

The relative importance of birds and insects as pollinators of the New Zealand flora

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Abstract: Native birds may have been underestimated as pollinators of the New Zealand flora due to their early decline in abundance and diversity on the mainland. This paper reconsiders the relative importance of birds and insects as pollinators to eight native flowering plants, representing a range of pollination syndromes, on two offshore island refuges. Experimental manipulations were made on five of these plant species to assess the relative effectiveness of bird and insect visitors as pollinators. In addition, foraging behaviour and the respective morphologies of flowers and visitors were measured at all eight plants to identify the main pollinators. The experimental measures showed that percentage fruit set was significantly higher in flowers exposed to birds than flowers from which birds were excluded in all manipulated plants. The observational measures revealed that for six of the flowering species (*Sophora microphylla*, *Vitex lucens*, *Pittosporum crassifolium*, *Pittosporum umbellatum*, *Pseudopanax arboreus* and *Dysoxylum spectabile*) the endemic honeyeaters were most likely to meet the conditions necessary for successful pollination. For the remaining two species (*Metrosideros excelsa* and *Geniostoma ligustrifolium*) the contribution by honeyeaters and insects to pollination was equivalent. The results suggest that the role of the endemic honeyeaters in pollination of the New Zealand flora, and the subsequent regeneration of native forest ecosystems, should be important considerations in ecosystem management.

Keywords: birds; ecosystem; effectiveness; flora; honeyeaters; insects; management; New Zealand; pollination.

Introduction

Early observations on the pollination ecology of the New Zealand flora suggested insects were by far the most common floral visitors (Thomson, 1927; Heine, 1938) and that most flowers conformed to an insect pollination syndrome (entomophily). Heine (1938) surmised that the largely generalised nature of the native flora allowed promiscuous pollination by a wide range of imprecise insects, while the relatively high incidence of dioecy provided a mechanism ensuring cross-pollination in spite of this simple floral structure. These unusual characteristics, and the rarity of specialised native pollinators such as nectar-feeding birds, have been reiterated in subsequent reviews on the pollination ecology of New Zealand (Godley, 1979; Primack, 1983; Lloyd, 1985; Primack, 1995).

The importance of Diptera as pollinators in the Old World (Proctor *et al.*, 1996) and the fact that pollination of flowers by birds was practically unknown in Britain and Europe (Thomson, 1927) may account for the historical bias that has persisted until recently against recognition of bird pollination in New Zealand. The rapid reduction and loss of bird species which accompanied European settlement may also explain

the general underestimation of bird visitation to native flowering species since the earliest scientific observations made in New Zealand. The relatively small suite of potential bird pollinators endemic to New Zealand (Ford *et al.*, 1979) and the paucity of bird-visited native plants which show obvious adaptations to bird pollination (Godley, 1979; Lloyd, 1985) has resulted in the role of birds being dismissed as relatively unimportant for the New Zealand flora (Primack, 1983; Lloyd, 1985). A review on the pollination of the New Zealand flora concluded that most bird visitation to flowers was incidental, that the birds carried pollen accidentally, and that birds were most likely to foster self-pollination (Godley, 1979).

A lack of further study in this field has allowed this view to survive unchallenged into the present literature (Clout and Hay, 1989; Proctor *et al.*, 1996). However, recent work suggests that birds may be more important in the pollination of the New Zealand flora than previously considered (Craig and Stewart, 1988; Ladley and Kelly, 1995; Castro and Robertson, 1997; Ladley *et al.*, 1997; Heenan, 1998; Heenan and deLange, 1999; Robertson *et al.*, 1999). On offshore island refuges where native bird abundance and diversity is high, birds persistently and regularly visit

species whose pollination is currently considered entomophilous, and are able to obtain sufficient energy rewards from these flowers (Castro and Robertson, 1997). This suggests that observations in ecosystems with depleted bird populations may provide an incomplete picture, and that the use of floral 'syndromes' (flower characteristics attractive to particular guilds of pollinators) to predict the probable pollination of a species in New Zealand may be limited (see also Buchmann and Nabhan, 1996).

The aim of this study is to reconsider the relative effectiveness of birds and insects as pollinators of the New Zealand native flora by measuring fruit set as the outcome of visitation to a flowering plant. Behavioural and morphological factors influencing this outcome, such as rate of visitation, pollen load, pollen transfer, and probability of cross-pollination, are used to identify the main pollinator for each plant. The observations were made on two island refuges where the avifauna more closely resembles that of pre-European New Zealand.

Methods

Site

The primary study site was Tiritiri Matangi Island (36° 36'S, 174° 53'E), which lies off the Whangaparaoa Peninsula in the Hauraki Gulf 28 km north of Auckland city. The 220 ha island is managed by the Department of Conservation as a Scientific Reserve free of mammalian predators. The original vegetation of the island was coastal broadleaf forest, and is described fully by Esler (1978). Restoration of the island following cessation of grazing by sheep and cattle in 1972 has included active planting over former grassland (Craig *et al.*, 1995), eradication of mammalian predators, and translocation of native bird species currently lost or threatened within their northern range on the mainland.

A second site, Little Barrier Island (36° 13'S, 175° 04'E) in the outer Hauraki Gulf, was used to study

P. umbellatum which was poorly represented on Tiritiri Matangi. This 3183 ha island reserve likewise comprises predominantly coastal broadleaf forest, is free of all mammalian predators except the Polynesian rat (*Rattus exulans*), and supports a population of bird species formerly found throughout northern New Zealand.

