



RESEARCH REPOSITORY

*This is the author's final version of the work, as accepted for publication following peer review but without the publisher's layout or pagination.
The definitive version is available at:*

<http://dx.doi.org/10.1071/PC14924>

Murphy, M., Howard, K., Hardy, G.E.St.J. and Dell, B. (2015) When losing your nuts increases your reproductive success: sandalwood (*Santalum spicatum*) nut caching by the woylie (*Bettongia penicillata*). *Pacific Conservation Biology*, 21 (3). pp. 243-252.

<http://researchrepository.murdoch.edu.au/id/eprint/28923/>

Copyright: © CSIRO 2015.
It is posted here for your personal use. No further distribution is permitted.

**When losing your nuts increases your reproductive success:
sandalwood (*Santalum spicatum*) nut caching by the woylie
(*Bettongia penicillata*)**

Marie Murphy, Kay Howard, Giles E. St J. Hardy and Bernard Dell

School of Veterinary and Life Sciences, Murdoch University, South Street, Murdoch, WA 6150,
Australia.

Abstract

To regenerate sandalwood (*Santalum spicatum*) stands in south-western Australia it is necessary to understand the complex relationship between woylies (*Bettongia penicillata ogilbyi*) and sandalwood. Sandalwood requires a seed disperser for successful recruitment and in the past the critically endangered woylie played an important role in dispersing and caching seeds, but it is not clear whether this mutualistic and antagonistic relationship is beneficial to regeneration efforts. An enclosure in a woodland and ⁴⁶Scandium-labelled seeds, enabled study of the *in situ* predation of seeds, caching, the fate of cached seeds, the detection of cached seeds and predation of germinated seeds. Woylies preferentially cached sandalwood, then *S. acuminatum* seeds, before any interest was shown in *Acacia acuminata* and *Gastrolobium microcarpum* seeds, which were virtually all eaten *in situ*. Of a further 500 radiolabelled and individually numbered sandalwood seeds deployed, 42.2%

were eaten *in situ*, 20.8% had an unknown fate and 37% were cached, with some seeds being recached up to four times. After nine months, only four cached seeds remained undisturbed. Olfaction appeared to be the primary method of cache detection. To examine the recruitment rate of cached seeds, the fate of 89 transplanted sandalwood seedlings at two study sites was followed. After one month 38% were intact and growing, but half of the transplanted seedlings were dug up and the remaining endosperm was eaten *in situ* or taken away. The results highlight the potential of providing seed supplies, including sandalwood seeds and seeds of their hosts, to seed-dispersal marsupials for passive ecosystem repair.

Additional keywords: caching, dispersal, regeneration, 46Scandium, scatter hoarding.

Introduction

Santalum spicatum (sandalwood) is an indigenous species of Western Australia that occurs within a wide range of arid to semiarid climates (Kealley 1991). Sandalwood is an obligate root hemi-parasite and typically grows with nitrogen-fixing hosts, such as *Allocasuarina* and *Acacia* species, and is particularly successful when parasitising *Acacia acuminata*. The scented heartwood is sought after for its oil which, is used in the perfume and other industries (Subasinghe 2013). Its geographical range has become constricted due to widespread clearing for agriculture (McKinnell 1990), and tree extraction from the wild is now restricted to arid ecosystems where recruitment remains problematic (Sawyer 2013).

Due to the large fruit of sandalwood, much of the seed remains below the parent tree after fruit fall, which results in low recruitment due to poor germination conditions, and competition with the parent and other seedlings for resources and hosts. Poor seed dispersal combined with the disappearance of the woylie (*Bettongia penicillata ogilbyi*) from central Western Australia may explain the reduced recruitment of natural sandalwood stands (Brand 2000). Over the past 200 years, woylies have become extinct over much of their geographical range and are now restricted to two remnant populations (Start *et al.* 1995; Wayne *et al.* 2015). The woylie is listed as critically endangered under

the *WA Wildlife Conservation Act 1950* and Endangered under the *Commonwealth Environment Protection and Biodiversity Conservation Act 1999* (Yeatman and Groom 2012). In the last 10 years, there has been a significant decline in the population in south-west Western Australia, and the indigenous persistent population currently numbers ~2000 (Pacioni *et al.* 2011; Wayne *et al.* 2013).

Several mammal species move seeds without killing them and transport them to microsites that favour seedling establishment (Theimer 2001; Dennis 2003; Murphy *et al.* 2005; Vander Wall *et al.* 2005). Woylies can cache hundreds of sandalwood seeds in individual scatter hoards that appear randomly placed, often uphill and always some distance from the source (Murphy *et al.* 2005). Recently, burrowing bettongs (*B. lesueur*) were also shown to move seed away from the parent plant, scatter hoarding them (Chapman 2015). Emus (*Dromaius novaehollandiae*) also disperse sandalwood seed, as eaten fruit are excreted intact (Erickson *et al.* 1973); however, they do not appear to be a major vector, as sandalwood seed dispersal and recruitment is low in areas where emus are abundant (Department of Environment and Conservation unpubl. data 2004). Thus, woylies have the potential to alter the fate of the seeds and subsequent sandalwood regeneration and to modify the distribution of sandalwood (Murphy *et al.* 2005). The bettongs' foraging activity has been shown to be important in ecosystem function (Garkaklis *et al.* 2004): as well as being a vector for mycorrhizal fungal spores, they can help create heterogeneity in nutrients (Noble 1993) and the water repellency of surface (Garkaklis *et al.* 1998) and subsurface soils (Garkaklis *et al.* 2000).

Seed dispersal by marsupials (in contrast to eutherian mammals) has been little studied. Until now, no formal research had been conducted to determine whether caching of sandalwood seeds by woylies has a positive impact on recruitment, although it has been demonstrated that the collection of seeds by scatter-hoarding rodents increases seedling recruitment (Vander Wall *et al.* 2005; Vander Wall 2008).

Tracking the fate of seeds depredated by mammals has relied on a range of techniques including: spool and thread (Forget 1993; Dennis 2003), fluorescent dyes (Longland and Clements 1995; Wróbel and Zwolak 2013), transponder tags (Suselbeek *et al.* 2013) and transponders with flagging tape for burrowing bettongs (Chapman 2015). In addition, ⁴⁶Scandium (⁴⁶Sc) has been used successfully for tracking seeds in the USA (Abbott and Quink 1970; Waitman *et al.* 2012). Labelled seeds can be

tracked using a Geiger Muller (GM) counter for up to one year (Primack and Levy 1988) to a depth of 30 cm (Vander Wall 1995). The isotope decays to titanium, a non-toxic substance and, due to its inert nature, ^{46}Sc does not pass through the food chain (Forget and Wenny 2005).

While the transportation of the seeds away from the parent plant and the subsequent burial of the seeds near potential host plants are the primary means of facilitating regeneration (Brand *et al.* 2014), it is important to investigate the relationship of the woylie and sandalwood to determine whether the reintroduction of woylies can improve recruitment as natural regeneration is low (Sawyer 2013; Brand *et al.* 2014). In this study, we examined the relationship between the woylie and Western Australian sandalwood to determine whether woylies play a role in the distribution and recruitment of sandalwood by caching the seeds. Across four experiments, we investigated the preferred seed for caching from four local species, the location and fate of cached seeds, the detection of cached seeds, and the fate of germinated seeds, using ^{46}Sc to locate deployed seeds.

Materials and methods

Experimental sites

Three experimental sites in the Dryandra Woodland Nature Conservation Reserve (32°48'S, 116°54'E), ~160 km south-east of Perth, were used in this study. The woodlands are managed by the Western Australia Department of Parks and Wildlife. The study area was predominantly native semiarid open wandoo (*Eucalyptus wandoo*) woodland and Sites A and B were selected as they were areas known to contain woylies and experimental sandalwood plots. Since 1931, 15 sandalwood plots have been established in the Dryandra Woodland (P. Jones, pers. comm.). Dryandra Woodland is home to one of the few extant populations of woylies (Department of the Environment 2015).

