

Dispersal of invasive *Berberis glaucocarpa* in secondary forest occurs mainly by exotic frugivores

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Abstract: Understanding plant invasions is important in conservation ecology and land management, as invasive plant species worldwide have caused irreparable damage and often incur substantial control costs. To record the dispersal vectors for the invasive barberry (*Berberis glaucocarpa*) in a New Zealand regenerating forest, video cameras were used to film 24 barberry plants in fruit in Kowhai Bush, Kaikoura. During 242 hours of video, a total of 101 foraging events were recorded by four bird species: silvereye (*Zosterops lateralis*), blackbird (*Turdus merula*), song thrush (*T. philomelos*), and starling (*Sturnus vulgaris*). The four bird species varied in visitation frequency, time spent on plants, and fruit removal rates. The estimated daily contribution to recorded barberry fruit removal was 42.8% by song thrush, 32.6% by silvereye, 24.3% by blackbird, and 0.2% by starling. No endemic bird species were observed feeding on barberry, despite bellbirds (*Anthornis melanura*) being common in Kowhai Bush. Removal rates for ripe barberry fruit were relatively modest (1.14% per day), but given the ~3 month fruiting season, represented a sizable seed rain in the surrounding forest. Although barberry is now sympatric with several introduced frugivores in New Zealand, none of its dispersers from its native range in Nepal and northern India are present. Instead, dispersal in New Zealand is facilitated primarily by introduced European bird species and native silvereyes.

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INTRODUCTION

The presence of an efficient seed disperser is a key predictor for the potential spread of a fleshy-fruited invasive plant species (Rejmánek & Richardson 1996). For many invasive fleshy-fruited plant species, birds are the main dispersal agents (Gosper *et al.* 2005). In New Zealand many endemic and native frugivorous bird species display generalist foraging strategies and disperse a wide array of native fleshy-fruited plant species (Thorsen *et al.* 2011). However, in the last 200 years, several additional

frugivorous bird species have become naturalised and are now widespread (Heather & Robertson 2000). For example, Eurasian blackbirds (*Turdus merula*) are key dispersers of weeds (Williams 2006), and facilitated the spread of the invasive hawthorn (*Crataegus monogyna*) in Porters Pass, New Zealand (Williams *et al.* 2010).

The combination of generalist foraging strategies in native and endemic frugivores, and the introduction of additional avian dispersal vectors, could promote the spread of invasive fleshy-fruited plants in New Zealand. As an increasing number of plants naturalise within native forests, understanding bird-mediated seed dispersal is important for both modelling and managing weed invasions (Overton *et al.* 2003). Despite this, only a few of

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the introduced fleshy-fruited plant species have had their dispersal vectors identified (Vitousek *et al.* 1996; Callaway & Aschehoug 2000; Mack *et al.* 2000; Wotton & McAlpine 2015).

Barberry (*Berberis glaucocarpa*) is a common invasive weed species found throughout much of New Zealand (Popay *et al.* 2010). Its primary dispersal vectors are frugivorous birds; however, the relative importance of native versus introduced birds in dispersal has not been well studied (Timmins & Williams 1987; Bakker *et al.* 1996). The objectives for this study were: (1) to determine the bird species feeding on barberry fruit in a regenerating native forest, (2) to measure fruit removal rates from fruiting plants and, (3) to quantify which disperser(s) removed the most fruit and subsequently were most likely to disperse barberry seeds.

To address these objectives, we used video cameras to document bird interactions with barberry. Video monitoring has been widely used in ecological research to record frugivore activity and fruit removal rates (Drummond 2005; Dumont 1999; Jayasekara *et al.* 2007; Kitamura *et al.* 2004; Levey *et al.* 2006; Tewksbury *et al.* 1999), making it a suitable method for this study.

METHODS

Study site and species

All observations were carried out at Kowhai Bush (173° 37' E, 42° 23' S), a 240 ha regenerating native forest near Kaikoura that is managed by Environment Canterbury. The areas to the north and east of Kowhai Bush are agricultural pastures while to the south and south-west are river shingle plains. Kowhai Bush is connected to lowland podocarp-hardwood forests in the foothills of the Kaikoura Range by a narrow strip of vegetation running along its north-western edge. This has created a corridor between the regenerating and older forests.

