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Seed dispersal by Australian digging mammals

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Cover image: Woylie (*Bettongia penicillata*). Image: Arthur Chapman, Flickr, CC BY-NC 2.0

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Executive summary

Mammal-seed interactions are important for structuring vegetation communities across a diverse range of ecosystems worldwide. Many Australian mammals consume seeds, but their role in seed dispersal has not been well explored. The translocation of Australian mammals for the purposes of ecosystem restoration is increasing. Digging mammals, i.e. species that dig to obtain food or create shelter, are commonly the focus of these translocations because they are ecosystem engineers but an understanding of their role in seed dispersal is lacking. We aimed to expand the understanding of endozoochory in Australian digging mammals by determining whether seeds consumed by select species remain viable and able to germinate. Firstly, we investigated the mean retention time and the post-consumption germination capacity of Australian seeds (*Acacia acuminata*, *Dodonaea viscosa* and *Gastrolobium calycinum*) likely to be consumed by quenda (*Isodon fusciventer*) and woylies (*Bettongia penicillata ogilbyi*) while in captivity. Secondly, we collected scat samples from five wild digging mammal species (boodie, *B. lesueur*; woylie, *B. penicillata*; bilby, *Macrotis lagotis*; golden bandicoot, *I. auratus* and quenda, *I. fusciventer*) known to consume seeds across nine sites in Western and South Australia. We searched the scat samples for seeds, identified the recovered seeds and then tested their viability and germination capacity. Mean excretion times in captive individuals were 14 hours for quenda and 24 hours for woylies, but some seeds were retained in their digestive passages for up to 39.5 and 55.5 hours, respectively. In captive settings, viable seeds of all plant species were retrieved from both quenda and woylie scats and only *G. calycinum* seeds ingested by quenda (62%) had a significantly higher germination percentage than control seeds (34%). In wild animals, we found that the abundance of intact seeds in scats was generally low but 70% of the retrieved seeds appeared viable. Five species of seed collected from scats of wild digging mammals germinated under laboratory conditions. Our results show that viable seeds are deposited in the scats of Australian digging mammals, indicating that these species may play a more important role in seed dispersal than previously considered. Digging mammals have the potential to contribute to ecosystem restoration efforts through the dispersal of viable seeds but there is also a risk that non-native species could be dispersed. These costs and benefits should be considered by practitioners when planning reintroductions of digging mammals.

Introduction

Mammal-seed interactions are important for structuring vegetation communities across a diverse range of ecosystems worldwide (Farwig & Berens 2012). The consumption of seeds by mammals may result in either predation (when the seed is destroyed) or dispersal (when the seed remains viable) and, consequently, can be either detrimental or beneficial for plants (Torres, Castaño & Carranza-Quiceno 2020). Mastication and exposure to stomach acids can damage seeds, leading to reduced germination and recruitment rates (Traveset, Robertson & Rodriguez-Perez 2007). However, for seeds that survive passage through the digestive tract, endozoochory, the dispersal of plant seeds via ingestion by a vertebrate animal, can be advantageous for plants in several ways. The removal of fruit pulp and scarification of the seed coat can increase germination capacity (Petre *et al.* 2015). Seeds may be dispersed at a greater distance from the parent plant than other forms of seed dispersal (Carlo, Aukema & Morales 2007), reducing both competition for resources and predation rates (Janzen 1970). Deposition in faeces may also provide moisture and nutrients, enhancing germination and growth rates (Traveset, Robertson & Rodriguez-Perez 2007). Additionally, seeds consumed by animals sometimes have increased germination rates (Cantor *et al.* 2010) due to the alleviation of seed dormancy (Traveset 1998).

Seeds form an important dietary component for many Australian mammals (Quin 1985; Murray *et al.* 1999; Gibson 2001; Bice & Moseby 2008). Australian seed-eating mammals are recognised as potentially important seed predators (Ballardie & Whelan 1986; Auld & Denham 1999; Mills, Gordon & Letnic 2018), but the extent to which they disperse seeds via endozoochory has received little research attention (Williams *et al.* 2000; Cochrane, Friend & Hill 2005). Seed predation should not automatically be equated with seed removal as some seeds may be dispersed via caching or endozoochory (Hulme 2002). Australian mammals including boodies (*Bettongia lesueur*), woylies (*B. penicillata*) and musky rat-kangaroos (*Hypsiprymnodon moschatus*) are known to cache seeds, leading to increased dispersal and germination potential (Dennis 2003; Chapman 2015; Murphy *et al.* 2015). In addition, research on endozoochory in Australian non-volant mammals also indicates that species such as Gilbert's potoroo (*Potorous gilbertii*) and common brushtail possums (*Trichosurus vulpecula*) may pass viable seeds (Cochrane, Friend & Hill 2005; Wotton & McAlpine 2015). However, the role of most non-volant seed or fruit-eating Australian mammals in seed dispersal through endozoochory is unknown.

Physical seed dormancy is an adaptive trait that acts to prevent germination when environmental conditions are suitable for germination, but not favourable for seedling survival (Merritt *et al.* 2007). Australian seeds in the genera *Acacia*, *Dodonaea* and *Gastrolobium*, for example, exhibit this adaptation and germinate only after exposure to high temperatures (Sweedman & Merritt 2006). Previous research suggests that germination capacity is increased if gut passage acts to break dormancy inhibitors such as removal of surrounding fruit pulp (Petre *et al.* 2015), or through seed coat scarification (Traveset 1998). However, the effect of consumption by marsupials on dormancy in Australian seeds is unknown. The time it takes an animal to pass a seed through its digestive tract (i.e. its gut passage time) will affect its effectiveness as a seed dispersal agent. Longer gut passage times may result in the dispersal of propagules over greater distances (Petre *et al.* 2015) and scarification in the gut can increase germination capacity by breaking seed dormancy. However, if gut passage times are too long seeds may be damaged or lose viability (Traveset *et al.* 2016). Whilst the gut passage times for several Australian mammals have been studied using markers that bind to solutes or small particles (e.g. Wallis 1994; Moyle, Hume & Hill 1995; Gibson & Hume 2000), there has been no research into the passage time of seeds.

Digging mammals may be important for seed dispersal dynamics as their diggings can trap seeds and provide favourable germination sites (James, Eldridge & Moseby 2010; Valentine *et al.* 2017). Their scats often contain viable, mycorrhizal fungi spores (Tay *et al.* 2018), which could lead to the beneficial co-dispersal of seeds and fungal spores (Theimer & Gehring 2007) if their scats also contain viable seeds. Many Australian digging mammals, such as bilbies (*Macrotis lagotis*), boodies and bandicoots, consume fruit and seeds (Quin 1985; Gibson 2001; Bice & Moseby 2008), but little is known about endozoochory in this group. For some species fruits and seeds are minor components in their diet (Thums, Klaassen & Hume 2005; Zosky *et al.* 2017) but for other species, particularly bilbies, fruit and seeds can form the bulk of their diet in certain seasons (Gibson 2001; Southgate & Carthew 2006).

