

Dispersal of banana passionfruit (*Passiflora tripartita* var. *mollissima*) by exotic mammals in New Zealand facilitates plant invasiveness

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Abstract: Banana passionfruit (*Passiflora tripartita* var. *mollissima*) is a noxious vine that is invasive in forest patches in coastal regions throughout New Zealand. We investigated the dispersal mechanisms that facilitate its spread in the Marlborough Sounds. To find out which animals act as dispersers, we monitored tagged fruits in the field. Fruits were removed quickly after ripening. Significantly fewer fruits were wholly removed from off-road locations than locations on road edges, but removal was high in both cases (70% and 93% respectively) indicating likely dispersal by both humans and wild animals. We found no evidence of dispersal by birds, but infrared cameras documented possums and rats consuming fruits in the field. To investigate the effect of fruit handling on germination, we compared germination success between hand-cleaned seeds, fleshy seeds and intact fruits in the field and glasshouse. Seeds germinated readily in all treatments, with no significant difference between treatments, so seeds do not require frugivore handling to germinate. In addition, we measured the germination of seeds extracted from 1.5 kg of feral pig faeces collected from *Sus scrofa* at Te Weuweu Bay and from faeces from captive possums (*Trichosurus vulpecula*) and Norway rats (*Rattus norvegicus*). Seeds extracted from pig and possum droppings readily germinated, with final germination success not significantly different from hand-cleaned or in-flesh seeds. None of the few intact seeds excreted by Norway rats germinated. Banana passionfruit has formed invasive mutualisms for both pollination (with introduced bees) and dispersal (with introduced mammals), exacerbating its spread. Weed management should combine direct weed control with limiting the spread of banana passionfruit, by managing feral pigs and possums.

Keywords: brushtail possum; feral pig; invasional meltdown; *Sus scrofa*; *Trichosurus vulpecula*; weed

Introduction

Some of the most damaging invasive plants are dispersed by frugivores (Richardson et al. 2000). Consequently, practical information describing the ways in which dispersal mutualisms affect the spread of weeds, particularly over long distances, is important for effective management and control and to prevent colonisation of new areas (Buckley et al. 2006; Sullivan et al. 2009). The adverse effects of exotic mammals in New Zealand are very diverse. Mammalian herbivory negatively affects many native plants (Sessions et al. 2001; Sweetapple et al. 2004; Forsyth et al. 2010), and exotic generalist herbivores typically disadvantage native plants and benefit exotic ones (Parker et al. 2006). Herbivores can reduce plant reproduction indirectly through leaf removal, and directly by consumption of flowers and fruits (Cowan 1991, 1992). Introduced mammals prey on native birds, reducing their abundance (Innes et al. 2010), and reducing pollination and/or dispersal services to native vegetation (Kelly et al. 2010; Anderson et al. 2011; Wotton & Kelly 2011). These interacting effects have been called ‘invasional meltdown’ (Simberloff 2006) whereby exotic herbivores, carnivores, and weeds facilitate each other’s spread.

However, the extent to which introduced animals enhance the invasiveness of exotic weeds specifically through dispersal mutualisms is not often addressed (Williams & Karl 1996), despite the fact that invasiveness of exotic species in new habitats is strongly dependent on patterns and mechanisms of seed dispersal (Constible et al. 2005). Some invasive species are unable to reproduce, and consequently would not have established, in the absence of frugivores (Panetta & McKee

1997). The invasive South American vine banana passionfruit (*Passiflora tripartita* var. *mollissima*, Passifloraceae) continues to spread throughout New Zealand (Beavon & Kelly 2012). However, little is known about its dispersal ecology in New Zealand, including the effect of ingestion and gut passage on germination (Williams & Buxton 1995). As a result, this study examined the frugivorous dispersal mutualisms of banana passionfruit in the Marlborough Sounds.

