

Endozoochory and the Australian bluebell: consumption of *Billardiera fusiformis* (Labill.) Payer (Pittosporaceae) seeds by three mammal species at Two Peoples Bay Nature Reserve, Western Australia.

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Abstract

Animals that feed on fruits have the potential to play a key role in vegetation dynamics, assisting in plant succession and maintenance of floral diversity. Seeds may be ingested, passed through the gut and voided to the soil. Through this action seeds are dispersed to new sites (endozoochory). Removal of pulp from fleshy fruits during transport through the gut may also assist in the stimulation of germination. This study compared the germination response of seeds of the Australian bluebell, *Billardiera fusiformis*, retrieved from faecal pellets of three native mammals (quokka *Setonix brachyurus*, Gilbert's potoroo *Potorous gilbertii* and bush rat *Rattus fuscipes*) with that of freshly collected and aged, but non-ingested seeds, from Two Peoples Bay Nature Reserve, Western Australia. Ingestion of seeds of *B. fusiformis* by quokkas, Gilbert's potoroos and bush rats increased germination by 58%, 31% and 2% respectively over a control (seeds physically removed from freshly collected fleshy fruit). When placed in dry storage for over a year, however, both ingested and non-ingested seeds displayed significant increases in percent germination.

Keywords: endozoochory, fleshy fruit, seed dispersal, gut passage, animal faeces

Introduction

Seed dispersal is important for reproductive success and is the critical mobile stage of a plant's life history. Dispersal may be accomplished through a variety of mechanisms and agents including wind, water, ballistics and animals. The main animal vectors of seed dispersal are vertebrates (especially mammals and birds) and ants. Animals have the ability to move seeds to new sites passively either on body surfaces (epizoochory) or actively by consuming fruits (endozoochory) or caching seeds. They may also play an active role in seed dispersal through digging and burrowing activities (Chambers & McMahon 1994). Diggings can trap plant litter, forming nutrient-rich microsites for the germination of seeds (Martin 2003). This soil disturbance is important in nutrient cycling and contributes to soil health (Martin 2003, Garkaklis *et al.* 2004). In Western Australia many small mammals create soil disturbance through their foraging for seeds, fungi, roots and invertebrates, or through burrowing activity. Seeds and spore-filled fruiting bodies of hypogeous fungi, such as those consumed by Gilbert's potoroos, are ingested, passed through the gut and voided to the soil (Nguyen *et al.* 2004).

Frugivores have an effect on the germination of seeds (rate and percent) in about 50% of plants they consume (Traveset 1998). In many cases only a proportion of

ingested seeds survive passage through the gut, with larger seeds suffering damage. Ingestion of seeds may increase their germinability by removal of dormancy. The removal of fleshy pulp prior to laboratory incubation of seeds has increased germination in a number of species (*e.g.*, *Persoonia* spp, *Leucopogon verticillatus*), suggesting that germination inhibitors may be present in the flesh (Baskin & Baskin 2001). The removal of fleshy fruit material from around seeds may also act to prevent seeds from being destroyed by bacteria before germination occurs (Witmer 1991). Passage through the gut may alter the seed coat or endocarp, aiding water permeability and thereby affecting germination through the action of chemicals or mechanical action (Baskin & Baskin 2001). Survival in the gut may also be dependent on seed size (Moussie *et al.* 2005).

The movement of seeds away from parent plants through zoochory can also have beneficial effects – colonisation of new areas, escape from seedling mortality near parent plant due to competition between parent and seedlings, and the creation of wider population genetic structure (Samuels & Levey 2005). Dispersal distance will be dependent on the foraging range of the animal disperser and, in the case of endozoochory, its gut retention time. The sum of these effects may play a key role in vegetation dynamics, and may be a significant force in plant succession and maintenance of floral diversity.

Amongst the multitude of studies on endozoochory and seed germination (*e.g.*, Milton & Dean 2001; Traveset *et al.* 2001; Paulsen & Hogstedt 2002; Stanley &

Lill 2002; Cosyns *et al.* 2005a,b; Couvreur *et al.* 2005; Mouissie *et al.* 2005) the majority have investigated the effects of ingestion of seeds in birds, rabbits or ungulates such as deer, donkeys and sheep, and few have been conducted in Australia. Traveset *et al.* (2001) and Barnea *et al.* (1991) reported differences in germination after passage through bird guts, dependent on species and gut retention time. Paulsen & Hogstedt (2002) reported increased seedling emergence after passage of seeds through birds; Stanley & Lill (2002) reported high viability after passage of native *Rhagodia* seeds through the gut of silvereyes (*Zosterops lateralis*). Williams *et al.* (2000) investigated the effect of ingestion of weed seeds by introduced rodents and possums on survival and subsequent germination of those seeds and considered that there was a major potential for ship rats (*Rattus rattus*) and brushtail possums (*Trichosurus vulpecula*) to disperse weed seeds in New Zealand. Native foxes (*Pseudalopex culpaesus*) have also been implicated in the spread of weed species in Chile through consumption of alien fruits and their defaecation (Silva *et al.* 2005).