Many of Australia's digging mammal species are threatened (Fleming *et al.* 2014), and the decline of these species is likely to have been accompanied by a loss of their roles within ecosystems, potentially contributing to ecosystem degradation (Valiente-Banuet *et al.* 2014). Reintroductions of locally extinct species may help to enhance overall restoration efforts (Lipsey & Child 2007), and reintroductions of digging mammals to restore ecosystem functions are becoming more common (Palmer *et al.* 2020). However, while the contributions of some of their digging activities to ecosystem function have received research attention (e.g. Garkaklis, Bradley & Wooller 2003; Valentine *et al.* 2018; Ross *et al.* 2020), the role of digging mammals in other ecosystem processes, such as herbivory and seed dispersal, is relatively unknown.

Here we investigated seed endozoochory in Australian digging mammals using two approaches. Firstly, using captive animals, we examined the i) rate at which seeds traverse the digestive tract of two species known to consume seeds, quenda (*Isodon fusciventer*) and woylies (*Bettongia penicillata ogilbyi*); and, ii) the germination capacity of seeds retrieved from their scats. Secondly, using wild animals, we examined the viability and germination capacity of seeds recovered from the scats of five commonly translocated digging mammal species (*B. penicillata*, *B. lesueur*, *I. auratus*, *I. fusciventer* and *M. lagotis*) known to consume seeds.

Methodology

Gut-passage time, viability and germination of seeds in captive digging mammals

Study animals

Two female adult quenda (*I. fusciventer*) and a male and female adult woylie (*B. penicillata*) held in captivity at Native Animal Rescue (NAR), Malaga (~10 km north of Perth), Western Australia were used in this experiment. During the experiment, conducted in June 2019, the animals were housed in individual enclosures approximately 2 x 3 m in size. The floors of the enclosures were cleared of leaf litter and excess foliage to facilitate the location of scats. A hollow log or nest box, and a small bundle of fresh foliage were retained in each enclosure. The animals' regular feed consists of fruit, vegetables and a boiled egg with the addition of mealworms, insectivore mix and aviary seed (quenda) or herbivore pellets (woylies). For one week prior to, and during the experiment, seeds and fruit containing seeds were substituted with other items (e.g. similar fruit or vegetables without seeds). Feed was provided daily in the late afternoon and remaining food was removed each morning. Water was provided ad libitum throughout.

Testing seed viability

We used commercially sourced seeds (Nindethana Australian Native Seeds – King River, WA) of three native species previously recorded in the diet of Potoroids or Peramelids: *Acacia acuminata*, *Dodonaea viscosa* and *Gastrolobium calycinum* (Christensen 1980; Bice & Moseby 2008) (Table S1). Prior to the start of the experiment, we determined the viability of the seeds using a Faxitron MX-20 Digital X-Ray Cabinet (Tucson, Arizona, USA). Seeds that appeared uniformly white/grey in the digital imagery were deemed to be viable (Erickson and Merritt 2016). Seeds that appeared shrivelled/empty or abnormal were deemed non-viable and were discarded. The viable seeds were not treated to break physical dormancy so that we could investigate how this was affected by consumption by our study species. The germination capacity of control seeds (i.e. seeds not consumed by the study animals) was determined in the laboratory by incubating 100 seeds of each species at 15°C with a 12 hour light-dark cycle, using water agar as a germination medium (Merritt 2006). Twenty-five seeds of a single species were sown onto each petri dish. Prior to sowing, seeds were rinsed in a 30 gL⁻¹ bleach solution and sterilised water to reduce fungal contaminants (Merritt 2006). The number of germinating seeds was then counted weekly for four weeks.

Scat collection

At the commencement of the feeding experiment, 150 viable seeds (50 of each species), taken from the same seed pool as the controls, were mixed into each animal's usual feed. The modified feed was provided to the animals at 1600 h on the first day of the experiment and the remains removed at 0700 h the following morning. Remaining feed and the enclosures were searched for unconsumed seeds or seed caches so that the exact number of seeds consumed by each animal (i.e. the number of seeds found subtracted from 150) could be determined (Table 1).

Scat collection commenced at 2400 h (approximately 8 hours after presentation of the seeds) and was conducted at approximately 0700, 1600 and 2400 h for four consecutive days. A final scat collection event was conducted at 0700 h on day five, giving a total of 14 collection events (over 107 h) for each animal. This time period was based on marker excretion times of three species of potorine marsupials (Wallis 1994). During each scat collection event, the floor of the enclosures, the refuges and fresh foliage were searched carefully for scats or loose seeds by one or two observers, and the start time and duration of search were recorded. The midpoint between the end and start times of consecutive checks was used as the excretion time for calculations, as per Wallis (1994). Collected scats were placed into paper bags and stored in a well-ventilated location at room temperature until the conclusion of the experiment. The samples were dried at 35°C for six days and then stored at room temperature until the scat analysis was conducted.

Scat processing, seed viability & germination

All scats were examined for seeds. Scats were soaked in water and then carefully teased apart. Whole seeds, with or without the elaiosomes, were removed, sorted by species and dried. Where the number of retrieved seeds was less than the number consumed by the animals, we assumed the missing seeds were destroyed during the digestive process. The viability of the retrieved seeds was retested using the x-ray method described above. We performed a germination trial, including the seed sterilisation step, as described above, on all retrieved seeds that appeared viable using separate petri dishes for each animal, seed species and collection event combination. Differences in the germination capacity of viable seeds retrieved from scats and control seeds were assessed using Chi-square analyses in R statistical software (R Core Team 2019). We used the percentage of seeds that germinated as the response variable.

Seed viability and germination capacity in wild digging mammals

Study species and collection sites

We collected scat samples from five digging mammal species known to consume fruit and/or seed: bilbies (*M. lagotis*), golden bandicoots (*I. auratus*), quenda (*I. fusciventer*), boodies (*B. lesueur*) and woylies (*B. penicillata*). Samples were obtained from nine sites located across Western and South Australia (Figure 1). The sites ranged from a small urban reserve in the Mediterranean climate of the Swan Coastal Plain (Craigie Bushland) to remote ex-pastoral leases and islands in the arid zone of Western Australia (e.g. Matuwa-Kurrara Kurrara and Hermite Island). The sites have a range of historical uses but are now all managed primarily for conservation purposes and support extant and reintroduced populations of a variety of threatened mammal species.

