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S04-3 Birds as pollinators and dispersers: a case study from New Zealand

Sandra H. ANDERSON[1], Dave KELLY[2], Alastair W. ROBERTSON[3], Jenny J. LADLEY[2], John G. INNES[4]

1. School of Geography and Environmental Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand; sh.anderson@auckland.ac.nz
2. Plant and Microbial Sciences Dept., University of Canterbury, Private Bag 4800, Christchurch, New Zealand; d.kelly@botn.canterbury.ac.nz
3. Ecology Dept., Massey University, Private Bag 11222, Palmerston North, New Zealand; A.W.Robertson@massey.ac.nz
4. Landcare Research, Private Bag 3127, Hamilton, New Zealand; InnesJ@LandcareResearch.co.nz

Abstract One special legacy of New Zealand's long biogeographic isolation is a distinctive flora and fauna. The flora is characterized by a high percentage of trees (33% of species), a high percentage of bird-dispersed species (72% of trees), and a low incidence of ornithophily (4% of genera). In the prehuman avifauna, twelve species dispersed seed, and five were pollinators. Native ecosystems have since suffered clearance of 71% of forests, extensive hunting, and the introduction of 14 now-widespread predatory or browsing mammals. As a result, pollinating and seed dispersing birds are either regionally or nationally rare (7 species), or extinct on the New Zealand mainland (6 species). Six of seven bird-pollinated plant species examined so far are pollen-limited, to some extent, at mainland sites. Three of eight fruiting species studied are suffering reduced dispersal on the mainland, where large (>1.4 cm) diameter fruits now depend on a single disperser, the New Zealand pigeon, *Hemiphaga novaeseelandiae*. Conservation of these plants requires management of native bird populations, especially the tui (*Prosthemadera novaeseelandiae*), bellbird (*Anthornis melanura*), and the pigeon to avert long-term shifts in vegetation composition. Intensive predator control has been shown to increase the densities of mutualist bird species, suggesting that New Zealand conservation managers can assist bird-serviced plant populations by controlling predators, a third-order ecological manipulation.

Key words Bird pollination, Bird dispersal, Mutualisms, New Zealand

1 Introduction

New Zealand provides an interesting test for the importance of birds as pollinating and seed-dispersing mutualists. The woody flora is overwhelmingly fleshy-fruited, and ornithophilous flowers (large, red, copious, unscented, with dilute nectar) are a small but important botanical element. Aside from one nectarivorous bat (Arkins et al., 1999) and several lizards (Whitaker, 1987), birds are the only vertebrates filling the two roles. Human influence has greatly reduced the density and diversity of native birds throughout the two main islands, hereafter the "mainland" (Brockie, 1992). Thirty-nine exotic birds have established themselves but few are important dispersers or pollinators. Therefore, if native birds are important to ecosystem function, there should be evidence in New Zealand of floristic change resulting from the decline of native birds.

Clout and Hay (1989) reviewed the relative importance of avian dispersal and pollination mutualisms in New Zealand. They stressed the negative effect of avian extinctions and range reductions on dispersal mutualisms, particularly for large-seeded trees which now rely on a single, possibly keystone, disperser, the New Zealand pigeon (*Hemiphaga novaeseelandiae*). Here we show that reduction in bird densities is also causing widespread pollination failure on the mainland. We argue that pollination has been affected as much as dispersal, and that two honeyeater species, the tui (*Prosthemadera novaeseelandiae*) and bellbird (*Anthornis melanura*), are probably also keystone species as the predominant pollination and dispersal mutualists on the mainland.

2 Prehuman situation

Before the arrival of man, almost all of New Zealand was forested. This is reflected in the flora, with a high percentage of trees (33% of species) compared to a mean of 9% for the temperate zone worldwide (Atkinson and Cameron, 1993; Begon et al., 1996, p 34). Unusually for a temperate area, the woody flora is overwhelmingly fleshy-fruited: 72% of trees cf. 17%–47% at comparable northern latitudes (Burrows, 1994). Plants with typically ornithophilous flowers are relatively few (4% of genera) but nonetheless prominent (Castro and Robertson, 1997, Webb et al., 1999). However, birds also visit and pollinate many flowers with non-ornithophilous syndromes, especially those of canopy trees and winter-flowering plants (Castro and Robertson, 1997; Anderson, 2003).

