SHORT COMMUNICATION

Seed dispersal of matai (*Prumnopitys taxifolia*) by feral pigs (*Sus scrofa*)

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Abstract: Introduced feral pigs (*Sus scrofa*) include native fruit and seed in their diet, and thus may act as seed dispersers if seeds are passed intact. The aim of this study was to determine whether pigs consume, and subsequently disperse, intact seeds of the New Zealand native tree matai (*Prumnopitys taxifolia*). Two captive pigs were fed 100 ripe fruit of matai and their faeces checked for seeds for 4 days. Fourteen intact seeds (14%) were recovered and 57% of these germinated under glasshouse conditions, comparable with germination from hand-cleaned seeds. We collected 3.5 kg of feral pig faeces from matai-dominated forest in Isolated Hill Reserve, southern Marlborough. This sample contained over 450 intact matai seeds; these seeds readily germinated in the glasshouse, reaching 68% germination after 22 months. These results indicate that pigs are consuming native fruit and passing some viable seeds out – thus acting as occasional seed dispersers.

Keywords: germination; gut passage; Isolated Hill Reserve; mammals; Podocarpaceae

Introduction

Feral pigs (*Sus scrofa*) include fleshy fruits and seeds as part of their diet both in New Zealand and elsewhere (Henry & Conley 1972; Wood & Roark 1980; Thomson & Challies 1988). However, pigs are known to grind up seeds in the process of consumption (Beveridge 1964; Fedriani & Delibes 2009) so this behaviour has rarely been linked to legitimate seed dispersal. Mammals have the potential to be important for long-distance seed dispersal because of their long gut passage times and wide-ranging behaviour (Jordano et al. 2007) and have elsewhere been found to disperse seeds (Abe 2007; Calvino-Cancela 2011; Shiels & Drake 2011). Here we test whether feral pigs are potential seed dispersers of a medium-sized native seed (mataī *Prumnopitys taxifolia*; mean fruit and seed diameters 9 and 7 mm respectively). Mataī is a gymnosperm, so technically produces single-seeded cones, but for simplicity we will use the term 'fruits' for all kinds of fleshy-coated diaspores.

Feral pigs occupy c. 35% of New Zealand, including 13 islands (Fraser et al. 2000). In theory, if pigs disperse a wide variety of native seeds, this could partly compensate for the decline or disappearance of native frugivores (Kelly et al. 2010). Northern Hemisphere diet studies show plant material makes up approximately 80% of the diet of feral pigs. Certain foods are readily consumed seasonally, especially mast seed crops such as acorns and hickory nuts (Henry & Conley 1972; Wood & Roark 1980; Baber & Coblentz 1987; Massei et al. 1996; Schley & Roper 2003).

A New Zealand study of pig diet showed plant material made up 72% of the annual diet, including two fruits (tawa *Beilschmiedia tawa* and hīnau *Elaeocarpus dentatus*) that together comprised 30.9% of the diet (Thomson & Challies 1988). Fruits of mataī, supplejack (*Ripogonum scandens*), miro (*Prumnopitys ferruginea*) and nīkau (*Rhopalostylis sapida*) are also eaten (Beveridge 1964; Knowles & Beveridge 1982; Thomson & Challies 1988). None of these studies recorded whether any seeds were viable, although Beveridge (1964) noted that 'a large quantity' of seeds were crushed.

Although fruit is common in pig diets, studies have been divided on to what extent they destroy the consumed seeds versus passing them out intact. In Hawai'i, pigs disperse viable seeds of the introduced *Passiflora mollissima* (LaRosa 1992). Work in New Zealand confirmed that pigs consume *Passiflora mollissima* fruit and excrete most of the seeds intact and viable (Beavon 2007). In Australia two-thirds of mesquite (*Prosopis pallida*) seeds consumed by feral pigs were undamaged; approximately 80% of these seeds then germinated (Lynes & Campbell 2000). However, in Argentina Campos and Ojeda (1997) found that all *Prosopis flexuosa* seeds found in pig faeces had been destroyed. Consequently, the presence of fruit in pig diets does not necessarily equate to seed dispersal.

We studied the viability of seeds of a native tree, mataī, following consumption by pigs. We hypothesised that pigs consume this native seed and release some intact in faeces, thereby acting at least partially as seed dispersers. Our study has two parts: first we conducted a feeding experiment using captive pigs to determine whether the resulting faeces contained viable seeds; second, faecal samples were collected from a patch of mataī-dominated forest to test whether intact seeds were also present in faeces of wild pigs.