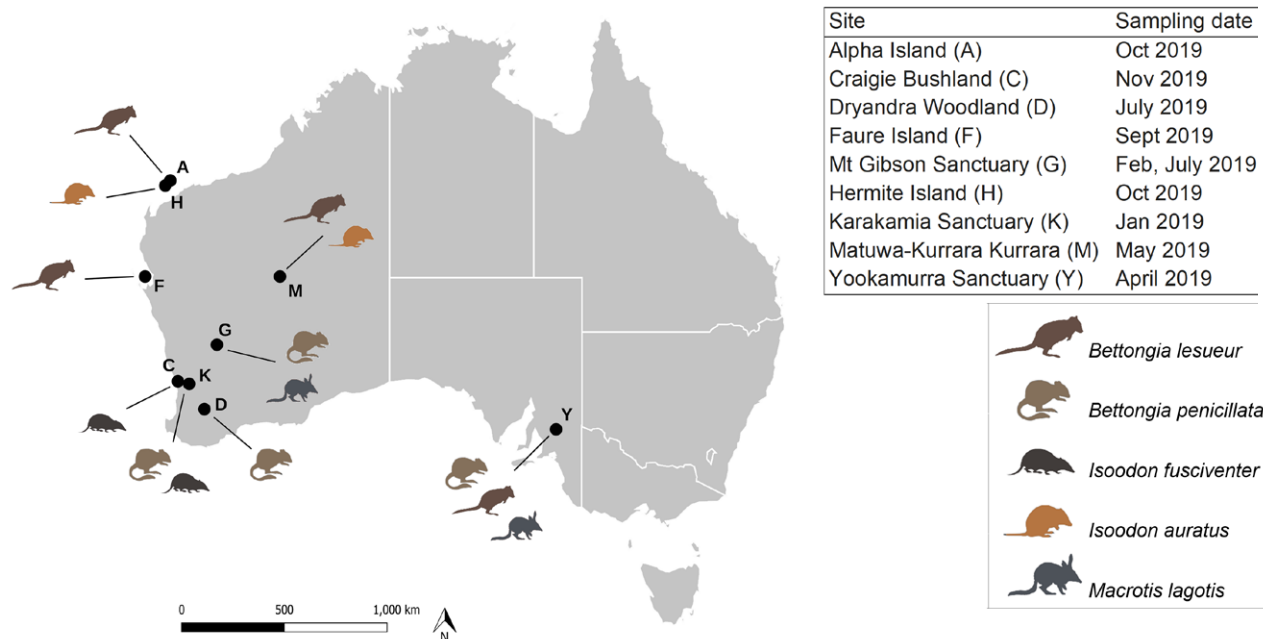


Figure 1. Scat samples were collected from five wild digging mammal species across nine sites in Western and South Australia on various dates throughout 2019.

Scat collection

Trapping was used to collect scat samples from individual animals. At Dryandra Woodland and Faure Island, we deployed 20 cage traps, spaced 200 m apart and baited with peanut butter and oats, for three nights in July (Dryandra Woodland) and September (Faure Island) 2019. Scat samples were collected from the base of traps occupied by the target species the following morning. Traps were cleaned and moved to a new location each day to facilitate the capture of a greater number of individuals. Existing monitoring programs were utilised to collect scat samples at the remaining study sites. Trapping methods involved various configurations of baited cage or aluminium box traps deployed in fixed locations for three or four nights. Sample collection commenced 5 h after trap deployment at Yookamurra Sanctuary but was carried out the following morning at the remaining sites. Traps, and the ground beneath them, were cleaned between captures. Scat samples from all locations were air-dried and stored at room temperature until processed. Because bilbies rarely enter traps, their scat samples were also collected along walked transects by surveyors trained to identify them from the scats of other co-occurring species. Samples were collected from widely spaced locations, but it was impossible to determine whether they represent unique individuals. We aimed to collect fresh samples (i.e. those that were unbroken, moist, soft and shiny) and rejected any that appeared excessively aged or degraded.

Scat processing

The scats of our study species typically consist of varying numbers of faecal pellets. For consistency, we randomly selected five pellets from twenty scat samples from each species and site combination for further analysis. For some species, at some sites, we obtained less than twenty samples containing five or more pellets. Where this was the case we selected the samples containing the largest number of pellets and used the entire sample for analysis if it contained less than five pellets (boodies – Alpha Island $n = 11$; bilbies – Mt Gibson Sanctuary $n = 14$; golden bandicoots – Hermite Island $n = 10$, Matuwa-Kurrara Kurrara $n = 4$). We only obtained seven samples for bilbies from Yookamurra Sanctuary, of which three had less than five pellets.

The scat samples were soaked in water for 1 to 2 h until they reached a soft consistency. Each pellet was then transferred to a clean petri dish, gently teased apart and then mixed with a small amount of water until the pellet was spread across the dish in a thin layer. This dish was carefully examined for seeds using a dissecting microscope at 10 x magnification. All whole seeds were removed, thoroughly dried and then stored in plastic vials at room temperature until they could be identified. The seeds were identified, to species or genus where possible, using reference guides (Sweedman 2006; Erickson *et al.* 2016; South Australian Seed Conservation Centre 2018) and expert opinion, with reference to the site flora inventories. Seeds that could not be identified were separated into distinct morpho-groups.

Seed viability and germination

We determined whether the seeds were viable, i.e. still contained an embryo, using the x-ray technique from Erickson and Merritt (2016). Specifically, the seeds were x-rayed using a Faxitron MX-20 Digital X-Ray Cabinet (Tucson, Arizona, USA). Any seeds that appeared uniformly white or grey in the digital imagery, or for which the embryo was visible, were deemed viable. Seeds that appeared abnormal or hollow were determined to be non-viable.

In a pilot study, the germination capacity of seeds retrieved from woylie scats collected from Dryandra Woodland in October 2018 was tested in a glasshouse by sowing the seeds onto potting mix and watering for 20 s, twice daily. Fungal contamination of the seeds was substantial and there was no germination after eight weeks. For the full study, therefore, we tested germination capacity in the laboratory where conditions could be more carefully controlled. Viable seeds were plated onto water agar (0.7% w/v) in 90 mm Petri dishes and incubated at 15°C with a 12:12 h photoperiod ($30 \mu\text{mol m}^{-2} \text{s}^{-1}$, 400-700 nm, cool-white fluorescent light). To reduce fungal and bacterial contaminants, seeds were rinsed in a 30 g L⁻¹ bleach solution and then sterilised water prior to plating (Merritt 2006). We recorded the number of germinating seeds in each sample weekly for four weeks, and then once more 10 weeks after the commencement of the experiment.



Woylie scats at Dryandra. Image: G. Beca

Results

Gut-passage time, viability and germination of seeds in captive digging mammals

Seed consumption and gut-passage time

The animals consumed most of the seeds presented to them (mean 71%, range 35-97%; Table 1) but many of the consumed seeds were damaged or destroyed. Seed fragments were found frequently in the scats but could not be identified to species and were discarded. Overall, less than half of the consumed seeds were retrieved whole, with or without the elaiosome, but recovery rates were highly variable between individuals (mean 46.8%, range 9-83%; Table 1).

