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## Post-dispersal seed predation on eleven large-seeded species from the New Zealand flora: a preliminary study in secondary forest

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**Abstract** Seed predation trials were conducted for 11 large-seeded species native to New Zealand in secondary forest. The species used were: *Alectryon excelsus*, *Beilschmiedia tawa*, *Coprosma grandifolia*, *Corynocarpus laevigatus*, *Hedycarya arborea*, *Myoporum laetum*, *Nestegis cunninghamii*, *Prumnopitys ferruginea*, *Prumnopitys taxifolia*, *Rhopalostylis sapida*, and *Ripogonum scandens*. Seed removal was monitored for 15 days for 160 seeds of each species, placed in piles of 5 seeds in each of 4 treatments at each of 8 sites in the Karori Wildlife Sanctuary, Wellington, in 1998. Removal of depulped seeds from treatments to which all species had access ranged from 3.8% to 23.8%, with a mean of 9.8%. No seeds were removed from the treatment that excluded all vertebrates. Presence of flesh on the seeds significantly increased seed removal rates in the three species tested with and without flesh. No relationship was found between seed removal and seed size, seed mass, or the proportion of the seed mass that was contributed by the seed coat. The seed removal rates reported here are exceptionally low, and suggest that the potential for post-dispersal seed predation to limit regeneration of native forest in New Zealand may have been over-estimated, at least in the forest type studied.

**Keywords** post-dispersal seed predation; New Zealand

### INTRODUCTION

For many years, people have believed that post-dispersal seed predation by introduced rodents may be limiting regeneration of native forest species in New Zealand (Campbell 1978; Fuller 1997). This idea has been indirectly supported by dietary analysis work on rodents, which has consistently shown that seeds of native New Zealand species are significant components of the diets of ship rats (*Rattus rattus*), Polynesian rats (*R. exulans*), Norway rats (*R. norvegicus*), and mice (*Mus musculus*) (Beveridge 1964; Best 1969; Atkinson 1972; Daniel 1973; Campbell 1978; Miller & Miller 1995). The effect of seed predation on forest regeneration in New Zealand ecosystems is largely unknown, but there is evidence that post-dispersal seed predation negatively affects regeneration overseas (Louda 1989), with seed removal rates of 100% being relatively common in the literature (Crawley 1992).

In this study we quantified the proportion of seeds from 11 New Zealand forest species that are removed by seed predators after arrival on the forest floor. It was not possible for us to estimate the proportion of seeds removed for all of the species within the forest community studied. We therefore decided to assess predation rates on a range of large-seeded species. Large-seeded species are likely to be more heavily affected by seed predation than small-seeded species for two main reasons. Firstly, large seeds are more likely to be removed by rodents than small seeds (Thompson 1987; Crawley 1992; Eriksson 1995; Hulme 1998). This is thought to be because large seeds are easier to find and slower to be incorporated into the soil profile (Thompson et al. 1994; Bekker et al. 1998), and provide greater nutritional rewards for predators than small seeds. Secondly, as there is a fundamental trade-off between producing many small or few large seeds (Eriksson & Jakobsson 1998; Jakobsson & Eriksson in press), loss of an

equal number of large and small seeds results in a proportionally greater reduction in seedling recruitment in the large-seeded species.

The following questions are addressed in this paper:

- 1) What proportion of seeds from a selection of large-seeded New Zealand forest species are removed over a 2-week period?
- 2) Does the presence of fruit pulp increase the chances that a seed will be removed?
- 3) Are larger seeds more likely to be removed than smaller seeds?
- 4) Is a high ratio of seed reserve mass (embryo and endosperm; "reward" for seed predators) to seed coat mass (defensive structures; hindrance for seed predators) related to high rates of seed removal?

