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# HONEYEATERS AND THE NEW ZEALAND FOREST FLORA: THE UTILISATION AND PROFITABILITY OF SMALL FLOWERS

**Summary:** New Zealand flowers are frequently considered unspecialised allowing easy access to pollen and nectar by a wide range of visitors. Most conform with a syndrome of insect pollination (entomophily). Pollination of forest flowers by birds has been described for a range of species whose flowers are morphologically ornithophilous. On Kapiti Island and Little Barrier Island, all three species of New Zealand honeyeaters have been described feeding on flowers currently assumed to be entomophilous or where the pollination system is unknown. The persistence and regularity of visits suggests that the birds are obtaining suitable rewards in the form of nectar and could be serving as pollinators.

We measured the nectar energetic value from flowers of three ornithophilous and five entomophilous species. Nectar production over 24 hours was highest in ornithophilous species, but the standing crop of nectar overlapped - ornithophilous species: *Metrosideros fulgens* (standing crop 6.6 J), *Metrosideros excelsa* (22 J), and *Fuchsia excorticata* (1.8 J); and entomophilous: *Pittosporum crassifolium* (23 J), *Pseudopanax arboreus* (1.5 J), *Dysoxylum spectabile* (3.7 early flowers - 6.7 J late flowers), *Pittosporum eugenioides* (2.7 J) and *Geniostoma rupestre* (1.8 J). The entomophilous species present the flowers in aggregation and as result birds can visit a large number flowers per minute. We found that the average estimated nectar consumption rate for all the entomophilous species except *G. rupestre* was enough to sustain the two smaller New Zealand honeyeaters (hihi energy requirements= 0.12 kJ min$^{-1}$, median energy obtained: 0.16 kJ min$^{-1}$ *D. spectabile* - 0.57 kJ min$^{-1}$ *P. crassifolium*); bellbird energy requirements = 0.10 kJ min$^{-1}$, median energy obtained: 0.14 kJ min$^{-1}$ *D. spectabile* - 0.68 kJ min$^{-1}$ *P. crassifolium*). However, we estimate that if the birds are able to selectively forage on the flowers with most nectar, the energetic returns of all species may be sufficient for hihi and bellbird (hihi: 0.18 kJ min$^{-1}$ *G. rupestre* - 0.93 kJ min$^{-1}$*; P. crassifolium*; bellbird: 0.12 kJ min$^{-1}$ *G. rupestre* - 1.11 kJ min$^{-1}$ *P. crassifolium*). If tui (energy requirements: 0.25 kJ min$^{-1}$), forages randomly, only *P. crassifolium* (0.80 kJ min$^{-1}$) and *D. spectabile* late in the season (0.30 kJ min$^{-1}$) provide sufficient returns, but if selective, *P. arboreus* (0.45 kJ min$^{-1}$) may also suffice.

We suggest that because (a) the nectar produced by entomophilous flowers provides sufficient energy to sustain the energetic requirements of birds, and (b) these plants flower in the cooler months when insect activity is reduced, birds might have played a wider role in pollination than previously considered. This finding is of particular importance because the abundance of New Zealand honeyeaters on the mainland has decreased considerably since human colonisation and this could be affecting forest regeneration.

**Keywords:** energetic value of nectar, bird-plant interactions, ornithophily, pollination, honeyeaters, New Zealand flora.

