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REVIEW ARTICLE

The role of lizards as seed dispersers in New Zealand

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ABSTRACT
There is growing awareness globally of the role lizards play as seed dispersers. In New Zealand, it has been suggested that lizards are effective dispersers, and white–blue fruits and divaricating shrubs are adapted to lizard dispersal. We present new data and review the lizard seed dispersal literature. Lizards eat fruits of at least 23 native species, five of which are divaricating. Birds also eat fruits of divaricating species. Lizards prefer white-blue fruits to red fruits, and eat white–blue-fruited species more frequently than expected given their occurrence in the flora. White–blue fruits are associated with divaricating shrubs and open habitats. Seeds in lizard scats have germination percentages ≤ control seeds in four species tested. Lizards generally disperse seeds < 20 m, but allow seeds to escape parent plants and reach safe establishment sites. Lizards can be important seed dispersers even at reduced densities on the mainland, where they may disperse a larger fraction of seeds than previously assumed. In shrublands lacking frugivorous birds, lizards may be the only remaining dispersers.

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Introduction

Dispersal is a key phase in the plant life cycle. Seeds dispersed even short distances beyond a parent plant's canopy often exhibit enhanced germination and seedling establishment relative to seeds dropped directly beneath it (Howe & Smallwood 1982). Seed dispersal can potentially confer three, non-mutually-exclusive, fitness advantages (Traveset et al. 2014): 1. escape from density-dependent mortality near the parent plant; 2. colonisation of newly-available sites, the occurrence of which is unpredictable in time and space; and 3. directed dispersal to specific, non-random sites particularly well-suited to germination and seedling establishment. In addition, separation of seeds from the surrounding fruit pulp or seed scarification by dispersers may either enhance or reduce germination in at least some animal-dispersed species (Traveset & Verdú 2002). The effects of scarification tend to be small and inconsistent, while those of pulp removal are larger (Robertson et al. 2006).

In forests and shrublands around the world, many (23%–90%) woody species produce fleshy fruits adapted for dispersal by vertebrates (Jordano 2014). Birds and mammals have long been regarded as the only ecologically and evolutionarily significant frugivorous seed

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dispersers. For example, in his 700-page review of seed dispersal, Ridley (1930) devoted only half a page to dispersal by lizards, and the next 50 years of research led van der Pijl (1982) to add only a handful more examples. However, the past 25 years have seen a growing awareness of the role that lizards may play; they were recently shown to be the most important animals in seed dispersal networks in parts of the Galápagos Islands (Heleno et al. 2013) and to have a higher seed dispersal effectiveness than birds for seven out of 11 species in a Canary Islands plant community (González-Castro et al. 2015). Lizard frugivory may be particularly important in island ecosystems, which often have naturally or human-induced depauperate frugivore faunas (Olesen & Valido 2003). In the Balearic Islands, local extinction of a lizard seed disperser has reduced recruitment in a lizard-dispersed plant species (Traveset et al. 2012).

Whitaker (1987) was the first to recognise the potential role of lizards as seed dispersers in New Zealand. In coastal shrublands on the mainland, lizard densities can reach 10,000 animals per hectare, and lizards may consume at least 1,000,000 seeds per hectare per year (Whitaker 1987), yet little is known about the fates of the seeds they ingest. Whitaker (1987) made a series of claims. Firstly, he observed that fruits eaten by lizards are generally sweet, small (< 6 mm diameter), more or less odourless, and white or translucent. In the New Zealand flora, several white-fruited species are polymorphic (also with blue, pink or red morphs), or have bicoloured white and blue fruits (Lord et al. 2002). Secondly, Whitaker noted that fruits of divaricating shrubs or tangled vines are eaten by lizards, and speculated that these fruits are largely inaccessible to birds because they are mostly located inside a dense tangle of branches and twigs. Thirdly, as noted above, lizards can consume huge quantities of fruits, even on the mainland. Fourthly,Whitaker observed that seeds ingested by lizards passed through the gut intact. However, the effect of lizard ingestion on seed germination had not been tested by comparing germination of seeds defecated by lizards with control seeds collected directly from plants. Finally, Whitaker observed that lizards tend to defecate in rocky crevices. He proposed that seed deposition in these sites might provide ideal conditions for seedling establishment, especially in arid or exposed environments.

Although Whitaker (1987) provided an important new perspective on seed dispersal in New Zealand, the evidence was largely anecdotal. We use data from three new sites plus a literature review to assess whether the evidence supports the following hypotheses based on Whitaker's (1987) observations: 1. lizards prefer white and blue fruits to other fruit colours; 2. fruits of divaricating shrubs are eaten by lizards and not birds; 3. lizards eat fleshy fruits in significant quantities when they co-occur; 4. seeds ingested by lizards are undamaged and germinate as well as control seeds collected directly from plants; and 5. lizards deposit seeds in safe sites for seedling establishment.

Methods

Skink dispersal of **Muehlenbeckia** *spp.*

We investigated whether skinks provided effective seed dispersal of *Muehlenbeckia astonii* at Kaitorete Spit, Canterbury, in 2011 and 2012. *Muehlenbeckia astonii* (Polygonaceae) is a nationally endangered (de Lange et al. 2013), small-leaved, divaricating shrub undergoing widespread recruitment failure (de Lange & Jones 2000). Individual plants are either female or inconstant male (de Lange & Jones 2000). *Muehlenbeckia astonii* occurs in Wairarapa, Wellington, Marlborough and Canterbury, where it is threatened by habitat loss, browsing and trampling by stock (de Lange & Jones 2000). We also collected data on lizard dispersal of *M. complexa*, the only other fleshy-fruited species at the study site. *Muehlenbeckia complexa* is a widespread dioecious liane forming compact, tangled masses (Allan 1961). *Muehlenbeckia astonii* and *M. complexa* fruits consist of a small (2–2.5 × 1.25 mm), black, three-angled achene (hereafter referred to as a seed), which is partly surrounded by fleshy, translucent white tepals (Allan 1961). Both *M. astonii* and *M. complexa* seeds have been found in lizard scats (Whitaker 1982; de Lange & Jones 2000; Wotton 2002), although whether lizards are effective dispersers of these species is unknown.

Kaitorete Spit (43°83′31″S, 172°52 ′03″ E) extends for c. 27 km to the west of Banks Peninsula, Canterbury (Lettink & Seddon 2007), and is the stronghold for *M. astonii*, with c. 2500 plants (de Lange & Jones 2000). The study was conducted within a 1.2 ha plot fenced to exclude stock and rabbits since 2001. The vegetation comprised native-dominated grassland with occasional native woody plants including *M. astonii*, *M. complexa* and *Carmichaelia australis*. Two skink species (*Oligosoma maccanii* and *O.* aff. *polychroma* Clade 5) occur in the study area (Lettink & Seddon 2007) and are potential dispersers of *Muehlenbeckia* seed. The only birds observed were skylarks (*Alauda arvensis*), magpies (*Gymnorhina tibicen*) and seagulls (*Larus* spp.; D Wotton, pers. obs.).

In February 2011 we selected 10 flowering or fruiting female *M. astonii* plants that were separated from conspecific adults by > 10 m. Around each plant we placed one artificial lizard retreat at each of six distances (0, 2, 4, 6, 8 and 10 m) from the canopy edge, each on a random compass bearing. Each retreat consisted of a double layer of corrugated Onduline roofing material measuring 400 mm × 280 mm (0.112 m^2), with small wooden dowels separating the two layers (Lettink & Cree 2007). Rocks were placed on top of each retreat to prevent them blowing away in strong winds.

Retreats were checked monthly from February to June in 2011 and February to May 2012, and any skink scats on top of or inside retreats were collected. All scats that accumulated at retreats between the two sampling periods were removed in late January 2012 and discarded. Skink scats were readily identified by their small size, cylindrical shape and white tip of uric acid. Any seeds in scats were removed and identified under a dissecting microscope with reference to seeds collected from the field and a seed atlas (Webb & Simpson 2001). We also measured distances from retreats to the nearest fruiting *M. complexa*. Fruiting intensity of the 10 focal *M. astonii* plants was assessed monthly from February to June 2012 using an ordinal scale ranging from 0 (no fruits) to 5 (fruiting heavily). Fruiting intensity was determined on the same day that scats were collected.