Frugivores vary in the extent to which they contribute to plant fitness through both dispersal quantity and dispersal quality (Schupp 1993). Effective seed dispersal depends on the number of visits made to the plant by a disperser, and the number of seeds dispersed per visit. There are many variables that might affect the quantity of fruits being dispersed including frugivore density, gape size, dietary constraints and preferences, as well as the size and availability of fruits (Buckley et al. 2006). The quality of seed dispersal also affects plant fitness, and depends on factors such as the treatment the seed receives in the mouth and gut of the frugivore, the distance the seed is dispersed from the parent plant, the level of competition with other seedlings, and the probability that it will be deposited in a site suitable for germination (Schupp 1993).

Robertson et al. (2006) discussed three ways that frugivores can directly affect success in seed germination and thus dispersal quality. Firstly, the pulp of some fruit contains chemical compounds that suppress germination so removal of pulp from the outside of the seeds may result in increased germination success; the *deinhibition effect*. Pulp removal may also reduce the likelihood of microbial or fungal damage to seeds (Traveset 1998). Secondly, gut passage of the seed may

increase the permeability of the seed coat allowing water and gas through and consequently resulting in increased germination; the *scarification effect* (Robertson et al. 2006). Gut passage of fruits may have a positive, negative, or no effect on seed germination (Traveset 1998) depending on the frugivore's morphological and physiological traits, such as the length of the digestive tract, the presence of teeth or a gizzard, the digestive fluids in the gut, and the probability that the animal will deposit seeds in an environment suitable for germination (Nogales et al. 2005). Whether a seed is positively, negatively, or not affected by ingestion depends on both of the species involved. No pattern appears to exist, regardless of the genetic relatedness of plant species (Nogales et al. 2005). Thirdly, there may be a *fertilisation effect* from faecal material that enhances germination success when seeds are deposited in nutrient- and microbe-rich faeces, though this effect is thought to be weaker (Robertson et al. 2006). The relative contributions of these effects, particularly deinhibition and scarification, need to be addressed in order to evaluate the frugivorous mutualisms that are important for the survival of a particular species.

Banana passionfruit is presumed to be dispersed by monkeys in its home range, although the indigenous disperser does not appear to have been documented (LaRosa 1992). The relative contributions of various birds and mammals to the dispersal of banana passionfruit in New Zealand are unknown (Williams & Buxton 1995). Little is known about the effects of ingestion and gut passage on seed survival. Williams and Buxton (1995) reported that fruits were eaten particularly by possums (*Trichosurus vulpecula*) but also by Norway rats (*Rattus norvegicus*), ship rats (*R. rattus*), and kiore (*R. exulans*). It is not known whether seeds survive and germinate following ingestion by mammals. Pūkeko (*Porphyrio porphyrio*), blackbirds (*Turdus merula*), and silvereyes (*Zosterops lateralis*) have also been observed eating fruit and excreting the seeds. None of the seeds ingested by silvereyes germinated (Williams & Karl 1996; Williams 2006). In contrast, Williams and Karl's (1996) study found that bellbirds (*Anthornis melanura*) and tūī (*Prosthemadera novaeseelandiae*) ignored the adventive fruits available (including *P. tripartita*), despite their availability in winter when few indigenous fruits are available.

The aims of this study were to investigate the relative contributions of frugivorous birds and mammals in the dispersal of banana passionfruit seeds, and test the hypothesis that seeds are primarily dispersed by introduced birds and mammals. The specific objectives were:

- To determine if seeds require removal from the fruit in order to germinate.
- To investigate the proportion of fruit being removed by frugivores in the field and the speed at which the fruits are being removed.
- To determine which frugivores are the primary consumers of fruits and to establish whether these frugivores excrete viable seeds.

Materials and methods

We used two sites in Queen Charlotte Sound (Marlborough) to monitor and collect fruits (see Beavon & Kelly 2012), located on the uphill side of Port Underwood Road (at 41°15.57' S, 173°58.97' E) and along Queen Charlotte Drive in Kaireperepe Bay (41°16.01' S, 173°58.97' E). Large pre-existing banana passionfruit plants were mostly located at the edges of

broadleaved forests on mid-successional native scrub and broadleaved species regenerating on slips, except for a couple of plants growing where the vegetation was predominantly gorse.

