Contribution by possums to seed rain and subsequent seed germination in successional vegetation, Canterbury, New Zealand

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Abstract: The contribution of seeds and fruit to the diet of the introduced brushtail possum (*Trichosurus vulpecula*) was examined in seral vegetation in lowland Canterbury, New Zealand. Fruit and seeds comprised *c.* 70% of total possum diet, and possums contributed 17% of the dispersed seed rain for the period of our study. The effect of gut passage on germination was measured for five seed species by germinating seeds recovered from faeces of captive and wild possums. At least one-quarter of seeds of four of the species germinated. Two seed species showed a negative effect, and one a positive effect of gut passage relative to uningested seeds. Although possums may increase the spread of invasive weeds, their seed dispersal behaviour may offer conservation benefits by accelerating succession in seral vegetation. Because of the reduction in numbers of large-gaped native birds (e.g. kereru, *Hemiphaga novaeseelandiae*), possums may now be the only dispersal agents for large-seeded native species in many areas.

Keywords: gut passage; possum diet; seed dispersal; *Trichosurus vulpecula*; vegetation succession.

Introduction

Consumption of fruits and seeds of indigenous New Zealand plants by the introduced brushtail possum (*Trichosurus vulpecula*) has been widely reported (e.g. Mason, 1958; Fitzgerald, 1976; Cowan, 1990), but few studies have addressed this behaviour in terms of seed dispersal. In Australia possums have been implicated in seed dispersal of mast-seeding cycads (Ballardie and Whelan, 1986), and in the spread of an introduced tree (Bass, 1990). Williams *et al.* (2000) offered the first quantitative treatment of the possible effects of possum dispersal in New Zealand, by investigating the effect of gut passage on germination. However, we have been unable to find any published material that uses field-collected data to directly assess the seed dispersal behaviour of possums.

We have started to fill this gap by evaluating the potential role of possums as seed dispersers in a successional environment in lowland Canterbury. As a consequence of the lack of original native vegetation across large areas of lowland New Zealand, regenerating seral vegetation offers potentially important opportunities for biodiversity conservation. Seral vegetation is often found in areas where biodiversity conservation is generally not a high priority for land management. With time and only minimal management inputs, seral vegetation can rapidly regenerate to a stage where native tree species dominate the vegetation (e.g. Wilson, 1994). Possums are common in such environments and are generally only controlled to reduce the threat that they pose as vectors for bovine tuberculosis (Coleman and Caley, 2000). Given their widely reported consumption of fruit and seeds, possums are potentially important dispersers of seed in lowland seral vegetation. Although foliage often forms most of the diet of possums, Nugent *et al.* (2000) consider that fruit is more preferred than foliage, and is an important source of energy and nutrients. Possums may offer benefits to biodiversity conservation in that they may be the only potential dispersal vector of large-seeded native species (Clout and Hay, 1989). However, their seed dispersal behaviour may also pose a conservation risk by increasing the spread of invasive weed species (Williams and Timmins, 1990; Williams *et al.,* 2000).

The seed rain of our field site has been described (Dungan *et al.,* 2001) and, although not a specific focus of that study, it became clear that seed dispersed by possums comprised a significant proportion of the total dispersed seed rain. Quantifying this contribution and the potential effects of gut passage on seed germination will clarify the potential importance of seed dispersal by possums. Schupp (1993) provides a framework for describing disperser effectiveness, incorporating both quantitative (e.g. number of disperser visits, disperser abundance, number of seeds dispersed per visit) and qualitative (e.g. damage during ingestion, effect on germination, spatial pattern of seed deposition) components. Our aim was not to quantify the effectiveness of possums as seed dispersers. Instead, we first investigated possum diet to illustrate the extent to which possums are consuming fruit and seeds in successional vegatation. We then quantified the contribution of possums to total dispersed seed rain, and examined the effect of ingestion and gut passage on the fate of seeds recovered from faeces of captive and wild animals. These data were used to make some tentative conclusions about the potential importance of possums as seed dispersers in successional vegetation in New Zealand.