The enclosure was 85 × 220 m, fenced with 2-m-high 5-mm mesh, with a 30-cm skirt running out from the fence along the ground to prevent animals digging their way in or out of the enclosure. The

fence was initially electrified, but this failed after Experiment 1, so small gates were left open so the woylies were free-living and could enter and leave the enclosure for Experiments 2 and 3.

The vegetation consisted of a large mature sandalwood stand, jam acacia (*Acacia acuminata*), a dense rock sheoak (*Allocasuarina huegeliana*) stand and occasional wandoo (*Eucalyptus wandoo*). The understorey was predominantly scattered sandplain poison (*Gastrolobium microcarpum*) clumps. The understorey was very open around the sandalwood stand. Several woylie-type nesting sites were constructed within the enclosure, where fallen branches and dead sandplain poison bushes were placed among the dense thickets of sheoak to provide areas with low, dense clumped vegetation as preferred by woylies for nest sites (Christensen and Leftwich 1980).

Site A was located within the Dryandra Woodland, parallel to the Wandering–Narrogin Road, adjacent to farmland (approximately $-32.763744, 116.968476$). This area also contained numerous mature sandalwood trees planted in the 1950s (J. Brand, pers. comm.), saplings and seedlings, interspersed with jam acacia, rock sheoak, a few wandoo and a sparse understorey. The soil was predominately sandy.

Site B was deeper in the Dryandra Woodland (approximately $-32.803595, 116.988980$), and had similar vegetation to Site A, but included dense thickets of sandplain poison throughout. Sandalwood was planted in rows within the native vegetation in the late 1970s to early 1980s (J. Brand, pers. comm.) but there were very few new sandalwood recruits at this site. The understorey was sparse except in the sandplain poison thickets. The soil type was predominantly sand overlaying clay, duplex soils.

The woylies

For Experiment 1 two woylies, one male and one female, were placed in the electrified enclosure on Day 1. The following day a further three males were added. These woylies came from a wildlife sanctuary in Pingelly, 40 km north-east of Dryandra, and had been kept away from human contact for at least nine months before their translocation. They were raised in captivity, fed special marsupial pellets and were due for release at ~1 year of age. They were, however, introduced to sandalwood

seeds at an early age. Trapping was carried out before the commencement to ensure that no other mammal was in the enclosure at the time of the experiment.

Trapping surveys confirmed that woylies were present at Sites A and B (Experiment 4), and within the enclosure area after gates were added (Experiments 2 and 3). Trapping sessions, over four consecutive nights per experimental site, were commenced in May 2002 and repeated at regular intervals until December 2005, giving a total of 1300 trap-nights at Site A and 1400 at Site B. The trapping sessions were carried out four times a year in each season. The minimum number of animals 'known to be alive' was calculated by counting the number of times an individual woylie was trapped over at least three sessions. A total of 11 individual females and 17 individual males were trapped between May 2002 and December 2005.

Brush-tail possums (*Trichosurus vulpecula*) were present at Sites A and B. The estimated population (using the Jolly–Seber method) of the possums was 17 possums at Site A (density of 1.4 ha⁻¹) and 70 at Site B (5.8 ha⁻¹) in spring 2003 compared with spring 2005, when there was an estimated 25 possums at Site A (density of 2.1 ha⁻¹) and 35 at Site B (2.9 ha⁻¹).

Radiolabelling and locating seed

The seeds, with intact shells, were radiolabelled using the method of Vander Wall (2000). One mCi of ⁴⁶Sc (PerkinElmer, Boston) was added to 40 mL of sterile water, the seeds were coated with the solution and left to dry for 48 h. This gave ~1 µCi (37 kBq) of activity per seed. The dry seeds were placed in zip-lock plastic bags and transferred to the site in lead pots. A GM counter (Radiation Alert™ Monitor 5 SE International, USA) was used to locate seeds, seed hulls, scats and caches. The GM counter was calibrated for cobalt-60, the isotope with the closest photon energy count (1.33 MeV 100%) to ⁴⁶Sc (1.12 MeV 100%) in October 2004. Faeces were located with the GM counter during the study and removed from the study site. At the conclusion of each experiment any partially eaten seed or seed hull found with the GM counter was removed from the study area.

Marking the location of caches

Any caches located were discretely marked with a small numbered and dated plastic marker (above-ground portion measured 6.5 cm wide × 2.5 cm high). Prior to the start of Experiment 3, 50 markers were placed in the ground throughout the site and checked after two weeks, in case the woylies had learned to associate the markers with caches. None of the areas that had the markers showed signs of digging, so it was concluded that using this type of marker would not alert woylies to cache locations.

Experiment 1: The fate of fallen seeds

In May 2005, 50 sandalwood seeds and 50 of the smaller *Santalum acuminatum* (quandong) seeds, and 450 seeds of each host species – *Acacia acuminata* (jam acacia) and *Gastrolobium microcarpum* (sandplain poison) – were used to examine *in situ* predation and caching behaviour (Fig. 1). All seeds are known to be a food source for woylies (Sampson 1971; Christensen 1980; Murphy *et al.* 2005). The quandong and sandalwood seeds were individually numbered with indelible ink. The quandong and jam seeds were obtained from Nindethana Seed Service Pty Ltd, Albany WA, the sandalwood was supplied by The Forest Products Commission of WA (Narrogin, provenance 2001), while the sandplain poison seed was collected from Dryandra Woodland in December 2004.

The sandalwood and quandong seeds were placed, using gloves and tongs, within the dripline of two separate sandalwood trees, 6 m apart, within the enclosure containing five woylies, to simulate natural fruit fall. After dark, the other seeds were placed in the same location on Petri dishes to reduce the risk of non-target predators such as birds and ants removing them. The seeds were observed from 5 m away for 30 min every hour overnight. While present, the observer remained quietly seated on a folding stool, as still as possible, using a night scope. Each dawn, the seeds were checked and recorded as remaining *in situ*, eaten *in situ*, removed (fate unknown) or cached. Any remaining seeds were collected and stored during the day. Remaining seeds were returned each night until the supply was exhausted. The seeds were tracked daily for the first week, then monthly for a total of seven months.

Experiment 2: The fate of cached seeds

To determine the fate of cached seeds, 500 individually numbered and radiolabelled sandalwood seeds were deployed in the enclosure. The enclosure had gates so that the woylies could come and go from the enclosure. Observation indicated that there were no more than five or six woylies in the area at the time of the experiment.

At dusk of the first evening in February 2006, 200 labelled seeds were placed under an adult sandalwood tree, positioned to simulate natural fruit fall. The seeds were observed continuously overnight from a distance of 5 m, again with the unconcealed observer using a night scope. At dawn, the seeds were checked as described in Experiment 1. Any remaining seeds were collected and stored during the day, and, while available, each evening 200 seeds were deployed.

The experiment continued until all the seeds had either been eaten or removed. The cached seeds were monitored every morning for a further week to determine if they had been left undisturbed, dug-up and eaten or re-cached elsewhere. Subsequent monitoring of the caches was carried out every two weeks for two months, then monthly for another seven months.

Gloves were worn to excavate the cache, with minimal disturbance, and the type and amount of seeds were recorded along with the seed number (for sandalwood and quandong). The cache depth and distance from the source of the seeds were measured. The seeds were returned to the cache, re-covered and checked each morning for one week to determine whether the seeds remained *in situ*, had been moved or had been eaten. After the first week, the caches were checked on a monthly basis for a year until the gamma emissions were too low to monitor.

Experiment 3: Detection of cached seeds by woylies

To determine how woylies locate buried seeds, 80 artificial caches, each containing radiolabelled and numbered sandalwood seed were set up throughout the fenced/gated enclosure in late February 2006, after the initial observation phase of Experiment 2. The caches were made to a depth of 5 cm with minimal disturbance to the surrounding soil. The seed was covered with soil and leaf litter to ensure the woylies could not see disturbed earth, making them rely on olfaction to locate the seeds in caches.