Famously, New Zealand lacked terrestrial mammals apart from several ground-foraging bats; and the 67 species of native forest birds filled many of the roles that mammals do elsewhere (Atkinson and Millener, 1991). Although Clout and Hay (1989) list 31 species which ate fruit, many were opportunistic insectivores or acted primarily as seed predators (moa, parrots). Holdaway (1989) and Atkinson and Millener (1991) record twelve bird species as responsible for most seed dispersal: piopio (*Turnagra capensis*), two moas with small gizzard stones (*Euryapteryx* spp.), huia (*Heteralocha acutirostris*), saddleback (*Philesturnus carunculatus*), New Zealand pigeon, tui, bellbird, hihi (*Notiomystis cincta*), kokako (*Callaeas cinerea*), whitehead (*Mohoua albicilla*) and the flightless weka (*Gallirallus australis*). Of eight flower-visiting species, the three putative Meliphagidae (tui, bellbird and hihi) were the most important pollinators (Craig et al., 1981; Angehr, 1986). The kaka (*Nestor meridionalis*) and saddleback also pollinated some flowers, while whiteheads and two parakeets (*Cyanoramphus* spp.) did so incidentally. This is in contrast to Australia, which has about 100 species of flower-visiting birds including nearly 70 species of Meliphagidae (Ford et al., 1979; Pyke, 1980).

3 Human impacts

Since human arrival some 700 years ago, forest cover has fallen to 23% of land area (Taylor and Smith, 1997: 8.27), and the remaining forests have been affected by introduced mammalian herbivores (Veblen and Stewart, 1982). Over the same time, there have been massive extinctions and range reductions in the avifauna, with 45% of native bird species eliminated from the mainland and 29% going extinct globally, largely due to introduced mammalian predators (Holdaway, 1989; King, 1990; Holdaway et al., 2001).

Of the avian pollinators, the hihi and saddleback are now extinct on the mainland, while the kaka, tui and bellbird are in lower numbers in smaller ranges there (Bull et al., 1985). None of the exotic birds introduced since are significant pollinators, although the European starling (*Sturnus vulgaris*) and recently self-introduced silvereye (*Zosterops lateralis*) pollinate some flowers (Delph and Lively, 1985; O'Donnell and Dilks, 1994).

Four avian dispersers of seed are now extinct. Of those remaining, the hihi and saddleback are confined to predator-free offshore islands, the kokako and weka have restricted distributions, the New Zealand pigeon is widespread but reduced in numbers, and the tui, bellbird and whitehead are absent from parts of the mainland as well. Of the introduced species, all widespread, the silvereye, European starling, Eurasian blackbird (*Turdus merula*), song thrush (*Turdus philomelos*), and common myna (*Acridotheres tristis*) also disperse seed (O'Donnell and Dilks, 1994).

4 Current status of pollination mutualisms

Work on current pollinator service to flowering plants shows that inadequate visitation by birds is resulting in a fall in seed set. This is apparent from data for the bird-pollinated forest shrub, *Rhabdothamnus solandri* (Gesneriaceae), which we studied at two mainland sites near Auckland, where only the tui is present, and at one offshore bird sanctuary (Little Barrier Island), where all extant native bird pollinators are abundant. We performed three pollination treatments: un-manipulated flowers accessible to birds, bagged flowers from which all pollinators were excluded, and hand-pollinated flowers. Fruit set in un-manipulated flowers (67%) on the bird sanctuary was almost as high as for hand-pollinated flowers (70%), showing that pollen servicing by birds was very thorough.