Methods

Study site

All field sampling was undertaken in Hoon Hay valley on the Port Hills of Canterbury, New Zealand (172° 37' E, 43°37' S; 50–500 m a.s.l., Port Hills Ecological District). Vegetation in the valley is a seral mosaic typical of marginally productive agricultural land in much of lowland New Zealand. With clearance for agriculture, the vegetation of Hoon Hay valley has changed from mixed lowland podocarp/angiosperm forest to a dynamic mosaic of highly modified vegetation at differing successional stages (Williams, 1983). The current vegetation ranges from open sites dominated by adventive grasses (e.g. *Dactylis glomerata* and *Lolium perenne*), through early successional vegetation dominated by *Pteridium esculentum* and introduced seral shrub species (especially *Cytisus scoparius* and *Sambucus nigra*), to relatively intact forest dominated by *Melicytus ramiflorus*, *Myoporum laetum* and *Sophora microphylla*. We limited our investigations to seral forest and scrub.

Possum diet

Ninety possums were caught in kill traps during 1996 (60 in summer, 30 in winter). Their stomach contents were washed through progressively finer sieves (2 mm and 1 mm mesh size) to aid sorting. All sieved material (seeds, fruit, foliage fragments etc.) was analysed and, where possible, identified to species level by comparison with field-collected material. Stomach contents generally retained the natural colour and consistency of fresh material, and were able to be identified under low magnification. Sorted material was dried to constant water content in a forced draught oven at 80°C for 48 hours and weighed, and the proportional contribution of fruit and seeds to the total dry mass of identifiable stomach material was calculated. Identifiable material was 47% of the dry mass of sieved stomach contents.

Seed rain

Seed rain was sampled between January and May 1996 using 80 circular seed traps (each 0.196 m^2). Traps were randomly situated (the first trap on each transect was positioned at a random distance from the transect origin, traps were spaced 30 m apart thereafter) on 13 transects positioned at random distances along an access track. The transects were perpendicular to the track, and extended to the seral scrub and forest boundary, between 100 and 300 m from the track. Each seed trap consisted of a wire ring, 50 cm in diameter, to which dense shade cloth ('Sarlon', Donaghy Industries, Christchurch, N.Z.) was attached around its circumference and tied at the base to form a large collecting cup. Traps were emptied fortnightly until the end of April, and once more 4 weeks later to give a total trapping period of *c.* 130 days, timed to coincide with the main period of seedfall for most of the species present (Burrows 1994a; 1994b).

Seeds (seeds less fleshy parental tissues; includes seeds within non-fleshy structures for wind-dispersed species), fruit, and possum faeces were separated from other material. There was only occasional evidence of direct possum interaction with the traps, so we presume that most faeces fell into the traps from the overhanging vegetation. Seeds were isolated from other faecal matter by either gentle crushing of dry faeces or crushing once faeces were softened after soaking in water. Seeds were identified to species by comparison with field-collected material. We assumed that all seeds of fleshy-fruited species that were recovered without parental tissue (other than those recovered from possum faeces) had been dispersed by birds. This approach underestimated the importance of dispersal by possums, as the fruits of several fleshy-fruited species (e.g. *Melicytus ramiflorus*) become very brittle once dry, and so seeds are readily removed from fruit in the traps and during transport of trap contents. Our method also underestimated dispersal by possums, as we did not attempt to recover faeces deposited on the ground or in dens.

Effect of gut passage on seed germination

To assess the effect of gut passage on seed germination, seeds were isolated from faeces of wild and fruit-fed captive possums. Fruit of five species that were widespread in the valley (*Melicytus ramiflorus*, *Muehlenbeckia australis*, *Myoporum laetum*, *Sambucus nigra*, *Solanum laciniatum*) were collected and stored at 4°C until captive possums were available. Feeding trials were conducted at the Landcare Research animal facility at Lincoln using caged animals. On three separate occasions individual animals were presented with 100 ripe fruits of each species. Fruits of *Melicytus ramiflorus* deteriorated during storage to the point where there was only enough suitable material for one presentation. Because of the large fruit size of *Solanum*, only 30 fruits were presented at any one time. Fruits were presented every morning and left for 24 hours. Faeces were collected daily, beginning 72 hours after fruit presentation, for 3 consecutive days and stored at 4°C until the commencement of germination trials. Faeces produced by field-trapped possums were collected, and stored in the same manner. To remove seeds, faeces were soaked in water for 24 hours and broken apart with gentle crushing. Damaged and undamaged seeds were then removed from other faecal material by sieving under running water.