Effects of seed pulp removal on seed germination

To determine the effect of removing banana passionfruit seeds from fruits we compared germination success using three main treatments: (1) seeds within flesh, i.e. seeds separated from other seeds but remaining in their small fleshy, orange capsule; (2) cleaned seeds, i.e. with all of the flesh removed; and (3) intact fruits. Fruits came from nine plants spread across the two sites. We germinated seeds in both the glasshouse and field (following Robertson et al. 2006) during two major fruiting periods: 15–27 February 2006 and 20 September to 1 November 2006. Each treatment had 10–14 replicate fruits from all nine plants. For fleshy and cleaned seed treatments, we divided fruits in half and allocated half of the seeds to the glasshouse and half to the field. We randomly selected 25 seeds for each treatment per half fruit.

In the glasshouse, we half-filled seed-raising trays with potting mix (containing 80% pH-adjusted horticultural bark and 20% Bioblend of blood and bone), divided it into four sections, and evenly scattered seeds from a randomly selected treatment in each quarter. We then covered the seeds with a thin layer of potting mix and enough fine shingle to prevent seed desiccation and reduce the growth of mosses and liverworts. We placed individual whole fruits on top of soil in a pot. We stored trays and pots in a heated glasshouse in which daytime temperatures across the year ranged from approximately 12°C to 32°C. The seeds were watered every 1–2 days throughout summer and every 4–5 days during winter, but received no additional fertiliser.

In the field near the fruit collection site, we cleared the ground of any vegetation and cultivated the soil so it was loose. Individual whole fruits were placed on top of the soil. For the fleshy and cleaned treatment we put segments of 65-mm-diameter plastic pipe approximately 70 mm long in the ground in groups of 20 (5 × 4) to contain the seeds (see fig. 1 in Robertson et al. 2006). Each tube had five seeds scattered evenly inside it from either the fleshy or clean treatment. We covered seeds with a thin sprinkling of soil and leaf litter to prevent desiccation. To avoid disturbance or predation we covered tubes and individual fruits with pegged-down wire mesh (6-mm aperture). We recorded the number of seeds that germinated each month for at least 6 months, removing new seedlings at each visit to ensure accurate counts.

Ingestion effects on seed viability

To measure the effect of pig ingestion on viability, we collected droppings of feral pigs (*Sus scrofa*) from an area of active pig foraging at Te Weuweu Bay in Tory Channel (41°15.13' S, 174°13.57' E) on 3 February 2006. We collected three patches of feral pig droppings (with banana passionfruit seeds visible in them) on the edges of pig-rooted areas, approximately 40–50 m apart. In the lab we weighed the air-dry droppings, then washed them through a 6-mm sieve (to remove large debris) placed above a 3-mm sieve (to catch the seeds and seed fragments). We removed and counted the cleaned seeds and planted a subsample in the glasshouse (9 February 2006) and another in the field (16–18 February 2006), as described above, to test for germination. We planted 800 seeds (in four trays of 200 seeds) in the glasshouse and 600 seeds (three groups of tubes with 10 seeds per tube) in the field and recorded germination success for 14 months.

For possums, we fed six fruits (from different plants) to six captive possums using animals from Pest Control Research in Christchurch on 24 November 2006 and collected the faeces 2 days later, finding 108 seeds in the faeces. We planted 100 randomly selected seeds from this collection in the glasshouse on 30 November 2006, and measured germination each month for 5 months.

To measure the effect of rats, we set up six live traps in Kaireperepe Bay for six nights, baited with banana passionfruit, in an attempt to collect ingested banana passionfruit seeds from feral rats. However, rats proved to be very wary of the traps. Two ship rats were caught and held in the traps for 2 days, but determining which seeds had been dropped rather than ingested was difficult. Consequently, six captive Norway rats (also from Pest Control Research in Christchurch) were offered fruit, each from a different plant, on 24 November 2006. Not all fruits were eaten although some were overripe and soft. The few intact seeds found in the faeces were planted in the glasshouse on 30 November 2006. Germination data were collected monthly for 5 months.

