be vulnerable to florivores and granivores. It is not surprising therefore that flowers often contain chemical defenses (Twigg and Socha, 1996; Hanley et al., 2009) and fruits may protect their seeds via warning

coloration, distasteful chemicals, woody fruits or sharp appendages (Schaeffer and Ruxton, 2011).

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. 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 summer drought/heat (Lamont et al., 2002; Groom et al., 2004), nutrient-impooverished soils (Lamont et al., 2002), disparate pollinators (Hanley et al., 2009) and 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

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in clusters, species resprout or are fire-killed, and they are bird- or insect-pollinated (Barker et al., 1999; Groom and Lamont, 1996b, 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 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 6000 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 reproductive traits key to its fitness in a nutrient-impooverished, 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 fruits (Groom and Lamont 1997), our overarching hypothesis was that these give the greatest protection against cockatoo granivores.

1.1. 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 pierce with much effort (Fig. 2). The endocarp of most species can be placed in the "high-density wood" category (>540 kg/m³, 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 or stems (Groom et al., 1994a; 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) 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

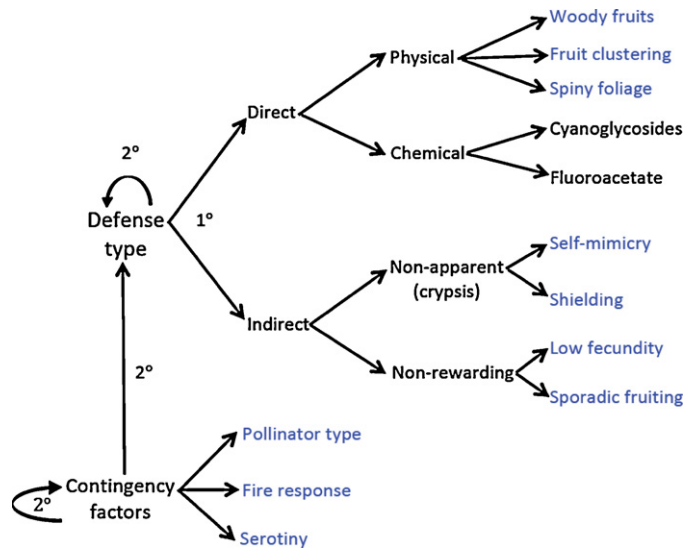


Fig. 1. Scheme showing relationships between the various possible seed-defense types and factors that modify their intensity through evolutionary time. For example, bird pollination promotes open foliage via a secondary (2°) pathway that favours production of large woody fruits, which protect seeds directly 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. 3). 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.

be expressed through the heavier seeds being held within larger woodier fruits, crypsis through camouflage or shielding, and/or protection by spiny leaves. Serotiny 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 direct and indirect defenses and contingency factors interacting with the defense factors, that involved several primary pathways and 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, (b) fruit crypsis, (c) large fruit size, (d) fruit clustering and/or (e) small seed store as alternative defenses available to hakeas. 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 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 (McKey, 1974; Stamp, 2003).

1.2. 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 deter florivory by non-pollinators, such as cockatoos. On the other hand, the inflorescences of insect-pollinated congeners are small and protected within dense, spiny foliage that deters vertebrate florivores but allows access to invertebrate pollinators (Table 1, Fig. 2). However, variation in floral defense strategies presents an evolutionary dilemma for the plant: while insect-pollinated flowers (and thus

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