Seeds from captive and wild animals were pooled to create a single 'ingested' treatment. Pooling of ingestion treatments takes no account of possible germination differences between wild and captive animals, but as our aim was simply to investigate the possible effect of gut passage on germination, the effect of pooling on our overall result was minor. Where more than 100 seeds of a species were recovered, two replicates of 50 undamaged seeds were randomly selected. Where fewer than 100 seeds were recovered, all seeds were used. Seeds were placed in controlled-climate growth cabinets (12 hour photoperiod: 20°C 65% humidity light phase; 15°C 60% humidity dark phase) on several sheets of standard filter paper that were kept moist (in petri dishes). Germinated seeds were removed and counted for 3 months (criterion for germination being splitting of testa for *Melicytus ramiflorus*, and first sign of radicle emergence for other species). As a control 50 seeds from ripe field-collected fruits of each species were submitted to the same germination protocol. To determine whether ingestion had a significant effect on germination we performed a chi-squared test for independence, with a null hypothesis that gut passage has no effect on germination success. We rejected this hypothesis if the χ^2 value calculated from a 2×2 contingency table was greater than the tabulated value ($\chi^2_{0.05,\,1} = 3.841$).

Results

Fruit and seeds in possum diet

Fruit (epidermis, fleshy pericarp of drupes, berries, arils etc.) and identifiable whole seeds contributed a substantial proportion of the total identifiable stomach material for the period of our study (87.3% and 0.5% by dry mass, respectively). Foliage contributed 10.9% with the remainder comprising stems (bark and wood; 0.8%), invertebrates (0.2%), birds (0.2%) and flowers (0.1%). Of the identifiable fruit material *Sambucus nigra* and *Melicytus ramiflorus* together contributed 65% of the total fruit consumed (34.7% and 29.9% respectively; Table 1).

Possum-dispersed seeds

Possum dispersal accounted for a substantial proportion of the total seed rain. The seed traps collected 70 021 seeds (whole seeds without fleshy parental material, but including dispersal structures for wind-dispersed species) from 46 predominantly woody species, of which possum-dispersal contributed 11 907 seeds (17%; Table 1). Possum dispersal accounted for up to 75% of the seed rain for each of the 14 possum-dispersed species. The species that were most commonly dispersed by possums were *Sambucus nigra* (75% of seed possum-dispersed), *Myoporum laetum* (41%), and *Melicytus ramiflorus* (17%). No seeds were recovered from four species that were present as fruit material in the stomachs of trapped animals (Table 1).

Effect of gut passage on germination success

Ingestion by possums can result in a significant proportion of mechanical seed damage (Table 2). Nearly 80% of *Sambucus* seeds removed from faeces of captive possums were visibly damaged, as were 75% of *Muehlenbeckia* seeds. There was no obvious damage to the large, woody, nut-like seeds of *Myoporum*.

The effect of gut passage on the germination of intact seeds varied widely between species (Table 3). Gut passage significantly impaired germination (relative to control seeds from ripe fruit) for *Melicytus* and *Muehlenbeckia*: 49% of *Melicytus* seeds removed from possum faeces germinated, compared to 86% of control seeds. No seeds of *Muehlenbeckia* removed from faeces germinated, whereas 40% of control seeds did. Germination of *Solanum* seeds was significantly enhanced, with 87% of recovered seeds germinating,

Table 1. Total number of seeds, by species, collected from 80 seed traps (each 0.196 m^2) under short-stature forest in lowland Canterbury, compared with the numbers of seeds in these traps that were were recovered from possum faeces. The proportion of the total seeds which were recovered from faeces (% in faeces), and the proportion of total fruit diet (% fruit consumed) for each species are listed. 'Other species' are those species which were recovered from seed traps, but which were not present in faeces.

Species	Total seeds	Seeds in faeces	% in faeces	% fruit consumed
Melicytus ramiflorus	39 218	6633	16.9	29.9
Sambucus nigra	5964	4477	75.1	34.7
Aristotelia serrata	2918	440	15.1	
Muehlenbeckia australis	1411	203	14.4	8.2
Myoporum laetum	299	123	41.1	11.8
Coprosma robusta	391	8	2.0	
Leycesteria formosa	1795	8	0.4	
Uncinia leptostachya	147	6	4.1	
Cytisus scoparius	3193	4	0.1	
Parsonsia spp.	2101	1	0.0	
Coprosma virescens	2273	1	0.0	
Pittosporum tenuifolium	253	1	0.4	0.1
Anthoxanthum odoratum	394	1	0.3	
Alectryon excelsus	146	1	0.7	
Solanum laciniatum				11.0
Rubus fruticosus				3.8
Fuchsia excorticata				0.4
Pennantia corymbosa				0.1
Total	60 503	11 907	19.7	
Other species	9518			
TOTAL	70 021	11 907	17.0	100%

Table 2. Total number of defecated seeds, and number and proportion of damaged seeds, collected from faeces of captive possums.