## Introduction

To ensure pollination, flowers possess adaptations related to the sensory abilities, mobility, and morphology of pollinators (Faegri and van der Pijl, 1979). To maintain the pollinator's interest in the flowers, plants offer nectar rewards which generally correlate with the size and energetic requirements of the pollinators (Faegri and van der Pijl, 1979). However, nectar is expensive to produce (Southwick, 1984) so a plant should produce only enough nectar to ensure pollinators will repeatedly visit it without being too easily satiated after one or a few visits (Heinrich & Raven, 1972). Considering that the optimal pollinator is the one that most effectively transfers pollen and produces the maximum seed set over a blooming season (Stebbins, 1970), selection should favour a level of nectar production that is dependent on the most effective pollinator. Flowers of different species often converge in the characteristics (syndrome) that they present to attract particular guilds of pollinators. For instance, flowers pollinated by insects, also called "entomophilous" are, in general, small, scented, and contain small amounts of concentrated

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nectar. "Ornithophilous" flowers (pollinated by birds) are usually large, red, orange or yellow, and contain large amounts of dilute and unscented nectar (Faegri and van der Pijl, 1979). However, specialisation for one particular pollinator or for one syndrome may not occur if the most consistent pollination results from visits from diverse pollinators (Herrera, 1996).

In New Zealand, the flowers of many native plants are structurally simple. They are often clustered and small, scented, mostly green, white or cream in colour (Cockayne, 1928; Godley, 1979), and a relatively large percentage of species are dioecious (have male and female flowers on separate plants; reviewed in Lloyd, 1985). These characteristics are usually associated with an entomophilous syndrome. Most New Zealand flowers are regarded as unspecialised and frequently promiscuous, receiving visits from several kinds of insects. New Zealand lacks many of the specialised pollinating animals found elsewhere (Heine, 1938; Godley, 1979; Webb and Kelly, 1993). There are no native long-tongued bees or hawkmoths and there are few butterflies, which are important pollinating species in other parts of the world. In New Zealand the pollinating role of these insects has possibly been taken over by Diptera (Thompson, 1927; Heine, 1938). Some pollination of plants has also been ascribed to reptiles (Whitaker, 1987), bats (Daniel, 1976; Ecroyd, 1996) and birds (Godley, 1979; Delph and Lively, 1989). Although birds are clearly the most likely pollinator for a handful of native plants (e.g. *Phormium*, *Metrosideros*, *Fuchsia*, *Sophora*) the wider extent or importance of bird pollination remains unclear. Of 30 New Zealand native species of plants visited by birds (Godley, 1979), only 13 display a typical ornithophilous syndrome. Godley (1979) suggested that the remaining species are probably visited by birds only incidentally, and that true ornithophily is not involved. He suggested that birds may foster self-pollination rather than cross pollination (except for the species with sexually dimorphic flowers).

New Zealand forests have lost a large number of bird species and suffered a severe reduction in the abundance of others (Holdaway, 1989). Offshore islands free of mammalian predators are the closest approximations to what the bird densities of New Zealand mainland forests may once have been (Diamond and Veitch, 1981). For this reason it is important to look in these refuges at the relationship between New Zealand birds and the pollination of forest plants. Today, all three species of native honeyeaters only co-exist on two off-shore islands: Kapiti Island near Wellington, and Little Barrier Island in the Hauraki Gulf.

Most flowers used by the birds on Kapiti I. do not display the typical ornithophilous syndrome, but seem entomophilous (Castro, 1995). Therefore we set out to determine whether these small flowers are energetically worthwhile to large visitors (i.e. honeyeaters) in comparison with more typically ornithophilous flowers.

In this paper we provide (i) a comprehensive list of New Zealand plants visited by the three native honeyeaters, (ii) data on the nectar energetic value of the flowers of eight forest plant species (three ornithophilous and five entomophilous species), and (iii) the energetic returns for honeyeaters visiting four of these entomophilous species on Kapiti Island.

# Methods

## Honeyeater ecology

Honeyeaters (family Meliphagidae) are common birds throughout Australasia, particularly Australia, where they pollinate many plant species (Paton & Ford, 1976). New Zealand has three endemic species of honeyeaters - the tui (*Prosthemadera novaseelandiae*[1] ), the bellbird (*Anthornis melanura*), and the hihi (stitchbird) (*Notiomystis cincta*). All three species feed on flower nectar, fruits, and insects in different proportions according to availability (Gravatt, 1970; Angehr, 1984; Rasch, 1985; Castro *et al.,* 1994). Hihi became extinct on the North Island mainland in the late 1800's (Oliver, 1955) and the overall abundance of honeyeaters has decreased since human colonisation on the New Zealand mainland (Diamond and Veitch, 1981; Rasch, 1985; Gill and Martinson 1991). The abundance of honeyeaters on some islands today is probably the closest to that on the mainland prior to the arrival of humans and introduced predators.

