Quantifying seed dispersal by birds and possums in a lowland New Zealand forest

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Published online: 22 September 2016

Abstract: Declines in native birds in New Zealand have raised questions about whether seed dispersal limits plant regeneration and whether introduced mammals such as brushtail possums (*Trichosurus vulpecula*) can replace absent native birds. We determined the relative contribution to seed dispersal by birds and possums in native secondary forest at Kowhai Bush, Kaikoura. The number of seeds dispersed per hectare per day by each animal species was determined based on the number of seeds per faecal pellet, the number of faecal pellets per animal per day, and the density of animals per hectare. Five dispersers had many seeds in their faecal samples: bellbirds (*Anthornis melanura*, mean 11.5 seeds per sample), silvereyes (*Zosterops lateralis*, 7.0), song thrushes (*Turdus philomelos*, 8.3), blackbirds (*Turdus merula*, 15.1) and possums (8.4). However, possums produced half as many faeces per day as birds and were present at lower densities than birds (1 possum, 3 bellbirds, 2.7 silvereyes, 6.4 song thrushes, and 3.2 blackbirds per ha). Consequently, on a per hectare basis, possums dispersed <3% of the total seeds, much less than bellbirds (22%), silvereyes (12%), song thrushes (33%) and blackbirds (30%). Possums also destroyed approximately 15% of seeds found in faeces, reduced the germination of gut-passed *Coprosma robusta* seed to half of that from bird faeces, and did not swallow fruit any larger (max 7 mm diameter) than those moved by birds. Consequently, possums provided little benefit from seed dispersal.

Key words: bellbird; bird abundance; blackbird; brushtail possum; frugivory; germination; seed dispersal; seed predation; silvereye; song thrush

Introduction

As a result of worldwide declines of frugivorous animals, there is an increasing need to understand the effects of disperser loss on plants (Bond 1994). Several studies have demonstrated negative impacts on seedling recruitment and plant regeneration through loss of their seed dispersers (e.g. Terborgh et al. 2008; Wotton & Kelly 2011). There is abundant evidence of widespread reduction of frugivores, primarily birds and mammals (Corlett 1998; Sodhi et al. 2004; Wright et al. 2007). Introduced species are also now widespread and can make up a substantial component of the fauna in some countries (Vitousek et al. 1997). Consequently, there is interest in whether introduced animals can function as effective seed dispersers and compensate for reductions in native dispersers (e.g. Staddon et al. 2010). The negative effect of species extinctions on seed dispersal processes could be lessened if other species are able to compensate for those that have been lost (Kawakami et al. 2009). New Zealand lacks native land mammals (apart from three bat species), but now hosts 32 species of introduced mammals, most of which are considered pests (King 2005). This change has raised questions about whether introduced mammals are useful seed dispersers in New Zealand (Kelly et al. 2010).

The Australian brushtail possum (*Trichosurus vulpecula*) was introduced to New Zealand in 1858 (King 2005). Possums eat a wide range of fleshy fruits (Coleman et al. 1985; Cowan 1990). Many of the seeds in fruits eaten by possums are destroyed, especially larger, thin-coated ones such as *Beilschmiedia tawa* (tawa), but seeds of some species (especially those with thickened seed coats) pass through the digestive system intact (Clout 2006). Dungan et al. (2002) argued that in sites with reduced numbers of large native birds such as kererū (*Hemiphaga novaeseelandiae*), possums may be the only remaining disperser for large-seeded native plant species. However, Williams (2003) argued against the value of possums as seed dispersers in native forest, on the basis that there is little evidence that possums disperse fruits greater than 10 mm diameter and seeds below this size are already dispersed by a suite of common bird species throughout New Zealand.

The relative effectiveness of possums compared to birds as seed dispersers is the focus of this study. Disperser effectiveness has both quantity and quality components (Schupp et al. 2010). A high quantity disperser removes a large number of seeds. Diet preferences of the dispersing animal and its local density affect the quantity of seeds removed. A high quality disperser causes little mortality in seeds it handles and deposits viable seeds in suitable habitat for establishment, especially away from the parent plant. In contrast, a low quality disperser destroys many seeds and deposits seeds in unsuitable habitat for establishment. A poor-quality disperser may have a negative effect on overall dispersal if fruits that it eats would otherwise have been consumed by a higher-quality disperser (e.g. in *Fuchsia excorticata* replacing high-quality dispersal by birds with low-quality dispersal by weta; Wyman et al. 2011).

We estimated the contributions by different animal species to total seed dispersal in a lowland secondary forest during the autumn fruiting period. Seed dispersal by each animal species was calculated by combining the number of seeds per defecation, the number of defecations per animal per day, and the density of animals per hectare. Our specific aims were to determine: (1) what is the overall contribution to seed dispersal by each animal species at Kowhai Bush; (2) do possums disperse larger fruits than birds; and (3) do possum-dispersed seeds germinate as well as bird-dispersed seeds?

Using this information, we discuss whether possum seed dispersal can compensate for bird declines and whether the benefits of possum seed dispersal outweigh the damage they cause through herbivory and predation on native dispersers.

Methods

Study site

This study was carried out at Kowhai Bush (173°36' E, 42°23' S, 80 m elevation), a 240 ha regenerating kānuka broadleaf forest, 7 km inland from Kaikoura. Kowhai Bush has little mammalian predator control, except for some poisoning of possums around the eastern edges where forest adjoins farmland. The forest canopy consists mainly of kānuka (*Kunzea ericoides*) and *Leptospermum scoparium*, with lesser amounts of *Melicytus ramiflorus*, *Pittosporum tenuifolium*, *Pittosporum eugenioides*, *Pseudopanax arboreus*, *Coriaria arborea*, *Dodonaea viscosa*, *Carpodetus serratus*, *Griselinia littoralis*, *Cordyline australis* and *Myoporum laetum*. The understory includes fleshy-fruited *Coprosma* and *Rubus* species (Hunt 1978; Starling-Windhof et al. 2011). Along its eastern margins, large areas have been invaded by the introduced fleshy-fruited woody weeds *Berberis glaucocarpa* and *Crataegus monogyna*.