Eighty control 'caches' (seedless) were dug to rule out disturbed earth as a visual clue to cache locations. A further 20 labelled seeds were carefully placed under the thick leaf litter created by the rock sheoak without disturbing the soil surface. Twenty control areas were set up by lifting leaf litter without seed placement to determine whether woylies could detect even the slightest disturbance in leaf litter.

Each cache had a plastic marker ~20 cm from the cache. To ensure that the woylies did not associate these markers with seed caches, 50 markers were placed in the ground throughout the site and checked after two weeks. None of the areas that had the markers showed signs of digging, so it was concluded that using this type of marker did not alert woylies to cache locations.

All caches (including controls) were checked daily, for three days, and the condition of each cache was recorded as either disturbed or undisturbed.

Experiment 4: Predation of germinated seeds

To determine whether woylies use emerging seedlings as markers to locate cached seeds, 89 greenhouse-grown seedlings were transplanted at two sites (Site A, $n = 46$; Site B, $n = 43$) in Dryandra Woodland in August 2003. Each of the seedlings was protected with an open-ended plastic bag staked into the ground to prevent any woylies accessing the seedlings. After one week, the protective plastic was removed, and the seedlings were observed for seven nights for signs of disturbance. The seedlings were classified as undisturbed or dug up, grazed or dead. The remaining epicarp of disturbed seedlings was either recorded as eaten *in situ*, dug up, or the endocarp removed.

Results

Experiment 1: The fate of fallen seed

Woylies ate or cached all the sandalwood seed on the first night before they interacted with seed from the other species. The sandalwood seeds were removed and cached (52%), or eaten *in situ* (48%) within 1 m of the source tree (Table 1).

At first encounter with the seeds, the woylies immediately manipulated the sandalwood seed with their forepaws before placing the seed in their mouths, leaving the area at a relatively high speed before returning to remove more seed. The return was rapid, suggesting that there was insufficient time to consume the seeds, thus the seeds were most likely being cached. Woylies can cache a seed within a matter of seconds, particularly if the cache is shallow and poorly covered, which was how many of the caches were found. It was only after several trips that some of the woylies started to eat the seeds *in situ*.

When the supply of sandalwood seeds was exhausted, the woylies started to consume the quandong seeds, which were all eaten or cached by the end of night 3. The woylies were observed sniffing the jam acacia and sandplain poison seeds during the first two nights but left the area without removing any of these seeds. After the large seeds had been removed or eaten, the woylies then collected or consumed the smaller seeds of the other two species. Jam acacia seeds were the third favoured seed, and were all consumed by one woylie after the sandalwood and quandong seed supply was exhausted; no cached jam acacia seeds were found. On the fifth night, one woylie ate most of the sandplain poison seeds *in situ*. The woylie then collected some seeds in its mouth and buried them 40 m from the source in a single cache. It returned to the source tree, collected more seeds and cached them very close to the first cache. It returned to the source and consumed the remaining seeds. No other sandplain poison seed caches were found and it was concluded that most seeds had been consumed by the one woylie (Fig. 2). After seven months, all of the cached seeds had been dug up and eaten *in situ*, with the exception of three sandalwood seeds, which were not found.

Experiment 2: The fate of cached seeds

In the first four nights, of the 500 sandalwood seeds deployed, 211 (42.2%) were eaten *in situ*, 185 (37%) were cached and the fate of 104 (20.8%) was unknown (Fig. 3). The caches all contained one seed, consistent with scatter hoarding, ranging from 3 to 88 m from the source tree. The seeds were buried between 1 and 6 cm deep (mean = 3.15 ± 0.11 cm) (Fig. 4). Of the primary caches, 61 (33%) caches were between 2 and 3 cm deep. There were 22 (12%) caches at depths greater than 5 cm.

Cached seeds

After nine months, 185 primary, 120 secondary, 52 tertiary, 35 quaternary and 17 quintic caches had been located. There did not appear to be any spatial pattern associated with the different caches in relation to the source tree. It remains unknown whether the same woylie that made a primary cache went on to move that seed four times, or whether several different woylies were involved in recaching individual seeds. Other than possums, there was no sighting of, or evidence of, other mammals in the enclosure.

Fate of cached seeds

Some seeds were recached up to four times (Fig. 5). The fate of each of the 185 cached seeds were: recaching (primary 65%, secondary 43%, tertiary 67%, quaternary 50%); dug up and eaten (primary 32%, secondary 32%, tertiary 13.5%, quaternary 34.2%, quintic 25%) or removed, fate unknown (30%).

Location of the caches

Generally, caches were located within 30 cm of vegetation (63%), with 50% of caches occurring near sandalwood host trees (Fig. 6). There was no significant difference ($\chi^2_{28} = 39.3$, $P = 0.77$) between the location of caches and a particular vegetation type or structure for primary through to quintic caches. No caches were located within 1 m of *E. wandoo*, the only large trees within the enclosure.

The number of primary caches declined further away from the source with a mean distance of 28.7 ± 1.5 m (range 4–89 m). In all, 42% of caches were found less than 15 m from the source.

Experiment 3: Detection of cached seeds by woylies

Olfaction appeared to be the principal method used by woylies to locate buried seeds, a process at which they are very efficient. There was a significant difference ($\chi^2_1 = 6.5$, $0.025 > P > 0.01$) in the number of artificially cached seeds dug up by woylies compared with disturbance of the control 'caches'. Of the 80 caches, 65 (81.2%) were located by woylies over three nights. During the same period, 39 (48.7%) of the control 'caches' showed signs of being disturbed, suggesting that woylies

were, at least in part, responding to the smell of disturbed soil as well as the actual seed. Furthermore, there was a highly significant difference ($\chi^2_1 = 7.5$, $0.01 > P > 0.005$) between the number of seeds located by woylies under leaf litter compared with the control. All of the 20 seeds under the leaf litter were located within two nights compared with only six (30%) of the control 'caches' in the leaf litter showing signs of disturbance. These findings strongly suggest that it was the buried seeds that the woylies smelt rather than any disturbance in the leaf litter. There were no visual clues left during the burial of any seeds, ruling out the use of visual clues as a method of locating buried seeds.

Experiment 4: Predation of germinated seed

There was no significant difference ($\chi^2_4 = 3.96$, $P < 0.25$) between the two sites for the fate of seedlings, so data for sites were combined (Fig. 7). In total, 44% of germinated seed were dug up and eaten *in situ*, while 10% were removed from the area, presumably to be eaten elsewhere rather than recached as they would have been split open during the germination process, therefore no longer suitable for storage. There were 38% of seedlings surviving after one month, although 10 seedlings had been heavily grazed by unknown animal(s), with very few leaves or stems remaining.

Discussion

This study provides evidence that woylies at Dryandra Woodland are efficient pre- and postdispersal predators of their preferred seeds, sandalwood, and were capable of consuming a significant amount of deployed, dispersed and germinating seeds. This study suggests that before European settlement woylies probably played an important role in the recruitment of new sandalwood stands through their caching activities.

The woylies demonstrated a clear preference for sandalwood, followed by quandong, then jam acacia and sandplain poison. The kernel of sandalwood at maturity contains 50–60% oils (Hettiarachchi *et al.* 2013), with ~40% lipids, 20% carbohydrates and 15% protein (Liu *et al.* 1997). Quandong kernels are also rich in oil, and contain 67% fat and 15% protein (Jones *et al.* 1999). Acacia seed has an

average of 8% fat and 2% protein (Brand-Miller and Holt 1998). Larger, more nutritious, seeds are preferentially cached over smaller seeds as they provide a more energetic return (Zhang *et al.* 2005; Taraborelli *et al.* 2009; Vander Wall 2010). Although the woylies initially selected sandalwood and quandong, the seeds of jam acacia and sandplain poison were consumed after the preferred seeds had been cached or eaten. This behaviour was in contrast to the theory of seed caching by mammals commencing once the animal is satiated (Jensen 1985). Rather, it reinforces that it is more profitable to transport and scatter hoard larger nuts. Other factors that would influence the choice to cache seeds include food perishability (Smallwood and Peters 1986) and increased handling time resulting in increased risk of predation (Hadj-Chikh *et al.* 1996). However, it is possible that the prior exposure by the woylies to sandalwood seed influenced their seed preference, and because they were reared in captivity they may have developed different foraging skills to wild-raised animals.