In 2012 we conducted experiments to compare germination of seeds in skink scats and seeds collected directly from plants and de-pulped by hand. *Muehlenbeckia astonii* seeds collected from scats during 2012 were pooled across collection dates then separated into two groups: ‘mature’ and ‘immature’. *Muehlenbeckia complexa* seeds from scats were pooled across 2012 collection dates. Owing to low seed numbers, seeds from each group were sown in a single pot (36 seeds per pot for each of the three *M. astonii* groups, and 14 *M. complexa* seeds per pot for hand-cleaned and skink treatments). Seeds were collected from nine plants of each species in early May 2012. All seeds were refrigerated to break dormancy (D Wotton, unpubl. data) from the time of collection until sowing in September 2012. Seeds were sown in 500 mL plastic pots containing potting mix, with a 4 cm layer of seed-raising mix on top. Pots were placed outside under shade cloth and watered as required. We checked pots fortnightly and recorded seed germination (emergence of cotyledons above seed-raising mix) for 6 months.

We analysed all data in R 3.0.0 (R Core Team 2013). We tested the hypothesis that *M. astonii* and *M. complexa* seeds ingested by lizards germinate as well as control seeds collected directly from plants using a Chi-squared test with Yates' continuity correction. We tested whether the frequency of seeds in skink scats at Kaitorete Spit was independent of month collected using a Pearson's Chi-squared test for each year.

Skink seed dispersal on Matiu-Somes Island

We documented frugivory and seed dispersal by skinks on Matiu-Somes Island to investigate whether lizards play a significant role in plant reproduction. Twenty cylindrical, 4L plastic pitfall traps (22 cm diameter) were buried in each of two habitats on Matiu-Somes Island in Wellington Harbour (41°25′85″S, 174°86′56″E): a planted habitat of rank exotic grass with 68% cover of 4 year-old planted shrubs, dominated by *Coprosma repens*, and an unplanted habitat of rank exotic grass with 62% cover of naturally established shrubs dominated by *Coprosma propinqua* and *Muehlenbeckia complexa*. Traps were evenly spaced at 4 m intervals in a 7 × 3 grid in the planted habitat and a 5 × 4 grid in the unplanted habitat. Traps were baited with tinned pears and monitored daily for five 5-consecutive-day periods at roughly fortnightly intervals between late January and early April 1997. All captured lizards were identified, measured and released.

Lizard scats that were found in traps with lizards were collected and examined for seeds, which were cleaned, identified to species and counted. Later, in the field, we measured the distance from the trap in which the seeds were deposited to the edge of the nearest fruiting plant of the same species, to derive a conservative estimate of seed dispersal distance.

Gecko frugivory on Stephens Island and germination of Piper excelsum

We documented frugivory by raukawa geckos (*Woodworthia maculata*) on Stephens Island, Cook Strait (40°67′07″S, 173°99′83″E) and tested the effect of gecko ingestion on germination of *Piper excelsum* seeds. Two other gecko species (southern striped gecko, *Toropuku stephensi*, and Marlborough green gecko, *Naultinus manukanus*) also occur on Stephens Island, but we did not confirm frugivory by these species. We collected fresh gecko scats during late February to early March 2009 and mid-to-late April 2009. *Piper excelsum* fruits were common during February and March but scarce by April. Ripe fruits of *Muehlenbeckia australis, M. australis* x *complexa*, *Melicytus obovatus*, *Myoporum laetum* and *Pittosporum tenuifolium* were also present. Scats were collected near fruiting *P. excelsum*, inside sheds used extensively as retreats by *W. maculata*, and during April from artificial retreats in *Muehlenbeckia australis* and from *W. maculata* captured from these retreats and held overnight. Scats were checked for seeds and any present were cleaned, identified and counted.

We compared germination of *P. excelsum* seeds collected from gecko scats during the first trip with seeds from 20 fruiting *P. excelsum* collected at the same time on Stephens

Island. We sowed seeds in April 2009 in three treatments: lizard-ingested, hand-cleaned and seeds in fruit pulp. *Piper excelsum* fruits contain many small seeds. In order to accurately measure germination percentage, we separated seeds from the pulp, counted them into batches of 100 and placed those in the 'pulp' treatment back into pulp. Seeds were sown in seed-raising mix in 800 mL plastic pots, with 14 replicates per treatment. Pots were placed in a randomised block design (one pot of each treatment per block) in a glasshouse at University of Canterbury where the temperature was maintained above 5 °C but otherwise unheated, and checked monthly until germination ceased in March 2010. We also measured 17 of these *P. excelsum* fruits, and counted the number of mature and immature seeds. Mature *P. excelsum* seeds were dark, while immature seeds were pale.

We tested the hypothesis that *P. excelsum* seeds ingested by geckos germinate as well as control seeds collected directly from plants. We analysed data using a generalised linear mixed-effects model with a binomial error distribution and block as a random effect in the R package *lme4* (Bates et al. 2014).

Literature review

We collated data on the frequency of occurrence of seeds in lizard scats or stomachs in New Zealand from published studies and unpublished theses. We also collated lizard frugivory observations, including information on the lizard species, plant species, fruit colour and width, and seed width. We used Google Scholar and searched for the term 'lizard diet New Zealand'. In addition, we searched the titles of papers published since 1987 in the bibliography maintained by the Society for Research on Amphibians and Reptiles in New Zealand (SRARNZ) for those likely to contain information on lizard diet, and searched the selected publications for information on fruit consumption.

We tested whether the percentage frequency of seeds in scats differed between skinks and geckos using a generalised linear model with a quasibinomial error distribution (to account for overdispersion). We used a Chi-squared test to test whether lizard consumption of white–blue fruits was more common than expected compared to the New Zealand fleshy-fruited flora (Lord et al. 2002), using our updated list of species eaten by lizards. We categorised any species with white, blue, bicoloured white and blue, or polymorphic fruits including a white colour morph as white–blue fruits, following Lord et al. (2002).

Results

Skink dispersal of Muehlenbeckia *spp.*

Between February and June 2011 we collected 528 skink scats from artificial retreats at Kaitorete Spit. In 2012 we collected 631 scats between February and May. In total, 110 (9.5%) of the 1159 scats collected contained seeds. The mean number of seeds per scat across all scats was 0.14. Scats containing seeds had on average 1.5 ± 0.94 (mean ± SD) seeds per scat, and up to five seeds. *Muehlenbeckia astonii* seeds occurred in 82 (7.1%) of the scats and *M. complexa* seeds were found in 31 (2.7%). Three scats had seeds of both *M. astonii* and *M. complexa*. Scats contained mature and immature *M. astonii* seeds, plus a few damaged *M. astonii* seeds and seed pieces (Table 1). All *M. complexa*

Table 1. *Muehlenbeckia astonii* and *M. complexa* seeds in 1159 skink (*Oligosoma maccanii* and *O.* aff. *polychroma* Clade 5) scats collected at Kaitorete Spit during February–June 2011 ($n = 528$) and February–May 2012 ($n = 631$).

			Number of seeds			
Plant species	Year	Mature	Immature	Damaged	Pieces	Total
Muehlenbeckia astonii	2011	28	8	1	0	37
	2012	42	32	6	5	85
	Total	**70**	**40**	**7**	**5**	**122**
Muehlenbeckia complexa	2011	15	0	4	2	21
	2012	16	0	1	5	22
	Total	**31**	**0**	**5**	**7**	**43**

seeds were mature, though a few were damaged or in pieces (Table 1). We found no fruit pulp in scats, and skinks apparently digest the soft *Muehlenbeckia* fruits completely.