The bird fauna at Kowhai Bush includes four species that have major fruit components in their diet: the native silvereye (*Zosterops lateralis*) and bellbird (*Anthornis melanura*), and the exotic song thrush (*Turdus philomelos*) and blackbird (*Turdus merula*) (MacFarlane et al. 2016). Additional species present that eat fruit occasionally are native brown creepers (*Mohoua novaeseelandiae*), grey warblers (*Gerygone igata*), fantails (*Rhipidura fuliginosa*), South Island robins (*Petroica australis*) and rifleman (*Acanthisitta chloris*), and exotic dunnocks (*Prunella modularis*) and starlings (*Sturnus vulgaris*). The two larger common native frugivores, tūī (*Prosthemadera novaeseelandiae*) and kererū, are rare in Kowhai Bush (Hunt 1978) and not recorded during this study, even though kererū are regularly seen in Fyffe-Palmer Reserve, just 5 km away (TW pers. obs.). Fyffe-Palmer Reserve has tall podocarp forest including *Prumnopitys ferruginea*, a favoured food of kererū (Clout & Hay 1989) that is absent in Kowhai Bush.

Seed dispersal quantity

Seeds per defecation

Bird seed dispersal was examined by catching birds in mist nets to collect faecal samples. Mist nets (38 mm mesh) were erected in forest clearings on 30 days over autumn 2012 (March, April, May) following the procedure of Whitaker (1972). Three pole rigs were used, one 8 m long and two 12 m long. Nets were operated for approximately 7–8 hours between 0730 and 1700 hours on fine, calm days and checked every 10 minutes. Any defecations done by birds in the nets were caught on plastic sheets 1 m wide placed below the nets. Birds were then removed from the net and placed in cotton bags for five minutes, during which time they usually defecated. Weight, gape width, species, sex, and age were recorded. Most birds were banded before being released, to enable recaptures to be identified. Individual faeces from known birds were refrigerated before being examined for seeds under a dissection microscope. Seeds were counted and identified, in most cases to species, with the aid of a reference collection. Due to the low numbers of blackbirds and song thrushes caught, we included similar data collected at Kowhai Bush in autumn 2011 by MacFarlane (2012) using identical methods for a total of 60 mist-netting days.

Seeds in possum faeces were examined through transect sampling in Kowhai Bush. Six 200 x 10 m transect lines were initially cleared of any possum faeces in March 2012. Fresh single faeces were collected from ground searches along transects over 14 days in autumn 2012 (March, April, May). Individual faeces were processed in the same way as for birds.

Fruit availability and size

To estimate fruit availability, observations were made approximately every two weeks from March to May 2012 of the number and ripeness of fruit present along six 200 x 10 m transect lines. All fleshy-fruited fruiting plants present on the transect lines were recorded including species, number of fruits and percentage of ripe fruit. The number of fruits per individual was estimated visually by counting the number of fruits in sequential sections. For small shrubs, the total number of fruits on the plant was counted.

To measure fruit size, fifteen fruit from each species were collected from at least three different individuals to measure the least diameter, which determines swallowing ability of birds (Kelly et al. 2010). The flesh was then removed and seeds were counted and stored as a reference collection to aid seed identification.

Defecations per day

To measure the defecation rate for wild birds in New Zealand that do not have constant access to food sources, we focused on bellbirds, a common and important mid-sized frugivore, in Kowhai Bush in spring 2012. They are observed easily in Kowhai Bush, being common, less disturbed by people than song thrushes and blackbirds, and having slower movements than silvereyes. Bird searches were for approximately 8 hours a day between 0730 and 1900 for 4 days by walking along tracks and observing the number of defecations from an individual bird over measured time intervals.

The average number of possum defecations per night was obtained from the literature. Three different studies all present similar numbers: Cowan (1992) found an overall average of 71.5 faecal pellets per night for field-trapped possums held overnight in 12 different months. Fitzgerald (1977) also trapped and held possums overnight and had a very similar average of 69.7 pellets. Similarly, feeding trials with captive possums gave an average of 71.1 pellets over a 24 hour period (Fitzgerald 1977).

Animals per hectare

We combined three types of information to estimate bird abundance per hectare in Kowhai Bush. Bellbird abundance in Kowhai Bush was estimated from territory mapping conducted in autumn 2011 by MacFarlane (2012), who recorded the number of territory-holding birds in a 7.8 ha area. This density estimate includes only territory-holding birds, not vagrant bellbirds that pass through the area in search of food.

Secondly, bird abundance was calculated using the number of active nests (nests with ≥ one egg or nestling) found in a 19 ha area searched intensively in the 2002 breeding season (JV Briskie unpubl. data). The number of nests per hectare was converted to birds per hectare by multiplying by two. Bellbird and silvereye nests are cryptic and difficult to find relative to the larger nests of blackbirds and song thrushes, so densities based on nests for those two species may be underestimates. Other potential sources of error include not allowing for unpaired or non-breeding birds, bias associated with recording in spring breeding season when bird abundance is low and birds like silvereyes are not flocking, and not correcting for multiple nests per pair per season.

Thirdly, we obtained estimates of bird abundance for lowland hardwood forest types from Kikkawa (1966), who conducted an in-depth survey of bird populations in forest habitats of the South Island of New Zealand.

Possum abundance was obtained by placing possum WaxTags at 20 m intervals along six 200 m transect lines in a similar method to that described by NPCA (2010). WaxTags were nailed to trees 30 cm above the ground and a blaze of flour and icing sugar (5:1 ratio) was applied from the ground up to the WaxTag. WaxTags were checked for possum bite marks after three nights and the bite mark index (BMI) was calculated. Possum density was then calculated using the linear correlation between bite mark index and possums per hectare given by Thomas et al. (2007).

Seed dispersal quality

Germination

To test for differential germination of seeds dispersed by different animal species, seeds of the dominant plant species found in faecal samples (*Coprosma robusta*) were sown in trays of potting mix and placed in an unheated glasshouse at the University of Canterbury. Hand-cleaned seeds of whole fruits collected from Kowhai Bush were used as a control (Robertson et al. 2006), with 700 control seeds in total divided across 14 trays. All seeds received at least 8 weeks cold treatment in a refrigerator prior to sowing. Seedling emergence was counted at 10 day intervals over the following 10 months, which is long enough to measure all germinable seeds (Burrows 1995). The final total germination of seeds from different animal species was analysed with trays as replicates (n = 24 trays; each tray averaged 42 seeds) and using a generalised linear model (GLM) with quasibinomial error distribution and logistic link function, using the R statistical program, version 2.15.1.

