A moving feast: the influence of landscape context on bird-mediated seed rain into conservation areas

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Summary To assess the influence of surrounding land on bird-mediated seed rain to an area, we compared the seed influx from European starling (*Sturnus vulgaris* L.) flocks arriving to roost on two islands, both similar distances from the nearest seed source but differing in proximity to weed infestation.

Seed collection trays on both islands received significantly higher seed rain at starling roost sites than at control sites. Seed influx at the roost sites also appeared higher over the winter, when starlings flock to roost on the islands, than during the summer when they disperse to breed. Composition of the seed rain at roost sites varied significantly between the islands. The seed rain on the island adjacent to land which lacked weed control (Motuihe) was dominated by adventive plant species, while on the island adjacent to weed-controlled land (Tiritiri Matangi) native species dominated.

The importance of landscape context in determining the direction of development of an area, and the implications of this for the selection and management of conservation areas are considered.

Keywords Starling, seed rain, dispersal, weed, long distance, landscape.

INTRODUCTION

Active management of areas is commonly undertaken in an attempt to redress native biodiversity decline. However, the impact of continual input from the surrounding unmanaged area is frequently underestimated by managers. Knowledge of incoming seed rain may be especially important in the context of ecological restoration projects aiming to promote recruitment of desirable native species while simultaneously minimising the spread of weeds (Ferguson and Drake 1999).

Dispersal by birds is one of the most common ways by which weeds establish (Timmins and Williams 1987, Cameron 1990, Williams and Karl 1996, Atkinson 1997). The non-native European blackbird (*Turdus merula* L.) and the self-introduced silvereye (*Zosterops lateralis* Latham) are major seed dispersers over large areas of New Zealand, and play an important role in weed diffusion, but are mainly responsible for short distance dispersal (Williams 2006). The non-native starling (*Sturnus vulgaris* L.), although a relatively minor frugivore (Burrows 1994), flocks in high numbers and flies large distances to roost sites (Brockie 1983) as well as having a relatively long gut retention time (Karasov and Levey 1990). These characteristics mean starlings may provide the long-distance stochastic dispersal important to weed spread. Their preference for roosts on predator-free islands (Brockie 1983), where conservation efforts are concentrated, presents a particular threat to biodiversity in New Zealand (Atkinson 1997).

Land use in New Zealand is undergoing a change from predominantly pastoral farming to increasingly 'lifestyle' development (Williams 2006). Within this landscape natural areas are weed controlled, despite the increased threat of weed invasion as a result of surrounding land use intensification (Timmins and Williams 1991). This study evaluates the influence of land use on the direction of development in adjacent areas, by examining the relationship between the surrounding landscape and the seeds dispersed by starlings to two island roosts. Such information is important for prioritising selection and management of conservation areas if the long-term goal is to establish self-sustaining ecosystems (Atkinson 1997).

MATERIALS AND METHODS

The study was undertaken on two islands, Motuihe and Tiritiri Matangi, in the Hauraki Gulf near Auckland, New Zealand. The islands have a parallel history of vegetation clearance for farming over 150 years (Esler 1978, Esler 1980), followed by recent efforts to eradicate pests and restore the forest cover. Both islands are now free of mammalian predators, are managed for conservation, have starling roosts and are a similar distance from the nearest seed source. The salient difference between them is their landscape context: the nearest land to Motuihe Is. is residential and rural land lacking weed control, while the nearest land to Tiritiri Matangi Is. is weed-controlled regional parkland.

On each island approximately fifteen 0.5 m^2 seed collection trays (Dijkgraaf 2002) were set up at a starling roost site and the same number at a control site of similar vegetation, but where starlings did not roost. The trays were cleared monthly throughout a year. Bird-dispersed seeds stripped of pericarp were

distinguished from intact fallen seeds and identified and counted. A transect of 200 m was walked through representative habitat (Dawson and Bull 1975) in at least four months and starlings within 50 m counted to assess the number of birds feeding on each island during the day. Five minute bird counts to 100 m (Dawson and Bull 1975) were made monthly where possible, before dusk at each site to identify resident fruit-eating bird species and their abundance. Counts were then made from a vantage point at dusk of the number of incoming starlings to roost. Seeds dispersed to roost sites were compared to the existing vegetation on each island.

RESULTS

The seed influx was significantly higher at starling roost sites than control sites on both islands (Motuihe $t = 10.7$ (288) $P < 0.0001$; Tiritiri Matangi $t = 4.1$ (198) $P < 0.0001$), despite similar resident bird populations at both sites (Table 1).