Skink fruit consumption (percentage of scats with seeds) differed among months in 2011 ($\chi^2 = 18.85$, d.f. = 3, $P = 0.0003$) and marginally so in 2012 ($\chi^2 = 6.88$, d.f. = 3, $P = 0.076$). In both years seeds were most frequent in scats between February and April (73.6% of all scats with seeds), even though ripe *M. astonii* fruits were available from February to June (Figure 1). Fruit consumption was highest between February and April 2011

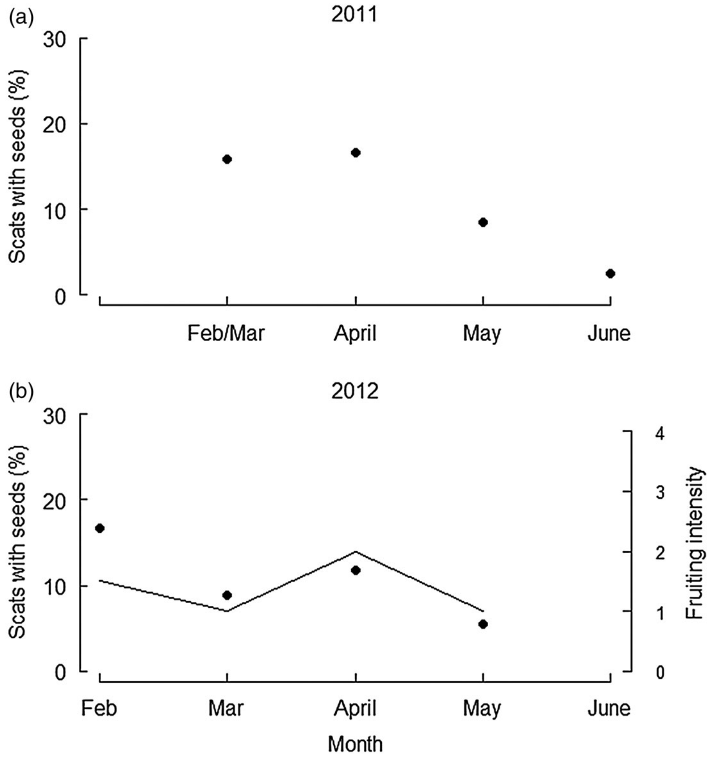

Figure 1. Percentage of skink scats containing seeds (●) during *Muehlenbeckia astonii* fruiting season at Kaitorete Spit. **A,** 2011; **B,** 2012. In 2011, scats were collected from mid-February to late June, while in 2012 scats were collected from the start of February to the end of May. The solid line indicates median availability of ripe fruit for 10 *M. astonii* focal plants. Fruiting intensity was assessed using a qualitative linear scale from 0–5.

and in February 2012 (16%–17% of scats with seeds) (Figure 1). During the study period, *M. astonii* plants on Kaitorete Spit produced few fruits compared to cultivated plants or those at Travis Wetland, Christchurch. When fruiting intensity was assessed in 2012, focal plants never had more than c. 30 ripe fruits at one time, though flowers were common (hundreds) on some plants. In contrast, individual plants at Travis Wetland had hundreds of ripe fruits.

Muehlenbeckia astonii seeds from skink scats collected at Kaitorete Spit had significantly lower germination success (25% of 'mature' and 0% of 'immature' seeds) than hand-cleaned mature seeds collected directly from plants (50%; $\chi^2 = 24$, d.f. = 2, $P < 0.0001$). Likewise, germination success was significantly lower for *M. complexa* seeds from scats (21.4%) than hand-cleaned seeds from plants (78.6%; $\chi^2 = 7$, d.f. = 1, $P = 0.008$).

Skink scats (with and without seeds) occurred at the highest densities in retreats furthest (8–10 m) from focal *M. astonii* plants, and tended to decline with increasing proximity to study plants (Figure 2). In contrast, seed density in retreats declined with increasing distance from the 'parent' plant (nearest fruiting *M. astonii*; Figure 2). Skinks dispersed *M. astonii* seeds up to at least 10 m from 'parent' plants (the maximum distance observable due to spacing between female *M. astonii* plants), although many seeds (48.4%) were deposited beneath the 'parent' canopy (Figure 2). *Muehlenbeckia complexa* seeds were found in scats up to 12.8 m from the nearest fruiting conspecific plant. Mean and median dispersal distances of scats containing seeds were 3.19 m and 2 m (± 3.24 SD) respectively for *M. astonii* and 2.30 and 3.80 m (± 0.75) for *M. complexa*.

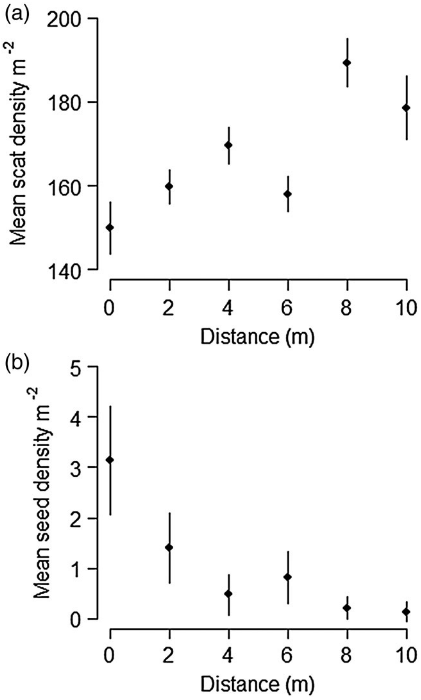

Figure 2. Mean densities in relation to distance from the nearest fruiting *Muehlenbeckia astonii* plant at Kaitorete Spit. **A,** Skink scats; **B,** *Muehlenbeckia astonii* seeds in skink scats. Error bars are 95% confidence intervals.

Skink seed dispersal on Matiu-Somes Island

We captured 476 skinks in 1000 trap nights in the two habitats: 80 and 210 northern grass skink (*Oligosoma polychroma*) and 83 and 103 spotted skink (*Oligosoma lineoocellatum*) in the planted and unplanted habitats, respectively. We recovered 128 scats (65 from *O. polychroma*, 31 from *O. lineoocellatum* and 32 where both species were captured together), 21 (16.4%) of which contained seeds of fleshy-fruited plants (Table 2). These scats contained 34 identified and 18 unidentified seeds. In the planted habitat, the seeds were mainly *C. repens* and were recovered from *O. lineoocellatum*. In the unplanted habitat, seeds were from *C. propinqua* and *M. complexa*, and were recovered mainly from *O. polychroma*. Seed dispersal distances ranged from 0–3.4 m from the margin of the nearest fruiting plant (Table 2). For each plant species, the mean seed dispersal distance was 1–2.4 m.

Gecko frugivory on Stephens Island and germination of Piper excelsum

We collected 82 gecko scats from Stephens Island, 66 (80.5%) of which contained seeds. Artificial retreats generally contained only *W. maculata*. One scat was collected from a retreat with both *W. maculata* and *T. stephensi*, which contained a single *M. australis* seed. Excluding this scat, 80.2% of remaining scats (either confirmed or likely to be from *W. maculata*) contained seeds. We observed *W. maculata* feeding extensively on *P. excelsum* fruits and almost all seeds in scats were from this species (65 scats contained 2034 mature, 366 immature and five damaged *P. excelsum* seeds, and six seed pieces). Scats with seeds had 36.5 ± 15.6 (mean ± SD) seeds per scat, with 5.5 ± 6.0 immature seeds per scat (15.1% of all ingested seeds were immature). *Piper excelsum* fruits measured 10.9 ± 0.7 × 30.3 ± 4.5 mm and contained 117.8 ± 32.8 seeds, of which 20.9 ± 16.6 (17.7%) were immature.

Woodworthia maculata consumption of *P. excelsum* fruits had no effect on germination percentage compared to seeds collected directly from plants, either via scarification of seeds (gecko ingested vs. hand-cleaned, $z = -1.351$, $P = 0.177$) or removal of fruit pulp (hand-cleaned vs. seeds in pulp, $z = 0.859$, $P = 0.391$). *Piper excelsum* seeds ingested by geckos germinated as well (67.9 ± 14.0%, mean ± SD) as hand-cleaned seeds (70.2 ± 16.3%) and seeds in pulp (71.6 ± 18.6%).

Lizard frugivory literature review

Lizard consumption of fleshy fruits is widespread in New Zealand, both geographically and taxonomically. Lizard frugivory has been reported from the Three Kings Islands in the far north (Parrish & Gill 2003) to Central Otago in the south (Tocher 2003). New Zealand has 42 extant gecko species and 55 extant skink species (Hitchmough et al. 2013). To date, six gecko species in four genera (*Hoplodactylus*, *Woodworthia*, *Dactylocnemis* and *Naultinus*) and 14 skink species (all New Zealand skinks are in the genus *Oligosoma*) have been reported eating fruits (Tables 3 and 4).