## METHODS

Seeds from the following relatively large-seeded species native to New Zealand lowland forests were collected for use in this study: *Alectryon excelsus*\*, *Beilschmiedia tawa*, *Coprosma grandifolia*, *Corynocarpus laevigatus*, *Hedycarya arborea*, *Myoporum laetum*, *Nestegis cunninghamii*, *Prumnopitys ferruginea*, *Prumnopitys taxifolia*, *Rhopalostylis sapida*, and *Ripogonum scandens*. These species were selected as they were large-seeded species native to the Wellington area whose seeds were available for collection. The term seed is used broadly in this paper to represent the persistent part of the diaspore; thus, for *Myoporum laetum* the units studied were the woody parts of the four-seeded drupes. Seeds were collected from three sites as they became available: 1) the Karori Wildlife Sanctuary (the site of the predation trials); 2) Otari Native Botanic Gardens (a reserve approximately 4 km from the study site which contains relatively intact late-successional native forest remnants); and 3) Wellington Botanic Gardens (located approximately 3 km from the study site). In all trials, seeds were used within a few days of collection in order to study the removal rates of each species at the time of year at which the seeds were normally available to seed predators. Fruit pulp was removed from seeds unless otherwise stated. Flesh was removed using a

paper towel, and seeds were allowed to dry before they were placed in trials.

Eight 15 m × 15 m quadrats were located in a gully running NNW in the upper Karori Wildlife Sanctuary (KWS), Wellington (Moles & Drake 1999). The KWS is the site of a mainland island restoration project, and is located approximately 5 km south-west of Wellington city centre. The gully site was chosen as it was relatively flat (thus allowing checking of traps with minimal disturbance to the area), and it was well away from tracks and therefore was less likely to be disturbed by human visitors to the Sanctuary. The forest in the gully was low secondary forest, dominated by *Melicactus ramiflorus*, *Pseudopanax arboreus*, *Coprosma grandifolia*, and *Geniostoma rupestre* var. *ligustrifolium*. The forest is known to contain *Rattus rattus*, *Rattus norvegicus*, and *Mus musculus*, as well as a range of native seed predators (Fuller 1997). Rat densities beneath native forest in KWS are thought to be comparable to those in other untreated North Island native forests (C. Gillies pers. comm.).

The eight quadrats were located at least 30 m apart. Sixteen treatment areas were located in a grid pattern within each quadrat such that each treatment was 5 m away from the next closest treatments.

Treatments used were: **open ground**, a simple depression (10 cm × 10 cm × 1 cm deep) in the ground, rimmed so that seeds could not wash away, each marked by a small piece of orange flagging tape on a nail at least 50 cm from the depression; **open pot**, square black polythene flower pots (112 × 112 mm wide; 92 mm tall) with most of one side cut away (the aperture was 55 mm across and came down 80 mm from the top) nailed to the ground and filled with soil so that the level of the soil surface was equal inside and outside the pot; **pot with coarse mesh**, open pots covered in 12-mm steel mesh (25 mm × 25 mm opening) to allow access to rodents but small enough to exclude larger vertebrates (e.g., brushtail possums, *Trichosurus vulpecula*); **pot with predator-proof mesh**, open pots covered in the 6-mm predator-proof fencing mesh designed to exclude all mammals from the KWS.

For each species a pile of five seeds was placed in each of the four treatments in each of the eight quadrats. At no time were seeds of two species present in the same location. The 16 species\*treatment combinations were randomly distributed in each quadrat. The positioning of five seeds together in each treatment was chosen to approximate the likely distribution of the seeds of these bird-disseminated species in natural situations,

\*Nomenclature follows Allan (1961), Moore & Edgar (1970), and Connor & Edgar (1987) for plants, and King (1990) for animals.

and to give an adequate sample size. Seeds of *Hedycarya arborea*, *Prumnopitys ferruginea*, and *Ripogonum scandens* were set out both with and without fruit pulp.

Removal of seeds was recorded over four 15-day periods in 1998, commencing on: 23 January, 14 February, 3 March, and 10 May. Seeds were classified as removed when they had been carried out of the treatment area, or when they had been gnawed to such an extent that it was unlikely the seed would be able to germinate. It is important to note here that some of the seeds that were removed from the area may have been further dispersed, and were not necessarily destroyed (Innes 1990). Measures of seed removal presented here are therefore likely to overestimate seed predation.

Differences in predation rates between treatments were assessed using a one-way analysis of variance, and Dunnett's post-hoc multiple comparison test was used to determine which treatments were significantly different (Zar 1984). Linear regressions (Zar 1984) were used to test for relationships between the number of depulped seeds remaining in the open treatments after 15 days, and seed length,  $\log_{10}$  seed mass, and the proportion of seed mass contributed by seed coats.