The forest interior of Kowhai Bush is a flood-induced successional patchwork of differing age, structure and species composition (Hunt & Gill 1979). The forest canopy ranges from 5–12 m high and is dominated by kanuka (*Kunzea ericoides*) and manuka (*Leptospermum scoparium*), with occurrences of *Melicytus ramiflorus* and *Pseudopanax arboreus* on the north-eastern side. Along the eastern margins, areas have an understory of barberry and hawthorn. Barberry is native to Nepal and northern India and was introduced into New Zealand in 1916 as a hedgerow species (Roy *et al.* 2004; Lakhey *et al.* 2024). It soon became naturalised and is now classified as a noxious weed species (Owen 1997; Froude 2002; Rahman *et al.* 2003; McAlpine & Howell 2024). If left unchecked in open or regenerating habitats, it can replace other shrubland species (Sullivan *et al.* 2007). Flowering of barberry in Kowhai Bush occurred from the start of October until end of November 2010. Flowers were small, yellow and occurred in clusters of 4–12 (MacFarlane 2012). Fruits are small and fleshy, ~8 mm in diameter, round, black or purplish, with a white surface bloom, typically containing two seeds (Webb *et al.* 1988). Fruit was ripe in Kowhai Bush from late February until late May in 2011 (MacFarlane 2012).

Video observations

To identify the bird species feeding on barberry fruit, video cameras were used to capture foraging events on 24 randomly selected barberry plants. Filming was carried out 24 Feb–20 May 2011, using two Sony DCR-SR68 video cameras. Video cameras were set up 5–7 m from plants so that the entire plant was visible plus a minimum margin of >1 m surrounding the plant. This increased the observer's ability to identify visiting birds. Although it was sometimes difficult to identify some birds while feeding, all could be

identified from their flight patterns as they entered and left the area. Filming was divided into morning and afternoon sessions to account for time-of-day effects. Morning sessions ran from dawn (6:30–7:30 h) to approximately 13:00 h, while afternoon sessions began the following day at the same time the previous morning session had ended and continued until dusk (17:30–19:00 h). This schedule was necessary due to the camera battery life, which was limited to eight hours, and the time required for recharging batteries. Together, these sessions spanned the period from sunrise to sunset, with each plant filmed for both a morning and afternoon session. A total of 242 hours of recordings were collected, with an average of 610 ± 30 minutes (mean $\pm 95\%$ CI) per plant.

The day after the afternoon filming, we estimated the total number of ripe, unripe and damaged fruit available on that plant. Due to the size and position of many of the plants it was not possible to count all fruit, and so 25 clusters of fruit were selected at random on each plant. From each cluster the total ripe and damaged fruit was recorded, and the average number of fruit per cluster calculated. The total numbers of clusters per plant was then counted, and total fruit per plant calculated by multiplying fruit per cluster times clusters per plant.

Video recordings were watched later, and for each bird landing on a plant we recorded: (1) bird arrival and departure times, to calculate total seconds spent on the plant, (2) species of bird, (3) whether a foraging event occurred, defined as fruit seen to be eaten or birds displaying feeding behaviours like pecking or swallowing motions, and (4) if possible, the total number of fruit eaten.

Analysis

The software package R version 2.13.2.2 was used for all statistical analyses. All selected models were checked for goodness of fit (Agresti & Kateri 2011), with the gof function, R package aods3 v0.4-1.1. Morning and afternoon filming sessions were combined to form one period. For all foraging events, the observer was able to record how long each individual bird remained feeding (seconds) on the plant.

While the number of fruits eaten could not be determined for every foraging event, time spent feeding was significantly correlated with fruit removal (see Results). Given this relationship, total feeding time was used as a proxy to estimate each bird species' relative contribution to fruit removal. A GLM with a Poisson distribution was used to estimate differences in fruit removal rates among the four bird species. Lastly, to estimate each bird species' overall contribution to barberry fruit removal, we first calculated feeding intensity for each monitored plant using the formula:

$$\text{Feeding Intensity} = \left(\frac{\sum \left(\frac{T}{H} \right)}{\sum F} \right) \times 1000 \times P$$

Where T is the total time a bird spent feeding on a plant (seconds), H is the total duration of video recording for that plant (hours), F is the total number of available fruits on the plant, and P is the proportion of plants visited by the species. Since this calculation applies to individual bird visits, we then averaged feeding intensity across all monitored plants (N) to obtain a final estimate for each species:

$$\text{Overall feeding intensity} = \frac{1}{N} \sum_{i=1}^N \text{Feeding intensity}_i$$

This final metric provides a standardised estimate of each species' feeding effort per 1000 available fruits per hour across all sampled plants, accounting for both visitation frequency and time spent feeding.