While woylies have been reported to bury small quantities of *Gastrolobium* seeds (Sampson 1971) and the toxic *G. bilobum* (Christensen 1980), this is the first study to provide evidence of woylies caching seeds of the highly toxic sandplain poison. The seeds are considered potentially nutritious but contain a lot of fibre, which may limit nutrient digestibility (Irlbeck and Hume 2003). Furthermore, due to the hard testa, many seeds are likely to pass through the gut intact, to be deposited in scats. Interestingly, no woylie scats were located containing any of the labelled *Gastrolobium* seeds. This alternative seed dispersal method of the sandalwood hosts potentially increases the distribution and range of these plants (Wang and Smith 2002).

Single sandalwood seeds were cached and recached by woylies up to four times, illustrating the complex nature of the seed-dispersal process. Chapman (2015) reported that recaching occurred up to six times by burrowing bettongs. Jansen *et al.* (2006) hypothesised that recaching seeds allows the animals to monitor food quality and quantity. As the woylies scatter hoard single seeds, sometimes at depths that favour germination and emergence, they provide the best chance that some of the buried seeds will not only escape detection but will also be buried in areas beneficial to germination (Pearson and Theimer 2004). In the current study the most frequent location of caches was near one of sandalwood's principal hosts, jam acacia, but this is probably coincidental due to the density of these

species in the area. In a bigger enclosure, Chapman (2015) found that 42% of seeds were cached near (<3 m) potential host plants. If undetected, the buried sandalwood seed may germinate and it is feasible that they will have an increased chance of survival by having easy access to the host's root system compared with non-dispersed seeds. Some seeds were located buried under fallen logs, which may partially protect the seed from detection and also protect the germinating seedling from grazing. In the current study, 37% of seeds were cached but only 12% of seeds were buried at a depth of 5 cm or more, the optimal planting depth for sandalwood (McKinnell 1990), while the burrowing bettongs completely covered (depth not provided) 21% of caches (Chapman 2015). More studies are required to determine the correct seed to animal ratio required to maximise sandalwood regeneration capacity.

In the current study, there was no pattern of cache location in relation to the source or previous cache position. There was a complex movement of sandalwood seed, with seed being recached often (nightly) and regularly being moved back closer to the source. As the current study was conducted in an enclosure, this may have restricted the distance travelled by the woylies while caching. Only five seeds were cached against the fence line, which could suggest either that woylies avoided the fence line or they reached the fence and diverted back into the enclosure to cache seed. Stapanian and Smith (1978) predicted that with increasing seed abundance rodents will cache further from the seed source in order to maintain a low density and high spacing of cached seeds to reduce pilfering. However, some rodent studies have shown that shorter dispersal distances result from increased seed abundance (Jansen *et al.* 2004; Moore *et al.* 2007; Puerta-Piñero *et al.* 2010). In the current study, the strategy of the woylies may have been to cache as many seeds as quickly as possible, then to further disperse these seeds by recaching but this was difficult to determine in a small enclosure. Retrieval and recaching, either by the original animal, or by a cache robber is common amongst mammals (Vander Wall *et al.* 2005). In a larger enclosure, Chapman (2015) was able to demonstrate that most of the recaching by *Bettongia lesueur* occurred progressively further away from the deployment area, resulting in 45% of seed being cached ≥ 40 m (maximum >80 m) from the source. Competition for sandalwood as a food source is high (Vander Wall 1990), as shown by the multiple recaching, and the

speed at which the woylies and the burrowing bettongs (Chapman 2015) took the sandalwood seeds from the source.

Post-dispersal seed predation was high, with up to 50% of the caches disturbed with the seed husk beside a dug-up cache. Scatter hoarding rodents are remarkably adept at recovering their own caches, with up to 98% of cached seeds being depredated (Vander Wall 1990). For large seeds, the opportunity to escape seed predation via burial or reduced seed density is limited (Hulme and Borelli 1999). For sandalwood, the greater the number of woylies present at seed fall could result in more scatter hoarding occurring to reduce competition for seed, and thus increase the chances of the successful recruitment. However, a large number of woylies later locating and consuming the cached seeds could be detrimental to recruitment.

Olfaction appears to be the primary method to locate buried seeds used by woylies with a combination of the smell of disturbed earth and the seed likely to have been used. Woylies have a well developed sense of smell as demonstrated by their ability to locate *Mesophellia* spp. deep within the soil, in the peak of summer, when the ground is very dry and hard (Christensen 1980). By observing the foraging behaviour of woylies, who are prolific diggers (Garkaklis *et al.* 2004), there is a strong possibility that a combination of olfaction and random foraging are the likely methods of cache location. Vander Wall (2000) noted that this combination was an effective way for rodents to locate buried seeds. However, some mammals use a combination of spatial memory and olfaction to locate their own caches, but olfaction only to locate caches made by other individuals (Vander Wall 2000; Winterrowd and Weigl 2006). Further research with a captive population of woylies is required to test this.

Sampson (1971) suggested that woylies used seedlings as 'markers' to assist in locating buried seeds and the current study provides evidence to support this theory: there were empty seed hulls found lying next to disturbed seedlings in most cases at both sites. The woylies only appeared to dig up small, newly germinated seedlings, when there would still be fatty epicarp remaining for consumption. Rodents and corvids are also known to use emerging seedlings to locate caches whereby they consume the remains of the seed (Abbott and Quink 1970; Vander Wall 1990; MacDonald 1997; Pyare and Longland 2000). Studies have demonstrated that this sort of seedling predation can

seriously impact the distribution and recruitment of many temperate and tropical species. In some cases, the seedlings probably provided additional clues to olfaction in the search for buried seeds; however, in some instances the seedlings alone appeared to ‘provide a sufficiently strong stimulus to elicit a digging response without additional olfactory motivation’ (Pyare and Longland 2000, p. 70). A combination of olfaction and visual clues from the emerging seedlings is the most likely way that woylies locate buried seeds. They were observed foraging in the area before locating the seedlings. The germinated seeds that escaped early detection by woylies were left undisturbed; furthermore, the woylies showed no interest in consuming these seedlings, unlike the red acouchies (*Myoprocta exilis*) that slow down the depletion of endosperm by removing, upon germination, the sprouts that help keep the seed alive (Jansen *et al.* 2006). The considerable level of postgermination predation may negatively impact sandalwood recruitment and spatial distribution, but this would depend on competition between woylies for food sources during that period.

Even with relatively few woylies in the area, predation on seeds and seedlings has the potential to be considerable. The predatory behaviour displayed by woylies is remarkably similar to the findings from other studies of small mammals, particularly rodents, that are attracted to concentrations of seed so their highest predation usually occurs under the parent canopy (Howe 1989; Forget 1993; Hulme and Borelli 1999; LoGiudice and Ostfeld 2002). Thus, seed predators, such as woylies, have the potential to affect plant populations by altering patterns of seed dispersal, and ultimately regeneration, by destroying emerging seedlings (Hulme 2002).

⁴⁶Sc proved to be a valuable tool, particularly as shown in the first experiment, in which all seeds were successfully tracked. The average caching depth of 5 cm falls within the 30-cm depth of GM counter detection. The 30% of undetected seeds in the second experiment appears to be relatively consistent with findings from other studies. For example, Vander Wall (2003) reported that 20–50% of pine seeds were not located using ⁴⁶Sc. It was assumed that some seeds that were missed in the current study may have been removed from the search area in Experiments 2 and 3. As the remaining seeds were stored during the day, birds could not be held responsible for the loss.

