

1 **Gut passage time and viability of seeds consumed by Australian marsupials**

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## 18 **Abstract**

19 Many Australian mammals consume seeds, but their role in seed dispersal has not been well  
20 explored. Here, we investigated the mean retention time and the post-consumption germination  
21 capacity of Australian seeds (*Acacia acuminata*, *Dodonaea viscosa* and *Gastrolobium*  
22 *calycinum*) likely to be consumed by quenda (*Isoodon fusciventer*) and woylies (*Bettongia*  
23 *penicillata ogilbyi*). Mean excretion times were 14 hours for quenda and 24 hours for woylies,  
24 but some seeds were retained in their digestive passages for up to 39.5 and 55.5 hours,  
25 respectively. Viable seeds of all plant species were retrieved from both species' scats and only  
26 *G. calycinum* seeds ingested by quenda (62%) had a significantly higher germination  
27 percentage than control seeds (34%). Our results show that viable seeds are deposited in the  
28 scats of quenda and woylies, indicating that these species may play a role in seed dispersal.

29

30 **Keywords:** endozoochory, granivory, seed dispersal, seed germination, potoroid, peramelid.

31

## 32 **Introduction**

33 Endozoochory, the dispersal of plant seeds via ingestion by a vertebrate animal, can be  
34 advantageous for plants in several ways. Seeds may be dispersed at a greater distance from the  
35 parent plant than other forms of seed dispersal (Carlo *et al.* 2007), reducing both competition  
36 for resources and predation rates (Janzen 1970). Deposition in faeces may provide moisture  
37 and nutrients, enhancing germination and growth rates (Traveset *et al.* 2007). Additionally,  
38 seeds consumed by animals sometimes have increased germination rates (Cantor *et al.* 2010)  
39 due to the alleviation of seed dormancy (Traveset 1998).

40 Seeds form an important dietary component for many Australian mammals (Quin 1985;  
41 Murray *et al.* 1999; Gibson 2001; Bice and Moseby 2008), and some groups, such as bettongs,  
42 disperse seeds via scatter-hoarding (Murphy 2009; Chapman 2015). Australian seed-eating  
43 mammals are recognised as potentially important seed predators (Ballardie and Whelan 1986;  
44 Auld and Denham 1999; Mills *et al.* 2018), but the extent to which they disperse seeds via  
45 endozoochory has received little research attention (Williams *et al.* 2000; Cochrane *et al.*  
46 2005).

47 Physical seed dormancy is an adaptive trait that acts to prevent germination when  
48 environmental conditions are suitable for germination, but not favourable for seedling survival  
49 (Merritt *et al.* 2007). Australian seeds in the genera *Acacia*, *Dodonaea* and *Gastrolobium*, for  
50 example, exhibit this adaptation and germinate only after exposure to high temperatures  
51 (Sweedman and Merritt 2006). Previous research suggests that germination capacity is

52 increased if gut passage acts to break dormancy inhibitors such as removal of surrounding fruit  
53 pulp (Petre *et al.* 2015), or through seed coat scarification (Traveset 1998). However, the effect  
54 of consumption by marsupials on dormancy in Australian seeds is unknown.

55 The time it takes an animal to pass a seed through its digestive tract (i.e. its gut passage  
56 time) will affect its effectiveness as a seed dispersal agent. Longer gut passage times may result  
57 in the dispersal of propagules over greater distances (Petre *et al.* 2015) and scarification in the  
58 gut can increase germination capacity by breaking seed dormancy. However, if gut passage  
59 times are too long seeds may be damaged or lose viability (Traveset *et al.* 2016). Whilst the  
60 gut passage times for several Australian mammals have been studied using markers that bind  
61 to solutes or small particles (e.g. Wallis 1994; Moyle *et al.* 1995; Gibson and Hume 2000),  
62 there has been no research into the passage time of seeds.