## RESULTS

The seed removal rates observed during this study were very low (Table 1; Fig. 1), with an average of 9.8% of the depulped seeds of all species being removed from the open treatments by the end of 15

days. The presence of rodent tooth marks on seeds, and rat droppings in the treatment areas suggest the involvement of rodents in the seed removal.

There were significant differences ( $F_{3,423} = 20.73$ ;  $P < 0.001$ ) in predation rates between seeds set out in the different treatments (Fig. 2). There was no significant difference between the number of seeds removed from the open pot and the open ground treatments ( $P = 0.98$ ). No seeds of any species were removed from pots covered with the 6-mm rodent-proof mesh at any point during the trials.

Removal rates of *Ripogonum scandens*, *Hedycarya arborea*, and *Prumnopitys ferruginea* seeds set out with flesh intact were 3.3, 4.7, and 5 times higher, respectively, than for seeds of the same species which were stripped of flesh before placement in the field (Fig. 1; Table 1).

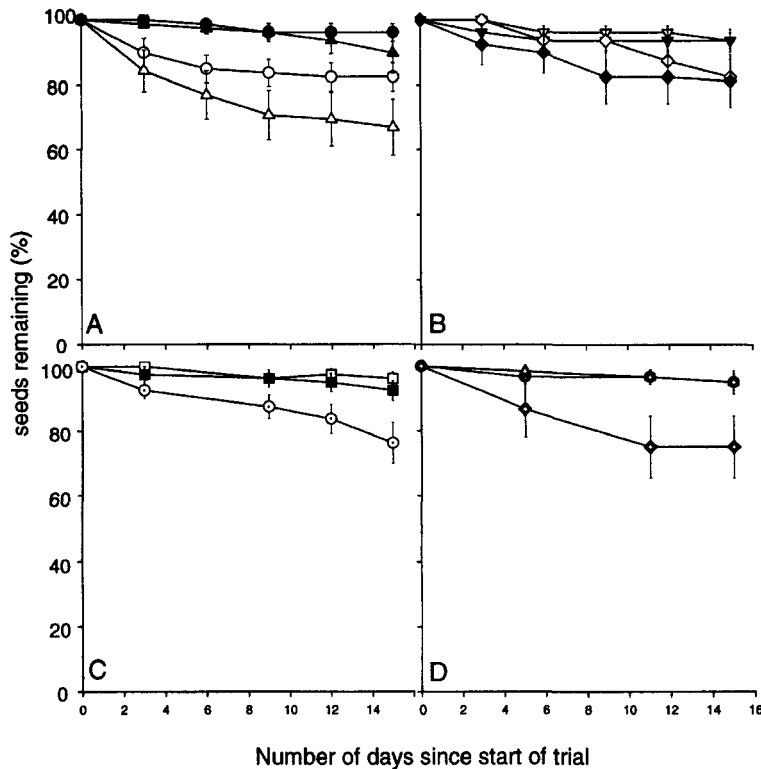
No significant relationships were found between the number of depulped seeds remaining in the open treatments after 15 days and seed length ( $P = 0.93$ ),  $\log_{10}$  seed mass ( $P = 0.99$ ), or the proportion of seed mass contributed by seed coats ( $P = 0.14$ ).

## DISCUSSION

The seed predation figures recorded in this study ( $\approx 10\%$ ) are far lower than those recorded in forests elsewhere in the world. For instance, Blate et al. (1998) found an average post-dispersal predation rate of 53% after 30 days in 40 species of Indonesian rainforest plants; Osunkoya (1994) found that an average of 41% of the seeds of 12 Australian rainforest species were removed within 28 days;

**Table 1** Means of seed size and weight parameters and mean predation rate for species used in the seed predation trials. \* from Wardle (1991).