The peak excretion (54% of seeds) for quenda occurred between 4-11.5 hours (Figure 2). For woylies, the peak excretion (59% of seeds) occurred between 19.5-24 hours (Figure 2). Mean gut passage time was similar to the time of peak excretion for both species: 14 ± 3 hours for quenda and 24 ± 2 hours for woylies.

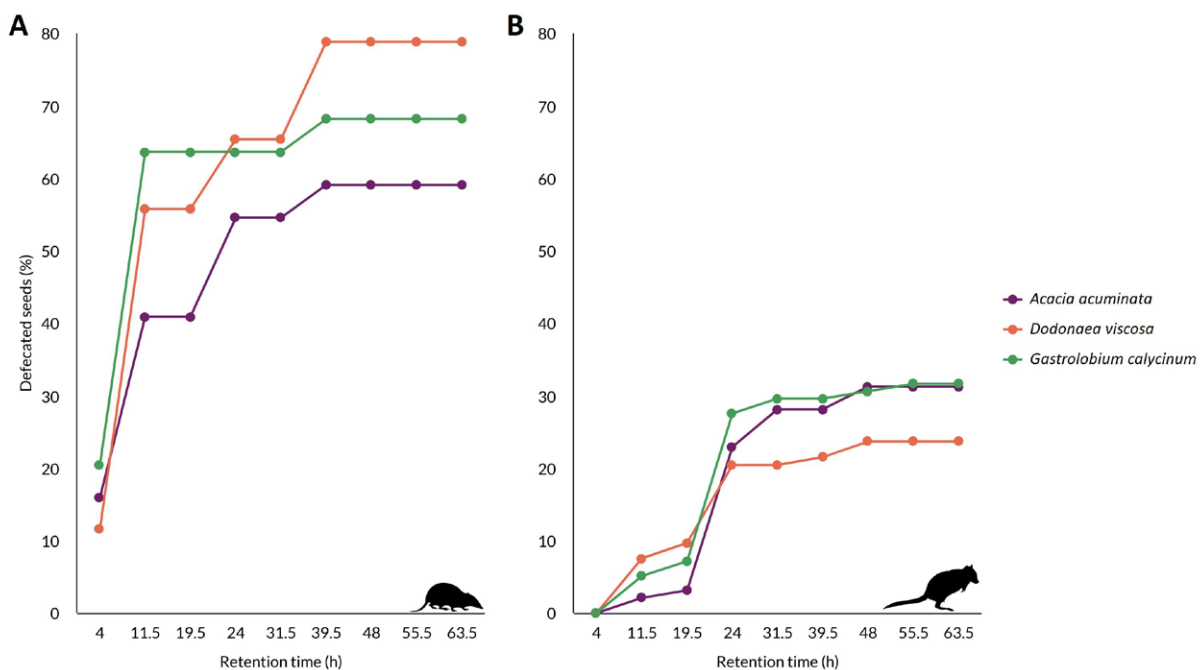


Figure 2. Relationship between the retention time (in hours) and the cumulative percentage of viable seeds of *A. acuminata*, *D. viscosa*, *G. calycinum* recovered from scats of (a) quenda and (b) woylies. The experiment was continued until 103.5 h after consumption, but the last seeds were recovered from the scats at 39.5 h (quenda) and 55.5 h (woylies).

Seed viability and germination

Of the seeds retrieved, 100% percent of *A. acuminata*, 96% of *D. viscosa* and 97% of *G. calycinum* seeds (97% overall) were viable after consumption by quenda. For seeds consumed by woylies, 100% of *D. viscosa*, 87% of *G. calycinum* and 80% of *A. acuminata* seeds (88% overall) remained viable. Germination of *A. acuminata*, *D. viscosa* and *G. calycinum* occurred in both control and ingested seeds (Table 2). There was no significant difference between the germination capacity of *A. acuminata* seeds ingested by quendas or woylies and the controls (Table 2). *Dodonaea viscosa* seeds ingested by quenda had a significantly lower germination capacity compared to the controls, but there was no difference between the seeds ingested by woylies and the control seeds (Table 2). *Gastrolobium calycinum* seeds ingested by quenda had a significantly higher germination capacity than the control seeds, but seeds consumed by woylies had a significantly lower germination capacity than the control (Table 2).

Table 1. Number of seeds of each species used in the experiment, their consumption (i.e. number of seeds found subtracted from presented seeds), recovery, viability and germination capacity. Numbers in brackets represent the percentage of the previous section's total.

	Seeds presented				Seeds consumed				Seeds recovered				Seeds viable				Seeds germinated			
	A	D	G	Total	A	D	G	Total	A	D	G	Total	A	D	G	Total	A	D	G	Total
Quenda 1 (♀)	50	50	50	150	13	16	24	53 (35%)	8	7	10	25 (47%)	8	7	10	25 (100%)	1	2	5	8 (32%)
Quenda 2 (♀)	50	50	50	150	31	36	20	87 (58%)	18	34	20	72 (83%)	18	32	19	69 (96%)	1	3	13	17 (25%)
Woylie 1 (♂)	50	50	50	150	49	48	49	146 (97%)	25	16	29	70 (48%)	20	16	26	62 (88%)	1	8	4	13 (21%)
Woylie 2 (♀)	50	50	50	150	47	45	49	141 (94%)	5	6	2	13 (9%)	4	6	1	11 (84%)	1	2	1	4 (36%)

A – *Acacia acuminata*, D – *Dodonaea viscosa*, G – *Gastrolobium calycinum*

Table 2. Number and percentage of viable seeds recovered from scats that germinated. Significant differences between viable seeds recovered from scats of quenda or woylies and the controls are indicated by bold font.

Seed species	Control		Quenda						Woylie			
	Germinants		Germinants		χ^2	p	Germinants		χ^2	p	Germinants	
<i>Acacia acuminata</i>	15 (15%)		2 (7.7%)		0.12	0.72	2 (8.3%)		1.91	0.17		
<i>Dodonaea viscosa</i>	51 (51%)		5 (12.8%)		22.84	<0.001	10 (45.4%)		0.32	0.57		
<i>Gastrolobium calycinum</i>	34 (34%)		18 (62.1%)		8.19	0.004	5 (18.5%)		4.57	0.03		

Seed viability and germination in wild digging mammals

Seed occurrence, abundance and identification

Seeds were found in the scats of all five mammals but not at all sites (Table 3). Overall, 23% of samples contained seeds, and seed abundance was generally low (median = 1 seed per sample, range = 0 – 78). Evidence of seed consumption was lowest for woylies and quenda (0-25% and 10-25% of samples contained seeds, respectively; Table 3). Seeds were most frequently retrieved from golden bandicoot scat (40% of samples from all sites contained seeds) and the sample that contained the highest number of seeds was from a golden bandicoot at Matuwa-Kurrara Kurrara (Table 3).