Species description

Eight flowering plants were selected for study, representing a diversity of form, pollination syndrome and flowering season (Table 1). These included the trees kowhai (*Sophora microphylla*), pohutukawa (*Metrosideros excelsa*) and puriri (*Vitex lucens*), which have relatively large-sized flowers (>20 mm), karo (*Pittosporum crassifolium*), kohekohe (*Dysoxylum spectabile*) and haikaro (*Pittosporum umbellatum*), which have smaller flowers (7–10 mm), and fivefinger (*Pseudopanax arboreus*) and the shrub hangehange (*Geniostoma ligustrifolium*), which have very small flowers (< 3 mm).

There is some conjecture regarding the pollination ecology of all the above species except *V. lucens*, which is commonly accepted as bird pollinated (ornithophilous) (Petrie, 1904). Although both *S. microphylla* and *M. excelsa* are usually regarded as ornithophilous (Godley, 1979), it has been argued that *S. microphylla* has a range of bird and insect pollinators (McCann, 1952–1954; Clout and Hay, 1989), while the shallow nectar cup and frequent insect visitation observed at *M. excelsa* has led to the suggestion that birds visit the unadapted brush flowers of this species as thieves and pollinate only by accident (McCann, 1952–1954). There is evidence that lizards and bats, both of which have been greatly reduced on the New Zealand mainland, may also play a role in pollen transfer in *M. excelsa* (Whitaker, 1987; Arkins *et al.*, 1999). The pollination of the remaining smaller-flowered species has received scant attention and, in the absence of obviously bird-adapted features, is considered entomophilous (Webb *et al.*, 1998).

All extant endemic avian floral visitors except

Table 1. Characteristics of flowering plants selected for study.

Species	Plant form	Syndrome	Season	Style (mm)	Breeding system
<i>Sophora microphylla</i>	Tree-canopy	Bird?	Late winter	36.1	Hermaphrodite
<i>Metrosideros excelsa</i>	Tree-emergent	Bird?	Early summer	30.8	Hermaphrodite
<i>Vitex lucens</i>	Tree-emergent	Bird	Winter	24.9	Hermaphrodite
<i>Pittosporum crassifolium</i>	Tree-subcanopy	Insect	Late winter	8.9	Dioecious
<i>Dysoxylum spectabile</i>	Tree-canopy	Insect	Early winter	7.6	Dioecious
<i>Pittosporum umbellatum</i>	Tree-subcanopy	Insect	Midwinter	7.2	Dioecious
<i>Geniostoma ligustrifolium</i>	Shrub-understorey	Insect	Spring	2.3	Gynodioecious
<i>Pseudopanax arboreus</i>	Tree-subcanopy	Insect	Midwinter	2.2	Dioecious

kaka (*Nestor meridionalis*) were represented on Tiritiri Matangi, including tui (*Prothemadera novaeseelandiae*), bellbird (*Anthornis melanura*), hihi (*Notiomystis cincta*), kakariki (*Cyanoramphus novaeseelandiae*), saddleback (*Philesturnus carunculatus*) and whitehead (*Mohoua albigilla*) (Heather and Robertson, 1996). On Little Barrier Island, kaka were also present. Various other bird species known to visit flowers, including the recently self-introduced silvereye (*Zosterops lateralis*), and the introduced rosella (*Platycercus eximius*), starling (*Sturnus vulgaris*) and myna (*Acridotheres tristis*), were present in relatively low numbers on the islands.

Tui, bellbird and hihi, the three endemic honeyeaters (Meliphagidae), are frequent nectar feeders (Craig *et al.*, 1981) and possess a channelled, bifurcated tongue, tipped with a brush of flattened hairs that serve as capillaries for the uptake of nectar (McCann, 1964). Kaka, kakariki, saddleback, silvereye, starling and rosella show less specialised adaptations to nectarivory, while whitehead and myna show none (McCann, 1964).

The insect orders associated with flower visitation in New Zealand—Hymenoptera (bees), Diptera (flies), Coleoptera (beetles) and Lepidoptera (butterflies and moths) (Godley, 1979)—were all represented on both islands. Hymenoptera were represented mainly by the native short-tongued Colletid and Halictid bees, which are essentially pollen gatherers (Godley, 1979). The introduced long-tongued honeybee *Apis mellifera* was present in lower numbers than the native bees, and is a nectar-collecting bee. Diptera are considered the most numerically abundant flower visitors in New Zealand (Heine, 1938), although there has been a lack of precise estimates of their effectiveness as pollinators (Lloyd, 1985). Coleoptera are also recognised as common pollen vectors, and numerous Lepidoptera have been found in association with native flowering plants (Thomson, 1927; Godley, 1979).