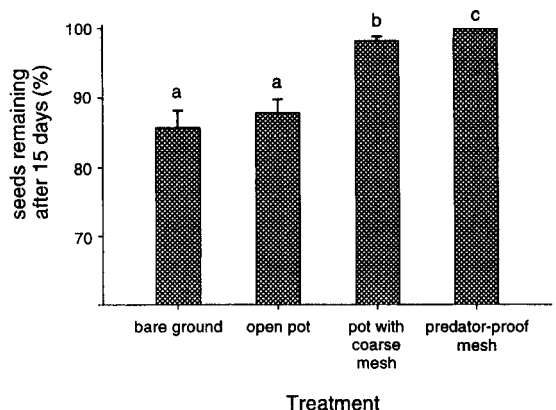
Species	dry mass of seed in flesh (g)	dry mass of seed w/o flesh (g)	ratio of hard outer layers to total dry mass (%)	greatest length without pulp (mm)	greatest width without pulp (mm)	% of depulped seeds removed after 15 days
<i>Alectryon excelsus</i>	–	0.17	45.5	7.3	7.4	6.25
<i>Beilschmiedia tawa</i>	–	1.28	17.4	24.0	9.8	6.25
<i>Coprosma grandifolia</i>	–	0.03	33.3	6.6	4.0	17.5
<i>Corynocarpus laevigatus</i>	4.60	1.98	18.3 *	20.6	13.3	18.75
<i>Hedycarya arborea</i>	0.56	0.36	23.3	11.0	8.4	3.75
<i>Myoporum laetum</i>	0.24	0.10	85.2	7.9	3.9	3.75
<i>Nestegis cunninghamii</i>	–	0.55	85.5	14.4	10.1	7.5
<i>Prumnopitys ferruginea</i>	1.39	0.52	86.1	10.6	6.4	5
<i>Prumnopitys taxifolia</i>	–	0.10	94.6 *	7.4	6.1	5
<i>Rhopalostylis sapida</i>	–	0.24*	28.0 *	8.3	5.3	23.75
<i>Ripogonum scandens</i>	0.49	0.25	3.0 *	7.6	6.3	10



**Fig. 1** Removal rates of seeds from the Karori Wildlife Sanctuary in each of the four 15-day trials, commencing on **A**, 23 January 1998; **B**, 14 February 1998; **C**, 3 March 1998; **D**, 10 May 1998. Percentage of seeds remaining  $\pm$  SEM, from the open ground and open pot treatments (data combined as there was no significant difference between means for these treatments) at all eight sites ( $n = 16$  locations  $\times$  5 seeds for each species). All seeds were without flesh unless specified. A: filled circles = *Hedycarya arborea*; open circles = *Hedycarya arborea* (with flesh); filled upwards triangles = *Ripogonum scandens*; open upwards triangles = *Ripogonum scandens* (with flesh). B: filled diamonds = *Corynocarpus laevigatus*; open diamonds = *Coprosma grandifolia*; filled downwards triangles = *Beilschmiedia tawa*; open downwards triangles = *Alectryon excelsus*. C: filled squares = *Nestegis cunninghamii*; open squares = *Myoporum laetum*; dotted open circles = *Rhopalostylis sapida*. D: Crossed filled upwards triangles = *Prumnopitys taxifolia*; crossed filled diamonds = *Prumnopitys ferruginea* (with flesh); crossed filled circles = *Prumnopitys ferruginea*.

Ostfield et al. (1997) found seed predation rates of 85% and 48% depending on rodent density in New York; and 43% of the seeds of *Virola surinamensis* had been lost after 2 weeks in tropical forest in Panama (Howe & Schupp 1985). Whilst seeds were exposed to predators for a shorter period of time in this study than in many of the studies summarised above, the post-dispersal seed predation rates in this study do seem exceptionally low. A study by Daniel (1973) also showed relatively low rates of predation on the seeds of native New Zealand species (359 of 1700 *Elaeocarpus dentatus* and 117 of 600 *Prumnopitys ferruginea* seeds removed over an unspecified time from the Orongorongo Valley, near Wellington, in 1971. It is unclear whether these seeds had been separated from the fruit pulp, and no information about seed density is given).

The low rate of seed predation observed in this study is surprising in an evolutionary context, as one would have expected native New Zealand plants to be highly vulnerable to predation by rodents due to the lack of exposure to mammalian seed predation throughout their evolution. Perhaps the pressure to maintain well-defended seeds to reduce seed



**Fig. 2** Total removal rates for seeds of all species from all traps in each of the four treatments. Bars represent the mean  $\pm$  1 SEM. Letters above the bars show the results of Dunnett T3 tests. Categories sharing the same letter are not significantly different ( $P > 0.05$ ).