Methods

Captive trial

Two adult, female kunekune pigs (*Sus scrofa*), a New Zealand breed, were kept in captivity at Willowbank Wildlife Reserve, Christchurch, New Zealand. Both were born in captivity and weighed approximately 130 kg. One hundred ripe mataī fruits (one seed per fruit) were fed in one session to the two pigs, with each eating approximately 50 fruits. Most of these fruits were hand-fed to the pigs, with others sandwiched between bread (for easy handling) or placed straight into the feeding trough. All seeds were ingested; none were spat out. Fruits had been collected from the Port Hills, Christchurch, mostly

under a single female mataī, approximately one month earlier, and refrigerated. Only ripe fruits were used.

The entire enclosure was cleaned of pig faeces within 30 min of the seeds being ingested. Pig faeces were then collected during daily cleaning for four consecutive days. These samples were taken back to the laboratory and sifted to recover seeds.

Field study

Field evidence of pig dispersal was collected in winter 2008 from Isolated Hill, a 2835-ha scenic reserve in southern Marlborough, New Zealand. Mataī-dominated forest makes up 8% of the reserve (Williams 1982). Feral pigs are present throughout the reserve, being especially abundant in areas containing mataī (Cochrane 1994). We observed on initial visits that pig faeces in this area appeared to contain large amounts of crushed mataī seeds. On a single day in June 2008 a 3.5-kg sample of pig faeces was collected from under c. 12 female mataī trees through a 1-ha area of mataī-dominated forest within the reserve (E2591170, N5924350, NZMG). Although pig faeces were most easily collected under female mataī trees, given the long gut passage times of pigs (see Results), mataī seeds are likely to be present in faeces deposited elsewhere. The samples were collected 1–2 months after mataī had finished fruiting; all faeces were solid and water was required to sift samples and retrieve seeds.

Germination

All intact seeds recovered from both the captive and field trials were potted in June 2008 and kept under glasshouse conditions as for previous studies (Kelly et al. 2010) at the University of Canterbury, Christchurch, New Zealand, for two spring/summer cycles until June 2010. Germination was recorded at least monthly, but weekly during the main period of germination (November to March each year for 2 years). We were unable to measure the germination rate of non-pig-processed seeds ourselves, as all the available fresh fruits collected were used in the captive feeding trials. We therefore compared our data to hand-cleaned and germinated mataī seeds presented by another study (Kelly et al. 2010, their table 2). The same glasshouse was used as for Kelly et al.'s study, but their seeds were sourced from elsewhere in the northern South Island, at Pelorus Bridge (Nelson) and Blue Duck Reserve (Kaikoura). In addition, we potted 20 seeds from Isolated Hill that were partially damaged from pig mastication. Overall germination success rates were compared between trials using chi-square tests on the totals.

Results

Captive trial

The captive pigs readily ate the mataī fruits offered to them, consuming all within 5 min. The pigs made loud crunching sounds as they chewed the seeds. Despite this, of the 100 seeds fed to the pigs, 14 intact seeds were retrieved from the collected faeces. The seeds were excreted over 4 days, with most collected on Day 3. In total 8 of the 14 seeds (57%) germinated in the glasshouse – seven in spring 2008, one in spring 2009 (Table 1). As the Day 4 sample still contained some mataī seed we cannot exclude that some seeds were excreted after the trial ended. The faeces contained an unquantifiable amount of shattered mataī seed coat; no partially damaged seeds were recovered.

Field study

The 3.5 kg of pig faeces collected from Isolated Hill contained abundant mataī seed-coat fragments (not quantified), many intact mataī seeds (c. 470), and some damaged seeds: 20 partially damaged mataī seeds (potted in glasshouse) and 20 mataī seeds broken in half with traces of the embryo present (not potted). If we apply the 14% recovery rate of intact seeds from the captive trials, then this would suggest approximately 3400 fruits were consumed by the pigs in question. No other food sources were identified in the faecal samples, indicating pigs were concentrating on mataī fruit in the area sampled at that time. There were no intact seeds from other plant species.

Germination

Glasshouse seeds began germinating in November 2008, 6 months after being planted. Germination continued throughout the next year, with low but consistent numbers over winter, followed by a second flush beginning in September 2009. No further germination was recorded after March 2010 (22 months after the seeds were planted). All three samples (hand-cleaned, captive, field) reached approximately 60% germination. We compared total germination success between the hand-cleaned seeds (from Kelly et al. 2010), captive trial and field trial. There was no significant difference between hand-cleaned seeds and either captive trial data ($\chi^2 = 0.04$, d.f. = 1, $P = 0.85$) or field data ($\chi^2 = 1.33$, d.f. = 1, $P = 0.25$). An additional 8 seedlings germinated from partially damaged seeds obtained from feral pig faeces.