63 In this paper we use two species known to consume seeds, quenda (*Isoodon fusciventer*) and  
64 woylies (*Bettongia penicillata ogilbyi*), to investigate endozoochory in Australian mammals.  
65 We sought to determine the rate at which these species pass seeds through their digestive tract  
66 and the germination capacity of seeds retrieved from their scats. We tested the following  
67 questions: (1) How long do quenda and woylies take to pass seeds through their digestive  
68 systems? and (2) Is the germination capacity of seeds retrieved from scats of quenda and  
69 woylies higher than unconsumed seeds?

70

## 71 **Materials and methods**

72 Two female adult quenda (*I. fusciventer*) and a male and female adult woylie (*B. penicillata*)  
73 held in captivity at Native Animal Rescue (NAR), Malaga, Western Australia were used in this  
74 experiment. During the experiment, conducted in June 2019, the animals were housed in  
75 individual enclosures approximately 2 x 3 m in size. The floors of the enclosures were cleared  
76 of leaf litter and excess foliage to facilitate the location of scats. A hollow log or nest box, and  
77 a small bundle of fresh foliage were retained in each enclosure.

78 The animals' regular feed consists of fruit, vegetables and a boiled egg with the addition of  
79 mealworms, insectivore mix and aviary seed (quenda) or herbivore pellets (woylies). For one  
80 week prior to, and during the experiment, seeds and fruit containing seeds were substituted  
81 with other items (e.g. similar fruit or vegetables without seeds). Feed was provided daily in the  
82 late afternoon and remaining food was removed each morning. Water was provided ad libitum  
83 throughout.

84 We used commercially sourced seeds (Nindethana Australian Native Seeds – King River,  
85 WA) of three native species previously recorded in the diet of Potoroids or Peramelids: *Acacia*

86 *acuminata*, *Dodonaea viscosa* and *Gastrolobium calycinum* (Christensen 1980; Bice and  
87 Moseby 2008) (Table S1). Prior to the start of the experiment, we determined the viability of  
88 the seeds using a Faxitron MX-20 Digital X-Ray Cabinet (Tucson, Arizona, USA). Seeds that  
89 appeared uniformly white/grey in the digital imagery were deemed to be viable (Erickson and  
90 Merritt 2016). Seeds that appeared shrivelled/empty or abnormal were deemed non-viable and  
91 were discarded. The viable seeds were not treated to break physical dormancy so that we could  
92 investigate how this was affected by consumption by our study species. The germination  
93 capacity of control seeds (i.e. seeds not consumed by the study animals) was determined in the  
94 laboratory by incubating 100 seeds of each species at 15°C with a 12 hour light-dark cycle,  
95 using water agar as a germination medium (Merritt 2006). Twenty-five seeds of a single species  
96 were sown onto each petri dish. Prior to sowing, seeds were rinsed in a 30 gL<sup>-1</sup> bleach solution  
97 and sterilised water to reduce fungal contaminants (Merritt 2006). The number of germinating  
98 seeds was then counted weekly for four weeks.

99 At the commencement of the feeding experiment, 150 viable seeds (50 of each species),  
100 taken from the same seed pool as the controls, were mixed into each animal's usual feed. The  
101 modified feed was provided to the animals at 1600 h on the first day of the experiment and the  
102 remains removed at 0700 h the following morning. Remaining feed and the enclosures were  
103 searched for unconsumed seeds or seed caches so that the exact number of seeds consumed by  
104 each animal (i.e. the number of seeds found subtracted from 150) could be determined (Table  
105 1).

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

118 All scats were examined for seeds. Scats were soaked in water and then carefully teased  
119 apart. Whole seeds, with or without the elaiosomes, were removed, sorted by species and dried.

120 Where the number of retrieved seeds was less than the number consumed by the animals, we  
 121 assumed the missing seeds were destroyed during the digestive process. The viability of the  
 122 retrieved seeds was retested using the x-ray method described above. We performed a  
 123 germination trial, including the seed sterilisation step, as described above, on all retrieved seeds  
 124 that appeared viable using separate petri dishes for each animal, seed species and collection  
 125 event combination. Differences in the germination capacity of viable seeds retrieved from scats  
 126 and control seeds were assessed using Chi-square analyses in R statistical software (R Core  
 127 Team 2019). We used the percentage of seeds that germinated as the response variable.