Lizards eat fruits from at least 23 native plant species in nine families (Table 3). Only five of these plant species are divaricating (*Coprosma propinqua*, *C. dumosa*, *C. rugosa*, *Melicytus alpinus* and *Muehlenbeckia astonii*), while a further four species are lianes

Table 2. Seeds in 128 skink (*Oligosoma polychroma* and *O. lineoocellatum*) scats collected from Matiu-Somes Island during February–April 1997, and mean dispersal distance to the nearest fruiting conspecific. Number of scats and dispersal distance range are presented in brackets.

Plant species	No. seeds (no. scats)	Mean dispersal distance in m (range)
Coprosma propinqua	10 (5)	1.31 (0.2–2.4)
Coprosma repens	6 (2)	2.4 (2.4)
Coprosma robusta	11 (7)	0.95 (0–2.8)
Muehlenbeckia complexa	6 (6)	0.99 (0–3.39)
Unknown	18 (4)	

with a tangled growth form (*Muehlenbeckia complexa*, *M. australis*, *M. axillaris* and *Cassytha paniculata*). So far, lizards have been recorded eating fruits of only one non-native species (Table 3). Lizards eat fruits from 3–13 mm wide with a mean diameter of 6.2 mm (± 1.3 mm), similar to fruits from the New Zealand fleshy-fruited flora (6.4 ± 3.8 mm; Lord et al. 2002). The largest fruits eaten by lizards are *Piper excelsum* (9–12 mm diameter fruits, which are eaten in pieces) and *Gaultheria* spp. (7–13 mm diameter).

The frequency of lizard stomachs and scats containing seeds is highly variable, ranging from 1%–58% and 2%–86%, respectively (Table 4). However, sampling has occurred at different seasons in different studies, and fruit consumption varies with spatial and temporal fruit availability. Seeds are more likely to be detected in stomachs than scats given the same sample size, because a single stomach can produce several scats. Both grand (*O. grande*) and Otago (*O. otagense*) skinks eat considerable quantities of fruit, particularly in autumn (Tocher 2003). *Oligosoma otagense* appear to specialise on fruits, with > 60% of droppings containing seeds in May (Tocher 2003). Fleshy fruits were the second most important food item by volume after invertebrates (c. 15%–18% of stomach contents) for *O. inconspicuum* and *O. maccanni* stomach contents sampled from September to June in Central Otago, but were less important for *O.* aff. *polychroma* Clade 5 (1%; Patterson 1992). *Coprosma propinqua* fruits comprised 8% of food items in *O.* aff. *polychroma* Clade 5 scats ($n = 10$), 39% in *W.* cf. *brunnea* scats ($n = 7$) and were absent from *O. maccanni* scats ($n = 29$) at Birdlings Flat, Canterbury (Freeman 1994). Seeds occurred more frequently in gecko scats (40.2 ± 29%, mean ± SD, $n = 13$) than those of skinks (25.5 ± 25.6%, $n = 6$). However, the difference was not statistically significant ($t = -1.089$, $P = 0.291$, d.f. = 18).

At Macraes Flat, the distribution of *O. grande* on rock tors was correlated with the diversity of fruiting shrubs, which was higher in tussock grassland than adjacent pasture (Whitaker 1996). However, there was no difference in *O. grande* body condition and reproduction between tussock and pasture, suggesting that fruit availability was not a limiting factor (Whitaker 1996). Skink distribution may have been influenced by vegetation attributes other than fruit availability. In dryland ecosystems such as Macraes Flat, *O.* aff. *polychroma* Clade 5 and *O. maccanni* favoured habitats dominated by indigenous vegetation rather than exotic pasture grasses (Walker et al. 2014).

Fruit colour preferences

In captive trials with fruits of four plant species, wild *Woodworthia* sp. 'Southern Alps' ate more fruits (30% of fruits offered) of species with blue or white fruits (*Coprosma petriei*

Table 3. Fleshy-fruited plant species eaten by lizards in New Zealand. Modified and updated from Whitaker (1987).

Plant family	Plant species	Growth form	Fruit colour	Fruit width (mm)	Lizard frugivores	Other frugivores	References
Rubiaceae	*Coprosma depressa*	Prostrate shrub	Red	5–6	*Oligosoma waimatense*	*Nestor notabilis*	Whitaker & Loh 1990, cited in Marshall 2005; Young et al. 2012
	C. dumosa	Divaricate shrub	Red or white	5	*O. otagense, O. grande*	–	Tocher 2003
	C. macrocarpa subsp. *macrocarpa*	Shrub	Orange	?	*O. fallai*	*Turdus merula*	Parrish & Gill 2003; Higgins et al. 2006
	C. propinqua	Divaricate shrub	White–blue	3–7	*Woodworthia maculata*, *O. waimatense*, *O. otagense*, *O. grande*, *W.* cf. *brunnea*, *Oligosoma* aff. *polychroma* Clade 5, *O. maccanni*, *O. lineoocellatum*, *O. polychroma*	*Sturnus vulgaris*, *Zosterops lateralis*, *T. merula*, *T. philomelos*, *Petroica macrocephala*, *Prosthemadera novaeseelandiae*, *Hemiphaga novaeseelandiae*, *Anthornis melanura*, *N. notabilis*	Whitaker 1985, cited in Whitaker 1987; Freeman 1994; Wotton 2002; Tocher 2003; this study; Ferguson & Drake 1999; Higgins & Davies 1996; Higgins et al. 2001, 2006; Young et al. 2012
	C. repens	Shrub or small tree	Orange	8	*O. smithi*, *O. lineoocellatum*	*A. melanura*, *S. vulgaris*, *Z. lateralis*	Falla 1936, cited in Whitaker 1987; this study; Higgins et al. 2001, 2006
	C. robusta	Shrub or small tree	Orange	4–5	*O. polychroma*, *O. lineoocellatum*	*T. merula*, *H. novaeseelandiae*, *A. melanura*, *P. novaeseelandiae*, *S. vulgaris*, *Z. lateralis*	This study; Higgins & Davies 1996; Higgins et al. 2001, 2006; Williams & Karl 1996
	C. rugosa	Divaricate shrub	White–blue	6–8	Not identified	–	Marshall 2005
Violaceae	*Melicytus alpinus*	Divaricate shrub	White–blue	5 (3–6)	*W.* sp., *O. waimatense*, *O.* aff. *polychroma* Clade 5, *O. otagense*, *O. grande*	*A. melanura*	Whitaker 1987; Tocher 2003; Higgins et al. 2001
Piperaceae	*Piper excelsum*	Shrub or small tree	Orange	11 (9–12)	*H. duvaucelii*, *Dactylocnemis* 'Poor Knights', *O. oliveri*, *O. alani*, *O. whitakeri*, *O. smithi*, *W. maculata*	*H. novaeseelandiae*, *P. novaeseelandiae*, *Z. lateralis*	Whitaker 1968 and Southey 1985, cited in Whitaker 1987; this study; Higgins & Davies 1996; Higgins et al. 2006
Ericaceae	*Gaultheria sp.*	Shrub	Red or white	7–13	*O. grande, O. otagense*	–	Tocher 2003
	Gaultheria ?antipoda	Shrub	Red or white	7–13	*O. grande, O. otagense*	–	Whitaker 1987
	Gaultheria depressa	Prostrate shrub	Red or white	7–13	*O. maccanni, O. inconspicuum, O.* aff. *polychroma* Clade 5	*N. notabilis, , Falco novaeseelandiae, Deinacrida connectens, Zealandosandrus maculifrons*	Patterson 1985; Young et al. 2012; Young & Bell 2010; Burns 2006; Larsen & Burns 2012
	Leucopogon fraseri	Shrub	Orange	4–6	*O. waimatense, O. maccanni, O. inconspicuum, O.* aff. *polychroma* Clade 5, *W.* sp., *O. otagense, O. grande*	*N. notabilis, F. novaeseelandiae*	Patterson 1985; Whitaker 1987; Tocher 2003; Young et al. 2012; Young & Bell 2010
	Pentachondra pumila	Prostrate shrub	Red	5.5 (4–7)	*O. grande, O. otagense*	*N. notabilis*	Tocher 2003; Young et al. 2012
Polygonaceae	*Muehlenbeckia astonii*	Divaricate shrub	White	?	*W.*sp., *O. macaanii, O.* aff. *polychroma* Clade 5	*Z. lateralis*	De Lange & Jones 2000; this study; Udy 2004

(*Continued*)

Table 3. Continued.