Species	Total	Damaged	%
Solanum laciniatum	5 638	1 481	(32.5)
Sambucus nigra	2 055	1 618	(78.7)
Myoporum laetum	218	0	(0.0)
Muehlenbeckia australis	65	49	(75.4)
Melicytus ramiflorus	44	12	(27.3)

Table 3. Germination success (number of seeds germinated) of seeds removed from fruits (i.e. non-ingested), and from possum faeces (ingested). Values in parentheses are the total number of seeds in each germination treatment.

Species	Seeds from fruits	Seeds from faeces	Effect	χ^2
Melicytus ramiflorus	43 (50)	39 (80)	–	16.8*
Muehlenbeckia australis	20 (50)	0 (23)	–	10.7*
Myoporum laetum	9 (50)	32 (100)	+	3.2
Sambucus nigra	26 (50)	42 (100)	+	1.0
Solanum laciniatum	22 (50)	87 (100)	+	28.9*

* denotes significant treatment effect at $\alpha = 0.05$ with 1 d.f.

compared with 44% of control seeds. No significant effect was observed for either *Myoporum* or *Sambucus*. Except for *Muehlenbeckia*, at least one-quarter of the seeds of each species germinated, indicating that although the effect of possum gut passage may be negative, it does not preclude passage of at least some viable seeds.

Discussion

It is clear that possums ingest significant quantities of fruit and seeds as part of their diet, and that once voided these seeds can be a large proportion of total seed rain (Table 1). Although possum ingestion can damage a significant proportion of seeds of most species (Table 2), in nearly all cases some seeds survive gut passage and are able to germinate (Table 3). Our results confirm that possums can and do disperse viable seeds.

Fruit and seeds in possum diet

Fruit and seeds comprised a significant part (69%) of possum diet for the period of our study. This high proportion is partly due to sieving bias, whereby larger fragments (e.g. fruit skins) are more likely to be retained by the sieves used (Sweetapple and Nugent, 1998). In spite of this bias, fruit and seeds comprised a high proportion compared with previous reports using similar techniques, which commonly list fruit and seeds as contributing much less than half of total possum diet (for review see Nugent *et al.,* 2000). For example, fruit consumption was less than 5% of annual diet in a lowland *Nothofagus* forest (Owen and Norton, 1995), and *c.* 25% in a subalpine shrubland (Parkes and Thomson, 1995). In a lowland podocarp/angiosperm forest, fruit use increased from 9% of total diet immediately prior to possum control, to 35% 2 years after control (Sweetapple and Nugent, 1998). This wide variability is explained by the tendency for possums to match their dietary intake to the availability of preferred food items (Nugent *et al.,* 2000). While foliage, particularly of soft broad-leaved seral species with relatively high foliar nutrient content, is generally the preferred food item, fruits offer a relatively energy- and nutrient-rich food source (Williams, 1982). Where fruit is available to possums it can become a favoured food item. The high proportion of *Melicytus* and *Sambucus* fruit in possum stomachs reflects both their relative abundance in the valley vegetation (Williams, 1983; Dungan *et al.,* 2001), and the fact that animal sampling coincided with the peak time of fruit availability for these species.

Contribution of possums to the overall seed rain

Possums dispersed 17% of the total numbers of seeds collected in the seed traps. This result suggests that possums are a significant seed dispersal vector. The only other published data that permit calculation of possum-dispersed seed rain are from Ahuriri Summit Reserve, approximately 3 km south of Hoon Hay valley (Burrows, 1994b). The contribution of possums to total seed rain can be estimated by recalculation of tabulated data (Table 2 and Appendix 2 of Burrows, 1994b). Possum dispersed seed accounted for at least 17 % of the total (all species) seed rain, although this ranged from <1% of seeds for *Pseudopanax arboreus* and *P. crassifolius* to *c.* 59% of *Fuchsia excorticata.*

Effect of gut passage on germination

The percentage of undamaged seeds that were recovered from captive animals varied among species. This may be a result of our seed storage and handling treatment, the physical properties of the seeds, or perhaps due to handling differences by the animals: seeds may be chewed during fruit consumption (e.g. *Sambucus*), or swallowed whole (e.g. *Myoporum*).