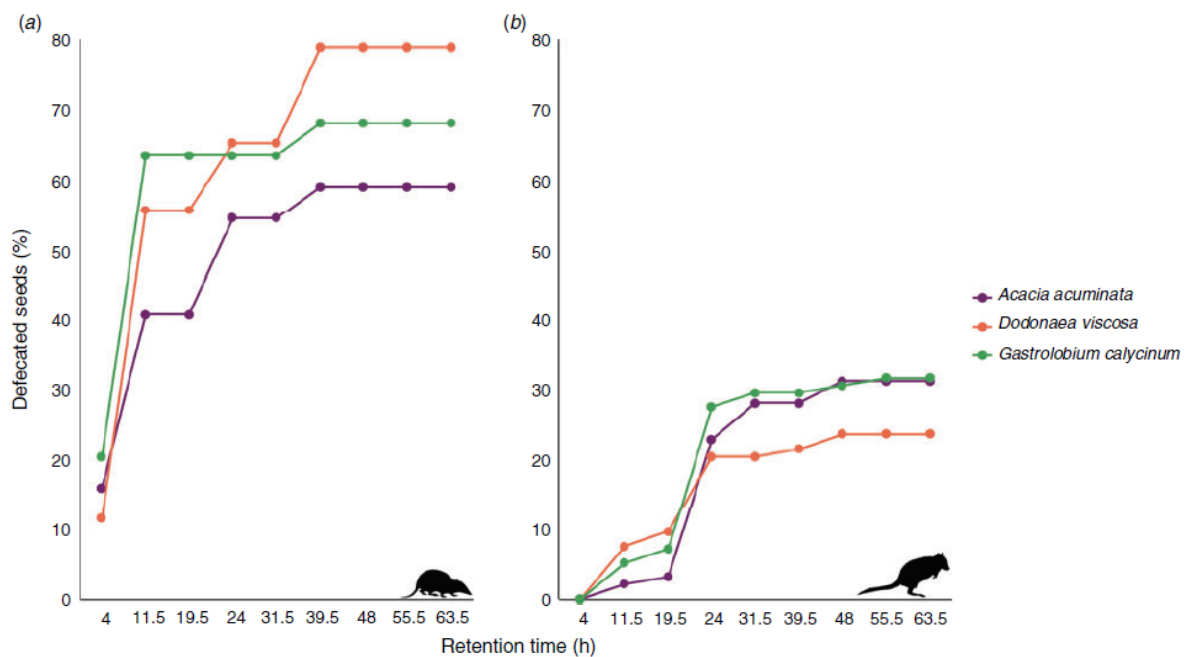
128

129 **Results**

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

135 The peak excretion (54% of seeds) for quenda occurred between 4-11.5 hours (Fig. 1). For  
 136 woylies, the peak excretion (59% of seeds) occurred between 19.5-24 hours (Fig. 1). Mean gut  
 137 passage time was similar to the time of peak excretion for both species:  $14 \pm 3$  hours for quenda  
 138 and  $24 \pm 2$  hours for woylies.

139



140

141 **Fig. 1.** Relationship between the retention time (in hours) and the cumulative percentage of  
 142 viable seeds of *A. acuminata*, *D. viscosa*, *G. calycinum* recovered from scats of (a) quenda and  
 143 (b) woylies. The experiment was continued until 103.5 h after consumption, but the last seeds  
 144 were recovered from the scats at 39.5 h (quenda) and 55.5 h (woylies).