Results

Seed dispersal quantity

Seeds in faecal samples

A total of 486 birds from 13 different species were caught in mist nets across both years (Table 1). The most commonly caught frugivorous birds were silvereyes (215) and bellbirds (88). Although song thrushes and blackbirds were common in the forest, low numbers (17 and 19 respectively; Table 1) were caught as they are wary of people. Only one tūī was caught as they are rare visitors to the bush. Starlings were frequently seen feeding on *Pseudopanax arboreus* fruit, but caught only once and the sample contained no seeds. No kererū were seen in Kowhai Bush during the study.

We collected 419 bird faecal samples and identified 2748 seeds, all intact, from 31 plant species. Of these, four plant species that were found in one faecal sample each (mostly one or two seeds) were not identified, and one seed found in a bellbird sample was identified to family (Cyperaceae). Seeds were present in the faeces of eight bird species. Four of these (silvereyes, bellbirds, blackbirds and song thrushes) contributed 98% of the seeds. The other four bird species are not considered further in this paper either because they were very rare (tūī) or because seeds were infrequent in their faecal samples (fantail, brown creeper, dunnock).

Silvereyes had the highest number of plant species represented with 21 different species. Blackbirds had a high mean number of seeds per sample (24), exaggerated due to one sample having 132 small *Coriaria arborea* seeds; excluding this sample gave a mean number of seeds per sample of 15.1. All seeds recovered from bird faeces were whole.

In possum faecal samples a total of 453 intact seeds from 12 plant species were identified, with the average number of seeds per sample similar to that of silvereye and song thrush (Table 1). Five seeds in two possum faecal samples were identified to genus level only (*Solanum* and *Lophomyrtus*). Eight possum

Table 1. Seeds found in faeces of birds and possums at Kowhai Bush ranked by number of seeds per faecal sample. Caught indicates the number of individual birds trapped in mist nets; not every caught bird produced a faecal sample. The blackbird mean seeds per sample excludes one sample, which had 132 *Coriaria arborea* seeds.

Species	Caught	Faecal sample	Samples with seeds	Intact seeds	Seed fragments	Seeds / sample	No. seed species
Tui	1	1	1	19	0	19	2
Blackbird	19	13	12	313	0	15.1	5
Bellbird	88	80	80	921	0	11.5	12
Song thrush	17	14	12	116	0	8.3	5
Silvereye	215	194	180	1355	0	7.0	21
Brown creeper	8	8	6	18	0	2.3	5
Dunnock	5	4	1	4	0	1	1
Fantail	81	63	1	2	0	<0.1	1
Grey warbler	43	33	0	0	0	0	0
Chaffinch	5	5	0	0	0	0	0
Redpoll	2	2	0	0	0	0	0
Starling	1	1	0	0	0	0	0
Sth Island robin	1	1	0	0	0	0	0
Possum	NA	54	43	453	177	8.4	12
Totals	**486**	**473**	**336**	**3201**	**177**		**(31)**

faeces contained seed fragments from two plant species. Seed fragments made up 88% of the total *Muehlenbeckia australis* seeds (100/113) and 21% of the *Carpodetus serratus* seeds (77/363). Our estimate of how many whole seeds were represented by the fragments indicates approximately 15% of the total number of seeds eaten by possums were reduced to fragments.

The number of faecal samples varied widely among animal species which could potentially affect the observed diet breadth. We calculated sample-based rarefaction curves (Gotelli & Colwell 2001), using the program EstimateS, version 8.2 (Colwell 2009). After rarefying back to the lowest sample size, overlapping 95% confidence intervals meant that none of the five frugivores could be definitely said to have a wider range of plant species dispersed than the others.

The most common seed dispersed was *Coprosma robusta* (56% of all seeds across the whole dataset; Table 2). *Coprosma robusta* made up more than half of all fruits eaten by each bird species and by possums (Table 2). Of the seeds that could be identified as native or exotic (99% of all seeds), 98% were native, with *Berberis glaucocarpa* and *Vitis vinifera* being the only exotic species found. Bellbirds dispersed only native seeds, while the introduced animals plus silvereyes had small percentages of their dispersed seeds being exotic (blackbird 1.7%, silvereyes and possum 1.8%, song thrush 7.8%).

Fruit availability

A total of 21 plant species were observed fruiting in Kowhai Bush during autumn 2012 (Table 2) and three were exotic (*Berberis glaucocarpa*, *Taxus baccata* and *Crataegus monogyna*). *Melicytus ramiflorus* was common in the forest but produced little fruit during the study period (Table 2). Fruiting was dominated by *Coprosma robusta*, *Pseudopanax arboreus*, *Coprosma rhamnoides* and *B. glaucocarpa*. The total fruit crop was approximately 720 000 fruit per hectare, corresponding to a seed crop of approximately 1 780 000 seeds per hectare. Seven plant species (making up 5.2% of available fruits) were not observed in the diet of any animal during this study (Table 2). There were four species with fruits with diameters larger than 9 mm (*Taxus baccata*, *Crataegus monogyna*, *Ripogonum scandens* and *Hedycarya arborea*: Fig. 1), none of which were found in faeces (Table 2).

Dispersal of large fruits

Despite being much larger animals, possums did not disperse larger fruits than birds. The largest-fruited species identified in faeces was *Coprosma grandifolia* (mean = 7.1 mm diameter ± 0.1 SE) and this was found in both bellbird and silvereye faeces (the two smallest animals). The invasive small tree *Berberis glaucocarpa* (mean = 6.6 mm ± 0.1) was the largest seed found in possum faeces, and was also present in silvereye, song thrush and blackbird faeces. The mean gape widths of song thrushes and blackbirds are larger than all fruits measured at Kowhai Bush (Fig. 1). Possums did disperse one plant species that was not found in bird faeces, *Carpodetus serratus*; however, this fruit is relatively small (c. 6 mm diameter) and has been reported in the diet of native birds elsewhere (O'Donnell & Dilks 1994) so *C. serratus* is apparently not reliant on only possums for dispersal.

Defecations per day, animals per hectare and total seed dispersal

Over the 4 days of observations, bellbirds were clearly observed for 3:00:23 hours in 102 sightings ranging from 5 seconds to 9:46 mins. During this time 43 defecations were observed. The data were divided into nine sequential blocks

Table 2. Fruit and seed abundance at Kowhai Bush (x 10^3 per hectare) and percentage of fruits in the forest (Kowhai Bush) and in the diet of dispersing animals. Asterisks indicate introduced plant species; (-) indicates fruiting species not recorded in animal diets. Sorted by descending number of fruit per hectare.