Germination analysis

Final germination success among treatments was analysed using two binomial generalised linear models (GLM) in R (v.2.10.1; R Development Core Team 2005). The response variable was the proportion of seeds that germinated, with tubes or pots as replicates. The first analysis used only the two treatments (cleaned and fleshy) for which source plant and starting number of seeds were known, and used predictors of source plant, location (glasshouse vs field), treatment (cleaned vs fleshy), and location \times treatment. Because the data were overdispersed, a quasibinomial error distribution and *F*-test were used.

The second analysis compared germination among all treatments: cleaned, fleshy, seed in whole fruits, and seeds excreted by pigs and possums. As the starting number of seeds was not known for whole fruits, we assumed that each fruit had started with the mean number of seeds per fruit (94) reported by Beavon and Kelly (2012). Here the predictors were treatment, location (glasshouse vs field), and location \times treatment, again with a quasibinomial GLM.

Fruit removal rates in the field

We selected, tagged, and monitored groups of 10 unripe fruits of similar size and maturity on 10 plants across our two sites from December 2005 to February 2006. We chose five plants on the roadside where fruits were easily accessible to humans (on road) and five on steep banks and slips in areas that would be little affected by anthropogenic disturbance or dispersal (off road). We tagged each fruit using three methods, to ensure it could be identified if it was found on the ground below the vine. Firstly, with a labelled paper tag with cotton tie attached on the fruit stalk; secondly, by tying a small length of blue wire at the fruit end of the stalk; and thirdly, by writing an identification number on the fruit itself using a felt pen. We revisited fruits every 3–4 weeks recording ripeness and whether each fruit was still on the vine, on the ground, wholly removed and/or partially eaten, until all the fruits had been removed or fallen off the vine. Five fruits from one plant were destroyed by a roadside mower so were excluded from analysis.

For analysis of fruit removal rates, we classified each fruit as either ‘taken’ or ‘not taken’. To determine whether there was a significant difference in the proportion of fruits taken

from on-road and off-road plants we ran a binomial GLM with a chi-squared significance test using location (on vs off road) and source plant as predictors. Two fruits were found partially eaten on the ground, so although some seeds were probably removed by the animal and possibly dispersed, they are entered as ‘not taken’ in this GLM.

Dispersal vectors

We took photos of partially eaten fruit (some still on the vine) while out in the field to record teeth marks and patterns of removal of fruit tissue. We placed an infrared time-lapse video camera out in the field from dusk (1800 hours) to dawn (0700 hours) for three nights (15, 17 and 19 June 2006) filming fruits, to determine which animals were eating the fruits. On the first night we left out two nearly ripe fruits, uncovered but pegged to the ground with wire pegs so they could not be dragged out of view of the camera. On the second and third nights, we placed three fruits underneath chicken wire (30 \times 40 mm mesh), which had previously failed to keep predators (rats) out. We took photos of the fruits before and after each night.

Results

Effects of seed pulp removal on seed germination

Germination occurred rapidly, with most occurring in the first few months. When comparing cleaned vs fleshy seeds and allowing for source (parent) plant, there was a large effect of germination location on seed germination (Table 1), but no significant effect of seed pulp removal (Table 2). Overall, germination was eight-fold higher in the glasshouse (64.5%) than the field (7.7%), which is to be expected because glasshouse seeds are well watered and protected from other hazards. Source plant was also significant, but neither treatment (clean vs fleshy) nor the location \times treatment interaction was significant.

Table 1. Germination success of banana passionfruit (*Passiflora tripartita* var. *mollissima*) seeds in cleaned and fleshy-seed treatments. Final percent germination (mean \pm SEM) is given for seeds planted in the glasshouse and field.