Jordano (1992) reported that between 82% and 88% of woody plants in Australian tropical and subtropical regions have fruits or seeds that are dispersed by vertebrates. The majority of these fruits are fleshy and are probably bird or bat dispersed, with few plant species having seeds adapted for dispersal by ground-foraging mammals or birds such as the cassowary (*Casuaris casuaris*) (Willson *et al.* 1989).

A number of Australian studies have investigated the relationship between endozoochory, seed germination and non-flying mammals. These include McGrath & Bass (1999) and Noble (1975) who investigated the ingestion and dispersal of seeds by the emu (*Dromaius novaehollandiae*) in New South Wales. Webber & Woodrow (2004) studied the effect of cassowary frugivory on seed germination of a rare rainforest tree in Queensland. There has been some investigation of caching of seeds by woylies (*Bettongia penicillata*) in Western Australia and their effect on seedling establishment (Murphy *et al.* 2005), and Parsons (1997) reported that *Carpobrotus* seeds from rabbit (*Oryctolagus cuniculus*) and eastern grey kangaroo (*Macropus giganteus*) faeces germinated readily in comparison to fresh seeds. In general though, the importance of non-flying mammals as agents of seed dispersal in Australia has been neglected. Fleshy fruits and endozoochory may be common in tropical and subtropical rainforests in Australia, but in most Australian sclerophyll woodlands and heaths less than 30% of plant species have fleshy fruits (Willson *et al.* 1989). In south western Australian plant communities seed dispersal by vertebrates is considered uncommon due to the low incidence of seeds enclosed by fleshy fruits (Bell 1994).

The objective of this study was to investigate and quantify plant-animal interactions associated with seed consumption. This paper reports the relationship between small native ground-dwelling mammals (quokka *Setonix brachyurus*, Gilbert's potoroo *Potorous gilbertii* and bush rat *Rattus fuscipes*) and seeds of the Australian bluebell, *Billardiera fusiformis*, (formerly *Sollya heterophylla*) in a Western Australian south coast nature reserve.

Methods

Study site

The study site is the Mount Gardner promontory within Two Peoples Bay Nature Reserve, situated 30 km east of Albany on the southern coastline of Western Australia. The site consists of granite headlands, small indented bays and hills covered in low heath vegetation. The area is an important refuge for threatened fauna, including the only known habitat of the critically endangered Gilbert's potoroo. Other native ground-dwelling mammals resident in the area include the quokka, bush rat, and quenda (*Isoodon obesulus*). The vegetation is comparable to other coastal sites and has been long impacted by the introduction of the plant pathogen, *Phytophthora cinnamomi* (Orr *et al.* 1995). Flora species abundant in the area include *Agonis flexuosa*, *Eucalyptus marginata*, *E. calophylla*, *Allocasuarina fraseriana*, *Melaleuca striata*, *Adenanthos barbigeros*, *Hakea ferruginea*, *Jacksonia spinosa* and *Leucopogon* species, with numerous sedges (e.g., *Anarthria scabra*) that provide important understorey cover for small mammals.

Faecal samples

A total of 275 scats from quokkas, Gilbert's potoroos, bush rats and quendas were assessed from the study site between September 2003 and February 2004. Samples comprising one or more fresh scats were taken from cage traps during trapping sessions to monitor the Gilbert's potoroo population, and opportunistically collected (in the case of quokka faeces) in the general vicinity of the trap lines. Scats were air dried as soon as possible after collection, weighed and seeds manually extracted from faeces. Seed type and load per scat were recorded and the mean number of seeds per scat and per gram of scat calculated for each mammal species.