Plant species	Fruit/ha x 10^3	Seeds/ha x 10^3	Percentage of fruits Forest	Bellbird	Silvereye	Thrush	Blackbird	Possum
Coprosma robusta	287.2	574.4	39.9	79.3	55.6	78.7	68.9	58.8
Coprosma rhamnoides	138.0	276.0	19.2	1.9	4.0	0.9	0	0
*Berberis glaucocarpa**	122.5	453.3	17.0	0	1.2	5.9	5.1	2.5
Pseudopanax arboreus	113.0	226.0	15.7	1.1	15.2	0.9	0	13.3
Hedycarya arborea (-)	12.5	12.5	1.7	0	0	0	0	0
*Crataegus monogyna**(-)	8.75	8.75	1.2	0	0	0	0	0
Pittosporum tenuifolium (-)	7.5	71.3	1.0	0	0	0	0	0
Myoporum laetum	5.0	5.0	0.7	0	0	0	0	1.2
*Taxus baccata**(-)	5.0	5.0	0.7	0	0	0	0	0
Coprosma grandifolia	3.5	7.0	0.5	0.6	0.2	0	0	0
Ripogonum scandens (-)	3.0	4.2	0.4	0	0	0	0	0
Cordyline australis	2.5	24.8	0.4	0.1	1.0	0	0	0
Coriaria arborea	2.5	12.8	0.4	0.6	5.6	0	23.5	1.8
Pittosporum eugenioides	2.5	18.5	0.4	0	0.1	0	0	0
Melicytus ramiflorus	1.85	12.14	0.3	0	1.6	0	0	0
Muehlen beckiaaustralis	1.5	1.5	0.2	3.0	8.2	0	0.9	15.0
Coprosma propinqua	1.21	2.41	0.2	8.4	4.9	0	0	0
Carpodetus serratus	1.0	65.2	0.1	0.0	0	0	0	5.1
Myrsine australis (-)	0.5	0.5	0.1	0	0	0	0	0
Corokia cotoneaster (-)	0.3	0.3	0.0	0	0	0	0	0
Ileostylus micranthus	0.3	0.3	0.0	2.5	0.2	0	0	0
Present outside transect	0	0	0	2.5	2.1	13.6	1.6	2.5
Total	720.11	1781.70	100%	100%	100%	100%	100%	100%

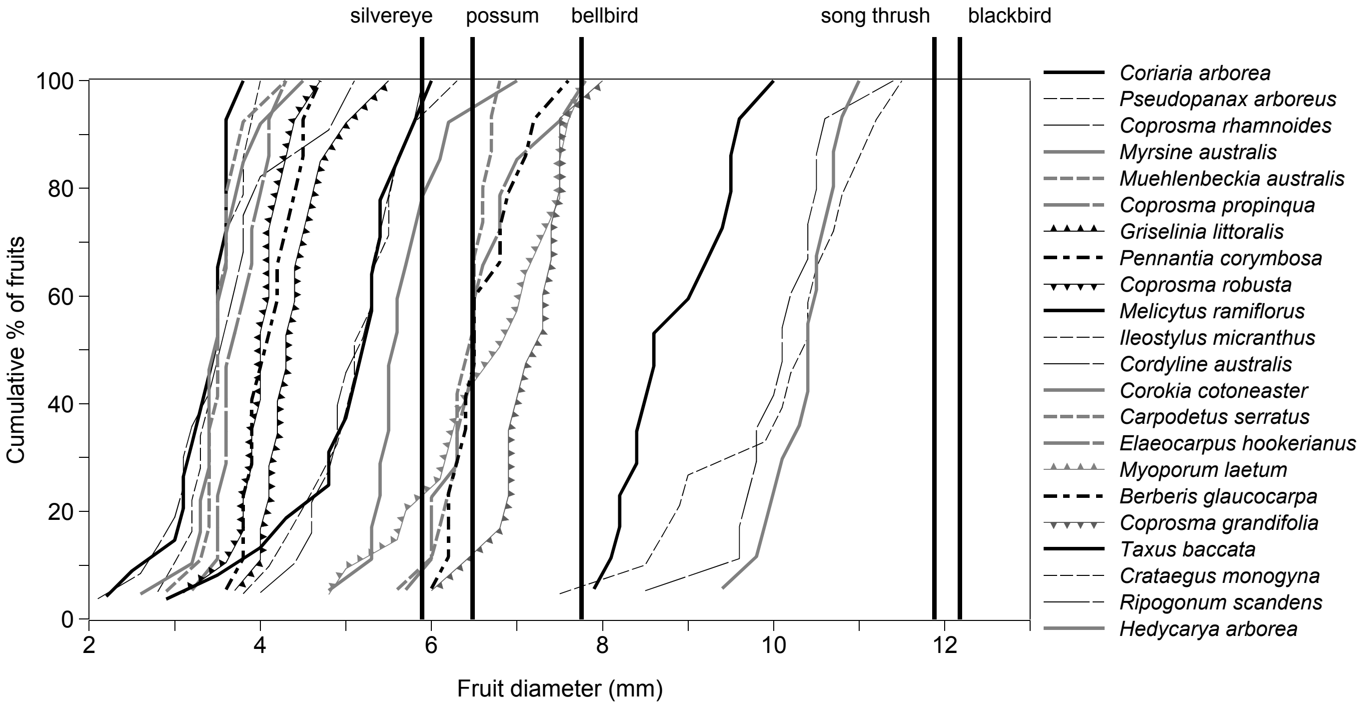

Figure 1. Cumulative distributions of fruit diameters for 22 plant species collected from Kowhai Bush. The mean gape width of silvereyes, bellbirds, song thrushes, and blackbirds is indicated by black vertical lines, although they are capable of swallowing larger fruits (see text); the line for possums indicates the mean fruit diameter of the largest seed excreted in faeces (*Berberis glaucocarpa*). Legend shows plant species ordered by increasing mean fruit diameter.

of approximately 20 minutes each, providing a mean of one defecation every 4.3 ± 0.6 minutes (mean ± 95% CI). Birds were assumed to be active for approximately 10 hours a day in the autumn fruiting season, so a defecation interval of 4.3 minutes over 10 hours equated to 140 faeces per bird per day. This estimate of defecation rate was also applied to silvereyes, song thrushes and blackbirds. The number of defecations per day for possums obtained from the literature (see Methods) was approximately 70.