Fruit and seed set

The relative contribution of birds and insects to fruit set was measured in five of the flowering species by experimentally manipulating visitation. Unopened buds were counted and exposed to one of two conditions; 1) open to visitation by all pollinators, or 2) enclosed in 2x2 cm mesh cages to exclude birds but not insects. In the hermaphrodite plant species, a third condition excluded all visitors by enclosing unopened buds in cotton gauze bags. These experimental conditions were replicated on approximately 10 individuals for each plant species. Validation tests by Schmidt-Adam (1999) to ensure that bee movement was not influenced by cage mesh enclosures showed no evidence of obstruction. Since bees were amongst the largest insect floral visitors observed during the study, it was assumed the cages did not impede insect movement. The

proportion of fruit set was recorded for each experimental condition. To investigate whether the standard measure of fruit set masked variability in the number of seeds set per fruit between open- and insect-pollinated conditions, the number of seeds per fruit was scored for a single species (*P. crassifolium*).

Flower visitation

Identification of visitors to flowers was achieved by observing approximately 10 individuals of each of the eight plant species, for one-hour periods, at comparable stages of flowering. To identify bird visitors to flowers, the plants were observed using 8x40 binoculars at sufficient distance to avoid deterring visitors, and the number of visits by each species recorded. A standard five-minute count of all birds seen or heard within 100 m (Dawson and Bull, 1975) was made during the observation period to measure the relative abundance of bird species.

To identify insect visitors to flowers, a sample was obtained by enveloping several inflorescences in a pillowcase and tapping the branch to dislodge insects. These were then captured using a collecting jar (Oldroyd, 1958), and killed by exchanging the lid with one under which a small wad of cotton wool soaked in ethyl acetate had been inserted. Specimens were later inspected and identified to order level. Samples were taken on at least three randomly selected individuals of all insect-visited plant species. In dioecious species, only female plants were sampled since the method was destructive and it was of most interest whether pollen-bearing insects were contacting the stigma of flowers.

Ten relative counts of insects and birds were obtained during the one-hour observation period by setting a timer to 4-minute intervals, and at each signal making an instantaneous scan of the plant using binoculars. To account for the possibility that the scan may have under-represented small or flightless insects, 100 flowers were inspected at close range at the end of the observation period and the proportion of flowers containing insects recorded. Logistical constraints on Little Barrier Is. meant that insect data were not collected for *P. umbellatum*, although no insect activity was observed at this species.

Pollen load

Floral visitors were sampled to identify whether they were carrying pollen, and in what location and quantity. Birds were captured in mistnets set in the vicinity of each selected flowering species. The bill and facial feathers were sampled separately by dabbing with a small (approx. 2x2 cm) piece of Sellotape in the direction of the feathers. This was stuck to a labelled microscope slide and inspected under 10x magnification, and the number of pollen grains of each flowering species scored on a log scale. The median

pollen score for each body area was calculated for each bird species. The pollen scores for each individual were also combined to give an estimate of total pollen load, and the median of these calculated for each bird species. A small dot of non-permanent 'Twink' was applied to the right tarsus of each bird on release, to avoid re-sampling the same individual.

To ascertain whether insect visitors were carrying pollen, the insects collected for identification were examined under 10x magnification with a dissecting microscope, and a median of the total pollen load obtained for each order.

Pollen transfer

To determine whether the pollen carried by floral visitors contacted the stigma of flowers visited, morphological measures of visitor and flower characteristics were made. The bill length of birds captured in mistnets was measured and a mean obtained for each species. The range in body length of insects for each order was obtained from specimens and the literature (Grant, 1999). Distance of the anthers and stigma from the nectary was measured for at least 10 randomly selected flowers of each plant species. All measurements were made using vernier calipers. The method of feeding by floral visitors was also identified by observation. The likelihood and means of pollen transfer was determined by comparing the morphological measures of bird and insect characteristics with those of flowers, along with information on pollen loads and feeding behaviour.

Cross-pollination

The duration (seconds) of each visit by a bird was recorded whenever possible, to assess frequency of movement between trees. Note was taken of whether visiting birds flew to a tree of the same species on termination of feeding, to obtain a measure of potential outcrossing. This could only be scored when the bird flew to a tree within sight of the observer. Duration of visits by insects and their potential outcrossing rate were not measured.

The SAS System was used for all statistical analysis, and the results are presented in the format

recommended by the SAS Users Guide (Hatcher and Stepanski, 1994). The statistics for results with a probability value higher than 0.1 are not reported.

Results

Fruit and seed set

The probability of fruit set was tested using the maximum likelihood ANOVA with chi-squared approximation, and showed a significant difference between the open and caged experimental conditions for all flowering species sampled (*P. arboreus* $\chi^2_{(1)} = 9577.6$, $P < 0.001$; *G. ligustrifolium* $\chi^2_{(1)} = 61.4$, $P < 0.001$; *P. crassifolium* $\chi^2_{(1)} = 19.6$, $P < 0.001$; *M. excelsa* $\chi^2_{(1)} = 337.4$, $P < 0.001$; *S. microphylla* $\chi^2_{(1)} = 31.1$, $P < 0.001$). For all species, a higher percentage of fruit were set in flowers accessible to birds relative to flowers from which birds were excluded (Table 2).