The effect of vertebrate gut passage on seed germination is highly variable and appears species specific. Some studies report positive effects of gut passage (Barnea *et al.,* 1990; Bustamante *et al.,* 1992), some report negative effects (Vila and D'Antonio, 1998), and others no detectable effects (Clout and Tilley, 1992; Izhaki *et al.,* 1995; Traveset and Willson, 1997). The effect of possum gut passage on seed germination has been investigated for a range of native and adventive woody plant species similar to those we investigated (Williams *et al.*, 2000). In that study captive possums were fed fleshy fruit of non-native weeds and native shrubs and trees. The proportion of intact seeds recovered ranged from 6% to 83%, and germination of seeds from possums ranged from 3% to 78%. Where a significant effect of gut passage was observed it was generally negative relative to non-ingested control seeds. Our results are broadly similar to those reported previously. The effect of possum ingestion on seed germination is variable among seed species. The physical characteristics of ingested seed, particularly their resistance to mechanical damage, and the way they are handled by possums, appears to have a significant effect. While some seeds of all species are viable and able to germinate, the effect of possum gut passage is generally negative compared with non-ingested seed.

It is difficult to compare the effect of possum gut passage with other possible dispersal vectors. It would be useful to know whether germination is more affected by possums than by avian frugivores such as kereru (*Hemiphaga novaeseelandiae*). In an Alaskan study Traveset and Willson (1997) compared the effects of gut passage through birds with passage through mammalian frugivores and found no significant disperser effect on germination.

Possible effects of possum dispersal

Given that possums can consume large quantities of fruit and seeds and that these can comprise a significant proportion of the dispersed germinable seed rain, we see at least three effects of seed dispersal by possums.

Firstly, the spatial effects of possum seed dispersal: possums can have large home ranges (typically 1 to 3 ha and occasionally up to 30 ha) and range widely (100–200 m) during the course of a single night (Cowan and Clout, 2000). As a consequence they have the potential to disperse seeds over quite large distances. They are also likely to have different defecation patterns from bird dispersers. Birds often deposit seeds close to perch sites, which can become nuclei accelerating vegetation succession (Yarranton and Morrison, 1974; McClannahan and Wolfe, 1993), whereas they are less likely to disperse seed to areas where perches are lacking.

Secondly, possums may enhance the spread of invasive weeds. This study, Bass (1990), and Williams *et al.* (2000) all show that possums can disperse large numbers of viable seeds of exotic weedy species. In areas with high biodiversity-conservation values, such as relatively intact forest remnants, this has the potential to be a significant negative effect. However, in areas where existing biodiversity-conservation values are lower, such as the seral vegetation in Hoon Hay valley, the ability of possums to disperse seeds may be enhancing vegetation succession. For example, possums in Hoon Hay valley disperse large numbers of *Sambucus* seeds. Although *Sambucus* is an aggressively invasive tree species, it can make a positive contribution to vegetation change (Voyce, 1998). Williams (1982) identified a predictable pattern of *Cytisus* → *Sambucus* → *Melicytus* → forest succession in Hoon Hay valley and it is possible that possums, through their preference for *Sambucus* and *Melicytus* fruits, are enhancing this succession by accelerating the spread of species from more- to less-advanced successional stages.

Thirdly, in many areas possums may be the only potential dispersal vector for large-seeded native species. In many parts of the country, large-gaped frugivorous birds are either absent or markedly less common than they have been historically (Clout and Hay, 1989). Consequently there is a suite of species with large diameter seeds that now lack a suitable dispersal vector. For example, *Myoporum laetum* seeds were present in possum faeces in significant numbers in Hoon Hay valley. Birds capable of dispersing large *Myoporum laetum* fruits (e.g. *Hemiphaga novaeseelandiae*) are less common in the valley now than they would have been prior to human settlement, so possums may represent a significant dispersal vector for this species.

These ideas are somewhat speculative, and are worthy of further investigation. While there is little doubt that there are many negative impacts of possums on indigenous ecosystems in New Zealand, especially forested ones (Payton 2000), it is clear that the interaction between possums and indigenous plant species is not always negative; possums can have positive benefits for ecosystem processes through their actions as seed dispersers. For some plant species, particularly those with large seeds, possums may be the only remaining vectors capable of effective seed dispersal. Our results do not provide an argument for disregarding possums as pests. Rather, we suggest that the interactions that occur between introduced fauna and indigenous flora are not always simple, and that in some circumstances possums can play ecologically beneficial roles for the conservation of indigenous biodiversity.

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