## Study area

Observations were made on Kapiti Island (1965 ha, 40°50' S, 174°55' E) on the south-western coast of the North Island of New Zealand from August 1991 to August 1994. Kapiti I. was largely cleared for agriculture in the 1800's but by 1930 all browsing animals with the exception of brush-tailed possums (*Trichosurus vulpecula*) had been eradicated (Cowan, 1992). Kapiti I. was freed of possums in

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[1] Bird names follow Turbott, 1990

1986 (Cowan, 1992). Kapiti I. forests cover approximately 1573 ha, and are divided into scrub and low forest (1029 ha) and tall forests (544 ha) of mahoe *Melicitus ramiflorus* [2] (9.9%);tawa *Beilschmiedia tawa* - hinau *Elaeocarpus dentatus* (33%); kamahi *Weinmannia racemosa* - tawa (3.2%); karaka *Corynocarpus laevigatus* ( 1.2%); and kohekohe *Dysoxylum spectabile* (52.6%). The remainder of the island is covered by low scrub, grass, tussock and flax (Fuller, 1985). At the time of this study there were Norway rats (*Rattus norvegicus*) and Polynesian rats (*Rattus exulans*) on Kapiti. A rat eradication attempt took place in 1997, which if successful would render Kapiti free of introduced mammalian predators. In the last ten years, there have been several bird transfers to Kapiti including hihi, saddlebacks (*Philesternus caruncalatus*), and kokako (*Calleas cinerea*).

## Bird observations

From April 1992 to July 1994 phenological observations were made of the plant species most frequently visited by honeyeaters in order to measure the presence and availability of fruits and flowers (Castro, 1995). Feeding by honeyeaters was recorded at fortnightly intervals during the non-breeding months (April-September), and almost daily during the breeding season (October-March). This information was collected along the island tracks during a study of hihi behavioural ecology (Castro, 1995). Wherever a hihi was found, we estimated the number of individual birds of each species of honeyeater in the adjacent area, the plant species they were feeding on, and the part of the plant they were using. We also recorded this information while collecting data for plant phenology (Castro, 1995). From August 1993 to August 1994 we recorded the flower handling times by honeyeaters on each of four plant species (*Geniostoma rupestre*, *Dysoxylum spectabile*, *Pseudopanax arboreus*, and *Pittosporum crassifolium*). During foraging bouts by birds, we recorded the number of flowers visited per minute. Observations were made on randomly chosen trees along any of the island's tracks whenever the trees were in flower. We aimed to follow at least five individual birds of each species and to collect at least 10 minutes of observation per species of bird. Collecting these data was not always possible, however, as the flowering season of the selected plants was short. In addition, some of the plant species were uncommon and in the case of hihi, there were only 30 to 35 birds on the island during this study. Most hihi on Kapiti were colour banded for individual identification, but we were unable to individually identify tui or bellbirds. To minimise the possibility of collecting all the data on a few individuals for these two species, the observations were made on trees located in several widely spaced areas.