Table 3. Mean number of seeds and seed species found in the scats of five species of digging mammals at nine sites in Western and South Australia. Numbers in brackets are the range. Sample sizes for boodies, woylies, golden bandicoot and quenda at all sites were n = 20. Sample sizes for bilbies were n = 22 at Mt Gibson and n = 7 at Yookamurra.

	Samples with seed		Seeds per sample, all samples	Seeds per seeded sample	Seed species per seeded sample
Species and site	No.	%			
Boodie					
Alpha Island	5	25	0.5 (0-3)	1.8 (1-3)	1 (1)
Faure Island	15	75	6.3 (0-47)	8.3 (1-47)	1.67 (1-3)
Matuwa-Kurrara Kurrara	1	5	0.1 (0-1)	1 (1)	1 (1)
Yookamurra Sanctuary	0	0	0	n/a	n/a
All sites	21	26			
Woylie					
Dryandra Woodland	0	0	0	n/a	n/a
Karakamia Sanctuary	5	25	1.0 (0-16)	4 (1-16)	1 (1)
Mt Gibson Sanctuary	0	0	0	n/a	n/a
Yookamurra Sanctuary	2	10	0.2 (0-2)	1.5 (1-2)	1.5 (1-2)
All sites	7	9			
Golden bandicoot					
Hermite Island	10	50	2.5 (0-16)	4.9 (1-16)	1.2 (1-2)
Matuwa-Kurrara Kurrara	6	30	4.3 (0-78)	14.3 (1-78)	1 (1)
All sites	16	40			
Quenda					
Craigie Bushland	2	10	0.3 (0-4)	2.5 (1-4)	2 (1-3)
Karakamia Sanctuary	5	25	0.6 (0-6)	2.2 (1-6)	1.2 (1-2)
All sites	7	18			
Bilby					
Mt Gibson Sanctuary	12	55	5.7 (0-37)	10.4 (1-37)	1.1 (1-2)
Yookamurra Sanctuary	0	0	0	n/a	n/a
All sites	12	41			

We recorded 38 types of seeds across all sites and mammal species, of which 23 were identified to family, genus or species (Figure 3; Table 4). The seeds ranged in size from 0.5 to 5 mm (mean 2.6 ± 0.2 mm). Most seeds (30/38) were 3 mm or less, but the seed species found in the most samples (all from boodies from Faure Island), identified as *Pimelea microcephala*, was 5 mm. Almost all of the samples contained just one species of seed, but nine contained two species, and four contained three species. We recorded the largest number of species ($n = 13$) in boodie scats (Figure 3). Although bilbies had the second highest proportion of samples containing seeds, we recorded the fewest species ($n = 5$) in their scat (Figure 3). Two seed species, *Cenchrus ciliaris* and a Fabaceae species, were recorded in the scat of more than one mammal species; and two species, *C. ciliaris* and *Cleome viscosa*, were recorded in scats at more than one site (Table 4). Of the seeds that were identified to at least family, most (14/23 species) were from shrubs. The remainder were herbs (four species), grasses (two species), trees (two species) and one species of unknown lifeform. Only four species, *P. microcephala* and three *Solanum* species, have fleshy fruits. The remainder have dry pods (e.g. *Acacia* spp.), capsules or nuts.

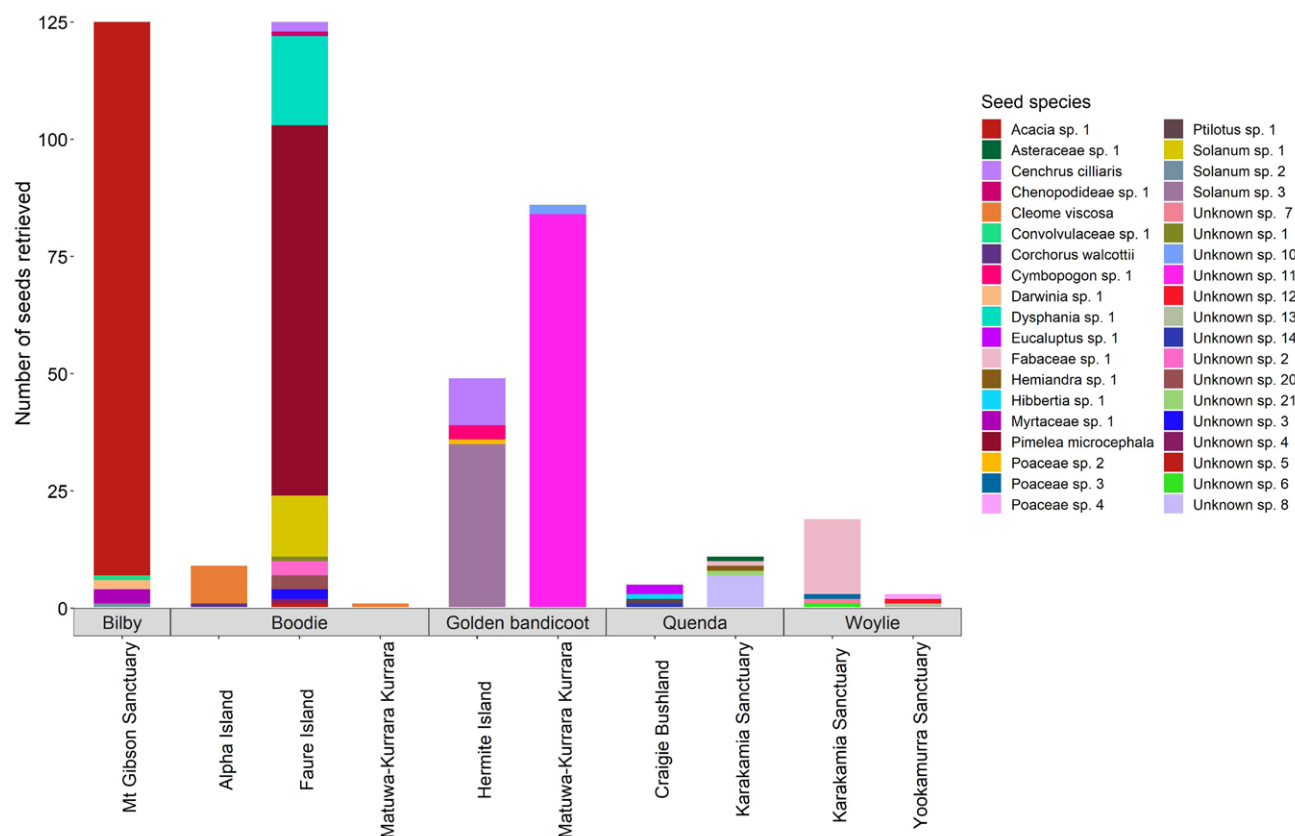


Figure 3. The number of seed species recovered from scat samples, and their overall abundance, varied considerably between mammal species and sites. Note that no seeds were recovered in scat samples from bilbies or boodies at Yookamurra Sanctuary, or from woylies at Dryandra Woodland and Mt Gibson Sanctuary.