A range of 34 plant species, 20 adventive (*Ficus macrophylla* Desf. ex Pers., *F. rubiginosa* Desf. ex Vent., *F. carica* L., *Iris foetidissima* L., *Olea* sp. L., *Physalis peruviana* L., *Phytolacca octandra* L., *Psidium guajava* L., *Lonicera japonica* Thunb., *Rhamnus alaternus* L., *Solanum nigrum* L., *S. americanum* Mill., *S. mauritianum* Scop., *Asparagus scandens* Thunb., *Rubus fruticosus* L., *Vitis vinifera* L., *Berberis glaucocarpa* Stapf., *Leycesteria formosa* Wallich., *Pyracantha angustifolia* Franch. and *Toxicodendron succedaneum* Kuntze) and 14 native (*Coprosma* sp., *Cordyline australis* Endl, *Melicope ternata* Forster et Forster f., *Melicytus ramiflorus* Forster et Forster f., *Muehlenbeckia* sp., *Myrsine australis* Allan, *Pittosporum crassifolium* Cunn., *Pseudopanax* sp., *Vitex lucens* Kirk, *Solanum aviculare* Forster f., *Dysoxylum spectabile* Hook f., *Podocarpus totara* D.Don, *Dacrycarpus dacrydioides* Laubenf. and *Leucopogon fasciculatus* A.Rich.), occurred in collection trays at the roost sites. Seed influx varied over the year, and appeared highest on Motuihe from March to August and on Tiritiri Matangi from March to July. This corresponds approximately with the number of starlings flocking in winter to roost and then dispersing over summer to breed (Figure 1). The relationship is clearer on Motuihe, except in July when a fire at the time of the roost count deterred birds from landing. On Tiritiri Matangi seed input decreased after April despite continuing high numbers of starlings roosting. A roost change on Tiritiri Matangi from August to December, resulting in loss of seed input to the trays, may have confounded the seasonal pattern for this island.

On Motuihe a small population of <50 starlings ($\bar{X} = 13.5$, $SE = 8.5$, $n = 6$) resided during the day. On Tiritiri Matangi a starling was sighted only once during transects ($\bar{X} = 0.2$, $SE = 0.2$, $n = 6$), although <6 birds were occasionally recorded during the day feeding on the grassed areas.

Table 1. Mean seed number per tray ± SE, and mean bird number per five minute count ± SE, at each site on both islands.

Island	Motuihe		Tiritiri Matangi	
Site	Control	Roost	Control	Roost
Seed no.	7.1 ± 1.2	42.3 ± 3.0	16.5 ± 4.5	109.7 ± 22.1
Bird no.	4.0 ± 0.5	9.5 ± 1.2	6.1 ± 0.6	8.6 ± 1.0

Composition of the seed rain varied significantly between the islands ($\chi^2 = 358$ (1), $P < 0.0001$). On Motuihe 78% ($n = 12$) of the seed rain was adventive species, while on Tiritiri Matangi most seeds brought in were native species (70%, $n = 12$). On both islands, grass seeds were more numerous at starling roosts than control sites (Motuihe 268:30; Tiritiri 143:0).

Of the fleshy-fruited weeds prioritised for management on each island (Graham and Lindsay 2004, Lindsay and Price 2005), starlings are the probable vector for 11 of the 18 species on Motuihe and six of the 17 species on Tiritiri Matangi. In addition, starlings imported four weed species new to Motuihe and eight to Tiritiri Matangi. Starlings also boosted the seed rain of a suite of common native plants to both islands, as well as importing two native species new to Motuihe and one to Tiritiri Matangi.

DISCUSSION

The high seed influx at starling roost sites relative to control sites demonstrates the capacity of mass flocking in starlings to disseminate relatively large amounts of seed. Although a small population of starlings resided on Motuihe Is., and occasional birds were observed feeding on Tiritiri Matangi during the day, the large majority of starlings on both islands arrived from the nearest landfall as roosting flocks in the evening and departed in the same direction at dawn. A number of fruiting plants which occurred in the seed rain at both roost sites, but were not present on either island, also indicate starlings were feeding off the islands. This is consistent with previous reports of starlings roosting on islands after foraging on the adjacent mainland during the day (Taylor 1968, Brockie 1983, Cameron 1990, Ferguson and Drake 1999, Meier-Behrmann 1999). Brockie (1983) suggests starlings choose to fly several km to roost on islands that are rat-free in order to avoid predation. These long-distance roost flights highlight the ability of starlings to provide gap-crossing 'saltation' dispersal of seeds described by