The percentage of fruit set in the absence of pollinators varied for the two hermaphrodite plant species (Table 2). No fruit set occurred in bagged *S. microphylla* flowers; however information was obtained for only six trees, due to loss of bags in adverse weather conditions. The proportion of bagged *M. excelsa* flowers that set fruit was relatively low. Selfing is probably enabled by the open structure of the blossom and a variable degree of self-compatibility in this species. The seedset measure for *P. crassifolium* was higher in flowers exposed to birds (32.9 ± 1.9) relative to flowers available only to insects (20.1 ± 5.1)

Flower visitation and pollen load

Birds were observed visiting all eight plant species, including those with small insect-syndrome flowers (Table 3). The rate of bird visitation was high (>8 visits/hour) to all species except *G. ligustrifolium* and *P. umbellatum*, which were visited regularly (>2 visits/hour). Tui and bellbird were the most prevalent flower-visiting bird species. A moderate to strong correlation between the visitation rate and abundance of each bird species on the island was revealed for all flowering plants analysed (Spearman's test for correlation: *P. arboreus*: $r_s = 1.0$; *V. lucens*: $r_s = 0.9$; *M. excelsa*: r_s

Table 2. Percentage fruit set under each experimental condition ($X \pm SE$ ($n = \text{no. flowers}$)).

Plant species	Experimental condition (pollinators)		
	Open	Insects only	None
<i>S. microphylla</i>	21.4 \pm 1.5 (754)	0.5 \pm 0.4 (397)	0 \pm 0 (128)
<i>M. excelsa</i>	57.9 \pm 1.1 (2173)	27.8 \pm 1.1 (1707)	15.7 \pm 0.5 (411)
<i>P. crassifolium</i>	70.1 \pm 4.4 (107)	26.3 \pm 7.1 (38)	n/a
<i>G. ligustrifolium</i>	6.0 \pm 0.3 (9200)	3.0 \pm 0.2 (7150)	n/a
<i>P. arboreus</i>	82.7 \pm 0.2 (29647)	35.0 \pm 0.4 (16787)	n/a

=0.8; *G. ligustrifolium*: $r_s=0.8$; *D. spectabile*: $r_s=0.7$; *P. umbellatum*: $r_s=0.4$), indicating that the relative use of flowers by birds was in proportion to the abundance of each bird species. *Pseudopanax crassifolium* and *S. microphylla* could not be included in the correlation analysis, since they were visited by only two bird species.

Insect visitation was noted at five of the seven study plants scored (Table 3). Hymenoptera, Diptera and Coleoptera were the most prevalent flower-visiting insect orders. Two orders not previously associated with flower pollination, Hemiptera (bugs) and Neuroptera (lacewings), were also recorded as visitors. Results from the instantaneous scans showed that insect activity was an order of magnitude greater than that of birds at *M. excelsa*, comparable to birds at *G. ligustrifolium* and *P. crassifolium*, but significantly lower than bird activity at the remaining species (Table 4). The proportion of insects per 100 flowers was strongly correlated with the measure of insect activity by scans for each flowering species ($r_s=0.87$).

Although not all visitors to a plant were captured for pollen sampling, especially where their visitation

rate to the plant was low, a representation of visitors to each flowering species was obtained. Bird species and insect orders varied in the median amount of pollen carried to different flowering plants (Table 5). Tui and bellbird, as well as being the most regular avian visitors, also routinely carried large pollen loads after feeding at flowers. Less information was obtained for hihi and silvereve, although they probably carried similar loads. Kakariki, whitehead and saddleback, although visiting a narrower range of flowering plants, were also capable of carrying large amounts of pollen. Rosella, myna and starling were not sampled, but were infrequent floral visitors. The most regular insect visitors, Hymenoptera and Coleoptera, carried moderately large pollen loads as a result of feeding at flowers. The insect orders Diptera, Hemiptera, Neuroptera and Lepidoptera generally carried smaller loads and were less regular floral visitors.

Pollen transfer

Some pattern was discernible in the location of the pollen load on bird visitors, with respect to the

Table 3. Bird visitation rate (mean visits/plant/hour \pm SE, n = observation hours), and main insect visitor(s), to flowering plants.

Birds	Plants							
	<i>S. microphylla</i> ($n=22$)	<i>M. excelsa</i> ($n=13$)	<i>V. lucens</i> ($n=13$)	<i>P. crassifolium</i> ($n=11$)	<i>D. spectabile</i> ($n=20$)	<i>P. umbellatum</i> ($n=18$)	<i>G. ligustrifolium</i> ($n=17$)	<i>P. arboreus</i> ($n=27$)
Tui	7.2 \pm 2.0	24.2 \pm 5	2.1 \pm 0.6	2.0 \pm 0.1	3.8 \pm 0.8	1.0 \pm 0.3	0.4 \pm 0.2	3.8 \pm 1.1
Bellbird	1.5 \pm 0.6	17.5 \pm 5.4	12.7 \pm 3.3	8.6 \pm 4.3	4.0 \pm 0.5	0.7 \pm 0.3	1.4 \pm 0.4	17.8 \pm 3.9
Hihi	0	0.2 \pm 0.1	0.6 \pm 0.4	0	0.1 \pm 0.1	0.1 \pm 0.1	0	0.2 \pm 0.2
Silvereve	0	3.8 \pm 1.1	0.3 \pm 0.3	0	0.3 \pm 0.1	0	0.4 \pm 0.4	0.2 \pm 0.2
Kakariki	0	0.8 \pm 0.3	0	0	0	0.4 \pm 0.3	0.5 \pm 0.3	0
Whitehead	0	0.5 \pm 0.5	0	0	0	0.1 \pm 0.1	0	0.5 \pm 0.3
Rosella	0	0	0.2 \pm 0.2	0	0	0	0	0
Saddleback	0	0.9 \pm 0.5	0	0	0	0	0	0
Myna	0	0.2 \pm 0.1	0	0	0	0	0	0
Starling	0	0.2 \pm 0.2	0	0	0	0	0	0
Insects	Coleoptera Diptera	Coleoptera Hymenoptera	none	Coleoptera Diptera	none	? none?	Coleoptera Diptera	Coleoptera Diptera
	Hemiptera Neuroptera			Hemiptera			Hymenoptera Lepidoptera	Hymenoptera Hemiptera

Table 4. Comparison of relative bird and insect activity (mean no. per plant per scan) at each flowering species.