Gabrielle Beca setting cage trap at Dryandra Woodland. Image: L. Valentine

Table 4. The characteristics, abundance, viability and germination capacity of seeds extracted from the scats of five species of free-living digging mammals.

Mammal species and site	Seed Species	Size (mm)	Fruit type	Plant life form	Number of samples	Number of seeds found	Number of seeds viable	Number of seeds germinated
Boodie								
Alpha Island	<i>Cleome viscosa</i> ^d	1.5	Pod	Herb	4	8	7	0
	<i>Corchorus walcottii</i>	2.5	Dry fruit	Shrub	1	1	0	0
Faure Island	<i>Cenchrus ciliaris</i> ^{ad}	3	Grain	Grass	2	2	0	0
	Chenopodiaceae sp. 1	1.5	Nut	Shrub	1	1	1	1
	<i>Dysphania</i> sp. 1	1.5	Nut	Herb	1	19	0	0
	<i>Pimelea microcephala</i>	5	Fleshy fruit	Shrub	9	79	76	11
	<i>Solanum</i> sp. 1	3	Fleshy fruit	Shrub	4	13	1	0
	Unknown sp. 1	0.5	Unknown	Unknown	1	1	1	0
	Unknown sp. 2	1.5	Unknown	Unknown	2	3	2	0
	Unknown sp. 3	1.5	Unknown	Unknown	2	2	1	0
	Unknown sp. 4	1	Unknown	Unknown	1	1	0	0
	Unknown sp. 5	1.5	Unknown	Unknown	1	1	0	0
	Unknown sp. 20	2	Unknown	Unknown	1	3	2	0
Matuwa-Kurrara Kurrara	<i>Cleome viscosa</i> ^d	1.5	Pod	Herb	1	1	0	0
Woylie								
Karakamia Sanctuary	Fabaceae sp. 1 ^e	3	Pod	Unknown	1	16	15	0
	Poaceae sp. 3	3.5	Pod	Shrub	1	1	0	0
	Unknown sp. 6	1.5	Unknown	Unknown	1	1	0	0
	Unknown sp. 7	1.5	Unknown	Unknown	1	1	0	0
Yookamurra Sanctuary	Poaceae sp. 4	5	Grain	Shrub	1	1	1	0
	Unknown sp. 12	1.5	Unknown	Unknown	1	1	1	0
	Unknown sp. 13	1	Unknown	Unknown	1	1	1	0

Mammal species and site	Seed Species	Size (mm)	Fruit type	Plant life form	Number of samples	Number of seeds found	Number of seeds viable	Number of seeds germinated
Golden bandicoot								
Hermite Island	<i>Cenchrus ciliaris</i> ^{a,d}	3	Grain	Grass	5	10	0	0
	<i>Cymbopogon</i> sp.	3	Grain	Grass	2	3	0	0
	Poaceae sp. 2	3	Pod	Shrub	1	1	0	0
	<i>Solanum</i> sp. 3	3	Fleshy fruit	Shrub	4	35	35	34
Matuwa-Kurrara Kurrara	Unknown sp. 10	4.5	Unknown	Unknown	2	1	1	0
	Unknown sp. 11	2.5	Unknown	Unknown	4	84	39	0
Quenda								
Craigie Bushland	<i>Eucalyptus</i> sp. 1	2.5	Capsule	Tree	1	2	2	0
	<i>Hibbertia</i> sp. 1	4	Capsule	Shrub	1	1	1	0
	<i>Ptilotus</i> sp. 1	5	Utricle	Shrub	1	1	1	0
	Unknown sp. 14	2	Unknown	Unknown	1	1	1	0
Karakamia Sanctuary	Asteraceae sp. 1	3	Grain	Herb or Shrub	1	1	0	0
	Fabaceae sp. 1 ^e	3	Pod	Unknown	1	1	1	1
	<i>Hemiandra</i> sp. 1	3	Nut	Shrub	1	1	1	0
	Unknown sp. 8	4	Unknown	Unknown	2	7	3	0
	Unknown sp. 21	2	Unknown	Unknown	1	1	0	0
Bilby								
Mt Gibson Sanctuary	<i>Acacia</i> sp. 1	3	Pod	Shrub	8	118	99	11
	Convolvulaceae sp. 1 ^b	5	Capsule	Herb	1	1	0	0
	<i>Darwinia</i> sp. 1	3	Nut	Shrub	2	1	0	0
	Myrtaceae sp. 1 ^c	1	Capsule	Tree	1	3	3	0
	<i>Solanum</i> sp. 2	2.5	Fleshy fruit	Shrub	1	1	0	0

^a Non-native species; ^b possibly *Duperreya* sp.; ^c *Eucalyptus* or *Melaleuca* sp.; ^d Species recorded at more than one site; ^e Species recorded in the scat of more than one mammal species

Seed viability and germination

Overall, 70% of the seeds recovered from the scats were viable and we recovered at least one viable seed from 23 of the 38 (60%) recorded seed species. However, viability varied widely for specific mammal-site combinations (Table 5). Extreme values tended to be recorded for mammal-site combinations for which only a small number of seeds were found; for example, only one, non-viable seed was recovered from boodie scats at Matuwa-Kurrara Kurrara.

The mean germination capacity of the viable seeds recovered from the individual mammal-site combinations ranged between 0 and 65.3% (Table 5). Five species of seeds germinated during the experiment: *P. microcephala* (11 seeds, 15% of the viable seeds of that species), a *Chenopodiaceae* species (1 seed, 100%), a *Solanum* species (34 seeds, 97%), an *Acacia* species (11 seeds, 11%) and a *Fabaceae* species (1 seed, 6%) (Table 4). These seeds came from the scats of four mammal species from four different sites: boodies from Faure, golden bandicoots from Hermite, bilbies from Mt Gibson, and quenda from Karakamia (Table 5). Germination occurred in 50% (2/4) of the species with fleshy fruits but in only 16% (3/19) of the species with dry fruits.

Table 5. Viability and germination rates of seeds found in the scats of five digging mammal species.