RESULTS

In total, 101 foraging visits to barberry plants were recorded. It was possible to identify all bird species and to measure their duration of feeding on barberry fruit for all visits. However, it was only possible to record how many fruits was eaten per visit for 35 birds. Four bird species were observed feeding on barberry fruit: the native silvereye (*Zosterops lateralis*), and introduced Eurasian blackbird, song thrush (*Turdus philomelos*) and common starling (*Sturnus vulgaris*) (Table 1). Endemic frugivorous birds (of which the most locally common was the bellbird, *Anthornis melanura*) were not observed feeding on barberry plants. Each plant was visited by 4.2 ± 1.7 (mean $\pm$ SE) birds during an individual filming period (morning and afternoon sessions combined), and each bird remained feeding for 47 ± 12.7 seconds per visit. Filmed barberry plants carried a mean of $1,324 \pm 463$ ripe fruits. For all bird species combined, a mean of 3.6 ± 1.1 fruits was removed per individual visit. This equates to 15.1 ± 4.6 fruits removed from each plant per day. For a filmed plant this would mean 1.14% of its fruit was removed daily. The fruiting season in 2011 lasted from late February until late May, a period long enough for most fruits to be removed.

Significant differences in fruit removal rates were detected among the four bird species ($\chi^2 = 34.92$, DF = 3, $P < 0.001$). This difference was driven by silvereyes, which made the most visits but removed fewer fruits per visit, compared to starlings which had the highest fruit removal rate per visit despite very few visits (Table 1). Blackbirds and song thrushes had intermediate values for both the number of visits and fruits removed per visit.

There was a significant relationship between the duration that birds remained on the plants and the total number of fruits they removed ($\chi^2 = 42.44$, DF = 1, $P < 0.001$,

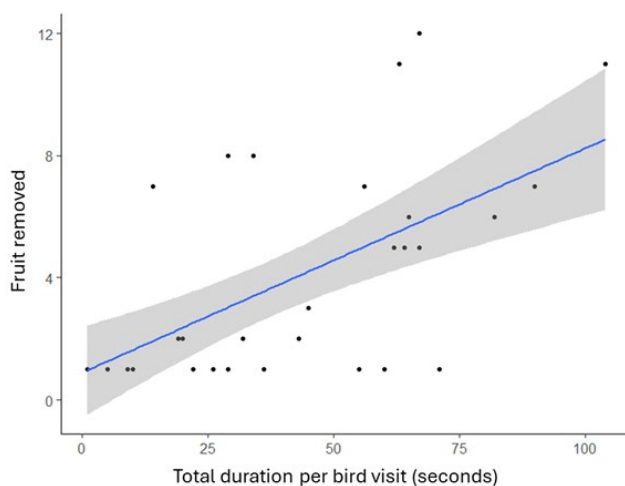


Figure 1. The relationship between mean duration of bird visits (seconds; model mean is indicated by the blue line) and the mean number of fruits removed per visit, with 95% CI.

Figure 1). The longer a bird remained on the plant the more fruits it removed. For this reason, using total time of visits per 1000 fruit is a reasonable estimate of each bird species' contribution to fruit removal. Overall, the daily contribution to recorded barberry fruit removal was 42.8% for song thrushes, 32.6% for silvereyes, 24.3% blackbirds, and 0.2% for starlings. These estimates suggest that song thrushes were the most important dispersal vector.

DISCUSSION

Consumption of barberry was restricted to one native and three introduced frugivorous bird species. Although silvereyes are native, they colonised New Zealand relatively recently, in the 1850s (Heather & Robertson 2000). The other three species were introduced to New Zealand from Europe between 1862 and 1883 (Heather & Robertson 2000). Of the four species recorded feeding on barberry, all except one (starling) were observed frequently enough to be considered a major dispersal vector of barberry in Kowhai Bush. Differences in feeding behaviours among silvereyes, blackbirds, song thrushes, and starlings contributed to the differences in seed dispersal dynamics. Blackbirds and song thrushes showed moderate visitation frequencies and fruit removal efficiencies and accounted for most seed dispersal. Silvereyes, despite spending shorter periods per visit and consuming fewer fruits on average, compensated with frequent visits. This pattern resulted in a substantial but still comparatively lower overall contribution to fruit removal. In contrast, starlings had high fruit consumption rates per visit but made few visits, suggesting they played a lesser role in dispersing barberry seeds.

Frugivore body size plays a key role in determining fruit consumption rates, as larger-bodied birds tend to consume greater quantities of fruit per feeding event due to their higher energy demands and they can consume larger fruits due to larger gape widths (Case & Tarwater 2020). In the Hawaiian Islands, the loss of large native frugivores and the introduction of smaller-bodied species reduced the dispersal of larger-seeded plants, altering plant-frugivore interactions (Case & Tarwater 2020). A similar pattern may explain the differences in fruit removal rates observed in this study. Blackbirds and song thrushes, both mid-sized frugivores, accounted for most barberry seed dispersal, while silvereyes, with their smaller size and gape, removed fewer fruits per visit. These results align with broader patterns in seed dispersal research, where frugivore body size influences both the quantity of fruit consumed and the effectiveness of seed dispersal (Howe & Smallwood 1982; Schupp 1993).