Plants	Birds	Insects	t	d.f.	P
<i>S. microphylla</i>	0.17	0.01	3.81	85	<0.0002
<i>M. excelsa</i>	3.81	37.39	4.69	32	<0.0001
<i>V. lucens</i>	1.17	0	7.2 ¹	51	<0.0001
<i>P. crassifolium</i>	0.38	0.31	0.35	31	0.7309
<i>D. spectabile</i>	0.90	0	5.82 ¹	49	<0.0001
<i>G. ligustrifolium</i>	0.63	0.60	0.10	34	0.9242
<i>P. arboreus</i>	1.71	0.47	8.90	134	<0.0001

¹ non parametric Wilcoxon scores reported (Z and t -test significance approximation)

Table 5. Variation in pollen load between bird and insect floral visitors to plants (n = no. of individuals).¹

Floral visitors	Plants							
	<i>S. microphylla</i>	<i>M. excelsa</i>	<i>V. lucens</i>	<i>P. crassifolium</i>	<i>D. spectabile</i>	<i>P. umbellatum</i>	<i>G. ligustrifolium</i>	<i>P. arboreus</i>
Tui	4 (5)	4 (1)	4 (1)	1 (1)	3 (5)	4 (3)	?	4 (2)
Bellbird	1 (3)	4 (7)	?	2 (11)	2 (2)	2 (8)	2 (2)	3 (27)
Hihi		?	?		?	3 (9)		?
Silvereye		?	2 (9)				?	?
Kakariki		4 (2)				?	3 (1)	
Whitehead	?					3 (8)		1 (2)
Saddleback	4 (1)							
Hymenoptera	4 (1)	3 (3)					?	2 (2)
Coleoptera	2 (4)	2 (1)		2 (73)			0 (5)	2 (12)
Neuroptera	2 (6)							
Diptera	0 (3)			0 (2)			0 (5)	2 (12)
Hemiptera	0 (1)		0 (1)		1 (2)			
Lepidoptera							0 (3)	

¹ 4 = 1000⁺ grains; 3 = 100-999 grains; 2 = 10-99 grains; 1 = 1-9 grains; 0 = no pollen; ? = not sampled

relationship between flower size and bird bill length (Table 6). In the large flowers (*S. microphylla*, *M. excelsa* and *V. lucens*) and the very small flowers (*G. ligustrifolium* and *P. arboreus*) foraging birds tended to carry more pollen on the facial feathers than the bill. Lack of pattern in the remaining flowers may have been a result of using categorical rather than numerical data to score pollen loads.

Observations of the feeding behaviour of visitors to flowers established whether successful transfer of the pollen load was likely to occur. The stigma of the smaller-flowered species (*P. arboreus*, *G. ligustrifolium*, *D. spectabile*, *P. umbellatum* and *P. crassifolium*) was likely to be contacted by all bird and insect visitors. However different feeding behaviours meant that not all visitors effectively transferred pollen. Kakariki typically fed destructively at *P. umbellatum* and *G. ligustrifolium* by crushing the flowers for nectar, while some insects visitors actually parasitised or fed on plant parts, e.g. Hemiptera and some Coleoptera on *P. crassifolium*. Transfer of pollen by visitors to stigma of the large-flowered species (*V. lucens*, *M. excelsa* and *S. microphylla*) was influenced by floral structure. The stigma of *V. lucens* flowers was likely to be contacted by all bird visitors, and there was no insect visitation observed for this species. Access to the stigma of the open brush-flowered *M. excelsa* depended on the approach of visitors. Larger birds positioned themselves over the flowers of *M. excelsa* while feeding and were likely to deposit pollen on the stigma. In contrast, the relatively small silvereye and whitehead frequently foraged from the base of the inflorescence, and were less likely to contact the stigma. Likewise, nectar-feeding honeybees gained access to the nectar from a position below the stigma, and contacted the receptive surface when exiting flowers

Table 6. Relative difference of anther to bill length ratio, and location of pollen load on the visitor, for each flowering species.