In contrast, un-manipulated fruit set (mean 16%) at both mainland sites was far lower than that for hand-pollinated flowers (83%). Birds visiting *Rhabdothamnus* flowers leave marks on the anther disk, and examination of flowers showed that 83% of flowers had been visited on the bird sanctuary, compared to 20% on the mainland. Evidently, inadequate visitation by avian pollinators is a primary contributor to low fruit set on the mainland. Moreover, ripening fruits contained more seed on the bird sanctuary (395 seeds per fruit) than on the mainland (168). The combined effect of lower fruit set and fewer seeds per fruit on the mainland produces a seed crop in *Rhabdothamnus* that is only 10% of production at sites where prehuman bird densities still exist.

Pollination failure is not restricted to *Rhabdothamnus*. Of seven bird-pollinated plants that were tested, only one, the self-compatible *Alepis flavida*, was found still pollinated adequately at all sampling sites (Table 1). We defined inadequate pollination as a "pollination index" of < 50%, i.e. unmanipulated fruit set was less than halfway between that for pollinator-excluded flowers (the worst-case scenario) and hand-pollinated flowers (the best case). Overall, pollination was inadequate at about half the sites; and in most cases there is evidence that low bird densities are the primary cause.

The reproduction of non-ornithophilous flowering plants pollinated by birds may also be compromised. Due to the decline in the avifauna, there is a widespread failure

Table 1 Percentage of study sites on mainland New Zealand where pollination is inadequate (pollination index < 50%) in bird-pollinated New Zealand plants

Species	Sites with PI < 50% (*n* sites)	Source*
Peraxilla tetrapetala	69% (29)	1
Peraxilla colensoi	30% (10)	1
Rhabdothamnus solandri	100% (2)	2
Fuchsia perscandens	100% (2)	3
Sophora microphylla	55% (11)	2
Fuchsia excorticata	22% (18)	2
Alepis flavida	0% (1)	4

*Sources: Robertson et al., 1999; this paper; Montgomery et al., 2001; Ladley et al., 1997.

of bird-pollination mutualisms on the New Zealand mainland. Some species, in particular the mistletoes (*Peraxilla* spp.), are entirely reliant on reproduction by seed (Robertson et al., 1999). It needs to be stressed that the effects of falls in seed production from such causes are not immediately obvious because most woody plants are long-lived; but ultimately they can lead to serious shifts in vegetation composition.

5 Current status of dispersal mutualisms

In several ways, seed dispersal seems to be less at risk than pollination. There are more widespread species of seed-dispersing birds on the mainland (New Zealand pigeon, tui, bellbird, whitehead, silvereye, European starling, Eurasian blackbird, song thrush, common myna) than pollinating birds (tui, bellbird, silvereye, European starling). Although the dispersal of seeds (> 1.4 cm diameter) of large-seeded trees may be limited to the New Zealand pigeon, which only it can swallow, only six tree species are so affected (Clout and Hay, 1989). Introduced mammals such as brush-tailed possums (*Trichosurus vulpecula*) may also disperse some large-seeded fruits (Williams et al., 2000).

Work on seed-disperser services to plants on the mainland shows that while dispersal of some fruiting plants (*Peraxilla* spp., *Alepis flavida*, *Tupeia antarctica*, and *Ileostylus micranthus*) is adequate in most seasons (Ladley and Kelly, 1996), it has been limited in others by the decline in the numbers of native birds. Comparisons for *Pittosporum crassifolium* between mainland sites near Auckland where only the tui is present and an offshore bird sanctuary (Tiritiri Matangi Island) where all extant native bird dispersers are abundant shows that, despite an equivalent visitation rate by birds, seed dispersal is significantly lower on the mainland (20%) than on the sanctuary (94%). This reflects the inability of introduced bird species at the mainland site to effectively disperse the seed. Similar studies of *Fuchsia excorticata* and *Rhopalostylis sapida* near Wellington also show that a larger proportion of fruits fall undispersed from plants on the mainland than on a neighboring bird sanctuary, Kapiti Island (McNutt, 1998).

