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

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11

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^{-1} 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

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±3 hours for quenda

138   and 24±2 hours for woylies.

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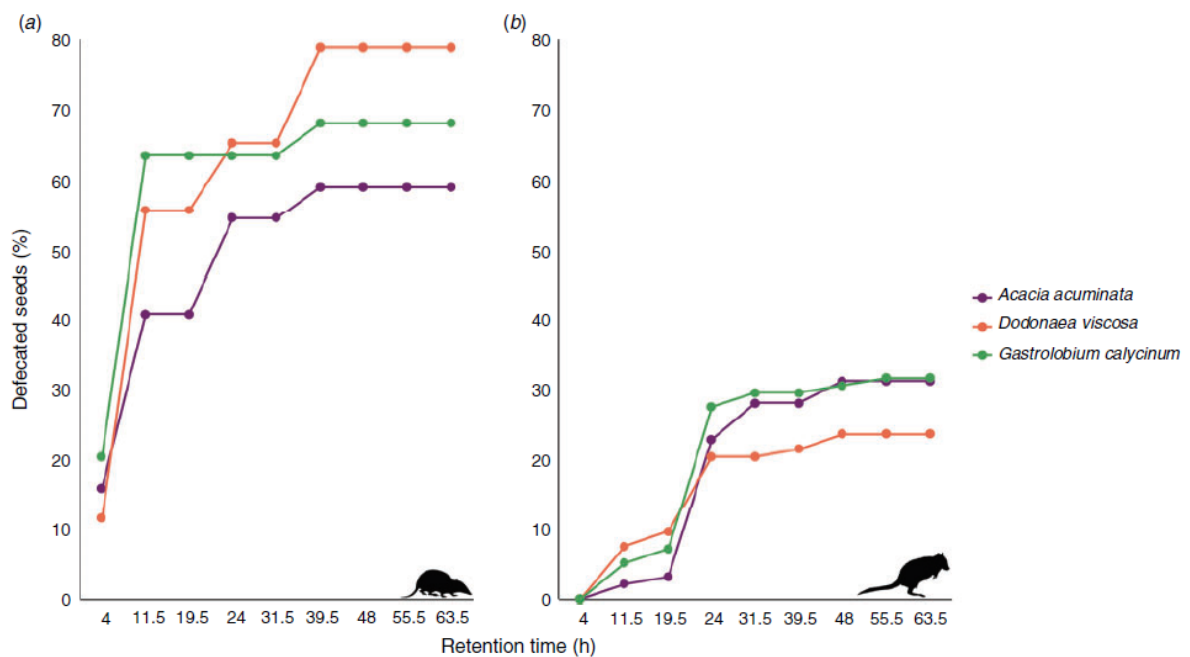
Fig. 1. Relationship between the retention time (in hours) and the cumulative percentage of viable seeds of *A. acuminata*, *D. viscosa*, *G. calycinum* recovered from scats of (a) quenda and (b) woylies. The experiment was continued until 103.5 h after consumption, but the last seeds were recovered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

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 germinants	Quenda Germinants	χ^2	P	Woylie Germinants	χ^2	P
Acacia acuminata	15 (15%)	2 (7.7%)	0.12	0.72	2 (8.3%)	1.91	0.17
Dodonaea viscosa	51 (51%)	5 (12.8%)	22.84	**0.001**	10 (45.4%)	0.32	0.57
Gastrolobium calycinum	34 (34%)	18 (62.1%)	8.19	**0.004**	5 (18.5%)	4.57	**0.03**

Discussion

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

Research on endozoochory in Australian marsupials is rare, but consumption by *Potorous gilbertii* and *Setonix brachyurus* increased germination in *Billardiera fusiformis* (Cochrane *et al.* 2005). Similarly, we found that consumption by quenda increased germination in *G. calycinum*. However, overall, the germination capacity of seeds consumed by 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 and Merritt 2006). Mastication or exposure to stomach acids may break physical seed dormancy, but can also damage seeds (Traveset *et al.* 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.

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 *et al.* 2007) and is more likely to occur to favourable locations (Carlo *et al.* 2007). For example, quenda and woylies forage extensively for subterranean food resources (Garkaklis *et al.* 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 and Eldridge 2017).

The mean excretion times we recorded for 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 and Strahan 2008; woylies 65 ha, Yeatman and 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.

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 *et al.* 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. 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). Field-based studies are required to determine how often free-living quenda and woylies consume seeds, and if this seed can germinate after consumption. Investigations on how consumption by other Australian mammals affects seed viability and germination capacity of a wide range of seeds, especially those already known to be part of their diet (Morton 1985), would also be useful. Our research demonstrates that endozoochory by Australian mammals is possible; future research will hopefully determine whether it contributes significantly to vegetation dynamics in natural settings.

Conflicts of interest

The authors declare no conflicts of interest.

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