Plant family	Plant species	Growth form	Fruit colour	Fruit width (mm)	Lizard frugivores	Other frugivores	References
	Muehlenbeckia australis	Tangled vine	White	?	*W. maculata* or *Toropuku stephensi*	*Z. lateralis*, *S. vulgaris*, *P. novaeseelandiae*, *H. novaeseelandiae*, *A. melanura*; *T. philomelos*	This study; Williams & Karl 1996; Higgins & Davies 1996; Higgins et al. 2001, 2006
	Muehlenbeckia axillaris	Tangled vine	White	5–7	*W.* sp., *O. grande*, *O. waimatense*, *W.* sp. 'Southern Alps'	*Z. lateralis*, *N. notabilis*	Whitaker 1985, cited in Whitaker 1987; Marshall 2005; Lawrence 1997; Higgins et al. 2006; Young et al. 2012
	Muehlenbeckia complexa	Tangled vine	White	?	*W. maculata*, *O.* aff. *polychroma* Clade 5, *O. maccanni*, *O. polychroma*, *O. lineoocellatum*, *O. moco*	*S. vulgaris*, *H. novaeseelandiae*	Whitaker 1982; Wotton 2002; this study; M. Baling pers. comm.; Higgins & Davies 1996; Higgins et al. 2006; Ferguson & Drake 1999
Lauraceae	*Cassytha paniculata*	Tangled vine	Green, yellow-green, red-green	4–7	*Naultinus grayi*	–	Whitaker 1987
Thymelaeaceae	*Pimelea oreophila*	Prostrate shrub	Orange	3	Not identified	–	Marshall 2005
	Pimelea prostrata	Prostrate shrub	White or red	?	*O. fallai*	*T. merula*	McCann 1955, cited in Whitaker 1987; Higgins et al. 2006
Solanaceae	*Solanum nodiflorum*	Shrub	Black	6	*H. duvaucelii*, *W. maculata*, *O. alani*, *O. oliveri*, *O. whitakeri*, *O. smithi*	–	Southey 1985, cited in Whitaker 1987
Coriariaceae	*Coriaria ?sarmentosa*	Shrub	Black	6–11	*O. otagense*	*N. notabilis*	Whitaker 1987; Young et al. 2012
Scrophulariaceae	*Myoporum laetum*	Tree	Purple	?	*O. fallai*	*T. merula*, *A. melanura*, *H. novaeseelandiae*, *P. novaeseelandiae*, *Z. lateralis*	Parrish & Gill 2003; Higgins & Davies 1996; Higgins et al. 2001, 2006
Phytolaccaceae	*Phytolacca octandra*[a]	Shrub	Black	8	*O. smithi*, *W. maculata*	–	Whitaker 1968, cited in Whitaker 1987; Wotton 2002

Fruit colour and width (mean and range) from Allen (1961), Webb et al. (1988), Young et al. (2012), Marshall (2005) and Flora of Australia Online.

[a] Non-native species.

Table 4. Frequency of seeds in lizard scats or stomachs ([a]) and months when samples were collected. *n* = number of scats or stomachs. Sites are listed from north to south.

Site	% freq	Months	*n*	Fruits eaten	Lizard species	Study
Middle Is	32	Dec–Mar	101	*Solanum nodiflorum*, *Piper excelsum*, *Coprosma spp.*	*Oligosoma alani*	Southey 1985, cited in Whitaker 1987
	11		89		*O. whitakeri*	
	9		49		*O. oliveri*	
Mana Is	39	Feb–Apr	154	*C. propinqua*, *Muehlenbeckia complexa*	*Woodworthia maculata*	Wotton 2002
Matiu-Somes Is	16	Jan–Apr	128	*C. repens*, *C. robusta*, *C. propinqua*, *M. complexa*	*O. polychroma* *O. lineoocellatum*	This study
Stephens Is	80	Feb–Apr	79	*P. excelsum*, *M. australis*	*W. maculata*	This study
Turakirae	58[a]	Jan–Feb	224	*M. complexa*, *C. propinqua*	*W. maculata*	Whitaker 1982
Wellington	6[a]	19 months	68	2 spp.	*O. polychroma*	Southey 1985, cited in Whitaker 1987
Nelson Lakes	5[a]	Jan–Dec	101	Unknown	*O. polychroma*	Spencer et al. 1998
	16[a]		84		*O. lineoocellatum*	
Birdlings Flat	43	Nov–Mar	7	*C. propinqua*	*W.* cf. *brunnea*	Freeman 1994
	20		10		*O.* aff. *polychroma* Clade 5	
	0		29		*O. maccanni*	
Kaitorete Spit	10	Feb–Jun	1159	*M. astonii*, *M. complexa*	*O.* aff. *polychroma* Clade 5 *O. maccanni*	This study
Cass	2	?	43	*M. axillaris*	*W.* sp. 'Southern Alps'	Lawrence 1997
Rock and Pillar Range and Lammermoor Range	4[a]	21 months, Sep–Jun	110	*Gaultheria depressa*, *Leucopogon fraseri*	*O. maccanni*	Patterson 1992
	3[a]		81		*O. inconspicuum*	
	1[a]		210		*O. polychroma*	
Macraes Flat	86	Feb	14	*M. axillaris*, *Melicytus alpinus*	*O. grande*	Whitaker 1987
Macraes Flat	32	Feb, May, Nov	167	*L. fraseri*, *Melicytus alpinus*, *Gaultheria* spp., *C. dumosa*, *Pentachondra pumila*, *C. propinqua*	*O. grande*	Tocher 2003
	39		78		*O. otagense*	
Macraes Flat	66	Feb–Mar	174	*C. propinqua*, *C. rugosa*, *C. dumosa*, *L. fraseri*, *M. alpinus*, *Pentachondra pumila*, *Pimelea oreophila*, *M. axillaris*	*O. grande* *O. maccanni* *O.* aff. *polychroma* Clade 5	Marshall 2005

and *Melicytus alpinus*) than species with red or orange fruits (*Acrothamnus colensoi* and *Leucopogon fraseri*, 22.7%; Lawrence 1997). However, because both red-fruited species were in a single family, other correlated fruit attributes may have influenced preferences. Captive feeding trials that controlled for phylogenetic influences showed a preference by two skink species (*O. maccannii* and *O.* aff. *polychroma* Clade 5) for white–blue fruits over red fruits (Marshall 2005). Skinks were more likely to approach white or blue *Coprosma* fruits (*C. cheesemanii* white morph, *C. dumosa*, *C. propinqua*, *C. rugosa*) before red fruits (*C. cheesemanii* red morph, *C. rotundifolia*, *C. decurva*, *C. robusta*), when offered fruits of each colour simultaneously on a green background (Marshall 2005). Although the conspicuousness of red or white–blue fruits against a green background was not measured (Marshall 2005), red or black *Coprosma* fruits are more conspicuous (in terms of human colour vision) against a foliage background than white, bluish or polymorphic fruits (Lee et al. 1994). In situ feeding trials at Macraes Flat, Otago, found that *O. grande* preferred white *C. cheesemanii* fruits to red fruits of the same species (Marshall 2005). However, there was no difference in lizard fruit removal rates of white- or red-fruited colour morphs of *Acrothamnus colensoi* in Canterbury subalpine shrublands (Young & Kelly 2014).

Lizard fruit colour preferences in feeding trials are supported by field observations of lizard frugivory. Among the 16 species reported by Whitaker (1987) as eaten by lizards, white–blue fruits were more common than expected compared to their prevalence in the New Zealand fleshy-fruited flora (Lord et al. 2002). Our analysis using an updated list of 23 species eaten by lizards confirms this finding ($\chi^2 = 6.9311$, d.f. = 1, $P = 0.008$; Figure 3). Nearly half (47.8%, 11 species) of the 23 species eaten by lizards have white–blue fruits (Figure 3), though white–blue fruits comprise only 21.5% of the fleshy-fruited flora (Lord et al. 2002).