There are several limitations of the current study that may have influenced the behaviour of the woylies in this study. Due to the endangered status of the woylie, only low numbers were available for the study, with little diversity in their ages. This may have had some impact on all experiments, particularly Experiment 1, as the food preference and foraging strategies may be influenced by age and sex. The amount of predation is likely to be influenced by the density of these seed predators, and the temporal and spatial effects on their energy requirements and the amount of alternative food sources available. Furthermore, the presence of an observer may have created a perception of increased predation risk, influencing the extent to which seeds were cached or eaten *in situ*. More research is needed to determine the extent of seed predation by natural populations of woylies, over several years, utilising remote cameras to capture more data.

In conclusion, woylies have both a mutualistic and antagonistic relationship with sandalwood and its propagules. Woylies are both pre- and postdispersal predators that consume seeds under the parent, seeds that have been dispersed away from the parent trees as well as cached and germinating seed. Woylies primarily scatter hoarded the sandalwood seed over other choices, made many small caches, and in some instances buried the seed at depths that favoured successful germination and emergence, but most importantly often buried them in protected areas at a distance from the parent tree. The reintroduction of woylies to areas within the natural range of sandalwood in Western Australia, and the provision of a structured supply of seeds, either as a diversionary food supply, as suggested by Longland and Ostoja (2013), or as a means of concurrently spreading seeds of sandalwood along with host plant seeds could form the basis of a passive restoration strategy. Generally, over a three-year period, survival of recruits that woylies had dispersed away from adult trees was significantly higher than for those recruits that had germinated beneath the adult crown in the sites with woylies. The provision of sandalwood seeds along with the seeds of host species could be the most cost-effective way to restore functioning ecosystems. However, as they are also seed predators a balance between woylie population and the seeds supplied requires careful consideration to enable successful restoration. While carrying out important ecosystem services, bettongs have the potential to provide natural regeneration of sandalwood in Western Australia.

Acknowledgements

We thank the Australian Research Council and the Forest Products Commission for financial support, the Department of Conservation and Land Management for permission to work with woylies at Dryandra woodland, John Lawson and Lisa Richards for their support at Dryandra, and Associate Professor Mike Calver for advice with statistics. Dr Adrian Wayne and two anonymous reviewers provided helpful comments on the first submission of the paper.

References

- Abbott, H. G., and Quink, T. F. (1970). Ecology of eastern pine seed caches made by small forest mammals. *Ecology* **51**, 271–278. doi:10.2307/1933663
- Brand, J. E. (2000). The effects of management regime and host species on sandalwood (*Santalum spicatum*) recruitment near Paynes Find, Western Australia. *The Rangeland Journal* **22**, 243–255. doi:10.1071/RJ0000243
- Brand, J. E., Sawyer, B., and Evans, D. R. (2014). The benefits of seed enrichment on sandalwood (*Santalum spicatum*) populations, after 17 years, in semi-arid Western Australia. *The Rangeland Journal* **36**, 475–482. doi:10.1071/RJ14026
- Brand-Miller, J. C., and Holt, S. H. A. (1998). Australian Aboriginal plant foods: a consideration of their nutritional composition and health implications. *Nutrition Research Reviews* **11**, 5–23. doi:10.1079/NRR19980003
- Chapman, T. F. (2015). Reintroduced burrowing bettongs (*Bettongia lesueur*) scatter hoard sandalwood (*Santalum spicatum*) seed. *Australian Journal of Zoology* **63**, 76–79. doi:10.1071/ZO14090
- Christensen, P. E. S. (1980). The biology of *Bettongia penicillata* (Grey, 1837) and *Macropus eugenii* (Desmarest 1817) in relation to fire. *Forests Department of Western Australia Bulletin* **91**, 1–90.
- Christensen, P., and Leftwich, T. (1980). Observations on the nest-building habits of the brush-tailed rat-kangaroo or woylie (*Bettongia penicillata*). *Journal of the Royal Society of Western Australia* **63**, 33–38.
- Dennis, A. J. (2003). Scatter-hoarding by musky rat-kangaroos, *Hypsiprymnodon moschatus*, a tropical rain-forest marsupial from Australia: implications for seed dispersal. *Journal of Tropical Ecology* **19**, 619–627. doi:10.1017/S0266467403006023
- Department of the Environment (2015). *Bettongia penicillata ogilbyi* – woylie. Biodiversity – species profile and threats database. Australian Government, Department of the Environment. Available at: http://www.environment.gov.au/cgi-bin/sprat/public/publicspecies.pl?taxon_id=66844 [accessed August 2015].

- Erickson, R., George, A. S., Marchant, N. G., and Morcombe, M. K. (1973). 'Australian Flora in Colour: Flowers and Plants of Western Australia.' (A.H. and A.W. Reed: Sydney.)
- Forget, P.-M. (1993). Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. *Oecologia* **94**, 255–261. doi:10.1007/BF00341325
- Forget, P.-M., and Wenny, D. (2005). How to elucidate seed fate? A review of marking methods used to study seed removal and secondary seed dispersal. In 'Seed Fate: Predation, Dispersal and Seedling Establishment'. (Eds P. M. Forget, J. Lambert, P. Hulme, and S. B. Vander Wall.) pp. 379–393. (CABI Publishing: Wallingford, UK.)
- Garkaklis, M. J., Bradley, J. S., and Wooller, R. D. (1998). The effects of woylie (*Bettongia penicillata*) foraging on soil water repellency and water infiltration in heavy textured soils in southwestern Australia. *Australian Journal of Ecology* **23**, 492–496. doi:10.1111/J.1442-9993.1998.TB00757.X
- Garkaklis, M. J., Bradley, J. S., and Wooller, R. D. (2000). Digging by vertebrates as an activity promoting the development of water-repellent patches in sub-surface soil. *Journal of Arid Environments* **45**, 35–42. doi:10.1006/JARE.1999.0603
- Garkaklis, M. J., Bradley, J. S., and Wooller, R. D. (2004). Digging and soil turnover by a mycophagous marsupial. *Journal of Arid Environments* **56**, 569–578. doi:10.1016/S0140-1963(03)00061-2
- Hadj-Chikh, L. Z., Steele, M. A., and Smallwood, P. D. (1996). Caching decisions by grey squirrels: a test of the handling time and perishability hypotheses. *Animal Behaviour* **52**, 941–948. doi:10.1006/ANBE.1996.0242
- Hettiarachchi, D. S., Liu, Y. D., Boddy, M. R., Fox, J. E. D., and Sunderland, V. B. (2013). Contents of fatty acids, selected lipids and physicochemical properties of Western Australian sandalwood seed oil. *Journal of the American Oil Chemists' Society* **90**, 285–290. doi:10.1007/S11746-012-2162-3
- Howe, H. F. (1989). Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* **79**, 417–426. doi:10.1007/BF00384323
- Hulme, P. E. (2002). Seed-eaters: dispersal, destruction and demography. In 'Seed Dispersal and Frugivory: Ecology, Evolution and Conservation'. (Eds D. J. Levey, W. R. Silva and M. Galetti.) pp. 257–273. (CAB International: New York.)
- Hulme, P. E., and Borelli, T. (1999). Variability in post-dispersal seed predation in deciduous woodland: relative importance of location, seed species, burial and density. *Plant Ecology* **145**, 149–156. doi:10.1023/A:1009821919855
- Irlbeck, N. A., and Hume, I. D. (2003). The role of acacia in the diets of Australian marsupials – a review. *Australian Mammalogy* **25**, 121–134. doi:10.1071/AM03121
- Jansen, P. A., Bongers, F., and Hemerik, L. (2004). Seed mass and mast seeding enhance dispersal by a Neotropical scatterhoarding rodent. *Ecological Monographs* **74**, 569–589. doi:10.1890/03-4042