	Cleaned (%)	Fleshy (%)
Glasshouse	65.93 \pm 3.56	63.07 \pm 5.66
Field	9.00 \pm 5.49	6.40 \pm 5.57

Table 2. Factors affecting final banana passionfruit (*Passiflora tripartita* var. *mollissima*) germination success for cleaned and fleshy seeds, using predictors of source plant, location (field vs glasshouse), and treatment (cleaned vs fleshy) in quasibinomial generalised linear models.

	d.f.	Deviance	F	P(>F)
Source plant	8	130.85	5.38	<0.001
Location	1	421.41	138.55	<0.001
Treatment	1	1.84	0.60	0.44
Location \times treatment	1	0.75	0.25	0.62
Residual	36	105.60		

Ingestion effects on seed viability

For feral pigs, we collected a total of 1509.9 g (three piles of 433.8 g, 423.6 g and 652.5 g) of air-dry droppings from which 2818 intact seeds (1250, 620 and 948 respectively) and 137 pieces of seed (63, 32 and 42) were extracted. Each fruit has 94 seeds on average, which means that the seeds found in 1.5 kg of pig droppings are the equivalent to approximately 30 fruits. This shows that feral pigs are targeting banana passionfruit as a food source. Seeds were viable following ingestion by pigs and many of the seeds collected from the pig droppings germinated (Fig. 1) and showed vigorous seedling growth.

The captive possums readily ate the banana passionfruit when offered them. There was audible crunching of seeds as they ate the fruits. One seed was found in the faeces of one of the animals, 49 from another and 58 from a third. The other three possums had no intact seeds in their droppings, but this may be because they had slower gut-passage times (see Discussion). After 5 months, 53 of the 100 possum-voided seeds had germinated in the glasshouse, a germination level that was similar to the other treatments (Fig. 1, Table 3).

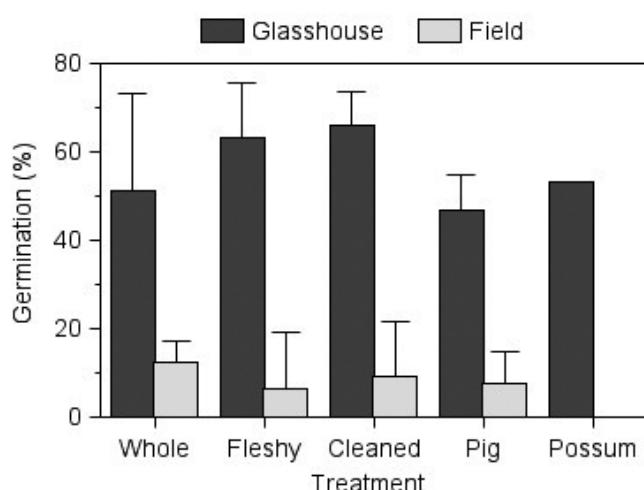


Figure 1. Effect of pulp removal and ingestion treatments on germination success (mean \pm 95% confidence interval) in seeds of banana passionfruit (*Passiflora tripartita* var. *mollissima*) from Queen Charlotte Sound, planted in the glasshouse (dark bars) and field (pale bars). Possum-ingested seeds were only germinated in the glasshouse with $n = 1$ so the confidence limits could not be calculated. There was a significant effect of glasshouse vs field, but no effect of treatment (see text).

Table 3. Effect on banana passionfruit (*Passiflora tripartita* var. *mollissima*) germination success of location (glasshouse vs field), all treatments (cleaned, fleshy, whole fruit, pig-ingested, and possum-ingested) and location \times treatment determined by quasibinomial generalised linear models. For whole fruit, ‘initial seeds per fruit’ was set to the mean of 94 seeds given by Beavon and Kelly (2012).

Factor	d.f.	Deviance	F	P
Location	1	1105.59	83.38	<0.001
Treatment	4	48.92	0.92	0.46
Location \times treatment	3	21.25	0.53	0.66
Residual	72	1019.29		

In contrast, the captive Norway rats did not excrete any viable seeds. Nearly all the seeds they consumed were ground up, again accompanied by audible crunching sounds. We found only four intact seeds in the rat faeces (all from one rat). Those seeds were planted in the glasshouse, but none of them germinated. With so few seeds found, the rat treatment was excluded from analysis of germination rates.