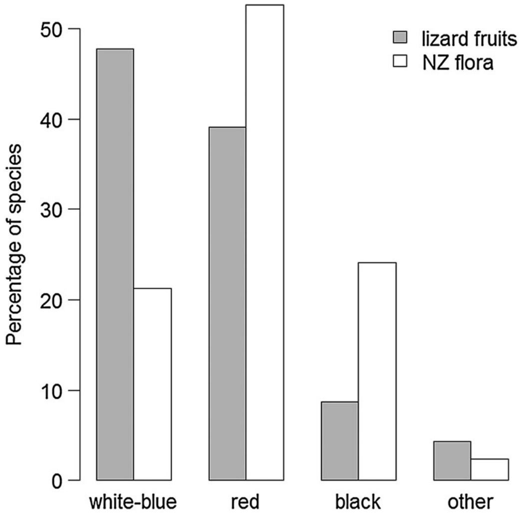

Figure 3. Percentage of fruits in each colour class eaten by lizards ($n = 23$) and in the fleshy-fruited New Zealand flora ($n = 245$, data from Lord et al. 2002). Lizards eat white–blue fruits more commonly than expected compared to their availability in the flora ($\chi^2 = 6.9311$, d.f. = 1, $P = 0.008$).

Bird frugivory of divaricating plants

Birds have been recorded eating fruits of at least 10 species of divaricating shrubs and three species of tangled vines. Three of the divaricating species whose fruits are eaten by lizards are also eaten by birds (Table 3). Birds also eat fruits of several divaricating shrub species which lizards have not yet been recorded eating (*Coprosma crassifolia*, *C. rhamnoides*, *C. rotundifolia*, *C. rigida*, *Myrsine divaricata*, *Neomyrtus pedunculata* and *Pittosporum divaricatum*) (Williams & Karl 1996; Higgins et al. 2006; Burns & Lake 2009). At three sites near Nelson, birds were not recorded eating fruits of the divaricating shrubs *C. crassifolia* and *C. propinqua*, though fruits of other divaricating species were eaten (Williams & Karl 1996). Of the 23 native species whose fruits are eaten by lizards, only 17 have been recorded as eaten by birds.

Seed dispersal quantity

Lizards can remove a significant proportion of available fruits. At high lizard densities on Mana Island, *W. maculata* removed at least 47% and up to 93% of *C. propinqua* fruits when birds were excluded (Wotton 2002). When both birds and lizards had access the percentage of fruits removed did not increase, compared to removal by lizards alone (Wotton 2002). Seagulls (*Larus* spp.) were the only birds observed at the site during the study period, and they occasionally eat fleshy fruits (Thorsen 2003). In Canterbury subalpine shrublands, lizards removed about half of the fruits removed by all frugivores (birds, mammals and lizards), despite their low abundance (Young & Kelly 2014). Lizard removal was particularly high for *C. propinqua* (c. 70% of all removed fruits), and lowest for *Gaultheria depressa* at one of the two sites (c. 38%).

On Mana Island, *W. maculata* deposited seeds (mostly *C. propinqua*) at mean densities of 98 m^{-2} (range 0–258 m^{-2}; Wotton 2002). Both fruit availability and lizard densities were high on Mana Island. However, at Kaitorete Spit the density of *Muehlenbeckia astonii* seeds deposited by skinks was much lower (Figure 2) probably due to both relatively low skink abundance (200–400 ha^{-1} at nearby Birdlings Flat; Freeman 1997) and low fruit availability. In coastal shrublands at Turakirae Head, lizard densities ranged from 4000–12,000 animals per hectare, and lizards may have dispersed at least 1,000,000 seeds ha^{-1} $year^{-1}$ (Whitaker 1987).

Seed dispersal quality

We know of only one other study that has tested the effect of lizard ingestion on seed germination (Wotton 2002). *Coprosma propinqua* seeds ingested by *W. maculata* germinated as well (72%) as hand-cleaned seeds (67%) and seeds in whole fruits (77%; Wotton 2002).

Seed dispersal distance is a function of gut passage time and movement patterns. For wild *W.* sp. 'Southern Alps' tested in captivity, gut passage time was negatively correlated with temperature (Lawrence 1997). Gut passage times were shortest (23 ± 4 h, mean ± SEM) at 20 °C, increased to 43 (± 4) h at 17 °C and 262 (± 19) h at 10 °C (Lawrence 1997).

Woodworthia maculata at Turakirae Head near Wellington occasionally moved more than 20 m between recaptures (Whitaker 1982), while *O. grande* at Macraes Flat, Otago, regularly moved between rock outcrops more than 10 m apart (Whitaker 1996). Between recaptures, individual *O. grande* moved on average more than 70 m between outcrops (Whitaker 1996). Adult female *O. grande* sometimes move more than 15 m to visit specific fruiting plants (Eiffler & Eiffler 1999). An adult *O. waimatense* was observed travelling 9 m across scree to feed on *C. depressa* fruits (Whitaker & Loh 1990, cited in Marshall 2005). At Pukerua Bay, Wellington, recaptures of five lizard species (*O. aneum*, *O. whitakeri*, *O. polychroma*, *O. zelandicum* and *W. maculata*) were mostly (75%–93% of movements) within 4 m of the site of first capture (Towns & Elliott 1996). While average movements were short (mean 2–6.3 m), lizards occasionally moved longer distances (29–64 m; Towns & Elliott 1996).

Lizards disperse seeds of several plant species up to at least 12 m (Wotton 2002; this study), enabling seeds to escape from the parent plant. Longer dispersal distances are possible, but can be difficult to measure due to the proximity of conspecific plants (Wotton 2002; this study). *Woodworthia maculata* deposited 66% of *C. propinqua* seeds ingested beyond the parent canopy (Wotton 2002). Skinks (*O. lineocellatum* and *O.* aff. *polychroma* Clade 5) dispersed 52% of *Muehlenbeckia astonii* seeds ingested away from the parent (Figure 2). Glasshouse trials indicate that for both *M. astonii* and *M. complexa* seedling growth was poorer in soil previously occupied by a conspecific plant than in soil occupied by another species (D Wotton, unpubl. data). Seed dispersal may enable *Muehlenbeckia* species to escape these negative soil feedbacks.

In shingle beach shrubland on Mana Island, *W. maculata* deposited *C. propinqua* seeds in rocky crevices. These sites provided suitable conditions for seedling establishment, and enhanced establishment compared to deposition in exotic grass (Wotton 2002).

Discussion

Lizard frugivory in New Zealand

Of the 97 extant native lizard taxa in New Zealand (Hitchmough et al. 2013), 21% are known to eat fleshy fruits. Most of the remaining lizard species probably eat fruits when they co-occur. Lizard frugivory has been recorded in shrublands (Freeman 1994; Lawrence 1997; this study), grasslands (Patterson 1992; this study), shingle beaches (Wotton 2002) and forests (Parrish & Gill 2003), and from lowland to subalpine elevations (Young & Kelly 2014). Not surprisingly, many of the lizard frugivory observations are from offshore islands, which often lack introduced mammalian predators and have much higher lizard densities than the mainland.

Do lizards prefer white–blue fruits?

Laboratory and field-based evidence suggest that New Zealand lizards prefer white and blue fruits to other fruit colours. This colour preference may be unique to New Zealand. A similar comparison between fruit colours in the flora and those eaten by lizards found no colour preference in either the Canary Islands or the Balearic Archipelago (Valido & Olesen 2007). Fruit size, colour and plant growth form are associated across the New Zealand flora (Lord et al. 2002), so lizards may be selecting fruits based on correlated, non-fruit traits. Blue and white fruits are correlated with small fruit size, shrub and divaricate growth forms, montane to alpine elevations and open habitats (Lord & Marshall

2001). Blue-fruited *Coprosma* species have narrower leaves than those with other fruit colours, while non-red (including blue) fruits are more frequent in small-leaved *Coprosma* species and at low elevation (Lee et al. 1988). Nutritional composition is not correlated with fruit colour, at least in *Coprosma*, where small, carbohydrate-rich and lipid-poor fruits appear to cater to a wide range of generalist frugivores (Markey 2005).