- Jansen, P. A., Bongers, F., and Prins, H. H. T. (2006). Tropical rodents change rapidly germinating seeds into long-term food supplies. *Oikos* **113**, 449–458. doi:10.1111/J.2006.0030-1299.14461.X
- Jensen, T. S. (1985). Seed–seed predator interactions of European beech (*Fagus sylvatica* L) and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. *Oikos* **44**, 149–156. doi:10.2307/3544056
- Jones, G. P., Watson, T. G., Sinclair, A. J., Birkett, A., Dunt, N., Nair, S., and Tonkin, S. Y. (1999). Santalbic acid from quandong kernels and oil fed to rats affects kidney and liver P450. *Asia Pacific Journal of Clinical Nutrition* **8**, 211–215. doi:10.1046/J.1440-6047.1999.00112.X
- Kealley, I. (1991). The management of sandalwood. Wildlife Management Program 8. Department of Conservation and Land Management, Western Australia.
- Liu, Y. D., Longmore, R. B., and Kailis, S. G. (1997). Proximate and fatty acid composition changes in developing sandalwood (*Santalum spicatum*) seeds. *Journal of the Science of Food and Agriculture* **75**, 27–30. doi:10.1002/(SICI)1097-0010(199709)75:1,27::AIDJSFA832.3.0.CO;2-5
- LoGiudice, K., and Ostfeld, R. S. (2002). Interactions between mammals and trees: predation on mammal-dispersed seeds and the effects of ambient food. *Oecologia* **130**, 420–425. doi:10.1007/S004420100810
- Longland, W. S., and Clements, C. (1995). Use of fluorescent pigments in studies of seed caching by rodents. *Journal of Mammalogy* **76**, 1260–1266. doi:10.2307/1382621
- Longland, W. S., and Ostoja, S. M. (2013). Ecosystem services from keystone species: diversionary seeding and seed-caching desert rodents can enhance Indian ricegrass seedling establishment. *Restoration Ecology* **21**, 285–291. doi:10.1111/J.1526-100X.2012.00895.X
- MacDonald, I. M. V. (1997). Field experiments on duration and precision of grey and red squirrel spatial memory. *Animal Behaviour* **54**, 879–891. doi:10.1006/ANBE.1996.0528
- McKinnell, F. H. (1990). Status of management and silviculture research on sandalwood in Western Australia and Indonesia. In ‘USDA Forest Service General Technology Report PSW-122’. (Ed. F. H. McKinnell.) pp. 19–29. (Department of Conservation and Land Management: Western Australia.)
- Moore, J. E., McEuen, A. B., Swihart, R. K., Contreras, T. A., and Steele, M. A. (2007). Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. *Ecology* **88**, 2529–2540. doi:10.1890/07-0247.1
- Murphy, M. T., Garkaklis, M. J., and Hardy, G. E. St. J. (2005). Seed caching by woylies *Bettongia penicillata* can increase sandalwood *Santalum spicatum* regeneration in Western Australia. *Austral Ecology* **30**, 747–755. doi:10.1111/J.1442-9993.2005.01515.X
- Noble, J. C. (1993). Relict surface-soil features in semi-arid mulga (*Acacia aneura*) woodlands. *The Rangeland Journal* **15**, 48–70. doi:10.1071/RJ9930048
- Pacioni, C., Wayne, A. F., and Spencer, P. B. S. (2011). Effects of habitat fragmentation on population structure and long distance gene flow in an endangered marsupial: the woylie. *Journal of Zoology* **283**, 98–107. doi:10.1111/J.1469-7998.2010.00750.X

- Pearson, K. M., and Theimer, T. C. (2004). Seed caching and pilfering by two species of *Peromyscus*: implications for pinyon pine establishment. *Oecologia* **141**, 76–83. doi:10.1007/S00442-004-1638-8
- Primack, R. B., and Levy, C. K. (1988). A method to label seeds and seedlings using gamma-emitting radionuclides. *Ecology* **69**, 796–800. doi:10.2307/1941028
- Puerta-Piñero, C., Gómez, J. M., and Schupp, E. W. (2010). Spatial patterns of acorn dispersal by rodents: do acorn crop size and ungulate presence matter? *Oikos* **119**, 179–187. doi:10.1111/J.1600-0706.2009.17793.X
- Pyare, S., and Longland, W. S. (2000). Seedling-aided cache detection by heteromyid rodents. *Oecologia* **122**, 66–71. doi:10.1007/PL00008837
- Sampson, J. C. (1971). The biology of *Bettongia penicillata* Grey, 1837. Ph.D. Thesis. The University of Western Australia, Western Australia.
- Sawyer, B. (2013). Sandalwood (*Santalum spicatum*) establishment in the semi-arid and arid regions of Western Australia. *The Rangeland Journal* **35**, 109–115. doi:10.1071/RJ12088
- Smallwood, P. D., and Peters, W. D. (1986). Grey squirrel food preferences: the effects of tannin and fat concentration. *Ecology* **67**, 168–174. doi:10.2307/1938515
- Stapanian, M. A., and Smith, C. C. (1978). A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. *Ecology* **59**, 884–896. doi:10.2307/1938541
- Start, A. N., Burbidge, A. A., and Armstrong, D. (1995). Woylie recovery plan. Wildlife Management Program No. 16. Department of Conservation and Land Management, Western Australia.
- Subasinghe, S. M. C. U. P. (2013). Sandalwood research: a global perspective. *Journal of Tropical Forestry and Environment* **3**, 1–8.
- Suselbeek, L., Jansen, P. A., Prins, H. H. T., and Steele, M. A. (2013). Tracking rodent-dispersed large seeds with passive Integrated Transponder (PIT) tags. *Methods in Ecology and Evolution* **4**, 513–519. doi:10.1111/2041-210X.12027
- Taraborelli, P., Borruel, N., and Mangeaud, A. (2009). Ability of murid rodents to find buried seeds in the Monte Desert. *Ethology* **115**, 201–209. doi:10.1111/J.1439-0310.2008.01605.X
- Theimer, T. H. (2001). Seed scatter-hoarding by white-tailed rats: consequences for seedling recruitment by an Australian rain forest tree. *Journal of Tropical Ecology* **17**, 177–189. doi:10.1017/S0266467401001122
- Vander Wall, S. B. (1990). 'Food Hoarding in Animals.' (The University of Chicago Press: Chicago.)
- Vander Wall, S. B. (1995). The effects of seed value on the caching behavior of yellow pine chipmunks. *Oikos* **74**, 533–537. doi:10.2307/3545999
- Vander Wall, S. B. (2000). The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). *Behavioral Ecology* **11**, 544–549. doi:10.1093/BEHECO/11.5.544
- Vander Wall, S. B. (2003). Mastings in pines alters the use of cached seeds by rodents and causes increased seed survival. *Ecology* **84**, 3508–3516.

- Vander Wall, S. B. (2008). On the relative contributions of wind vs. animals to seed dispersal of four Sierra Nevada pines. *Ecology* **89**, 1837–1849. doi:10.1890/07-0409.1
- Vander Wall, S. B. (2010). How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Philosophical Transactions of Royal Society B* **365**, 989–997. doi:10.1098/RSTB.2009.0205
- Vander Wall, S. B., Kuhn, K. M., and Beck, M. J. (2005). Seed removal, seed predation and secondary dispersal. *Ecology* **86**, 801–806. doi:10.1890/04-0847
- Waitman, B. A., Vander Wall, S. B., and Esque, T. C. (2012). Seed dispersal and seed fate in Joshua tree (*Yucca brevifolia*). *Journal of Arid Environments* **81**, 1–8. doi:10.1016/J.JARIDENV.2011.12.012
- Wang, B. C., and Smith, T. B. (2002). Closing the seed dispersal loop. *Trends in Ecology & Evolution* **17**, 379–385. doi:10.1016/S0169-5347(02)02541-7
- Wayne, A. F., Maxwell, M. A., Ward, C., Vellios, C., Ward, B., Liddelow, G. L., Wilson, I., Wayne, J. C., and Williams, M. R. (2013). The importance of getting the numbers right: quantifying the rapid and substantial decline of an abundant marsupial, *Bettongia penicillata*. *Wildlife Research* **40**, 169–183. doi:10.1071/WR12115
- Wayne, A. F., Maxwell, M., Ward, C. G., Vellios, C. V., Wilson, I., Wayne, J. C., and Williams, M. R. (2015). Sudden and rapid decline of the abundant marsupial, *Bettongia penicillata* in Australia. *Oryx* **49**, 175–185. doi:10.1017/S0030605313000677
- Winterrowd, M. F., and Weigl, P. D. (2006). Mechanisms of cache retrieval in the group nesting Southern Flying Squirrel (*Glaucomys volans*). *Ethology* **112**, 1136–1144. doi:10.1111/J.1439-0310.2006.01268.X
- Wróbel, A., and Zwolak, R. (2013). The choice of seed tracking method influenced fate of beech seeds dispersed by rodents. *Plant Ecology* **214**, 471–475. doi:10.1007/S11258-013-0183-0
- Yeatman, G. J., and Groom, C. J. (2012). National Recovery Plan for the woylie *Bettongia penicillata*. Wildlife Management Program No. 51. (Department of Environment and Conservation: Perth.)
- Zhang, Z. B., Xiao, Z. S., and Li, H. J. (2005). Impact of small rodents on tree seeds in temperate and subtropical forests, China. In 'Seed Fate: Seed Predation, Seed Dispersal and Seedling Establishment'. (Eds P. M. Forget, J. Lambert, P. E. Hulme and S. B. Vander Wall.) pp. 269–282. (CABI Publishing: Wallingford, UK.)