Species and site	Total seeds found	Mean viability (% of seed found)	Mean germination (% of all seed found)	Mean germination (% of viable seed)	Total number of seeds germinated	Total number of species germinated
Boodie						
Alpha Island	9	73.3	0	0	0	0
Faure Island	125	64.9	15.9	22.1	12	2
Matuwa-Kurrara Kurrara	1	0	0	0	0	0
Woylie						
Karakamia Sanctuary	20	18.8	0	0	0	0
Yookamurra Sanctuary	3	100	0	0	0	0
Golden bandicoot						
Hermite Island	49	50	32.6	65.3	34	1
Matuwa-Kurrara Kurrara	86	70	0	0	0	0
Quenda						
Craigie Bushland	5	75	0	0	0	0
Karakamia Sanctuary	11	55.6	16.7	25	1	1
Bilby						
Mt Gibson Sanctuary	125	87.4	4.5	6.1	11	1



Food for captive woylies with seeds embedded. Image: G. Beca

Discussion

Our study shows that viable seeds, capable of germinating under laboratory conditions, were deposited in the scats of quenda and woylies after ingestion in captivity. Further, the presence of viable seeds in the scats of five species of wild digging mammals, and the germination of several species of those seeds, demonstrates that Australian digging mammals can disperse seeds via endozoochory and may play a more important role in seed dispersal dynamics than previously considered. Of the seeds consumed in captivity, only 42% were retrieved whole from the scats, suggesting that quenda and woylies may also act as seed predators. Similarly, the abundance of intact seeds in the scats collected from wild animals was low but this varied considerably between mammal species, sites, and even individuals. We collected scat samples from wild animals at each site at only one time point and, consequently, our results may have been influenced by seasonal variations in seed availability or the dietary preferences of our species. The importance of endozoochory by digging mammals likely varies by season and location, but our results show that its occurrence is widespread and that further, more detailed investigations are warranted.

Research on endozoochory in Australian marsupials is rare, but consumption by *Potorous gilbertii* and *Setonix brachyurus* increased germination in *Billardiera fusiformis* (Cochrane, Friend & Hill 2005). Similarly, we found that consumption by captive quenda increased germination in *G. calycinum*. However, overall, the germination capacity of seeds consumed by captive woylies and quenda was half that of the control seeds. Physically dormant seeds, such as those used in our study, require high temperature cues or mechanical scarification to render the seed coat permeable to water and allow germination to occur if conditions are suitable (Sweedman & Merritt 2006). Mastication or exposure to stomach acids may break physical seed dormancy, but can also damage seeds (Traveset, Robertson & Rodriguez-Perez 2007). We showed that dormancy was alleviated in the seeds that experienced the shortest gut passage time, *G. calycinum* consumed by quenda. However, the low number of intact seeds we recovered, and similar or lower germination capacity in the remaining species, indicates that consumption by quenda and woylies most often damages seeds.

The mean excretion times we recorded for captive quenda and woylies are within the range of published values for marker excretion times for other Peramelids and Potoroids (Wallis 1994; McClelland *et al.* 1999), suggesting that standard digestive rate methods provide reasonable estimates of seed retention times. Most seeds in this study were passed quickly, with excretion rates peaking at 11.5 and 24 hours for quenda and woylies, respectively. Both species, however, retained some seeds for at least 39.5 hours. The gut passage times we recorded, combined with their home range sizes (quenda ~5 ha, (Van Dyck & Strahan 2008); woylies ~65 ha, (Yeatman & Wayne 2015), indicate that quenda and woylies may disperse seed over substantial distances. This may confer advantages, such as reduced competition with parent or sibling plants, to those seeds that remain viable after excretion and serve to counteract the negative impact of seed predation on plant populations.

Although consumption by woylies or quenda improved germination capacity in only one seed species, endozoochorous dispersal offers other advantages to seeds. The deposition of seeds within scats may provide nutrients and protection from seed predators (Traveset, Robertson & Rodriguez-Perez 2007) and is more likely to occur to favourable locations (Carlo, Aukema & Morales 2007). For example, quenda and woylies forage extensively for subterranean food resources (Garkaklis, Bradley & Wooller 2004; Valentine *et al.* 2012) and often defecate next to their foraging pits (B. Palmer *pers. obs.*). These scats may be covered by the ejected soil during pit creation or fall into the pits. Seeds in foraging pits are more likely to germinate (Valentine *et al.* 2017), exhibit higher growth rates (Valentine *et al.* 2018) and are less likely to be predated (Radnan & Eldridge 2017).

Of the scats collected from wild animals, 58 seeds from five species (13% of all seeds found) germinated during the study period, demonstrating that seeds consumed by digging mammals can germinate. A further 238 seeds (55%) appeared to have remained viable and, most likely, dormant. The seeds of many Australian plants exhibit dormancy, which is a germination delaying mechanism that prevents recruitment when environmental conditions are conducive to germination but not favourable for seedling survival (Merritt *et al.* 2007). Although passage through the gut of an animal can break seed dormancy (Traveset & Verdú 2002), some seeds require germination cues such as smoke or suitable environmental temperature and moisture conditions before germination will occur (Merritt *et al.* 2007). The seeds that remained un-germinated here may still be capable of germinating under the right conditions or with additional germination or dormancy breaking cues. We were unable to compare the viability and germination capacity of the seed species we recorded to unconsumed seeds from the same source, and hence how consumption affected their viability and germination capacity is unknown.

The wild digging mammal species consumed seeds from a wide range of plant types, including herbs, shrubs, trees and grasses, with a variety of fruit and seed types. This indicates that omnivorous digging mammals are opportunistic consumers of fruits and seeds. The abundance of fruit and seed in the diet of digging mammal species is likely to vary with availability relative to other food resources. Bice and Moseby (2008) found, for example, that bilbies and boodies vary the amount of seed in their diet in response to seasonal changes in its abundance. Similarly, we found eight species of seed, with an average of four seeds per sample, in woylie scats from Dryandra during our pilot study in October 2018 (G. Beca *pers. obs.*) but no seeds were found when we repeated the survey in July 2019 (Table 3). Although the contribution of digging mammals to seed dispersal dynamics may be episodic or vary with location or season, endozoochorous dispersal during times of peak seed abundance may be particularly important for reducing competition between establishing seedlings (Ballardie & Whelan 1986). In Australia's arid zones, where the germination of many plant species may only occur after prolific seeding following episodic rainfall events (e.g. Wright, Zuur & Chan 2014), endozoochorous dispersal at these key times could enhance plant species' chances of persistence and contribute to the maintenance of habitat quality.

Australian seed removal studies often assume that seed removal results in predation (Auld & Denham 1999; Gordon & Letnic 2016; Mills, Gordon & Letnic 2018; Mills & Letnic 2018) but Auld, Denham and Turner (2007) showed that nearly all of the seeds consumed by swamp wallabies (*Wallabia bicolor*), previously thought to be seed predators, remained viable after consumption. Similarly, Mills and Letnic (2018) assumed that *Dodonaea viscosa* seeds removed by woylies were predated, but in our study we showed that *D. viscosa* seeds consumed by captive woylies are able to germinate. We found that the abundance of intact seeds in the wild scat samples was generally low, possibly indicating that most seeds do not survive passage through the digestive tracts of bettongs, bandicoots and bilbies. We note, however, that this could also be because only small numbers of seeds were consumed. Even if predation does occur more often than endozoochory, the benefits of occasional dispersal of seeds to more favourable locations, such as the more fertile microsites offered by their foraging diggings (James, Eldridge & Moseby 2010) or sites at greater distances from the parent plant (Carlo, Aukema & Morales 2007), may help to offset the negative impacts of seed predation by digging mammals.