Germination analysis

The combined analysis compared germination under all conditions, including whole-fruit treatments and mammal-excreted seeds. Both seeds in whole fruits and mammal-excreted seeds germinated well (Fig. 1). Although we had expected whole fruits to inhibit germination, the whole fruits tended to break down and seeds started germinating very quickly, which was surprising given the size of the fruits. In one fruit, the first seedling had germinated only a month after the fresh fruit was put in the glasshouse. In another fruit, 85 seedlings germinated in under 3 months. A number of seeds from the whole fruits in the field (and some in the glasshouse) had not germinated by the final data collection date, but may have been dormant rather than dead, so our counts are minimum estimates.

In the combined analysis (Table 3), there was no significant difference among the treatments, but as before there was a large effect of location, with higher germination in the glasshouse than the field (Fig. 1). Hence we found no evidence that gut passage or hand-cleaning of seeds affected germination percentages.

Fruit removal rates in the field

Fruits in the field took 2–3 months to ripen but were removed quickly, often before fully ripe. On average, it took 3.7 ± 0.15 months (mean \pm SE) for all 10 fruits to be removed from the vine. A significantly higher percentage of fruits (Table 4) were wholly removed from roadside plants (92%) compared with off-road plants (70%; Fig. 2) but in both cases most fruits were removed, showing that animals are targeting fruits. For the off-road plants we found 6% of fruits either partially eaten on the ground, or partially eaten on the vine but later removed. The remainder of fruits, 8% by the road and 24% off-road, were found on the ground below the parent vine. There was no significant effect of plant. Although fruit removal rates were significantly higher by the road, most fruits are being removed in both areas.

Table 4. Effect of fruit location on the proportion of tagged fruit removed from banana passionfruit (*Passiflora tripartita* var. *mollissima*) vines in Queen Charlotte Sound, from a binomial generalised linear model analysis.

Factor	d.f.	Deviance	$P(\chi^2)$
On/off road	1	7.92	0.005
Plant	8	8.52	0.384
Residual	85	72.82	

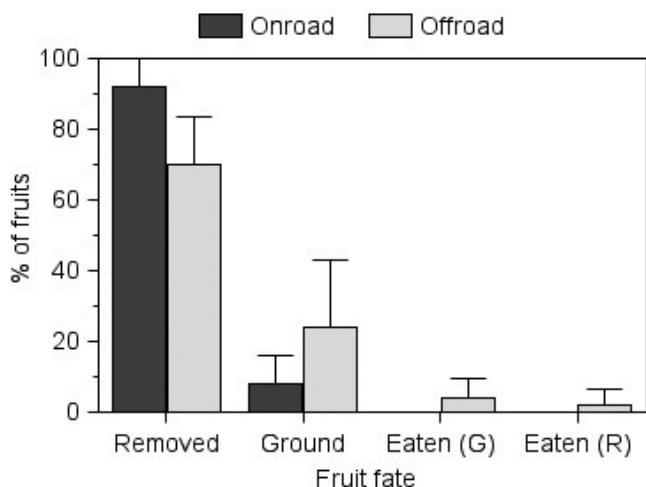


Figure 2. Fates (mean \pm 95% CI) of fruits of banana passionfruit (*Passiflora tripartita* var. *mollissima*) tagged by the roadside (dark bars) and off the road (pale bars) at two sites in Queen Charlotte Sound: Removed = tagged fruit disappeared from the area; Ground = found on the ground; Eaten (G) = found on the ground partially eaten; Eaten (R) = partially eaten but later removed. Fates were significantly different between roadside vs off-road (see text).

Dispersal vectors

No fruits were found with evidence of peck marks, despite our having observed hundreds of fruits and there being frugivorous birds throughout the area (including blackbirds, silvereyes, and bellbirds). This suggests that banana passionfruit is not a targeted food source for frugivorous birds, and birds are unlikely to be dispersing the seeds. Many fruits were found partially eaten, some with teeth marks, on both the ground and vines. Partially eaten fruits on the ground were typically found surrounded by piles of removed fruit skin.