Fig. 1. Mean seed weight (\pm s.e.) of *Santalum spicatum*, *S. acuminatum*, *Acacia acuminata* and *Gastrolobium microcarpum* seeds (left to right) used in Experiment 1 (May 2005), a radiolabelling study in Dryandra Woodland, Western Australia. Scale bar = 1 cm.

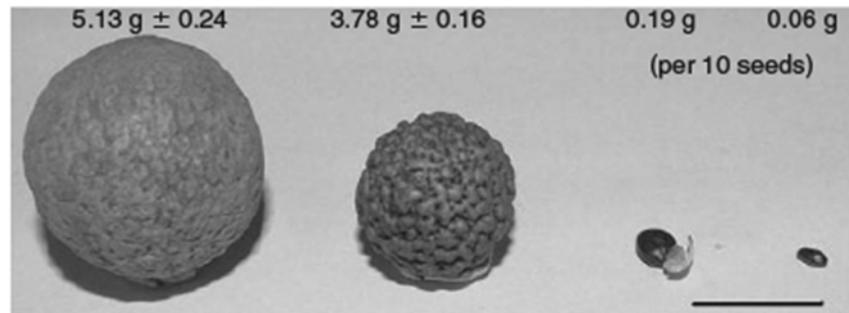


Fig. 2. The spatial distribution, in metres, of *Santalum spicatum* (•), *S. acuminatum* (□) and *Gastrolobium microcarpum* (?) seed caches made by woylies in May 2005 in an enclosure (85 × 220 m) in Dryandra Woodland. The seed source was located at the plot origin (0, 0).

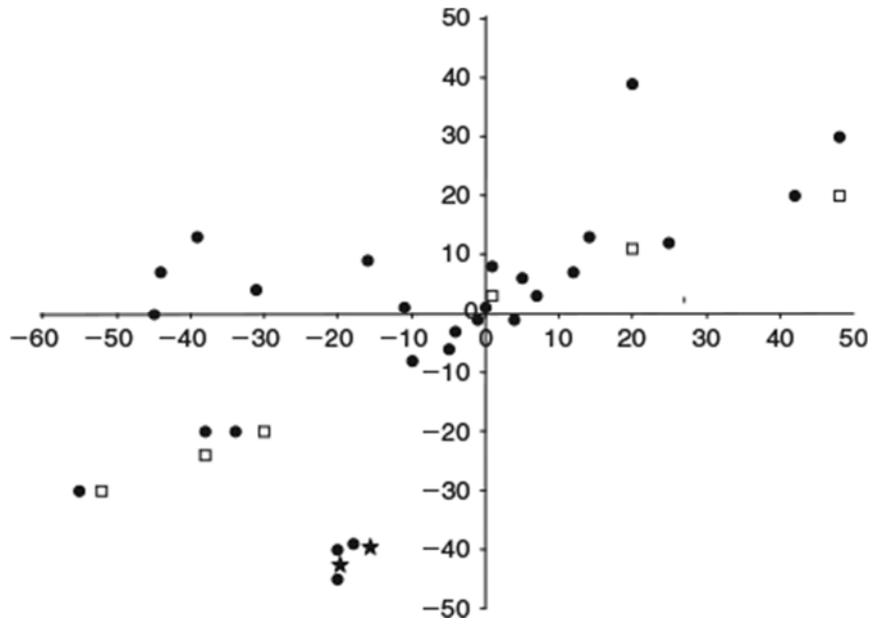


Fig. 3. The fate of *Santalum spicatum* seed over four nights following interaction by *Bettongia penicillata ogilbyi* in February 2006 in an enclosure in Dryandra Woodland, Western Australia. Black bars, eaten seeds; dark grey bars, cached removed seeds; light grey bars, fate of seeds unknown; and white bars, seeds remaining at the end of the night. n = no. of seed deployed.

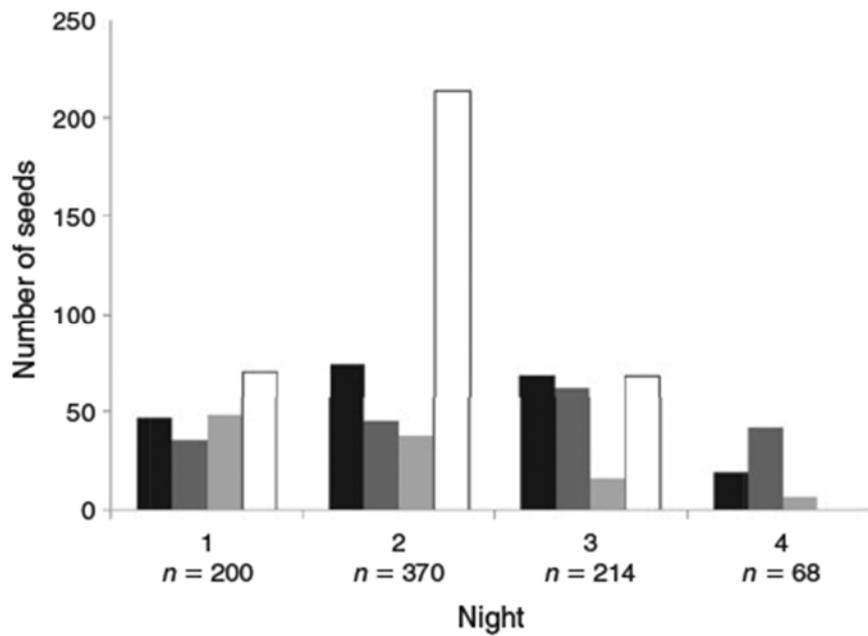


Fig. 4. Depth of primary caches of individual *Santalum spicatum* seed dug by *Bettongia penicillata* *ogilbyi* in February 2006 in Dryandra Woodland, Western Australia.

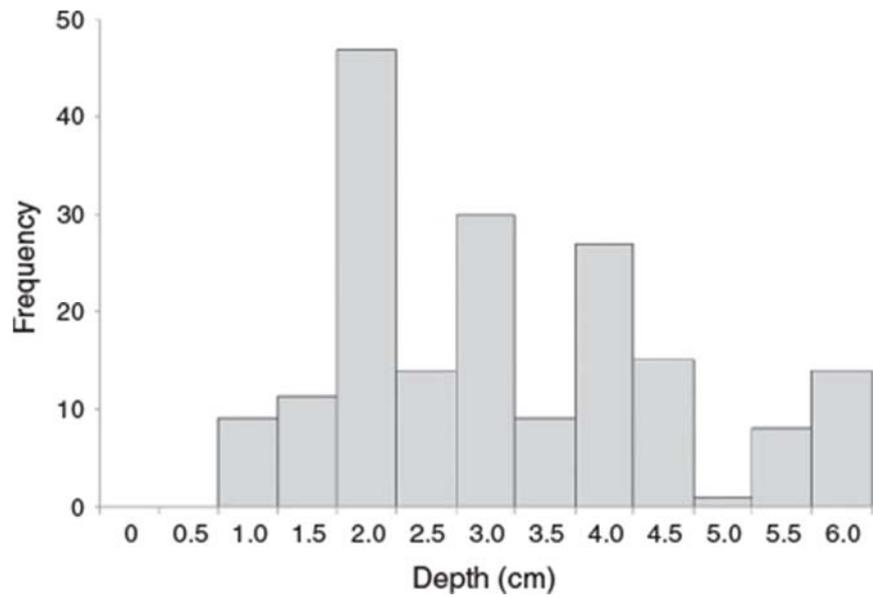


Fig. 5. The fate of 185 *Santalum spicatum* seed cached by *Bettongia penicillata ogilbyi* from February to November 2006 at Dryandra Woodland, Western Australia. Seed were recached up to four times (no. of seeds recached shown in arrow). The seeds were removed (fate unknown, black), untouched (light grey), eaten (white) or recached (dark grey).