Seed germination

Seeds retrieved from scats were identified by comparison with seeds found on plants in the study area. Seeds of *Billardiera fusiformis* were germinated as they were the only seeds found in the scats of more than one mammal species. Seeds were incubated without treatment on filter paper over moistened sponge (5 ml deionised water) in 90 mm Petri dishes in an incubator at 15°C with a 12 hour photoperiod. The experiment consisted of three replicates of 20 (quokka, bush rat and control), and 15 (Gilbert's potoroo) seeds from freshly retrieved seeds. In addition to germinating seeds from freshly collected faecal matter, seeds recovered from faeces were germinated after more than one year of storage (approx. 15 months in dry storage at 21°C). Where enough seeds were available a smoke treatment was applied to aged seeds (bush rat and Gilbert's potoroo only). This treatment consisted of soaking seeds for 24 hours in a 10% solution of Smokemaster® and rinsing seeds in deionised water prior to incubation as above. Each treatment contained four replicates of 25 seeds. Germination trials were concluded after 124 days.

In order to compare germinability of ingested seeds with that of non-ingested seeds, we incubated freshly collected and aged seeds of *Billardiera fusiformis* under the same conditions. Prior to incubation fleshy material

was removed from seeds by rubbing flesh away from seeds under water. Flesh was also removed from seeds before storing dry in paper bags for over 15 months at room temperature (approx 21°C and 50% relative humidity). Seeds were incubated without treatment (control) and under five different treatments (Table 4). Germination trials were concluded after 127 days.

Data Analyses

Percent germination data were arcsine square root transformed prior to Analysis of Variance (ANOVA) using StatView®. Mean time to germination (MTG) was calculated for the treatments that gave maximum germination for each species, using the equation:

$$MTG = \Sigma (nd) / N$$

where: n = number of seeds germinated between scoring intervals; d = the incubation period in days at that time point and N = total number of seeds germinated.

Results

Faecal analysis

Seed material was found in less than one third of the faecal samples from quokkas, Gilbert's potoroos and bush rats. Scats ranged in weight and number of seeds retrieved (Table 1). There was no visible evidence of damage to seeds and the only type of seeds common to all three mammals was the Australian bluebell, *Billardiera fusiformis* (Labill.) Payer (Pittosporaceae). *Billardiera fusiformis* is an evergreen climber with blue bell-shaped flowers and cylindrical fleshy drupe containing 30–50 seeds embedded in the mucilaginous pulp. This species is endemic to Australia and is commonly found in temperate regions of WA, SA, NSW and Tasmania. Scats of bush rats contained greater numbers of *B. fusiformis* seed per gram than those of either quokkas or Gilbert's potoroos, with more than 30

seeds retrieved per gram (Table 1). Only potoroo samples contained seeds of other plant species (*Marianthus* sp., *Astroloma* sp. and *Leucopogon* sp.) No seeds were recovered from the 57 quenda scats examined.

Seed germination

Ingested seed

Percentage germination of freshly retrieved seeds of *Billardiera fusiformis* was highest in seeds retrieved from quokka scats (58%) and lowest in seeds retrieved from bush rat scats (2%), with 31% germination of seeds retrieved from faecal pellets of Gilbert's potoroo (Table 2).

First germination occurred after 21 days for seeds recovered from both quokka and Gilbert's potoroo faeces. Ageing increased percentage germination of seeds ingested by Gilbert's potoroos and bush rats, but not quokkas. Treating aged ingested seeds with smoke compound further increased germination (Table 2). An estimation of the numbers of germinable seeds per gram of faecal matter was made for both fresh and aged seeds retrieved from faecal material. Germinable seeds per gram dry weight of faecal matter increased from 1.95 (fresh) to 1.66 (aged) in quokka and 0.14 (fresh) to 0.22 (aged) in Gilbert's potoroo. After ageing, there was a five-fold increase in germination of *B. fusiformis* seeds ingested by bush rats (from 0.75 to 4.80 germinable seeds per gram dry weight of faecal matter).

Non-ingested seed

Fresh non-ingested seeds of *B. fusiformis* were dormant on collection. Laboratory treatment of seeds increased germination, as did ageing (Table 3). Application of smoke stimulated some germination (12%) as did the combined effects of heat shock and smoke (28%). Heat shock alone did not provide a cue for germination, and limited germination occurred after the application of potassium nitrate.

Table 1

Occurrence of *Billardiera fusiformis* seeds in scats of four ground-dwelling mammals at Two Peoples Bay Nature Reserve, Western Australia.

Species	Total no. scats	Mean scat weight (g) n=10	Total scat dry weight (g)	Total no. <i>B. fusiformis</i> seeds retrieved	Mean no. seeds per scat (range)	No. seeds of <i>B. fusiformis</i> per g of scat
Quokka	16	1.076	19.48	66	4.13 (0-29)	3.4
Gilbert's potoroo	141	0.361	41.01	18	0.13 (0-4)	0.4
Bush rat	61	0.038	2.61	79	1.29 (0-20)	30.3
Quenda	57	0.210	19.10	0	0	0

Table 2

Percentage germination of *Billardiera fusiformis* seeds retrieved from faecal samples (fresh and aged) collected between September 2003 and February 2004 compared to seeds collected from plants (control).