All eight of the fruits that were laid out in front of the infrared camera were eaten overnight, seven of them completely so. Fruits were not common in June so some of them were not completely ripe and the one fruit that was half-eaten was particularly green. We found that ship rats were responsible for regularly shredding fruits into piles of fragments, by first removing the skin before eating the seeds and fleshy capsules. In the field, ship rats started visiting fruits at dusk and spent an average of 12% of the night (average total time 1 h 31 min per night), and as much as 17%, eating the three fruits. Up to four rats were visible at any one time. On average it took slightly under 20 min for rats to completely disassemble fruits. One of the fruits was half disassembled after only 4 min. Multiple rats would feed on a fruit but typically not at the same time, often taking away chunks to eat elsewhere.

The camera also captured possums eating fruits on six separate occasions, for a total of 9 min, across the two nights of 15–16 and 17–18 June 2006. When fruits were accessible (i.e. removed from under the chicken wire) possums continued to disassemble and eat fruits. Although we have evidence that in the field ship rats and possums eat fruits on the ground, we do not know whether fruits that are found partially eaten on the vine were eaten by rats or possums.

On two nights a mouse was seen either briefly eating the remains of the fruit or just running past after all the rats had left for the night, at 0645 and 0840 hours, respectively. Mice are unlikely to swallow (and therefore disperse) intact seeds.

Discussion

Our germination trials showed higher final germination percentages in the glasshouse than the field, as is usually found (e.g. Kelly et al. 2010), but no strong effect of fruit pulp removal. Intact fruits decomposed and seeds germinated surprisingly quickly for such a large fruit. This is consistent with data for a wide range of other plants showing that the deactivation effect (of pulp removal) is usually small under glasshouse and field conditions (Robertson et al. 2006; Traveset et al. 2007; Kelly et al. 2010). There was also no difference between animal-excreted and hand-cleaned seeds, showing no scarification effect (Robertson et al. 2006). That banana passionfruit seeds and fruits do not require handling by frugivores to successfully produce seedlings contributes to its weediness. Research on banana passionfruit in Hawai‘i has found that most seeds within a cohort germinate fairly rapidly once dormancy is broken, but some delay germination and persist in the seed bank for 8 months or longer (LaRosa 1992). Consequently, our counts of final germination success are minimum estimates.

The number of fruits removed by frugivores is an important component in determining the number of seeds that will be dispersed (Schupp 1993). By tagging fruit we found that most fruits were taken away from the plant, sometimes before they were fully ripe. The majority of fruits were taken within 2 months after ripening. This shows that dispersal is not failing from lack of frugivore attention in New Zealand, which leads to the question about what animals are removing fruits.

Of the four major groups of potential frugivores (birds, rodents, large mammals, and humans), from our study only the latter two appear to be important dispersers of banana passionfruit. Both native and exotic birds appeared to ignore the fruits. The skin of the fruit is soft, so although the fruits are large, even small birds could eat the fruit in sections, and there are reports of blackbirds and silvereyes feeding on them (Williams 2006). However, throughout this study no bird feeding on fruits was observed, and fruits were never seen with peck marks. This suggests that in the Marlborough Sounds birds are not important consumers of banana passionfruit.

Rodents also do not appear to be important dispersers. Rats actively consumed fruits, but we found no evidence that any seeds survived gut passage through a rat. Mice were rarely seen and were not confirmed to swallow seeds. This is consistent with earlier work that found that rodents are primarily seed predators: rats ground up all but the smallest seeds, and mice ground up everything (Price & Jenkins 1986; Williams et al. 2000). The only possible exception is that rats may contribute to short-distance dispersal given their propensity to hoard and cache seeds (Richardson et al. 2000). We know of no evidence for rat seed caching in New Zealand, although in our study rats were observed carrying away sections of banana passionfruit. But overall, the net effect of rodents may be to reduce spread by acting as seed predators.