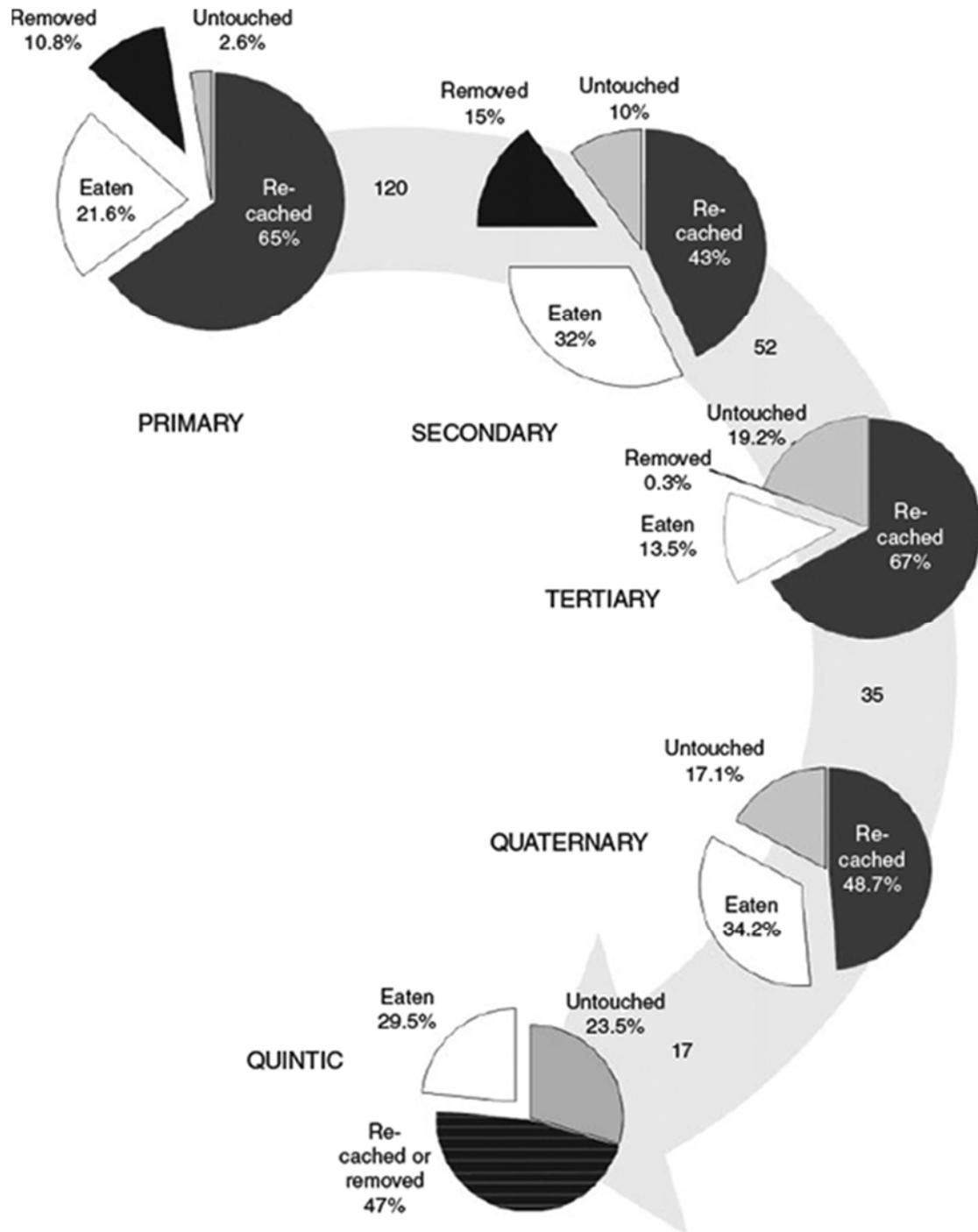


Fig. 6. Percentage of *Santalum spicatum* seed caches by *Bettongia penicillata ogilbyi* located within 30 cm of a particular vegetation type between February and November 2006 in Dryandra Woodland, Western Australia.

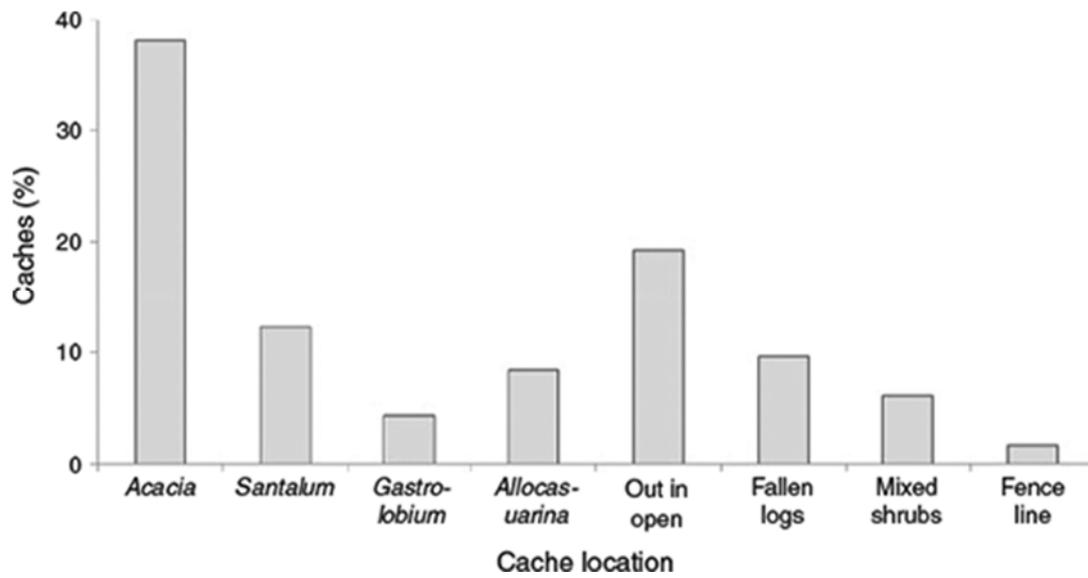


Fig. 7. The fate of planted *Santalum spicatum* seedlings (n = 89) after one month in Dryandra Woodland in the presence of *Bettongia penicillata ogilbyi*.



Table 1. The fate of *Santalum spicatum*, *S. acuminatum*, *Acacia acuminata* and *Gastrolobium microcarpum* seeds radiolabelled with ⁴⁶Scandium following interaction by *Bettongia penicillata ogilbyi* in May 2005 in an enclosure in Dryandra Woodland, Western Australia

All seeds were cached or eaten *in situ*

	<i>Santalum spicatum</i>	<i>Santalum acuminatum</i>	<i>Acacia acuminata</i>	<i>Gastrolobium microcarpum</i>
No. of seeds placed at source	50	50	450	450
Order of removal from source	1st	2nd	3rd	4th
No. of seeds eaten	24	44	450	414
No. of caches	26	6	0	2 ^A

^ATwo caches, one with 22 seeds, the other with 15 seeds.