Plant	Bird	Anther/bill ratio	Pollen load ¹	
			Face	Bill
<i>S. microphylla</i>	Tui	+	4	4
	Bellbird	+	1	0
<i>M. excelsa</i>	Tui	+	4	?
	Bellbird	+	4	2
	Kakariki	+	4	2
<i>V. lucens</i>	Saddleback	-	4	0
	Tui	=	3	3
<i>P. crassifolium</i>	Silvereye	+	2	0
	Tui	-	1	0
<i>D. spectabile</i>	Bellbird	-	1	1
	Tui	-	1	2
<i>P. umbellatum</i>	Bellbird	-	2	0
	Tui	-	2	4
	Hihi	-	3	2
	Bellbird	-	2	1
<i>G. ligustrifolium</i>	Whitehead	-	2	2
	Bellbird	-	2	1
	Kakariki	-	3	3
<i>P. arboreus</i>	Tui	-	4	3
	Bellbird	-	3	2
	Whitehead	-	1	0

¹ 4 = 1000⁺ grains; 3 = 100-999 grains; 2 = 10-99 grains; 1 = 1-9 grains; 0 = no pollen

on only 6% of foraging bouts ($n = 17$). Pollen-gathering honeybees appeared more likely to contact the stigma while crawling over the surface of the brush flowers in search of pollen. The more numerous native bees, although predominantly pollen gatherers, are smaller than *A. mellifera* (6-10 mm cf. 13 mm) and contacted the stigma in 10% of flowers visited ($n = 91$). Pollen

transfer to the stigma of the more complex *S. microphylla* flower was likely to be routinely achieved only by foraging tui. Bellbird were most frequently observed probing down the outside of the flower to reach the nectary without contacting the stigma. The distance between the stigma and the nectary in *S. microphylla* blossoms precluded foraging insect visitors from contacting the stigma. The pollen-bearing Coleoptera (Chrysomelid leaf beetles and Curculionid weevils), which occurred on *S. microphylla*, feed destructively on the plant parts.

Cross pollination

Only tui and bellbird were sufficiently frequent floral visitors to allow measurement of movement between plants, and hence possible cross-pollination. Comparison between tui and bellbird across all flowering species revealed a significant difference in visit duration ($t_{(365)} = -2.39$; $P < 0.001$). Tui spent significantly longer visiting a plant than bellbird (tui 224 ± 28.4 sec; bellbird 153 ± 9.8 sec). Both tui and bellbird were highly likely to fly to another plant of the same species on termination of a feeding bout (76%, $n = 621$ and 73%, $n = 349$ respectively).

Discussion

The findings of this study challenge some of the prevailing assumptions regarding the pollination ecology of the New Zealand flora. The need for attention to fruit set as the final outcome of flower visitation, as validation of the apparent pollination systems of the native flora, has long been acknowledged (Godley, 1979). Despite most of the plants being presumed insect-pollinated, experimental manipulations to measure the relative effectiveness of birds and insects as pollinators highlight the contribution of native birds to successful fruit set. When birds were excluded from inflorescences, fruit production was reduced in all species. This was most marked in plants that flowered over the colder months (*S. microphylla*, *P. crassifolium* and *P. arboreus*), when insect activity would be lowest and food requirement by birds high. Preliminary investigation of seed set suggests that, in addition, birds may be more effective pollinators than insects for plants with multi-seeded fruits, resulting in higher numbers of seed set per fruit in bird-visited flowers. These results agree with other studies comparing the relative pollinating effectiveness of birds and insects, which report a higher fruit set in bird-visited flowers than in those to which only insects had access (Carpenter, 1976; Waser and Real, 1979; Ramsey, 1988; Vaughton, 1996), and higher numbers of seeds per fruit as a result of bird visitation (Stewart, 1989; Schmidt-Adam, 1999). The absence of self-compatible

S. microphylla suggests that present selection pressure on the study population may favour an outbreeding system, since self-pollinating individuals are known to occur within populations elsewhere (Rattenbury, 1979). A relatively low proportion of self-set seed in *M. excelsa* may indicate the occurrence of selective seed maturation favouring outcrossed seed (see Craig and Stewart, 1989).

Comparison between the range of birds and insects visiting each flowering plant, in terms of their ability to meet the conditions required for successful pollination, allows the most important pollinators to be identified. Regular visitation is a basic condition of pollination, since it potentially results in greater pollen deposition over a longer time period and a higher likelihood of fruit set (Turner, 1982). The prevalence of the native honeyeaters, especially bellbird and tui, as visitors to all flowering species in this study suggests they are reliable floral visitors. The lower prevalence of hihi and silveryeye as floral visitors may be due to the smaller populations of these species on Tiritiri Matangi Island. However, the same pattern was observed on Little Barrier Island where hihi numbers are higher, suggesting they may be less nectarivorous than the other honeyeaters (see also Craig *et al.*, 1981). Less regular visitation to a narrower range of plants by other bird species suggests their importance is more limited. Burquez (1989) notes that only rarely do bird species other than the avian pollinator group particular to a geographical area serve as pollinators.

The most prevalent insect visitors were Diptera, Hymenoptera and Coleoptera, and regular insect visitation to half the study plants (*P. crassifolium*, *M. excelsa*, *P. arboreus* and *G. ligustrifolium*) implies a contribution by insects to the pollination of these species. Low or lack of insect visitation to the remaining four species suggests insects are unlikely to be important to their pollination. These findings are at variance with the accepted view that New Zealand's pollination ecology is dominated by a generalised insect pollinating fauna (Lloyd, 1985) with little contribution by birds (Godley, 1979). However, most observations of visitation to native flowers have been made on the post-European mainland of New Zealand, where rapid reduction or extinction of honeyeater populations accompanied colonisation. The use of flowers by birds in proportion to bird abundance demonstrated in this study suggests that such a reduction would adversely affect the rate of bird visitation to flowers. Reduced bird density would also be likely to affect the range of flowering species visited, since competitive pressure at higher densities results in visitation to a wider range of food sources (Villem *et al.*, 1984). Observations on offshore island refuges, where bird densities more closely represent pre-European New Zealand, show that the native honeyeaters are persistent visitors to a

wide range of flowers not normally associated with bird visitation on the mainland.