The various bird abundance estimates were broadly similar (Table 3). Bellbird territory mapping revealed that 24 birds held territories in the 7.8 ha area searched in 2011, equating to three birds per hectare (A. MacFarlane unpubl. data). The number of nests found in the 19 ha area searched in 2002 ranged from 11 (bellbird) to 61 (song thrush) (JV Briskie unpubl. data). After allowing for two birds per nest, the estimated number of birds per hectare ranged from 1.2 (bellbird) to 6.4 (song thrush) (Table 3), although these are thought to be minimum estimates for bellbirds and silvereyes because their nests are cryptic. In selecting bird density estimates for calculating seed dispersal per hectare, we used Kowhai Bush estimates where these were considered reliable (bellbird territories, blackbird and song thrush nests). For silvereyes we used the Kikkawa (1966) estimate, which would be consistent with density from Kowhai Bush nests if one-third of silvereye nests had escaped detection.

Table 3. Estimates of bird abundance (birds per ha), with bold plus asterisks indicating numbers selected to use for seed dispersal calculations.

	Bellbird	Silvereye	Song thrush	Blackbird
Territory mapping	**3.0***	-	-	-
Nests	1.2	1.8	**6.4***	**3.2***
Kikkawa 1966	2.5	**2.7***	3.9	3.7

Table 4. Summary of quantitative seed dispersal at Kowhai Bush, showing average seeds per defecation, defecations per animal per day, animals per hectare, and seeds dispersed per hectare per day for the five primary dispersing animals.

	Bellbird	Silvereye	Song thrush	Blackbird	Possum	Total
Seeds defecation^{-1}	11.5	7.0	8.3	15.1	8.4	
Defecations animal^{-1} day^{-1}	140	140	140	140	70	
Animals ha^{-1}	3	2.7	6.4	3.2	1	
Seeds ha^{-1} day^{-1}	4830	2646	7437	6765	588	22 266
Percentage	21.7	11.9	33.4	30.4	2.6	100

Of the 60 WaxTags laid, eight had possum bite marks. The BMI was calculated to be 13.3% ± 3.3 SE, equating to approximately one possum per hectare using the method in Thomas et al. (2007).

We calculated total seed dispersal per hectare per day over the autumn fruiting peak, using the estimates of the number of seeds per defecation together with the number of defecations per animal per day and animals per hectare for bellbirds, silvereyes, song thrushes, blackbirds and possums (Table 4). Total seed dispersal by these animals was approximately 22 300 seeds per hectare per day. Given a total seed crop of 1 780 000 seeds per hectare (Table 2), if 22 300 seeds were removed per hectare per day it would take 80 days for frugivores to consume the whole fruit crop, a period similar to the duration of the fruiting period. This provides a figure to ensure the various estimates are of the correct magnitude.

Birds contributed 97% of the total seed dispersal and dispersal by introduced birds represented over half (64%) (Table 4). The contribution by introduced birds would have been even higher if we had not excluded one blackbird pellet with 132 *Coriaria arborea* seeds (see Methods). Possum dispersal was less than 3% of the total seed dispersal in Kowhai Bush and that number was insensitive to using alternative bird density estimates for silvereyes or song thrushes from Table 3. Although possums had a similar number of seeds per faecal pellet as birds (Table 1), the number of defecations per day and their abundance per hectare was much lower, so the seed dispersal contribution of possums was consequently small.

Seed dispersal quality

Germination

Seeds of *Coprosma robusta* defecated by different animals varied significantly in their germination in the glasshouse ($F_{(5, 32)} = 4.941$, $p = 0.002$). Germination of seeds from possum faeces was significantly lower (31%) than seeds from faeces of all bird species (61–74%) and hand-cleaned seeds (Fig. 2). A model re-run without possum ingested seeds showed non-significant ($F_{(4, 29)} = 1.460$, $p = 0.240$) differences among the other treatments (birds and hand-cleaned).

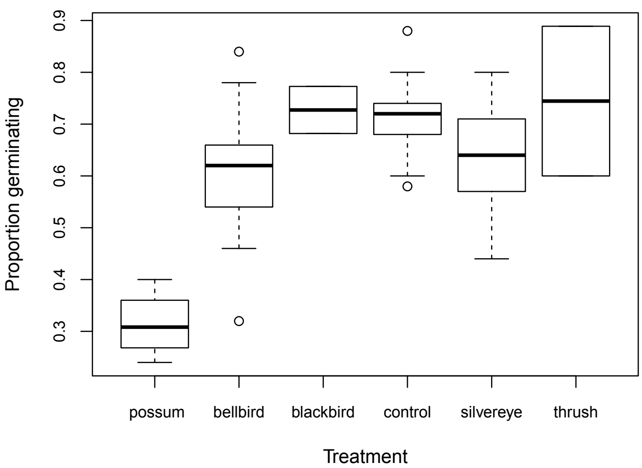

Figure 2. Proportion of *Coprosma robusta* seeds germinating after passing through various animal species or hand-cleaned (control). Box plot shows the median and upper and lower quartiles in the box, and minimum and maximum values in the whiskers (excluding outliers). Open circles show outliers, which are >1.5 times the interquartile range beyond the first or third quartiles.

Discussion

Possums made a trivial contribution to seed dispersal of plants in Kowhai Bush, dispersing less than 3% of the total seeds compared to four bird species (12–33% of the total seeds by each species). Furthermore, possums destroyed 15% of the seeds they consumed, and *Coprosma robusta* seeds that survived possum gut passage intact had only half the germination percentage of bird-dispersed seeds. In addition, there was no evidence that possums fill the role of large-gaped frugivorous birds that have been lost or reduced in abundance in parts of New Zealand, because possums defecated no seeds larger than those moved by silvereyes.

Seed dispersal quantity

The possum contribution to total seed dispersal at Kowhai Bush was quantitatively small, because they were at lower density and had lower defecation rates per day than each of the four frugivorous birds. Possum density is variable over New Zealand, being generally lower in beech forest (around one per hectare) than mixed lowland forest (5–10 per hectare) reflecting the abundance of food sources (Clout 2006). Our estimate for Kowhai Bush (~1 possum per hectare) is relatively low for a low-elevation forest, perhaps influenced by past possum control or a lack of den sites in the early successional forest. However, to make a large contribution to seed dispersal at a site, possum abundance would have to be much higher because there are 16.2 birds per hectare across the four main frugivore species. For example, at Kowhai Bush, if possum densities increased five-fold (and bird abundance and seeds per faecal sample were unchanged), possums would still disperse only 12% of all seeds moved.