Many digging mammal species are endangered, and reintroductions are commonly used to improve their conservation status (Burbidge, Harrison & Woinarski 2014). Digging mammal reintroductions are increasingly incorporating goals relating to ecosystem restoration (Palmer *et al.* 2020), and our results show that bettongs, bandicoots and bilbies may be able to contribute to these goals through the dispersal of plant seeds. Reintroducing mammals could assist restoration efforts by increasing the dispersal of native plants (Cantor *et al.* 2010; Genes *et al.* 2019). However, animals can also disperse exotic species (Dovrat, Perevolotsky & Ne'eman 2012), and this should be considered when predicting the ecological outcomes of a translocation. Given the gut passage times we recorded, during wild-to-wild translocations quenda and woylies would probably excrete most seeds consumed prior to their capture during the holding or transport stage, but some seeds could be excreted at the release site. Further, we recorded a small number of buffel grass (*Cenchrus ciliaris*) seeds in the scats of golden bandicoots from Hermite Island and boodies from Faure Island, two of the three study sites where buffel grass occurs. Although these seeds did not appear viable and did not germinate, buffel grass is a highly invasive environmental weed (Marshall, Lewis & Ostendorf 2012) and, as such, the potential for its endozoochorous dispersal during translocations warrants further attention. We suggest that scats excreted during holding and transport are retained and disposed of where germination cannot occur, unless dispersal of plant species from the source site is desirable. Where the source site supports exotic species absent at the release site, post-release monitoring for seedling recruitment of species of concern may be warranted.

Our study used only four captive animals and may not be representative of what happens in natural systems. For example, bettongs and bandicoots feed on mycorrhizal fungi and the co-occurrence of seeds and mycorrhizal fungal spores in scats may alter germination or growth rates (Tay *et al.* 2018). By testing the germination capacity of the viable seeds in the laboratory where conditions can be controlled, we provide an estimate of the potential germination of seeds consumed by digging mammals. In natural settings, this potential may not be realised. For example, fungi in the soil, or co-dispersed in the scats (Zosky *et al.* 2017; Tay *et al.* 2018), may restrict seed germination, as occurred during our pilot study. However, our research clearly demonstrates that endozoochory by Australian digging mammals is possible; future research will hopefully determine whether it contributes significantly to vegetation dynamics in natural settings.

Datasets

Access to data used in this report can be found via the UWA Research Repository: <https://research-repository.uwa.edu.au/en/datasets/gut-passage-time-and-viability-of-seeds-consumed-by-australian-ma> DOI: 10.26182/3fxh-g711

Ethics statement

This project was undertaken in accordance with the regulations of University of Western Australia Animal Ethics Committee. This project was conducted in accordance with the conditions of the following ethics permits: University of Western Australia Animal Ethics Committee (Captive trial RA/3/100/1655; Dryandra RA/3/100/1667), the DBCA Animal Ethics Committee (Alpha and Hermite Islands 2019-38C; Craigie 2016-46; Faure, Karakamia and Mt Gibson 2016-41; and Matuwa 2016-10 and 2018-02), and the South Australian Wildlife Ethics Committee (Yookamurra 36/2016).

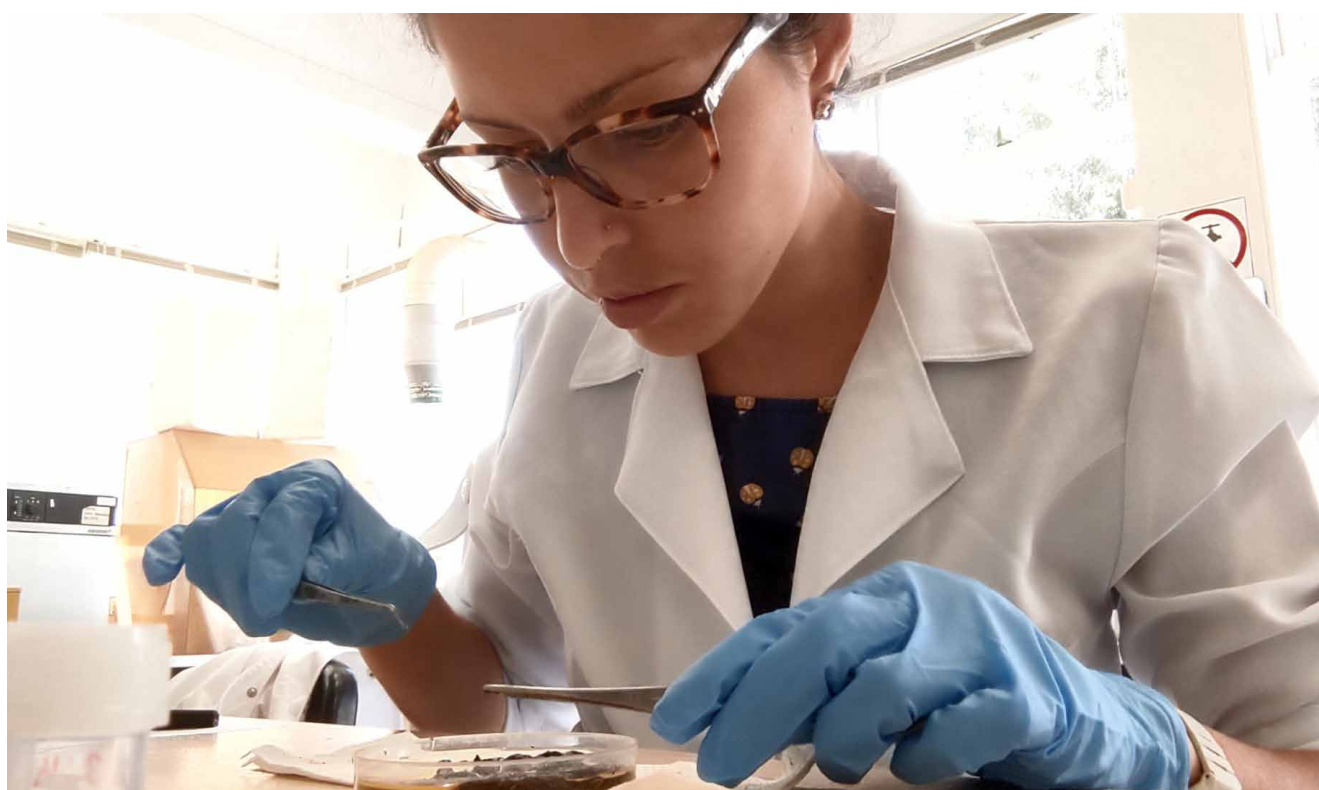
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Gabrielle Beca sorting scats in lab. Image: G. Beca



Further information:

<http://www.nespthreatenedspecies.edu.au>

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