A further condition for successful pollination is the donation of sufficient pollen, and the amount of pollen a visitor carries can be used as another indicator of their effectiveness (Stewart, 1989). The consistently large amounts of pollen carried by foraging honeyeaters observed in this study is in agreement with findings by Paton and Ford (1977), Collins *et al.* (1984), and Ford *et al.* (1979) for Australian honeyeaters and highlights the reliability of honeyeating birds as pollen vectors. Other less regular avian floral visitors were also capable of carrying large pollen loads. This may explain the relatively high seed set in bird-visited flowers observed for *P. crassifolium*. Hymenoptera were prevalent pollen-bearing insect visitors and were represented by the native Halictid and Colletid bees (*Lasioglossum* sp. and *Leioproctus* sp.), which typically carry large loose pollen loads, and by the introduced Apidae (honeybees and bumblebees) which carry pollen packed wet on the legs (Buchmann and Nabhan, 1996). The moderate pollen loads regularly carried by flower-visiting beetles confirms these as common pollen vectors (Proctor *et al.*, 1996). Neuroptera and Hemiptera, observed as occasional pollen vectors in this study, have not previously been associated with pollination in New Zealand. The variability of pollen transport by flower-visiting Diptera does not support the general perception of these insects as the most important pollinators of the native flora (Thomson, 1927; Heine, 1938), although their relative importance may increase with altitude.

In addition to carrying pollen, an effective floral visitor must also deposit pollen on the receptive stigma of a flower of the same species (Ford *et al.*, 1979). The ability to do this may be influenced by variation in foraging behaviour and morphology between pollen vectors (Paton and Ford, 1977; Wyatt, 1982). Location of the main pollen load on the facial feathers of birds visiting the larger flowered plants (*V. lucens*, *M. excelsa* and *S. microphylla*) meets requirements for successful pollen transfer in plants where anther-nectary distance is greater than the bill length of visiting birds (Paton and Ford, 1977). However birds visiting the smallest flowers (*G. ligustrifolium* and *P. arboreus*), where the distance from the anther to the nectary was smaller than the bill, also carried the main pollen load on the facial feathers, and not on the bill as predicted. This confirms the description by Castro and Robertson (1997) of birds feeding at the dense floral arrangements of these plants and brushing against anthers with the head and throat, which become covered in pollen that is likewise donated to stigma.

While the foraging behaviour of most pollen-bearing birds at flowers was likely to result in pollination, the behaviour of some compromised

successful transfer. Kakariki usually fed at flowers destructively, and are unlikely to be reliable pollinators. Bellbird were unable to reach the gap between the dorsal pair of stamens at the base of the kowhai flower, which permits access by the tongue to the tightly caged nectar (McCann, 1952-1954), and usually fed from the side without contacting stigma or anthers (see Heather and Robertson, 1996). This behaviour may explain the relatively light load of *S. microphylla* pollen and low visitation rate by bellbird to this flowering plant. Similar behaviour by silvereye and whitehead at *M. excelsa* was also unlikely to result in frequent pollen deposition on the stigma. Studies by McNee (1995) on *Eucalyptus rhodantha*, Stewart (1989) on *Feijoa sellowiana*, and Delph and Lively (1985) on *Fuchsia excorticata* likewise show that small birds often fed at larger flowers without transferring pollen.

Morphology suggests that most pollen-bearing insects were likely to contact the stigma of the smaller-flowered species during a visit. Insects foraging at the larger flowers were either pollen predators (e.g. Coleoptera at *S. microphylla*) or tended to localise their activity below the stigma. Studies comparing stigma contact rate for flower-visiting honeybees and honeyeating birds support a low contact rate for bees relative to birds (Ramsey, 1988; Buchmann and Nabhan, 1996), although this may increase to 27% for honeybees involved in both nectar and pollen collection (Schmidt-Adam, 1999). However, the relatively infrequent contact rate by bees visiting *M. excelsa* was compensated by high visitation, resulting in an overall pollinating effectiveness comparable to birds (see also Paton, 1993). This is in contrast to observations by Schmidt-Adam *et al.* (2000) of low insect visitation to *M. excelsa* at the same site and is probably explained by the early season of those observations (G. Schmidt-Adam, Massey University, Auckland, New Zealand, *pers. comm.*), since insect activity increased progressively over the flowering season as temperature increased.