The relative contribution of possums was also low because of high densities per hectare of the four frugivorous birds. Blackbirds and, especially, song thrushes were very abundant. Kikkawa (1966) noted that disturbed lowland forest near to settlements held the highest densities of these two introduced birds, with their abundance in podocarp and *Nothofagus* forests being an order of magnitude lower (about 0.5 blackbirds and 0.2 song thrushes per hectare). The locally high density of blackbirds and song thrushes in Kowhai Bush probably explains their much higher contribution to seed dispersal in this site than in the review presented by Kelly et al. (2006). In the latter study, blackbirds made only 3.9% of all visits to native fruiting plants (using visits as a proxy for number of fruits eaten). Most of the 39 cases in Kelly et al. (2006) were from mature native forest. A recent study in secondary forests around urban Wellington found blackbirds were the second most frequently observed frugivore (Burns 2012), consistent with blackbirds being more important in successional forest near settlements than elsewhere.

The relative contributions to total seed dispersal also depend upon defecation rates (faeces per day). This is well known for possums (see Methods), but not for birds. Our sole estimate is for bellbirds. There could be errors in applying this rate to the other three bird species, since gut retention time varies inversely with body site (Wotton et al. 2008), although how gut retention time affects defecation rate is unclear. Also, our defecation observations were conducted in spring rather than during the autumn fruiting season. The number of defecations per day is likely to vary with diet. Gut retention time varies inversely with the degree of frugivory (Levey & Karasov 1994), and may also be affected by the particular species of fruit eaten, but unfortunately we have no data on that.

The contribution by possums to seed rain has been estimated once previously in New Zealand. Dungan et al. (2002) sampled seed rain in seed traps in seral vegetation in Hoon Hay (lowland Canterbury) and found that seeds in possum faeces contributed 17% of the dispersed seed rain, higher than at Kowhai Bush (3%) but still a small part of the total. Both the Hoon Hay study and ours agree on the relatively minor role of possums as seed dispersers in New Zealand forests compared to birds (Williams 2003).

Dispersal of large fruits

Possums might benefit dispersal by eating large fruits, especially in New Zealand where these fruits are now largely dispersed by a single frugivore, the kereru (Wotton & Kelly 2011). However, previous work, confirmed by this study, shows that possums do not swallow any fruit larger than those swallowed by silvereyes, despite being much larger (2.5 kg for possums vs. 13 g for silvereyes). Silvereyes disperse fruits up to 9.9 mm mean diameter (*Crataegus monogyna*; Williams & Karl 1996), while there is no evidence that possums disperse any fruits greater than 10 mm diameter (Williams 2003). Possums ate only the pulp of six species of fruits >9 mm diameter (*Rhopalostylis sapida*, mean fruit diameter 9.1 mm; *Elaeocarpus dentatus* 9.2 mm; *Prumnopitys taxifolia* 9.4 mm; *Hedycarya arborea* 9.7 mm; *Ripogonum scandens* 10.5 mm; *Prumnopitys ferruginea* 13.0 mm; Cowan 1990, 1992; Williams et al. 2000; Kelly et al. 2010). Cowan (1990) found one *R. scandens* seed in possum faeces, apparently the largest fruit recorded as dispersed by a possum, but this fruit is also dispersed by silvereyes (O'Donnell & Dilks 1994). While possums did disperse a large number of *Carpodetus serratus* seeds, which were not found in bird faeces in our study, these small fruits (6 mm wide) are within the range of dispersal for silvereyes, bellbirds, blackbirds and tui, which have all been recorded eating them elsewhere (O'Donnell & Dilks 1994).

Seed dispersal quality

A high quality seed disperser should induce little seed mortality. Possums at Kowhai Bush destroyed 15% of *Coprosma robusta* seeds and halved germination of intact seed compared to birds. Our estimates of seed damage may be an underestimate since any completely ground up seeds would be undetected. Other studies have reported similarly low values for seed survival and germination in possums. Williams et al. (2000) showed that possums significantly reduced germination of *C. robusta* seeds (from 70% for hand-cleaned to 4%) and across 11 plant species, possums destroyed on average 66% of the seeds they swallowed. Dungan et al. (2002) reported that 75% of *Muehlenbeckia australis* seeds from possum faeces were visibly damaged and none of the intact defecated seeds germinated (compared with 40% germination in hand-cleaned seeds). We found that 88% of *M. australis* seeds were visibly damaged in possum faeces, but did not test for germination.

High-quality dispersers would also move seeds away from the parent plants and deposit them in sites suitable for germination. We have no direct information about movement distances in birds or possums, but both are likely to move seeds considerable distances for different reasons. Birds have short gut passage times (here 18–180 minutes; Sorensen 1984; French et al. 1992; Stanley & Lill 2002; O'Connor 2006; Wotton et al. 2008; Wotton & Kelly 2012) but can move seeds a long way in a short time (Wotton & Kelly 2012). Possums move more slowly but have long gut passage times (1.5–3 days; Nugent et al. 2000). There is little information about microhabitat of seed deposition for either birds or possums, except for possums in the subalpine zone (Young 2012) where possums mainly defecated under forest.

The evidence shows that possums destroy seeds and reduce germination, potentially limiting plant fitness. Fruits eaten by possums are taken also by birds, therefore, possums reduce the overall quality of seed dispersal. This is analogous to the interaction between tree weta (*Hemideina* spp.) and *Fuchsia excorticata* (tree fuchsia), whereby the low dispersal distances and low survival rate of seeds consumed by tree weta potentially replaces high-quality dispersal by birds with low-quality dispersal by weta (Wyman et al. 2011).