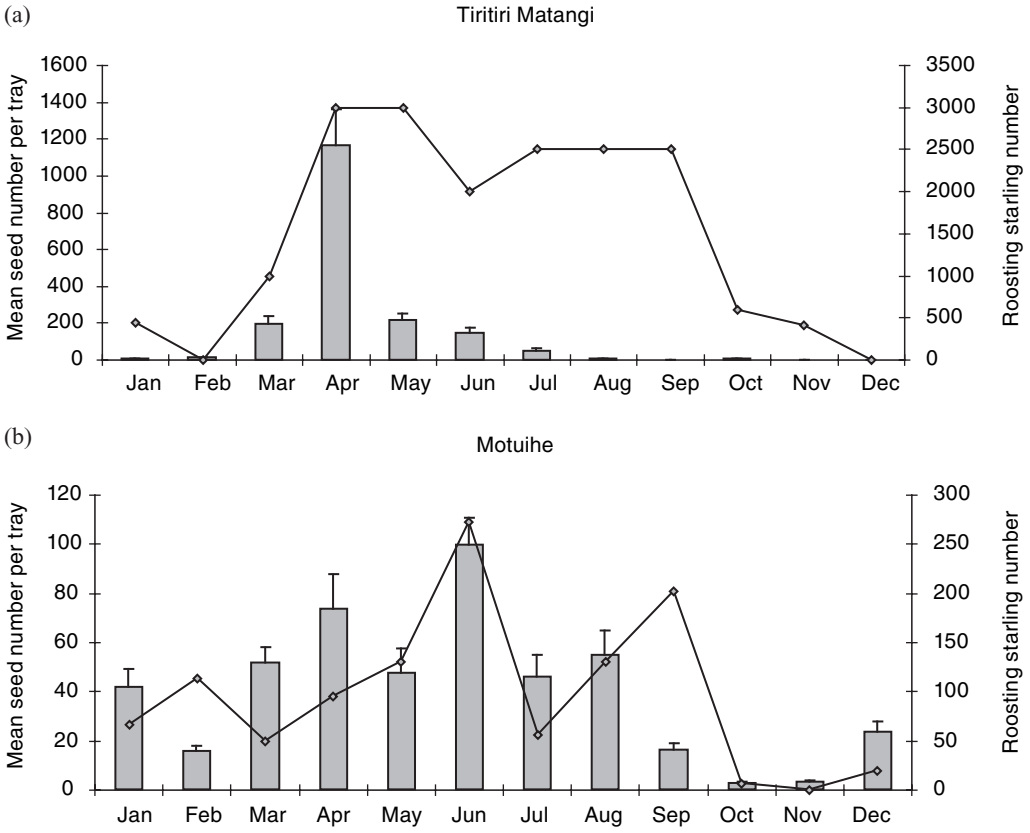

Figure 1. Mean seed number per tray ± SE (bars) at roost site, against number of starlings in roost flight (line), throughout the year for each island.

Davis and Thompson (2000) which is likely to generate new invasive loci for weed species (Williams 2006).

The seasonal trend of starlings forming large flocks from autumn has been noted previously (Snow and Snow 1988, Williams and Karl 1996). The close relationship between starling numbers and seed input on Motuihe may reflect the extended seasonal availability into winter of adventive fruits, which dominated the seed rain to this island. Most weeds originate from horticultural introductions (Timmins and Willliams 1987), some specifically to provide colour in winter gardens (Williams and Karl 1996). On Tiritiri Matangi the falloff in seed input as winter advanced, despite continuing high numbers of roosting starlings, may reflect the decreasing availability of native fruits, which dominated the seed rain at this island. Meier-Behrmann (1999) also reported that on Pudding Is., where native species dominated the starling-disseminated seed rain at roost sites, the highest seed input during the March to August study was for the months March to May. Although the apparent reduction in seed input over summer may have been confounded on Tiritiri Matangi by a shift in roost site, seed input at the control site confirmed peak fruiting for native species around April, as in other New Zealand studies (Ferguson and Drake 1999, Meier-Behrmann 1999). The difference in the proportion of native:adventive seeds imported to each island by starlings suggests that fruit selection is strongly influenced by surrounding land management. Coleman (1977) has also shown that the relative importance of components in the starling diet varies according to land use and local species abundance. Although starlings are restricted by morphological limitations (Snow and Snow 1988, Williams and Karl 1996) as well as their digestive system (Martinez del Rio and Stevens 1989) in the fruit they are able to access and utilise, within this range the choice of fruit is largely determined by availability. This is reflected in spatial differences in dietary composition locally and on a wider geographic

scale (Coleman 1977, Moeed 1990, Williams and Karl 1996, Meier-Behrmann 1999). The flexibility of starlings in response to available food types is considered a likely factor in their success (Feare 1993). Starlings foraging on land adjacent to Motuihe before flying to the island to roost have access to predominantly adventive fruits of residential gardens and lifestyle blocks, while parkland adjacent to Tiritiri Matangi offers predominantly native fruits. This is mirrored in the composition of seed loads carried by starlings to each island. These results underline the importance of landscape context in determining the direction of development of an area, since the outcome for biodiversity conservation of the seed rain from non-native birds, such as starlings, largely depends on their seed loads (Williams and Karl 1996).