Table 1. Germination tests on seeds of mataī (*Prumnopitys taxifolia*) that have passed through captive and feral pigs. Seeds were sown in a glasshouse (University of Canterbury, Christchurch, New Zealand) and germination recorded over two spring–summer cycles.

	Captive pig trial	Feral pig study		Hand-cleaned (Kelly et al. 2010)
	Intact seeds	Intact seeds	Partially damaged	
No. planted	14	472	20	200
No. germinated				
Spring–summer 1	5	115	3	114
Spring–summer 2	3	208	5	13
Total germinated (*n*)	8	323	8	127
Total germinated (%)	**57.1**	**68.4**	**40.0**	**63.5**

Discussion

This study shows that feral pigs consume mataī fruits in the wild and deposit a proportion of intact, viable seeds following gut passage. Though pigs are known to disperse introduced weeds (Beavon 2007), this appears to be the first New Zealand report of viable native seeds being dispersed by pigs.

Generally, pigs have been thought to be largely nomadic (Wodzicki 1950); however, studies both in New Zealand and elsewhere have shown distinct home ranges and small daily travel distances (Martin 1975; McIlroy 1989; Saunders & Kay 1991; Caley 1997). New Zealand studies showed home ranges up to 2 km^2 and immature pigs moving up to 3 km in a 24-hour period (Martin 1975; McIlroy 1989). Mammalian home ranges can be much larger than those of birds (Jordano et al. 2007).

This slow gut passage of seeds (2–4 days) has large implications for potential dispersal. With pigs possibly covering several kilometres in a 24-hour period (McIlroy 1989), seeds could be moved kilometres away from the parent tree. Also significant is that seeds were defecated over the space of 3 days. Rather than all seeds consumed at the same time being defecated in one spot, they could be spread over a larger area, reducing spatial clumping of seeds. Long gut passage times in pigs may negatively affect seed germination, as has been found in other studies (Fedriani & Delibes 2009), but no such lowered germination was found in mataī when compared with hand-cleaned seeds. This may be due to the thick endocarp of mataī (Thorsen et al. 2009).

It is possible that other introduced mammals may provide some dispersal services to native plants, as demonstrated for ship rats (*Rattus rattus*) in Hawai′i (Shiels & Drake 2011) and Japan (Abe 2007), rabbits (*Oryctolagus cuniculus*) in Australia (Calvino-Cancela 2011), and carnivores (badgers, foxes and stone martens) in Spain (Jordano et al. 2007). In New Zealand, ship rats passed only very small seeds intact (Williams et al. 2000), while brushtail possums (*Trichosurus vulpecula*) have been found to include small fruits in their diet, and excrete intact and viable seeds (Dungan et al. 2002). Mataī seeds have been retrieved from possum faeces and germination percentages of 40–50% recorded (J. Ladley, University of Canterbury, pers. comm.). However, the importance of possums as dispersers of larger native fruit is still controversial (Williams 2003). There is little information about possible seed dispersal by larger introduced mammals such as deer or feral cattle (Kelly et al. 2010).

While pigs may make a relatively small numerical contribution to dispersal of native seeds, in New Zealand's modified environment this may assist in maintaining dispersal. The loss of native avifauna has been well documented (Bell 1991), and the implications for mutualisms discussed and studied (Clout & Hay 1989; Kelly et al. 2004, 2010). In several cases it appears that, despite reduced densities of native birds and little contribution by introduced birds to fruit dispersal (Kelly et al. 2006), adequate dispersal service is still being provided to native plants (Kelly et al. 2010; Wotton & Kelly 2011). However, pigs could provide an important addition to the current suite of dispersers, given their likely long-distance dispersal. This is similar to the study of Jordano et al. (2007), which showed that c. 85% of dispersed *Prunus mahaleb* seeds in Spain were moved by frugivorous birds, but that terrestrial mammals (badgers, foxes and stone martens) contributed 67% of long-distance dispersal events.

This study has shown that feral pigs are consuming and passing intact viable seeds of one New Zealand species. Coupled with daily movement across several square kilometres, feral pigs are probably important in the long-distance dispersal of seeds, both of native plants and of introduced weeds.

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