Some plants appear able to regenerate from undispersed fruit in the vicinity of the parent (Burrows, 1994; Bell, 1996), while others may not (Ladley and Kelly, 1996; Trass, 2000). Without knowing its frequency, we cannot fully evaluate the consequences of poor dispersal service.

6 Restoring mutualism service

Pollination and dispersal services may be restored on the New Zealand mainland if the representation and numbers of key bird species can be raised. In the last decade, intensive control of introduced mammal pests, especially brush-tailed possums, stoats (*Mustela erminea*) and ship rats (*Rattus rattus*), has frequently increased native bird numbers, including the tui, bellbird and New Zealand pigeon (James and Clout, 1996; Innes et al., 1999). Sustained control of mammal pests is difficult and expensive, and currently confined to areas under 6000 ha (King, 1984; Saunders and Norton, 2001); but options are widening rapidly, including the use of mammal-proof fences (Clapperton and Day, 2001).

7 Conclusions: birds as keystones in New Zealand?

Although Clout and Hay (1989) have argued that pollination failure was likely to have a much less serious effect on the New Zealand flora than seed dispersal failure, it is now clear that pollination failure is a widespread problem for many native plants. The New Zealand temperate flora was unusually reliant on avian mutualists, and severe reductions in the avifauna are having downstream effects on plants. That both pollination and dispersal are continuing to function on the mainland is largely due to three surviving endemic species: tui, bellbird and New Zealand pigeon. Of these, the first two act as both pollinators and dispersers, and despite their low biomass per hectare, are crucial for continued ecosystem function. They could justifiably be called keystone species, and their continued protection is probably necessary to prevent large-scale, long-term changes in the surviving native forests of New Zealand.

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References

Anderson SH, 2003. The relative importance of birds and insects to pollinators of the New Zealand flora. New Zealand J. Ecol. 27: 83–94.

Angehr GR, 1986. Ecology of honeyeaters on Little Barrier Island: a preliminary survey. In: Wright AE, Beever RE ed. The Offshore Islands of Northern New Zealand. Wellington: New Zealand Dept. Lands and Survey, 1–11.

Arkins AM, Winnington AP, Anderson S, Clout MN, 1999. Diet and nectarivorous foraging behaviour of the short-tailed bat (*Mystacina tuberculata*). J. Zool. 247: 183–187.

Atkinson IAE, Cameron EK, 1993. Human influence on the terrestrial biota and biotic communities of New Zealand. Trends Ecol. Evol. 8: 447–451.

Atkinson IAE, Millener PR, 1991. An ornithological glimpse into New Zealand's pre-human past. In: Williams MJ ed. Acta XX Congressus Internationalis Ornithologici. Wellington: New Zealand Ornithological Congress Trust Board, 129–192.

Begon M, Harper JL, Townsend CR,1996. Ecology, 3rd edn. Oxford: Blackwell Science.

Bond WJ, 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Phil. Trans. Roy. Soc. Lond. B 344: 83–90.

Bell R, 1996. Seed Dispersal by Kereru (*Hemiphaga novaeseelandiae*) at Wenderholm Regional Park. MSc thesis, University of Auckland, New Zealand.

Brockie R, 1992. A Living New Zealand Forest. Auckland: David Bateman.

Bull PC, Gaze PD, Robertson CJR, 1985. The Atlas of Bird Distribution in New Zealand. Wellington: Ornithological Society of New Zealand.

Burrows CJ,1994. The seeds always know best. New Zealand J. Bot. 32: 349–363.

Castro I, Robertson AW, 1997. Honeyeaters and the New Zealand forest flora: the utilisation and profitability of small flowers. New Zealand J. Ecol. 21: 169–179.

Clapperton BK, Day TD, 2001. Cost-effectiveness of Exclusion Fencing for Stoat and Other Pest Control Compared with Conventional Control. Wellington: Department of Conservation.