These results suggest that the use of floral morphology to predict the likely pollinators of flowers (floral 'syndromes') has tended to be a mental straightjacket when applied to the smaller-flowered trees and shrubs of the New Zealand flora (see Faegri and van der Pijl, 1971). As a result many of these have been considered entomophilous in the absence of qualifying ornithophilous features. Despite a similar lack of ornithophilous characters, many Australian species are recognised as bird pollinated (Ford *et al.*, 1979; Keighery, 1982; Collins and Rebelo, 1987; Ippolito and Armstrong, 1993; McNee, 1995), probably due to greater persistence of the native avifauna in the landscape. Recent theory suggests that bird-plant associations may in fact be more closely related to variables such as perch size or body mass than flower

morphotype (Brown and Hopkins, 1995; Stanley and Lill, 2001). In this respect, the small-flowered *P. arboreus* and *D. spectabile*, which are heavily bird-visited but do not conform to the general floral syndrome for bird pollination, may be well suited to use by native honeyeating birds. These mass-flowering plants all present portions of bare stem, stalk and flower bract convenient for the access of flowers by perching nectarivorous birds (Proctor *et al.*, 1996). Tui, the largest and heaviest of the honeyeaters, are excluded from perching on the less robust portions such as inflorescence stalks (Craig *et al.*, 1981) and are restricted to flowers accessible from the plant stem. In contrast, the lighter and more subordinate bellbird and hihi are able to access flowers from perches along the more fragile flower bracts. The flowers of *P. arboreus* and *D. spectabile* are aggregated to form a highly concentrated resource, sufficient to meet the energy requirements of birds in the size range of the native honeyeaters (Castro and Robertson, 1997). Consideration of such variables may be useful in reassessing the accommodation of floral visitors by native plants.

A final condition for successful pollination in many plants is the delivery of outcross pollen. The extent to which this is met is determined by the movement of pollen vectors within and between plants (Levin, 1979; Kearns and Inouye, 1993). The flowering plants in this study ranged from dioecious species, which rely on movement of the pollen vector between plants, to hermaphrodite species with varying ability to self-fertilise. Birds are generally believed to effect high levels of outcrossing (Ford *et al.*, 1979), and the high constancy shown by bellbird and tui while feeding at a flowering species suggests they are likely to effect cross-pollination. The degree to which this occurs is influenced by the diversity, density and status of foraging birds present (Webb and Bawa, 1983; Craig and Stewart, 1988). Where the honeyeater species coexist, the larger more dominant tui is capable of defending a flowering tree and spending longer intervals feeding, while the smaller subordinate bellbird and hihi are often displaced and have characteristically shorter feeding intervals (see also Castro and Robertson, 1997). Ford *et al.* (1979) note that in defended plants, cross-pollination is mostly achieved by such displaced birds, which visit only a few flowers on each plant before being chased.

The relative probability of outcrossing by birds and insects was not assessed quantitatively. Insects, especially native bees, are known to be effective cross-pollinators for some native shrubs (Delph, 1990; Webb, 1994; Webb, 1985). However, studies by Stiles (1978), Webb and Bawa (1983), and Stewart (1989) indicate that in plants visited by both birds and insects, birds are generally responsible for greater pollen flow and are

more likely to outcross than insects. In native dioecious flowering trees and shrubs, a variable degree of insect pollination would be expected. Where individuals of dioecious species grow in proximity, flower-visiting insects may successfully transfer pollen between plants. This is evident in *P. arboreus*, where male and female trees occurred in mixed stands, and caged flowers achieved good fruit set. However, where individuals are separated by distance, the activity especially of less mobile insect visitors would be reduced (see also McNee, 1995; Waser, 1982). This is illustrated by a higher contribution to fruit set by birds relative to insects, despite equivalent visitation, in the dioecious flowering tree *P. crassifolium*. The same effect was not evident in *G. ligustrifolium*, which was also visited equally by birds and insects, since the main bird visitors (kakariki) destroyed the flowers without pollinating. The limitations of insect visitors would be further accentuated for canopy flowering trees. This can be seen in *M. excelsa* where despite a tenfold higher visitation rate by insects, fruit set attributable to birds and insects was equivalent. Schmidt-Adam *et al.* (2000) observed that birds, rather than insects, clearly promoted cross-pollination in *M. excelsa*, and that outcrossed seeds produced larger, more vigorous plants than selfed seeds.

Until recently, the advantage of bird visitation to plants in New Zealand was unclear. Godley (1979) maintained that birds were most likely to foster self pollination, especially in hermaphroditic plants, and this perception is reinforced by the apparent lack of interaction and displacement between foraging honeyeaters on mainland New Zealand, where native honeyeater populations are much reduced. The hypothesis that solitary birds would divide a large nectar source into individual territories, reducing the pollen flow to below that achieved by insects, has been used to explain the apparent lack of bird-pollinated trees in the New World (Stiles, 1978). The fact that approximately 44% of New World canopy rainforest species, many of them dioecious, are pollinated by large bees is used to support this (Stiles, 1978). However, while dioecious canopy trees are also common in New Zealand forest, long-tongued bees are under-represented in the native pollinator fauna and the flowers are visited instead by native honeyeating birds. The native honeyeaters are relatively large, perch to feed and often congregate in areas of high resources. These attributes and the resulting social interactions predispose native honeyeaters to foraging in, and successfully cross-pollinating, flowering canopy trees.

Studies of pollinator effectiveness, in place of the usual lists of floral visitors, are recommended if a meaningful understanding of pollination ecology is to be attained (Johnson and Steiner, 2000). The present

study suggests that interactions between the native honeyeaters and the New Zealand flora may have important ecological consequences for native forest communities. Drastic reduction in the abundance and diversity of honeyeaters throughout mainland New Zealand may be limiting the regenerative capacity of a wide range of native flowering species. The 'invisible' nature of this impact means that increasingly impoverished communities are mistakenly considered the natural vegetation cover. The implications of this process disruption on species persistence and forest composition needs to be recognised in native biodiversity management.

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