Most lizard families investigated have either trichromatic or tetrachromatic colour vision, with sensitivity reaching into ultraviolet wavelengths (New et al. 2012). Ultraviolet reflectance may not be important for fruit colour detection by New Zealand lizards, given that only one out of 41 native plant species tested had strong ultraviolet reflectance from fruits (Lee et al. 1990). At least some nocturnal gecko species are capable of colour vision, and can distinguish blue from grey at light intensities equivalent to dim moonlight (Roth & Kelber 2004). Given the sensitivity of lizards' colour vision, examination of the reflective qualities of fruits of lizard-dispersed species against foliage backgrounds in both sunlight and moonlight/starlight could provide insight into the role that fruit colour plays in lizard frugivory, and the role that lizard frugivory plays in evolution of fruit colour.

Are divaricating plants dispersed by lizards, not birds?

Divaricating species are unusually common in New Zealand, comprising nearly 10% of the woody flora (Greenwood & Atkinson 1977). Nevertheless, lizards have been recorded eating fruits of only five divaricating species to date. This may be due to a paucity of studies investigating lizard frugivory. Birds have been observed feeding on fruits of several divaricating plant species, contrary to Whitaker's (1987) observation that these fruits are largely inaccessible to birds. Birds probably eat fruits on the exterior of some divaricating species (Wotton 2002). Only two studies have quantified fruit removal rates from divaricating plants by birds and lizards; in both cases, when birds were excluded, lizards removed most *C. propinqua* fruits, and fruit removal did not increase when birds had access (Wotton 2002; Young & Kelly 2014). Divaricating plants may be ideal habitat for lizards, providing food, concealment and refuges from predators.

Plant trait evolution

The combination of traits associated with putative lizard dispersal (shrub and divaricate growth form, small leaves and white–blue fruits) appears to be unique to New Zealand (Lee et al. 1988; Markey 2005). *Coprosma* is the largest fleshy-fruited genus in New Zealand, with drupes exhibiting a range of colours (Lee et al. 1988). Red fruits are less common in New Zealand *Coprosma* (46%) than in *Coprosma* elsewhere (> 70%; Lee et al. 1988). Small-leaved, divaricating plants are unusually common in the New Zealand flora, and may have evolved in response to moa browsing (Greenwood & Atkinson 1977) or climate (McGlone & Webb 1981). The first evidence for the divaricate growth form in New Zealand dates from the early Miocene (20–16 Ma; Campbell et al. 2000). Cycles of mountain building and glaciation led to novel montane-alpine habitats, enabling colonisation and rapid speciation by many genera including *Coprosma*. At least some lizards were present in New Zealand throughout the *Coprosma* radiation.

Fruit size, colour and plant growth form appear to have evolved in concert in at least some New Zealand plant groups, possibly influenced by lizard dispersal (Lord et al. 2002).

White–blue fruits and small leaves have evolved independently several times in *Coprosma*, which may indicate selection for these traits by lizards (Markey 2005). Tree wētā (*Hemideina crassidens*) also prefer blue and white fruits and may have similarly influenced plant evolution in New Zealand (Fadzy & Burns 2010). However, wētā destroy a much greater proportion of ingested seeds than lizards (Fadzy & Burns 2010; Larsen & Burns 2012).

Testing the ultimate evolutionary question of the extent to which white–blue fruits and divaricating plants are adapted to lizard dispersal may not be possible, given the decline and extinction of so many birds since human arrival in New Zealand. Around 24% of all bird species are extinct (Tennyson 2010), with a disproportionate loss of flightless frugivores (80% extinct; Thorsen et al. 2011). Although only two lizard species have gone extinct (Hitchmough et al. 2013), remaining species have undergone major declines in abundance and distribution (Towns & Daugherty 1994). Nevertheless, it is not possible to say whether lizards were more or less important in the past than they are now. Seed dispersal mutualisms evolved under the influence of these past disperser communities, which may have exerted different selection pressures than the subset of dispersers remaining today. Bird dispersal of low-growing fleshy-fruited plants, including divaricating shrubs, may also be less common now than in pre-human times, due to behavioural changes. On offshore islands lacking introduced mammalian predators, endemic birds such as kererū (*Hemiphaga novaeseelandiae*) often forage on the ground, but they rarely do so on the mainland.

Do lizards eat fleshy fruits in significant quantities?

Like many omnivores that include fruit in their diet, New Zealand lizards appear to eat fleshy fruits when they are available. Fruits comprise a significant component of many lizards' diets, at least on a seasonal basis. Fruit consumption at Kaitorete Spit was probably low due to a paucity of fleshy fruits. Fruit consumption by lizards also appears to be greater at higher temperatures, both in captivity (Lawrence 1997) and in the field; lizards ate more *M. astonii* fruits earlier in the season at Kaitorete Spit (this study).

Outside New Zealand, some of the best documentation of the importance of fruits in the diets of island lizards include studies of seven *Podarcis* species in the western Mediterranean (Pérez-Mellado & Corti 1993) and two *Gallotia* species in the Canary Islands (Valido & Nogales 1994; Valido et al. 2003). These lizards are generally more omnivorous than those on nearby continents, and some are highly frugivorous. For example, in 8 months out of the year, fruit remains are found in > 50% of *Gallotia galloti* droppings in the Canary Islands (range 2% in January to 95% in April). In a review of herbivory in over 450 lizards species, Cooper & Vitt (2002) determined that, after correcting for lizard phylogeny, insularity was the only ecological variable associated with consumption of plants (leaves, flower resources and/or fruit). Numerous hypotheses have been proposed to explain this, including reduced prey availability on islands, but none have been confirmed.

The quantity of seed dispersed by lizards depends on both degree of frugivory and lizard abundance. Lizard densities similar to those likely in pre-human times now occur only at mainland sites with good protective cover (e.g. Turakirae Head, Wellington), and on offshore islands lacking invasive mammalian predators (Whitaker 1987). The contribution of lizards to seed dispersal at mainland sites where densities are low has previously been thought limited. However, even at low lizard densities fruit removal rates can be surprisingly high (Young & Kelly 2014), so their importance should not be discounted.

Do lizards damage ingested seeds?

Data for the four New Zealand species tested so far show that <10% of ingested seeds are visibly damaged by lizards. However, skinks ate many *M. astonii* fruits before seeds were mature, effectively killing 42.6% of seeds (both immature seeds and those damaged by gut passage). Passage through geckos had no effect on germination percentage of *Piper excelsum* (this study) and *C. propinqua* (Wotton 2002), but skink ingestion decreased germination of two *Muehlenbeckia* species (this study), though the latter results should be treated with caution due to the small sample sizes. Kaitorete Spit is the southernmost location for *M. astonii* and seeds there may ripen later than further north, where the climate is warmer and the growing season longer. It would be useful to know whether skinks commonly ingest unripe seeds in other *M. astonii* populations. Lizard fruit consumption and gut passage rates increase with temperature (Lawrence 1997), which may influence seed viability. Longer gut passage times reduce seed viability in some species (Murray et al. 1994), but have no effect in others (Castilla 2000).

Data from other islands also show that lizard gut passage effects on germination are generally small and inconsistent (Valido & Nogales 1994; Valido et al. 2003; Nogales et al. 2005; Rodríguez-Pérez et al. 2005; Rodríguez-Pérez & Traveset 2010; Zuel et al. 2012; Rumeu et al. 2011). A meta-analysis ($n = 39$ species) found that seed passage through reptiles' guts had no significant effect on germination percentage (Traveset & Verdú 2002).

Do lizards deposit seeds in safe sites?

Lizard seed dispersal distances are on a local scale (generally < 20 m, though potentially > 70 m), and colonisation of new sites via long-distance lizard dispersal is unlikely. Nevertheless, the short distances over which lizards disperse seeds can be advantageous in two respects. Firstly, lizards in New Zealand enable most seeds ingested to escape beyond the influence of parent plants (Wotton 2002; this study). Seeds in the vicinity of adult conspecifics can suffer disproportionate mortality due to host-specific seed and seedling predators or pathogens (Janzen 1970; Connell 1971). These effects are apparent in at least two *Muehlenbeckia* species, likely caused at least in part by host-specific soil pathogens (D Wotton, unpubl. data).