Our observations suggest that barberry does not appear to be dispersal-limited in New Zealand, despite being introduced and no longer sympatric with its native dispersers in Nepal and northern India. This pattern is consistent with broader trends, as ~32.9% of New Zealand's 295 environmental weed species produce fleshy fruits adapted for animal-mediated dispersal (Wotton & McAlpine 2015). Among these, blackbirds, silvereyes, song

Table 1. Visitation and fruit removal rates to barberry *Berberis glaucocarpa* at Kowhai Bush by four bird species (means $\pm$ 95% CIs from 242 hours of videos on 24 plants).

Bird species	Silvereye	Blackbird	Song thrush	Starling
Total number of visits	42	27	29	3
N fruit removed per visit	1.4 ± 0.47	3.5 ± 1.8	3.6 ± 1.8	9.3 ± 2.6
Proportion of plants visited by each bird species	0.46	0.37	0.42	0.08
Duration per visit (seconds)	31.5 ± 5.1	81.2 ± 47.9	42.4 ± 12.2	44.3 ± 22.6
Overall feeding intensity (seconds of feeding per 1000 fruits per hour)	3.96	2.95	5.20	0.02

thrush, and starlings have been identified as key dispersers, playing a significant role in accelerating plant invasions. Similarly, Williams & Karl (1996) found that introduced birds, such as blackbirds and song thrushes, consumed fruits from both native and exotic plants, whereas endemic species showed a stronger preference for native fruits. This pattern is also evident in Kowhai Bush, where barberry was largely ignored by endemic seed dispersers despite the presence of several frugivorous native birds, including bellbirds, South Island robins (*Petroica australis*), and the occasional visiting tūi (*Prosthemadera novaeseelandiae*) and kererū (*Hemiphaga novaeseelandiae*). The adaptability of introduced birds, along with their ability to thrive in human-modified landscapes, likely enhances their effectiveness as vectors of weed proliferation, often outcompeting or replacing native dispersers in disturbed ecosystems (Kelly *et al.* 2010).

An estimated 1.14% of barberry fruit per plant was consumed daily by birds. This dispersal estimate is likely higher, as possums (*Trichosurus vulpecula*) were also recorded dispersing barberry seeds at Kowhai Bush (Wyman & Kelly 2017). However, as the barberry fruiting season in 2011 at Kowhai Bush lasted from late February until late May, even rates of 1.14% of fruit eaten per day would have been sufficient for nearly all fruits to be removed. Indeed, by the end of May, few fruits remained on the barberry plants in Kowhai Bush, suggesting most had been eaten (AETM *pers. obs.*). This indicates that many plants likely were receiving adequate fruit removal services.

Apart from rates of fruit removal, the quality of seed dispersal depends on the treatment given to a seed in the mouth and gut, as well as the quality of seed deposition site (Schupp 1993). None of the four bird species that we observed eating barberry fruits are considered seed predators, and all barberry seeds collected from blackbird, silvereye, and song thrush faecal samples were intact (MacFarlane *et al.* 2016). Movement of seeds by dispersers away from parent plants is usually advantageous, as seedlings that germinate under parent plants can have higher predation rates and additionally will have to compete with both the parental plants and siblings as they grow (Schupp *et al.* 2010). The longer that a frugivore remains on the parent plant the more likely it is to deposit the seeds under this plant (Pratt & Stiles 1983). Birds that visited barberry plants remained feeding for 47 seconds on average and the maximum time was 493 seconds. Gut passage time normally averages c. 30 minutes for blackbirds (Sorensen 1981; Barnea *et al.* 1991), 20 minutes for silvereyes (Stanley & Lill 2002), 43 minutes for song thrushes (Herrera 1984) and 38 minutes for starlings (Karasov & Levey 1990; LaFleur *et al.* 2009). Therefore, it is likely that most barberry seeds were defecated away from the parental plants by all the foraging bird species.

Successful dispersal away from the parent plant, and germination of dispersed seed, means there is likely to be continued expansion of barberry into Kowhai Bush in the future. Barberry has only recently become established in Kowhai Bush, and its stands are still relatively small and young. It could be assumed that as stands increase in density there will be increased fruit availability and, subsequent increased visitation from frugivores and dispersal of seeds. Similar trends have been observed with hawthorn dispersed by blackbirds at Porters Pass, New Zealand (Williams *et al.* 2010). Barberry has the potential to negatively affect native biota by successional replacement of native seral species (Sullivan *et al.* 2007) and may compete with other native fruiting shrubs such as *Coprosma* species for resources. This could reduce habitat quality and eventually food availability for endemic frugivorous bird species, which do not appear to feed on barberry.

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