Possum impacts

The negative effects of possums on New Zealand ecosystems are well documented. As herbivores, possums damage native forests through selective browsing resulting in the canopy die-back of trees such as *Metrosideros* spp., *Podocarpus totara*, *Alectryon excelsus*, *Sophora* spp. and *Dysoxylum spectabile* (Clout 2006). Possums eat large quantities of native flowers and unripe fruit (Cowan 1990), reducing seed production in species like *D. spectabile*, *Rhopalostylis sapida* and *Elaeocarpus dentatus* (Cowan & Waddington 1990; Cowan 1991). In addition, possums are important predators of native birds including kaka (*Nestor meridionalis*), kokako (*Callaeas cinerea*) and kererū (Brown 1993; Sweetapple et al. 2004). As a result, possums disrupt fruit dispersal by damaging plants, reducing bird densities, and competing for food with native frugivorous birds (Atkinson et al. 1995). Once seeds have been dispersed, possums have been shown to reduce recruitment in forests through seedling herbivory (Wilson et al. 2003).

Possum seed dispersal may also create a conservation risk by spreading invasive weed species. In their native Australia, possums disperse seeds of the European weed hawthorn (Bass 1990). In New Zealand, possums are known to disperse seeds of the noxious weeds *Passiflora mollissima* (Beavon & Kelly 2015) and *Leycesteria formosa* (Dungan et al. 2002), while we found that possums dispersed some *Berberis glaucocarpa* seeds. They are also potentially important seed dispersers of a range of other alien plant species (Williams et al. 2000; Wotton & McAlpine 2015).

Conclusion

Birds, both native and introduced, were by far the most important seed dispersers in secondary broadleaved forest at Kowhai Bush. We found that the contribution to seed dispersal by blackbirds and song thrushes was higher than previously reported and suggest they may be particularly important in secondary forest near towns. In contrast, possums were not effective seed dispersers in Kowhai Bush in terms of quantity or quality, nor did they provide dispersal of any fruits larger than those moved by silvereyes. For these reasons, possums are not critical seed dispersers in native forest. Since their omnivory threatens faunal and floral native biodiversity, ongoing possum control would always be expected to provide conservation benefits.

Acknowledgements

We thank James Briskie and Archie MacFarlane for help with field work and access to unpublished data, Colin Webb for help with seed identification, and Margaret Stanley, Bill Lee, and two anonymous referees for helpful comments on the manuscript. The Canterbury Ecological Research Trust helped with logistics. This research was carried out with animal ethics approval from the University of Canterbury Animal Ethics Committee (AEC: 2012/10R). TW was supported by a PhD scholarship from the School of Biological Sciences, University of Canterbury, and a Royal Forest and Bird Protection Society (North Canterbury Branch) Stocker Scholarship.

References

Atkinson IAE, Campbell DJ, Fitzgerald BM, Flux JEC, Meads MJ 1995. Possums and possum control: effects on lowland forest ecosystems. Science for Conservation. Wellington, New Zealand, Department of Conservation. 32 p.

Bass DA 1990. Dispersal of an introduced shrub (*Crataegus monogyna*) by the brushtailed possum (*Trichosurus vulpecula*). Australian Journal of Ecology 15: 227–229.

Beavon MA, Kelly D 2015. Dispersal of banana passionfruit (*Passiflora tripartita* var. *mollissima*) by exotic mammals in New Zealand facilitates plant invasiveness. New Zealand Journal of Ecology 39: 100–107.

Bond WJ 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Transactions: Biological Sciences 344: 83–90.

Brown K 1993. Evidence that possums prey on and scavenge birds' eggs, birds and mammals. Notornis 40: 169–177.

Burns KC 2012. Are introduced birds unimportant mutualists? A case study of frugivory in European blackbirds (*Turdus merula*). New Zealand Journal of Ecology 36: 1–6.

Burrows CJ 1995. Germination behaviour of seeds of the New Zealand species *Aristotelia serrata*, *Coprosma robusta*, *Cordyline australis*, *Myrtus obcordata*, and *Schefflera digitata*. New Zealand Journal of Botany 33: 257–264.

Clout MN 2006. Keystone aliens? The multiple impacts of brushtail possums. In: Allen RB, Lee WG eds. Biological invasions in New Zealand. Berlin, Germany, Springer-Verlag. Pp. 265–279.

Clout MN, Hay JR 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. New Zealand Journal of Ecology 12: 27–33.

Coleman JD, Green WQ, Polson IG 1985. Diet of brushtail possums over a pasture-alpine gradient in Westland, New Zealand. New Zealand Journal of Ecology 8: 21–35.

Colwell RK 2009. EstimateS: statistical estimation of species richness and shared species from samples. Version 8.2. http://viceroy.eeb.uconn.edu/estimates/.

Corlett RT 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. Biological Reviews 73: 413–448.

Cowan PE 1990. Fruits, seeds, and flowers in the diet of brushtail possums, *Trichosurus vulpecula*, in lowland podocarp mixed hardwood forest, Orongorongo Valley, New Zealand. New Zealand Journal of Zoology 17: 549–566.

Cowan PE 1991. Effects of introduced Australian brushtail possums (*Trichosurus vulpecula*) on the fruiting of the endemic New Zealand nikau palm (*Rhopalostylis sapida*). New Zealand Journal of Botany 29: 91–93.

Cowan PE 1992. Analysis of the characteristics of fruit eaten by possums, *Trichosurus vulpecula*, in New Zealand. New Zealand Journal of Zoology 19: 45–52.

Cowan PE, Waddington DC 1990. Suppression of fruit production of the endemic forest tree, *Elaeocarpus dentatus*, by introduced marsupial brushtail possums, *Trichosurus vulpecula*. New Zealand Journal of Botany 28: 217–224.

Dungan RJ, O'Cain MJ, Lopez ML, Norton DA 2002. Contribution by possums to seed rain and subsequent seed germination in successional vegetation, Canterbury, New Zealand. New Zealand Journal of Ecology 26: 121–127.

Fitzgerald AE 1977. Number and weight of faecal pellets produced by opossums. Proceedings of the New Zealand Ecological Society 24: 76–78.

French K, Odowd DJ, Lill A 1992. Fruit removal of *Coprosma quadrifida* (Rubiaceae) by birds in South-Eastern Australia. Australian Journal of Ecology 17: 35–42.

Gotelli NJ, Colwell RK 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379–391.

Hunt DM 1978. Kowhai Bush: a valuable remnant of lowland forest. Forest and Bird 210: 18–21.

Kawakami K, Mizusawa L, Higuchi H 2009. Re-established mutualism in a seed-dispersal system consisting of native and introduced birds and plants on the Bonin Islands, Japan. Ecological Research 24: 741–748.