	Gilbert's potoroo	Quokka	Bush rat	Control
Fresh (no treatment)	31 ± 9.2	58 ± 1.4	2 ± 11.3	0
Fresh (+ smoke)	n/a	n/a	n/a	12 ± 1.6
Aged 15+mths (no treatment)	50 ± 12.8	49 ± 7.7	32 ± 4.2	16 ± 5.3
Aged 15+mths (+ smoke)	62 ± 5.0	n/a	64 ± 4.4	91 ± 3.4

Table 3

Treatment conditions and results of laboratory germination of fresh and aged seeds of *Billardiera fusiformis*.

Treatment Type	Condition	Percent Germination	
		Fresh seeds	Stored seeds 15 mths
Control	No treatment	0	16
Heat shock	68 hours at 80°C	0	53
Smoke	2 ml Smokemaster® on filter paper	12	91
Gibberellic acid	2 ml Gibberellic acid as GA ₃ on filter paper	0	8
Heat shock + Smoke	68 hrs 80°C + 2 ml Smokemaster® on filter paper	28	93
Potassium nitrate	2 ml KNO ₃ at 100 mg/L ⁻¹ on filter paper	2	47

Table 4

Results of two way ANOVA comparing the effects of ageing and smoke treatment and the interaction of these variables on percent germination in *Billardiera fusiformis*.

Source of variation	df	Mean square	F	Significance
Ageing	1	1.701	24.778	<.0001
Treatment	1	0.286	4.165	0.0477
Ageing x treatment	1	0.689	10.030	0.0029

When smoke was applied to aged non-ingested seeds germination reached 91%. Germination was also high (93%) when heat shock and smoke were applied sequentially, although heat shock alone produced only 53% germination in aged non-ingested seeds. The application of potassium nitrate (KNO₃) to non-ingested seeds increased germination to 47%. Ageing of both ingested and non-ingested seeds had a highly significant effect on percent germination (Table 4). There was also a significant interaction between ageing and smoke treatment on percent germination of both freshly collected and ingested seeds of *B. fusiformis*.

Time to first germination for non-ingested aged seeds was 23 days, and similar to first germination for ingested aged seeds (25 days). Mean time to germination was greater than 30 days for all but non-ingested aged and smoke-treated seeds (Table 5).

Discussion

This investigation has demonstrated that a functional relationship exists between mammals at Two Peoples Bay and the Australian bluebell, *Billardiera fusiformis*. It has highlighted the presence of inter-specific differences

Table 5

Mean time to germination (days) for fresh and aged ingested and non-ingested seeds of *Billardiera fusiformis*.

	Ingested			Non-Ingested
	Gilbert's potoroo	Quokka	Bush rat	
Fresh	31.1	37.4	42.0	-
Fresh + smoke	-	-	-	60.0
Aged	39.0	30.5	43.1	33.6
Aged + smoke	41.6	-	44.9	25.3

between dispersers with respect to their effects on seed germination. The significant differences seen in germination response of seeds from faeces of the three mammal species reflect differences in digestive tract morphology and gut retention time. Like other species of *Rattus*, bush rats have a relatively simple digestive system and short gut passage time. Both potoroos and quokkas exhibit foregut fermentation, but in potoroos the peptic hindgut is more important in digestion and digesta do not remain as long in the forestomach as in macropodids including the quokka (Hume & Carlisle 1985). Gut passage time is greater in the quokka at 38 hours (Calaby 1958) than the 24–30 hours observed in other potorooids, the long-nosed potoroo *Potorous tridactylus*, rufous bettong *Aepyprymnus rufescens* and woylie (Wallis 1994).

Frugivores may provide an essential service by freeing seeds from fruit pulp in addition to their role as seed dispersers. Release from germination inhibitors and high osmotic pressures by removal of flesh are mechanisms that can alter germination rate or percent (Samuel & Levey 2005). The removal of pulp from *B. fusiformis* seeds occurred much more rapidly through gut passage compared to natural fruit pulp decomposition that may take several months (pers. obs. A Cochrane). Little of the fleshy fruit was removed during passage of seeds through the gut of bush rats, perhaps contributing to reduced germination amongst seeds that they have eaten. The type of food ingested with the fruits may also affect germination by chemical and mechanical abrasion of the seed coat (Traveset 1998). The different speeds of germination promoted by different rates of gut passage may increase the probability that seeds will recruit successfully at a given time and in a given place (Traveset *et al.* 2001). Early seedling emergence in unpredictable environments may assist in maximising seedling survival.