Invasive species in the seed load of starlings may pose a threat to conservation land (Timmins and Willliams 1987, Williams and Karl 1996) and the presence of starling roosts is identified as one of the main contributing factors to weed invasion on New Zealand offshore islands (Atkinson 1997). Several weeds on Middle Is. attributed to roosting starlings by Cameron (1990), including exotic grasses and the first record of *T. succedaneum* in the wild, were confirmed at starling roost trays in this study. A disproportionate amount of adventive seed in the starling-disseminated seed rain on Motuihe suggests that the long-term restoration success of this island may be compromised by proximity to weed sources, while the arrival of a range of weed species new to Tiritiri Matangi highlights the need for monitoring. Many large-fruited adventive plants have not yet reached their potential range in New Zealand, probably due to their reliance largely on blackbirds which are predominantly short distance dispersers (Williams 2006), but dispersal events by roosting starlings may alter this dynamic. Although not all seeds arriving to an area successfully germinate (Meier-Behrmann 1999), identification of incoming seeds allows regeneration to be forecasted. A significant number of weed species imported by starlings in this study were not yet recognised as an issue in current weed management plans for either island (Graham and Lindsay 2004, Lindsay and Price 2005). Characteristics of incoming weed species which influence their potential to become invasive, such as history of invasiveness, shade tolerance and ability to use available pollinators (Richardson *et al.* 2000), should be used to predict weed issues and inform management throughout any restoration process.

Conversely indigenous fruit in the seed loads of starlings may be important for biodiversity conservation (Williams and Karl 1996). The dominance of native seeds in the seed rain from starlings on Tiritiri Matangi was also found in two previous studies of seeds dispersed to island starling roosts in New Zealand (Ferguson and Drake 1999, Meier-Behrmann 1999). Normally the density and species richness of seedbanks tends to decline as succession progresses (Young *et al.* 1987, Dalling *et al.* 1998), but profuse bird-mediated input by starlings to forested roosts ensures continual enrichment of the forest seedbank (Ferguson and Drake 1999) and may boost restoration efforts. The seed rain to both islands in this study included the native *D. dacrydioides* not present on either island but known to have existed on Motuihe historically (Heiss-Dunlop *et al*. in press) and to be highly attractive to starlings (Beveridge 1964, Williams and Karl 1996). Similarly Towns (2002) suggests that starlings may have been responsible for introducing the native *Streblus banksii* (Cheeseman) to Korapuki Is. from neighbouring islands. However, seed rain may not be a reliable indicator of the seedbank, since adventive species from the northern hemisphere are characterised by seed longevity and may be differentially favoured relative to native species, which do not have persistent seedbanks. For example on Mana Island, despite native species dominating the seed rain, the seedbank was dominated by adventives (Ferguson and Drake 1999). The implications of this are graphically illustrated in the regeneration of Motunau Is., where the replacement vegetation following rabbit removal has been vigorous invasion of boxthorn (*Lycium ferocissimum* Miers) dispersed to the island by starlings (Taylor 1968).

Despite studies showing the influence of land characteristics outside the managed area on the restoration process, New Zealand managers have tended to be more aware of animal pests than plant pests as a problem in reserves (Timmins and Williams 1991). This study supports the recommendations of Atkinson (1997) that wherever practicable mainland sources of problem weeds on islands should be located and destroyed. Weed control of coastal land may be a cost-effective means of preventing continual weed export to valuable island reserves via mobile bird seed dispersers. The potential for invasion should also be used in prioritising areas for restoration activities at a landscape scale (Atkinson 1997).

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REFERENCES

Atkinson, I.A.E. (1997). Problem weeds on New Zealand islands. Science for Conservation No. 45. (Department of Conservation, Wellington, NZ).

Beveridge, A.E. (1964). Dispersal and destruction of seed in central North Island podocarp forests. *Proceedings of the New Zealand Ecologist* 11, 48-55.

Brockie, R.E. (1983). Starling (*Sturnus vulgaris*) roosts and flightlines near Wellington. *Notornis* 30, 217-23.

Burrows, C.J. (1994). Fruits, seeds, birds and the forests of Banks Peninsula. *New Zealand Natural Sciences* 21, 86-107.