Secondly, lizards may provide directed dispersal (Howe & Smallwood 1982) for at least one plant species by depositing seeds in microsites that provide suitable conditions for seedling establishment (Wotton 2002). Overseas data provide mixed evidence as to whether lizard dispersal confers an advantage by directing seeds to suitable establishment sites. In coastal sand dunes in Brazil, the lizard *Tropidurus torquatus* deposits seeds on sandy substrates in the open where few seeds germinate (Fialho 1990). In coastal shrublands of the Balearic Islands, *Podarcis lilfordi* is the only disperser of the shrubs *Daphne rodriguezii* (Rodríguez-Pérez & Traveset 2010) and *Cneorum tricoccon* (Celedón-Neghme et al. 2013). Lizard-dispersed seeds of *Daphne rodriguezii* have higher seedling survival than seeds remaining under conspecifics, and undispersed seeds of *Cneorum tricoccon* fail to recruit beneath parents.

Effects of lizard body size

Overseas studies suggest lizard herbivory and frugivory are associated with large body size (Herrel et al. 2004; Meiri 2008). Size-based resource partitioning may have occurred among lizard species on Matiu-Somes Island. For example, the larger *O. lineoocellatum* were the main consumers of the larger *C. repens* fruits, while the smaller *O. polychroma* mainly consumed *C. propinqua* and *M. complexa*. However, small sample sizes and confounded species distributions make this difficult to test statistically. Both the size and quantity of fruits consumed were correlated with body size in Jamaican *Anolis* lizards, with larger species eating more fruits (Herrel et al. 2004). In addition, polychrotid lizards that eat fruit are larger than those that do not (Herrel et al. 2004). Two of New Zealand's largest lizards (*O. otagense* and *O. grande*) both eat significant quantities of fruit. *Oligosoma otagense* is the larger of the two, and eats more fruits than *O. grande* when the two species co-occur (Tocher 2003). Large frugivores are important not only because they can eat more fruits and disperse larger seeds, but also because they disperse seeds further (Wotton & Kelly 2012). In the Canary Islands, seedling recruitment in the lizard-dispersed plant *Neochamaelea pulverulenta* was greater in populations dispersed by large-bodied lizard species than in those dispersed by smaller lizard species (Pérez-Méndez et al. 2015).

Conservation implications

Seed dispersal services in New Zealand have almost certainly undergone major changes since the decline and extinction of many lizards and birds following human arrival (Towns & Daugherty 1994; Tennyson 2010). Of the 97 native lizard species in New Zealand, 32 are threatened with extinction, while a further 50 are 'At Risk' (Hitchmough et al. 2013). Declines in frugivore abundance and diversity can reduce both dispersal quantity and quality (Garcia & Martinez 2012), with potential flow-on effects for plant regeneration (Wotton & Kelly 2011). The loss of lizard dispersal may have contributed to the rarity of at least two plant species in the Balearic Islands, Spain (Traveset & Riera 2005; Traveset et al. 2012). While lizards have declined in New Zealand, they are still important seed dispersers at some mainland sites, at both high (Whitaker 1987) and low lizard densities (Young & Kelly 2014).

Lizards may persist as seed dispersers in some ecosystems where birds no longer play a major role. Fleshy-fruitedness is unusually common in the New Zealand alpine flora (12%) compared to other temperate regions (Lord 1999). There are at least 117 fleshy-fruited alpine species in New Zealand (Thorsen et al. 2011), many of which are blue- or white-fruited (Lord & Marshall 2001). Kea (*Nestor notabilis*), the main bird consuming fruit in alpine ecosystems, has experienced massive declines in abundance and distribution (Young et al. 2012). Fruit removal rates were high (67%–99%) at two Canterbury sites with both kea and lizards (Young & Kelly 2014). In alpine areas lacking kea, lizards may be particularly important seed dispersers. However, lizard dispersal is on a local scale and cannot replace the long-distance dispersal service that kea provide (Young et al. 2012).

Prior to human arrival, the eastern South Island had much more woody vegetation (McGlone 2001), which provides safe perching and nesting sites for fruit-eating birds (e.g. Williams et al. 2010) and increases native bird diversity (Walker et al. 2014). In some eastern South Island communities the most common birds (e.g. *Carduelis flammea*, *C. carduelis*, *Emberiza citrinella*, *Prunella modularis* and *Fringilla coelebs*; Walker et al. 2014) are primarily seed predators (Wotton & McAlpine 2015). However, common native lizards are not restricted to woody vegetation, and occupy both grassland and shrubland (Walker et al. 2014). In these South Island rainshadow ecosystems, lizards are likely to play an important seed dispersal role.

Different dispersers often produce different seed dispersal patterns, both in terms of the distance seeds are moved and the type of microhabitat they are deposited in (Jordano et al. 2007). Because lizards are primarily short-distance dispersers, loss of bird dispersers may compromise long-distance seed dispersal and colonisation of new sites, and mean that gene-flow between plant populations is mainly through pollination. Birds and lizards are also likely to deposit seeds in different microsites, though how this may affect plant regeneration is largely unknown. Restoration of native lizard and bird communities may increase seed dispersal effectiveness, enable seeds to reach a wider range of available microsites and promote the persistence of fleshy-fruited native plant communities.

Additional research avenues

As we have shown, reports of lizard frugivory are increasingly common, suggesting that lizards are likely to be important seed dispersers, especially on islands and in shrubland habitats. Yet research on frugivory and seed dispersal by lizards lags far behind that on birds and mammals. Because dispersal by lizards typically operates on a small spatial scale, the system lends itself to research questions that are difficult to address in mammal or bird dispersal systems. Overseas, at least two sets of studies have taken advantage of this: one involving *Timon lepidus* dispersing four species on Monteagudo Island, northwestern Spain (Piazzon et al. 2012) and another with *Podarcis lilfordi* dispersing *Daphne rodriguezii* in the Balearic Islands (Rodríguez-Pérez et al 2012a, b). Both studies reported complex relationships among patterns of lizard movement and foraging, plant community structure, and seed deposition and seedling survival, much of which seems ultimately to depend on small-scale features of habitat heterogeneity, including plant distribution. Recent advances in animal tracking technology (Latham et al. 2015) and molecular identification of species from their scats (e.g. Davison et al. 2002) can be used to quantify seed deposition patterns and identify dispersers, making it easier to conduct these detailed studies. These techniques could be used to address additional questions, including whether lizard body size influences fruit consumption and the relative importance of lizards and birds as seed dispersers.

Anecdotal evidence suggests fruit removal from divaricating plants is greater on predator-free islands than on the mainland, and on rock outcrops with lizards than without (Whitaker 1987). Nevertheless, lizard fruit removal rates when birds are excluded can be surprisingly high even at low lizard densities (Young & Kelly 2014) and their contribution to seed dispersal on the mainland has probably been underestimated. Research on whether lizard abundance affects fruit removal rates could shed light on the importance of lizards as seed dispersers in contemporary ecosystems.

Predatory birds in the Canary Islands frequently consume frugivorous lizards (Padilla et al. 2012). In bird pellets containing lizard remains, seeds of 78 different plant species were found, of which at least 32 species remained viable. Viability was affected by a number of possible factors, including the identity of the bird, lizard and plant species, plus the lengths and numbers of gut treatments. An important implication is the relatively long distance over which dispersal may occur when birds act as secondary dispersers (Padilla et al. 2012). New Zealand falcons (*Falco novaeseelandiae*) have been observed feeding directly on fruits (Young & Bell 2010) so seeds can occur in raptor scats without being consumed first by lizards. Nevertheless, secondary dispersal may be worth investigating in New Zealand.

Conclusion

Nearly 30 years after Whitaker (1987) first proposed that lizards play an important role in seed dispersal in New Zealand, surprisingly little research has been done on this topic. We found good evidence to support hypothesis 1 (lizards prefer white and blue fruits to other fruit colours) and hypothesis 3 (lizards eat fleshy fruits in significant quantities when they co-occur). There is some evidence that lizards deposit seeds in safe sites for seedling establishment (hypothesis 5), though this hypothesis needs further testing. We found mixed support for hypothesis 4 (seeds ingested by lizards are undamaged and germinate as well as control seeds), and hypothesis 2 (fruits of divaricating shrubs are eaten by lizards and not by birds) was not supported. Based on the evidence to date, lizards appear to be important dispersers even at low densities, particularly in shrublands. Seeds of divaricate plants are not dispersed exclusively by lizards; although they may be particularly suited to lizard dispersal, some fruits are removed by birds, at least from the exterior of plants. At some sites, lizards may play a key role as the last remaining dispersers that enable seeds to escape from negative parental effects and reach safe establishment sites.

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