145

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

157

158 **Table 1.** Number of seeds of each species used in the experiment, their consumption (i.e.  
 159 number of seeds found subtracted from presented seeds), recovery, viability and germination  
 160 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%)

161

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

163

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

Seed species	Control	Germinants	Quenda	<i>P</i>	Germinants	Woylie	<i>P</i>
	germinants		$\chi^2$			$\chi^2$	
<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	<b>0.001</b>	10 (45.4%)	0.32	0.57
<i>Gastrolobium calycinum</i>	34 (34%)	18 (62.1%)	8.19	<b>0.004</b>	5 (18.5%)	4.57	<b>0.03</b>

167

168

169 **Discussion**

170 Our study shows that viable seeds, capable of germinating under laboratory conditions, are  
171 deposited in the scats of quenda and woylies. Only forty-two percent of the consumed seeds  
172 were retrieved whole from the scats suggesting that quenda and woylies may act as seed  
173 predators. However, the high viability and germination of some seeds retrieved from the scats  
174 indicate that these species may also play a role in seed dispersal through endozoochory.

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

188 Although consumption by woylies or quenda improved germination capacity in only one  
189 seed species, endozoochorous dispersal offers other advantages to seeds. The deposition of  
190 seeds within scats may provide nutrients and protection from seed predators (Traveset *et al.*  
191 2007) and is more likely to occur to favourable locations (Carlo *et al.* 2007). For example,  
192 quenda and woylies forage extensively for subterranean food resources (Garkaklis *et al.* 2004;  
193 Valentine *et al.* 2012) and often defecate next to their foraging pits (B. Palmer *pers. obs.*).  
194 These scats may be covered by the ejected soil during pit creation or fall into the pits. Seeds in  
195 foraging pits are more likely to germinate (Valentine *et al.* 2017), exhibit higher growth rates  
196 (Valentine *et al.* 2018) and are less likely to be predated (Radnan and Eldridge 2017).

197 The mean excretion times we recorded for quenda and woylies are within the range of  
198 published values for marker excretion times for other Peramelids and Potoroids (Wallis 1994;  
199 McClelland *et al.* 1999), suggesting that standard digestive rate methods provide reasonable  
200 estimates of seed retention times. Most seeds in this study were passed quickly, with excretion  
201 rates peaking at 11.5 and 24 hours for quenda and woylies, respectively. Both species, however,  
202 retained some seeds for at least 39.5 hours. The gut passage times we recorded, combined with

203 their home range sizes (quenda 5 ha, Van Dyck and Strahan 2008; woylies 65 ha, Yeatman and  
204 Wayne 2015), indicate that quenda and woylies may disperse seed over substantial distances.  
205 This may confer advantages, such as reduced competition with parent or sibling plants, to those  
206 seeds that remain viable after excretion and serve to counteract the negative impact of seed  
207 predation on plant populations.

208 Reintroducing mammals could assist restoration efforts by increasing the dispersal of native  
209 plants (Cantor *et al.* 2010; Genes *et al.* 2019). However, animals can also disperse exotic  
210 species (Dovrat *et al.* 2012), and this should be considered when predicting the ecological  
211 outcomes of a translocation. Given the gut passage times we recorded, during wild-to-wild  
212 translocations quenda and woylies would probably excrete most seeds consumed prior to their  
213 capture during the holding or transport stage, but some seeds could be excreted at the release  
214 site. We suggest that scats excreted during holding and transport are retained and disposed of  
215 where germination cannot occur, unless dispersal of plant species from the source site is  
216 desirable. Where the source site supports exotic species absent at the release site, post-release  
217 monitoring for seedling recruitment of species of concern may be warranted.

218 Our study used only four captive animals and may not be representative of what happens in  
219 natural systems. For example, bettongs and bandicoots feed on mycorrhizal fungi and the co-  
220 occurrence of seeds and mycorrhizal fungal spores in scats may alter germination or growth  
221 rates (Tay *et al.* 2018). Field-based studies are required to determine how often free-living  
222 quenda and woylies consume seeds, and if this seed can germinate after consumption.  
223 Investigations on how consumption by other Australian mammals affects seed viability and  
224 germination capacity of a wide range of seeds, especially those already known to be part of  
225 their diet (Morton 1985), would also be useful. Our research demonstrates that endozoochory  
226 by Australian mammals is possible; future research will hopefully determine whether it  
227 contributes significantly to vegetation dynamics in natural settings.

228

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240

#### 241 **Conflicts of interest**

242 The authors declare no conflicts of interest.

243

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