For the most part, endozoochory provides an advantage for germination of *B. fusiformis* through partial release of dormancy in "fresh" seeds. Chemical and mechanical abrasion and de-pulping of seeds have apparently combined with the moist environment of the faeces to partially overcome dormancy. Germination was greater and more rapid in seeds retrieved from scats than in freshly collected seeds. Germination was also greater in seeds collected from plants and aged, indicating an after ripening requirement that implies the presence of primary dormancy (Mandujano *et al.* 1997). *B. fusiformis* has a rudimentary embryo within a white granular endosperm, often referred to as underdeveloped (Baskin

& Baskin 2001). The embryo is small and consequently has to grow before the seeds can germinate. Growth of the embryo takes place after the fruits have fallen. Dormancy delays germination until favourable conditions are met for seedling establishment and growth. For *B. fusiformis* smoke and seed ageing were partner cues for germination in the absence of ingestion to break dormancy. Smoke has been reported to cause intense chemical scarification and alteration of the permeability of seed coats (Egerton-Warburton 1998) and it is possible that smoke is acting in a similar way as the environment of the gut in overcoming dormancy.

Dispersal can affect plant dynamics (Bullock *et al.* 2002) and animal seed dispersers may play an important role in maintaining regional biodiversity, in linking patches of remnant vegetation (McGrath & Bass 1999) and in increasing species-richness in restoration projects (Traba *et al.* 2003). Differences in disperser action on the seeds of plants they consume can contribute to heterogeneity of plant communities (Traveset *et al.* 2001). Being sedentary, plants cannot move across the landscape unaided. Endozoochory may confer ecological benefits by promoting substantial and dispersed seedling recruitment. For seeds that rely on endozoochory for movement across the landscape dispersal distance will be related to animal home range dimensions. The greatest distances moved by non-dispersing individual quokkas, Gilbert's potoroos and bush rats, measured by trapping at Two Peoples Bay, are 475 m, 870 m and 540 m respectively (JA Friend unpub.). Although *B. fusiformis* is widespread at Two Peoples Bay Nature Reserve, no plants were recorded adjacent to trap lines where faecal samples were collected. Further investigations would be needed to determine whether seed abundance in faecal matter is correlated with abundance of plants in the vegetation.

Seeds adapted to survive ingestion have similar properties to those adapted to survive in the soil seedbank, namely small round, hard seeds (Pakeman *et al.* 2002). Seeds that can build up in the soil seedbank can have a significant effect on species richness and abundance after disturbance events. In the colonisation of new sites or those subjected to extreme disturbance (such as extensive wildfire or volcanic eruption), vegetation dynamics may be driven by immigrant seeds where a pre-existing soil seedbank is absent or depauperate. Seeds dispersed in faeces have a ready supply of nutrients and should have a competitive advantage for germination in nutrient-poor sites. And in fire-driven environments, when fire is absent for long periods of time, endozoochory may be an important contributor to successful seed germination and establishment of plant species.

The question of whether seeds are being eaten selectively or in proportion to their availability remains unanswered, though it is unlikely that *Billardiera* is a critical food resource for these small mammals, given its relative rarity at the study site and its seasonal availability. We have not attempted to determine seasonal variation in consumption of seeds and it is possible that considerable seasonal variation, as reported by Bennett & Baxter (1989) for long-nosed potoroos, occurs. With 30 to 50 seeds per fruit, the quantity of fruit consumed by the three mammals during the sampling

period appears low. We do not know how passage through the gut has affected seed survival as we have no information about the original quantity of seeds consumed by each animal. Seeds of *B. fusiformis* are small (< 2 mg in weight) and are likely to have escaped destruction by mastication. Ingestion of *Billardiera* is more likely to be opportunistic and of more benefit to the plants themselves. When plants depend on animals for seed transport they are susceptible to dispersal failure if their seed vectors become rare or extinct (Willson 1992). Where natural regeneration is dependent on seed dissemination, failure to disperse propagules could deplete plant populations. Low seedling recruitment and even local extinction of populations may occur. Small mammal species have experienced declines or complete extinction in many parts of Western Australia due to the introduction of foxes and cats, land clearing and changed fire regimes. Their demise may contribute to changes in the balance of vegetation communities. Future investigations should address the demographic and genetic effects of seed dispersal for plant populations.

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