In contrast, large mammals (possums and pigs) are important dispersers of banana passionfruit. Brushtail possums were observed consuming fruits in both the lab and field. This is consistent with previous work showing that possums favour fruit when it is available (Nugent et al. 2000; Dungan et al. 2002; Buckley et al. 2006) and can disperse smaller seeds (<10-mm diameter; Williams 2003). Since possum-excreted seeds germinated readily, possums are likely to be important dispersers of banana passionfruit.

Similarly, many viable seeds were found in feral pig

droppings. The foraging behaviour of pigs may enhance their effectiveness as dispersers because seeds are likely to be excreted in areas of rooting, where competition from native plants will be reduced (LaRosa 1992; Starr et al. 2003). This is important for banana passionfruit seedlings, which need at least 2% of full sunlight to establish (Baars & Kelly 1996). Thus, pigs may deposit seeds in areas that have favourable conditions for banana passionfruit establishment (Constible et al. 2005). In Hawai'i pigs appear to be greatly enhancing the dispersal of banana passionfruit seeds by depositing large numbers of viable seeds in fertile, disturbed sites ideal for germination (LaRosa 1992).

Mammals can provide good long-distance dispersal because they have large home ranges, long gut-passage times, and can ingest large numbers of seeds (Nogales et al. 2005). Pigs travel up to 3.6 km a day, with home ranges of 0.7 to 11.7 km² (McIlroy 2005). Possums usually range over 1–3 ha but sometimes up to 30 ha, often moving 100–200 m in a single night (Dungan et al. 2002). Both also have long gut retention times. Possums took 2–9 days to excrete ingested banana passionfruit seeds (Williams et al. 2000), and pigs took 3–4 days to excrete mataī seeds (*Prumnopitys taxifolia*; O'Connor & Kelly 2012). Therefore, both species could carry seeds long distances.

Humans are another potential disperser of banana passionfruit, as the plant is deliberately cultivated for its fruit (Webb et al. 1988) and people also harvest wild fruits. Dispersal might be achieved accidentally (when uneaten fruits are thrown away) or deliberately (to establish a new source of fruit). We have no direct evidence of human-mediated dispersal, although a significantly higher number of fruits were removed from roadside patches than off-road patches. This could be due to human harvesting of fruits, and/or animals preferentially moving along or foraging on forest edges (Kelly et al. 2004). Human-mediated dispersal of a different weed (*Tradescantia fluminensis*) in the Marlborough Sounds has been shown by an association with road traffic density and proximity to settlements (Butcher & Kelly 2011). However, although humans definitely assist the invasion of exotic plant species into indigenous ecosystems (Sullivan et al. 2005; Butcher & Kelly 2011), this study shows that invasive mutualisms between *Passiflora tripartita* var. *mollissima* and introduced frugivorous mammals also assist the spread of this weed. Importantly, pigs and possums can spread the weed to areas rarely visited by humans, making it hard to find and control new infestations.

Banana passionfruit has coped well despite the loss of its native mutualists, by forming mutualisms with exotic generalist pollinators and dispersers in New Zealand. Exotic honey bees and bumble bees were important for seed production (Beavon & Kelly 2012). Here we have shown that banana passionfruit also relies on invasive mammals (and humans) for seed dispersal. In the absence of introduced animals, banana passionfruit would have much lower seed output and little seed dispersal, so would have much slower spread in New Zealand.

In the Marlborough Sounds, as throughout New Zealand, invasive species have numerous interacting effects on ecosystems. Disturbances by introduced animals (and humans) create gaps that allow vines to overtop native canopy trees (Baars & Kelly 1996). Pollination and dispersal by introduced animals aids invasiveness in banana passionfruit through novel mutualisms. Therefore, exotic animals reduce the vigour and abundance of native plant species, and facilitate the spread of invasive plants. The abundance of exotic generalist pollinators

and dispersers makes New Zealand's ecosystems more easily invaded, indicative of an invasional meltdown (Simberloff 2006).

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