Cameron, E.K. (1990). Flora and vegetation of Middle Island, Mercury Islands Group, eastern Coromandel, northern New Zealand. *Journal of the Royal Society of New Zealand* 20, 273-85.

Coleman, J.D. (1977). The foods and feeding of starlings in Canterbury. *Proceedings of the New Zealand Ecological Society* 24, 94-105.

Dalling, J.W., Swaine, M.D. and Garwood, N.C. (1998). Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology* 79, 564-78.

Davis, M.A. and Thompson, K. (2000). Eight ways to be a coloniser, two ways to be an invader: a proposed nomenclature scheme for invasion ecology. *Bulletin of the Ecological Society of America* 81, 226-30.

Dawson, D.G. and Bull, P.C. (1975). Counting birds in New Zealand forest. *Notornis* 22, 101-9.

Dijkgraaf, A.C. (2002). Phenology and frugivory of large-fruited species in northern New Zealand'. PhD thesis, University of Auckland, Auckland, New Zealand.

Esler, A.E. (1978). Botanical features of Tiritiri Island, Hauraki Gulf, New Zealand. *New Zealand Journal of Botany* 16, 207-26.

Esler, A.E. (1980). Botanical features of Motutapu, Motuihe, and Motukorea, Hauraki Gulf, New Zealand. *New Zealand Journal of Botany* 18, 15-36.

Feare, C.J. (1993). Nectar feeding in European starlings. *Wilson Bulletin* 105, 194.

Ferguson, R.N. and Drake, D.R. (1999). Influence of vegetation structure on spatial patterns of seed deposition by birds. *New Zealand Journal of Botany* 37, 671-77.

Graham, S. and Lindsay, H. (2004). 'Weed survey Motuihe Island 22–24 March 2004'. (Department of Conservation, Wellington, NZ).

Heiss-Dunlop, S., Deng, Y., Craig, J.L. and Nichol, S.L. (in press). Using the fossil pollen record to guide ecological restoration of Motuihe Island, Hauraki Gulf, northern New Zealand. *Journal of the Royal Society of New Zealand*.

Karasov, W.H. and Levey, D.J. (1990). Digestive system trade-offs and adaptations of frugivorous passerine birds. *Physiological Zoology* 63, 1248-70.

Lindsay, H. and Price, I. (2005). Weed control programme report, Tiritiri Matangi Island. (Department of Conservation, Wellington, NZ).

Martinez del Rio, C. and Stevens, B.R. (1989). Physiological constraints on feeding behaviour: intestinal membrane disaccharidases of the starling. *Science* 243, 794-6.

Meier-Behrmann, D. (1999). 'The impact of mass roosting starlings (*Sturnus vulgaris*) on the vegetation of Pudding Island, Otago Harbour'. Postgraduate Diploma in Ecology, University of Otago, Dunedin, NZ.

Moeed, A. (1990). Diets of adult and nestling starlings (*Sturnus vulgaris*) in Hawke's Bay, New Zealand. *New Zealand Journal of Zoology* 7, 247-56.

Richardson, D.M., Allsop, N., D'Antonio, C.M., Milton, S.J. and Rejmanek, M. (2000). Plant invasions – the role of mutualisms. *Biological Review* 75, 65-93.

Snow, D. and Snow, B. (1988). 'Birds and berries: a study of an ecological interaction'. (T. and A.D. Poyser, Calton, UK).

Taylor, R.H. (1968). Introduced mammals and islands: priorities for conservation and research. *Proceedings of the New Zealand Ecological Society* 15, 61-7.

Timmins, S.M. and Willliams, P.A. (1987). Characteristics of problem weeds in New Zealand's protected natural areas. *In* 'Nature conservation: the role of remnants of native vegetation', eds D.A. Saunders, G.W. Arnold, A.A. Burbridge and A.J.M. Hopkins, pp. 410. (Surrey Beatty in association with CSIRO and CALM, Chipping-Norton).

Timmins, S.M. and Williams, P.A. (1991). Weed numbers in New Zealand's forest and scrub reserves. *New Zealand Journal of Ecology* 15, 153-62.

Towns, D.R. (2002). Korapuki Island as a case study for restoration of insular ecosystems in New Zealand. *Journal of Biogeography* 29, 593-607.

Williams, P. (2006). The role of blackbirds (*Turdus merula*) in weed invasion in New Zealand. *New Zealand Journal of Ecology* 30, in press.

Williams, P.A. and Karl, B.J. (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, 127-45.

Young, K.R., Ewel, J.J. and Brown, B.J. (1987). Seed dynamics during forest succession in Costa Rica. *Vegetatio* 71, 157-73.