Kelly D, Robertson AW, Ladley JJ, Anderson SH, McKenzie RJ 2006. The relative (un)importance of introduced animals as pollinators and dispersers of native plants. In: Allen R, Lee WG eds. Biological invasions in New Zealand. Berlin, Germany, Springer-Verlag. Pp. 227–245.

Kelly D, Ladley JJ, Robertson AW, Anderson SH, Wotton DM, Wiser SK 2010. Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit-dispersal in New Zealand. New Zealand Journal of Ecology 34: 66–85.

Kikkawa J 1966. Population distribution of land birds in temperate rainforest of southern New Zealand. Transactions of the Royal Society of New Zealand 7: 215–277.

King CM 2005. The handbook of New Zealand mammals. Melbourne, Oxford University Press. 596 p.

Levey DJ, Karasov WH 1994. Gut passage of insects by European starlings and comparison with other species. The Auk 111: 478–481.

MacFarlane AET 2012. Frugivorous mutualisms in a native New Zealand forest, the good the bad and the ugly. MSc thesis, University of Canterbury, Christchurch. 118 p.

MacFarlane AET, Kelly D, Briskie JV 2016. Introduced blackbirds and song thrushes: useful substitutes for lost mid-sized native frugivores, or weed vectors? New Zealand Journal of Ecology 40: 80–87.

NPCA 2010. Possum population monitoring using the WaxTag® method. Wellington, New Zealand, National Possum Control Agencies. 28 p.

Nugent G, Sweetapple P, Coleman J, Suisted P 2000. Possum feeding habits: dietary tactics of a reluctant folivore. In: Montague TL ed. The brushtail possum: biology, impact and management of an introduced marsupial. Lincoln, New Zealand, Manaaki Whenua Press. Pp. 10–23.

O'Connor S-J 2006. Modelling seed dispersal by tui. BSc Honours thesis, University of Canterbury, Christchurch. 41 p.

O'Donnell CFK, Dilks PJ 1994. Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. New Zealand Journal of Ecology 18: 87–107.

Robertson AW, Trass A, Ladley JJ, Kelly D 2006. Assessing the

benefits of frugivory for seed germination: the importance of the deinhibition effect. Functional Ecology 20: 58–66.
Schupp EW, Jordano P, Gómez JM 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188: 333–353.
Sodhi NS, Koh LP, Brook BW, Ng PKL 2004. Southeast Asian biodiversity: an impending disaster. Trends in Ecology & Evolution 19: 654–660.
Sorensen AE 1984. Nutrition, energy and passage time: experiments with fruit preference in European blackbirds (*Turdus merula*). Journal of Animal Ecology 53: 545–557.
Staddon S, Compton S, Portch A 2010. Dispersal of fig seeds in the Cook Islands: introduced frugivores are no substitutes for natives. Biodiversity and Conservation 19: 1905–1916.
Stanley MC, Lill A 2002. Avian fruit consumption and seed dispersal in a temperate Australian woodland. Austral Ecology 27: 137–148.
Starling-Windhof A, Massaro M, Briskie J 2011. Differential effects of exotic predator-control on nest success of native and introduced birds in New Zealand. Biological Invasions 13: 1021–1028.
Sweetapple P, Fraser K, Knightbridge P 2004. Diet and impacts of brushtail possum populations across an invasion front in South Westland, New Zealand. New Zealand Journal of Ecology 28: 19–33.
Terborgh J, Nuñez-Iturri G, Pitman NCA, Valverde FHC, Alvarez P, Swamy V, Pringle EG, Paine CET 2008. Tree recruitment in an empty forest. Ecology 89: 1757–1768.
Thomas M, Hickling G, Coleman J, Pracy L 1993. Long-term trends in possum numbers at Pararaki: evidence of an irruptive fluctuation. New Zealand Journal of Ecology 17: 29–34.
Thomas MD, Morgan DR, Maddigan F 2007. Accuracy of possum monitoring using WaxTags (Pest Control Research Contract Report: 2007/7). New Zealand, Animal Health Board. 50 p.
Vitousek PM, D'Antonio CM, Loope LL, Rejmanek M, Westbrooks R 1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21: 1–16.

Editorial board member: Margaret Stanley
Received 9 June 2015; accepted 29 May 2016

Whitaker AH 1972. An improved mist net rig for use in forests. Bird-Banding 43: 1–8.
Williams PA 2003. Are possums important dispersers of large-seeded fruit? New Zealand Journal of Ecology 27: 221–223.
Williams PA, Karl BJ 1996. Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. New Zealand Journal of Ecology 20: 127–145.
Williams PA, Karl BJ, Bannister P, Lee WG 2000. Small mammals as potential seed dispersers in New Zealand. Austral Ecology 25: 523–532.
Wilson DJ, Lee WG, Webster RA, Allen RB 2003. Effects of possums and rats on seedling establishment at two forest sites in New Zealand. New Zealand Journal of Ecology 27: 147–155.
Wotton DM, Kelly D 2011. Frugivore loss limits recruitment of large-seeded trees. Proceedings of the Royal Society B: Biological Sciences 278: 3345–3354.
Wotton DM, Kelly D 2012. Do larger frugivores move seeds further? Body size, seed dispersal distance, and a case study of a large, sedentary pigeon. Journal of Biogeography 39: 1973–1983.
Wotton DM, McAlpine KG 2015. Seed dispersal of fleshy-fruited environmental weeds in New Zealand. New Zealand Journal of Ecology 39: 155–169.
Wotton DM, Clout MN, Kelly D 2008. Seed retention times in the New Zealand pigeon (*Hemiphaga novaezeelandiae novaeseelandiae*). New Zealand Journal of Ecology 32: 1–6.
Wright SJ, Stoner KE, Beckman N, Corlett RT, Dirzo R, Muller-Landau HC, Nuñez-Iturri G, Peres CA, Wang BC 2007. The plight of large animals in tropical forests and the consequences for plant regeneration. Biotropica 39: 289–291.
Wyman TE, Trewick SA, Morgan-Richards M, Noble ADL 2011. Mutualism or opportunism? Tree fuchsia (*Fuchsia excorticata*) and tree weta (*Hemideina*) interactions. Austral Ecology 36: 261–268.
Young L 2012. Seed dispersal mutualisms and plant regeneration in New Zealand alpine ecosystems. PhD thesis, University of Canterbury, Christchurch. 165 p.