predation by invertebrates has resulted in seeds that are resistant to post-dispersal seed predation by mammals despite the lack of a direct selective pressure. Defences evident in the species in this study include thick, hard seed coats or endocarps (e.g., *Nestegis cunninghamii*, *Prumnopitys taxifolia*, and *Myoporum laetum*, Table 1), and toxic compounds (e.g., *Beilschmiedia tawa*, *Corynocarpus laevigatus*, and *Hedycarya arborea* (Campbell 1978)). The low rate of seed predation could also be due to a diversification of rodent diet in New Zealand, where rodents eat a wide variety of plant and animal foods (King 1990). The time of year at which our study was conducted is unlikely to have biased our results, as seed predation on each species was assessed at the time of year at which it was usually available to seed predators. However, seed predation rates may be higher if seed predators cue on the faecal smell associated with seeds dispersed by natural dispersers.

In order to test whether post-dispersal seed predation is limiting regeneration in New Zealand forests, a manipulative experiment involving the addition of extra seed to the forest understorey and determining whether recruitment was enhanced could be performed. However, with such low rates of seed removal (an overestimate of actual seed predation) even in large-seeded species, it seems highly unlikely that post-dispersal seed predation by rodents is limiting forest regeneration. On the other hand, rodents may be acting as pre-dispersal seed predators, damaging seedlings or reducing seed production through consumption of leaves and flowers. Although no species experienced extremely high levels of post-dispersal seed predation, the rates of seed predation were variable across the 11 species. Differential predation rates can alter community composition if predation rates are high enough to limit regeneration in some species (Brown & Heske 1990; Heske et al. 1993; Weltzin et al. 1997).

The higher predation rate on seeds set out with fruit pulp suggests that some seeds are removed by frugivores that are not attracted to depulped seeds, or that seed predators use olfactory or visual cues from the seeds or fruit in foraging. The use of the fruit pulp by seed predators as a cue for locating seeds has also been observed overseas (Nystrand & Granstrom 1997). Seeds that are transported away from the parent plant by vertebrates such as birds are usually stripped of flesh during dispersal (Kollmann 1995). These seeds are at an advantage over seeds from the same parent plant that were not dispersed, as they are less likely to be located by seed predators after dispersal due to the absence of the fruit pulp.

The lack of a significant relationship between the number of seeds remaining after 15 days and seed length or  $\log_{10}$  seed mass is probably due to the design of the experiment, which did not give high leverage on the question of whether large seeds were preferentially removed, as a small number of species were used and all had relatively large seeds. However, it is surprising that no correlation was found between number of seeds remaining after 15 days and the proportion of seed mass contributed by seed coats. This is contrary to the results of Blate et al. (1998), who showed that predation rates for 40 species in South-east Asian rainforest were negatively associated with seed size and thickness and hardness of seed coats.

Significant differences were recorded between the number of seeds removed from the coarse mesh treatment and the open pots. It is probable that this difference was at least partially caused by the reluctance of seed predators to enter the enclosed space offered by the container in this treatment. Rodents have previously been shown to be wary of novel food containers (Inglis et al. 1996). However, it is possible that some larger animals (e.g., brushtail possums) were responsible for some of the predation recorded. No significant difference was found between removal rates of seeds that were placed in hollows on the ground and those that were placed in open pots (Fig. 2). This suggests that seed predators were neither avoiding the pots nor using them as visual aids to assist with the location of seeds.

No seeds of any species were removed from pots covered with the 6-mm rodent-proof mesh at any point during the trials. Whilst many of the seeds were too large to be removed from the pots enclosed with the 6-mm rodent-proof mesh, the absence of damage to any of the seeds in this treatment indicates that no small invertebrates are important post-dispersal seed predators of these species at this site, at least on the large-seeded species tested. This is in marked contrast to many ecosystems around the world where ants are major seed removal agents (e.g., Australia; Hughes & Westoby 1990).

Evidence that rodents are destroying the seeds of some native New Zealand forest species is abundant from studies of scats, stomach contents, and husking stations. However, this study was one of the first to assess the proportion of the seeds of native New Zealand species removed by post-dispersal seed predators. The low rate of removal observed in this study suggests that the effect of post-dispersal seed predation on forest regeneration is minimal at this time of year, in secondary growth lowland forests

in the lower North Island. Further research into the effects of rodents on plant species at other stages of the life cycle is needed, as are further studies on levels of seed predation in other New Zealand ecosystems.

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