Clout MN, Hay JR, 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. New Zealand J. Ecol. 12 (Suppl.): 27–33.

Craig JL, Stewart AM, Douglas ME, 1981. The foraging of New Zealand honeyeaters. New Zealand J. Zool. 8: 87–91.

Delph LF, Lively CM, 1985. Pollinator visits to floral colour phases of *Fuchsia excorticata*. New Zealand J. Zool. 12: 599–603.

Ford HA, Paton DC, Forde N, 1979. Birds as pollinators of Australian plants. New Zealand J. Bot. 17: 509–519.

Holdaway RN, 1989. New Zealand's pre-human avifauna and its vulnerability. New Zealand J. Ecol. 12 (Suppl.): 11–25.

Holdaway RN, Worthy TH, Tennyson AJD, 2001. A working list of breeding bird species of the New Zealand region at first human contact. New Zealand J. Zool. 28: 119–187.

Hughes L, Westoby M, 1994. Climate change and conservation policies in Australia: coping with change that is far away and not yet certain. Pacific Cons. Biol. 1: 308–318.

Innes J, Hay R, Flux I, Bradfield P, Speed H, Jansen P, 1999. Successful recovery of North Island kokako *Callaeas cinerea wilsoni* populations, by adaptive management. Biol. Cons. 87: 201–214.

James RE, Clout MN, 1996. Nesting success of New Zealand pigeons (*Hemiphaga novaeseelandiae*) in response to a rat (*Rattus rattus*) poisoning programme at Wenderholm Regional Park. New Zealand J. Ecol. 20: 45–51.

King CM, 1984. Immigrant Killers: Introduced Predators and the Conservation of Birds in New Zealand. Auckland: Oxford University Press.

King CM, 1990. The Handbook of New Zealand Mammals. Auckland: Oxford University Press.

Ladley JJ, Kelly D, 1996. Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): dependence on birds. New Zealand J. Ecol. 20: 69–79.

Ladley JJ, Kelly D, Robertson AW, 1997. Explosive flowering, nectar production, breeding systems and pollinators of New Zealand mistletoes (Loranthaceae). New Zealand J. Bot. 35: 345–360.

McNutt KL, 1998. Impacts of Reduced Bird Densities on Pollination and Dispersal Mutualisms in New Zealand Forests. MSc thesis, Massey University, New Zealand.

Montgomery BR, Kelly D, Ladley JJ, 2001. Pollinator limitation of seed set in *Fuchsia perscandens* (Onagraceae) on Banks Peninsula, South Island, New Zealand. New Zealand J. Bot. 29: 559–565.

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

Pyke GH, 1980. The foraging behaviour of Australian honeyeaters: a review and some comparisons with hummingbirds. Aust. J. Ecol. 5: 343–369.

Robertson AW, Kelly D, Ladley JJ, Sparrow AD, 1999. Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). Cons. Biol. 13: 499–508.

Saunders A, Norton DA, 2001. Ecological restoration at Mainland Islands in New Zealand. Biol. Cons. 99: 109–119.

Taylor R, Smith I, 1997. The State of New Zealand's Environment 1997. Wellington: GP Publications.

Trass AP, 2000. Invasion of Woody Species into Weed Infested Areas. MSc thesis, Massey University, New Zealand.

Veblen TT, Stewart GH, 1982. The effects of introduced wild animals on New Zealand forests. Annals Assoc. Amer. Geog. 72: 372–397.

Webb CJ, Lloyd DG, Delph LF, 1999. Gender dimorphism in indigenous New Zealand seed plants. New Zealand J. Bot. 37: 119–130.

Whitaker T, 1987. The roles of lizards in New Zealand plant reproductive strategies. New Zealand J. Bot. 25: 315–328.

Williams PA, Karl BJ, Bannister P, Lee WG, 2000. Small mammals as potential seed dispersers in New Zealand. Aust. Ecol. 25: 523–532.