## Nectar Sampling

During 1993 and 1994 we sampled nectar from three ornithophilous flowers: *Metrosideros fulgens*, *Metrosideros excelsa* and *Fuchsia excorticata*; and five entomophilous flowers: *Pittosporum crassifolium*, *Pseudopanax arboreus*, *Dysoxylum spectabile*, *Pittosporum eugenioides* and *Geniostoma rupestre*. Nectar samples were taken by absorption onto filter paper "wicks" (McKenna and Thomson, 1989). Occasionally it was necessary to redissolve dried nectar on the flower with a small drop of water (Cresswell, 1990) prior to the application of the wick. For each species, the nectar in the flowers of three to eight separate plants was sampled. The number of flowers sampled per plant varied according to species (Table 2). Some of the flowers had large visitors excluded by means of mesh bags ("bagged") and some were left open to possible visitations ("unbagged"). Bagged nectar samples were taken (a) to measure the maximum quantities of nectar a bird could find (particularly early in the morning); and (b) to assess nectar utilisation by birds (comparing the total nectar produced by the plant vs. what is present after the flowers have been visited). The mesh bags, 20 cm x 30 cm, made of mosquito netting, were left on the flowers for 24 hours prior to the samples being collected. We placed two bags on each individual plant sampled. Each bag covered either a whole inflorescence or a section of a branch bearing flowers, depending on flower arrangement.

In the case of *D. spectabile,* flowers from the same plants were sampled both early and late in the flowering season. The nectar contained in the flowers is referred to as "standing crop".

Nectar samples were collected between 09:00 and 11:00 hr.

The sugar content of nectar (sucrose equivalent) per flower was calculated using an anthrone colorimetric assay of the sugar redissolved from the filter paper wicks (McKenna and Thomson 1989). The energetic values of flowers were calculated assuming that 1 mg sucrose = 16.8 joules. The average energetic value per inflorescence of each

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[1] Plant names follow Allan 1961; Moore and Edgar 1970; and Connor and Edgar 1987.

species was estimated from the product of the average energetic value of the standing crops and the average number of flowers in an inflorescence. To calculate the average number of flowers per inflorescence we counted the flowers in at least ten inflorescences of each species. Similar values could not be obtained for *Dysoxylum spectabile* and *Geniostoma rupestre* because the flowers are not arranged in a compact inflorescence, but form panicles (*D. spectabile*) or arise directly and spread along the branches (*G. rupestre*).

Nested ANOVA's were used to partition the variance in the amount of sucrose per flower into a treatment effect (bagged vs. unbagged), individual tree effects, the tree by treatment interaction, in some cases a season effect (early or late), and/or an inflorescence effect. Type III, or partial sums of squares, are presented in the analysis of variance table. The statistical package SAS was used for all analyses (SAS Institute 1988).

### Honeyeater energy requirements

The metabolic requirements of New Zealand honeyeaters were estimated using a formula that scales the requirements of another honeyeater species *Lichmera indistincta* by a factor proportionate to body mass (Collins and Newland, 1986). Winter conditions were assumed as: nine hour day length; 13°C day temperature; 9°C night temperature. These conditions reflect average winter conditions on Kapiti Island and also were the conditions used to produce the formula to estimate *Lichmera indistincta*'s energetic needs. Furthermore, we assumed that the New Zealand honeyeaters, like *L. indistincta*, spent 94% of their time in activities other than flying (Castro, unpub. data support this assumption). There are body mass differences between males and females in all three New Zealand honeyeater species (Hihi: male: 40.2 g; female: 30.3 g. Bellbird: male: 30.7 g; female: 25.0 g. Tui: male: 121.2 g; female: 87 g) (Craig *et al,* 1982). We used a mean of the average weights for males and females to simplify the results (Hihi = 35.25 g; Bellbird = 27.85 g; and Tui = 104.10 g). Under the above environmental conditions and using average weights, the energetic requirements were estimated to be 116 J min$^{-1}$ for hihi; 100 J min$^{-1}$ for bellbirds; and 252 J min$^{-1}$ for tui.

### Estimated Energetic Returns

Australian honeyeaters were estimated to leave 0-30% of the initial nectar volumes in flowers (Paton and Collins, 1989). In our calculation, we initially assumed that the birds were taking all the nectar in each flower.

It is not known whether the New Zealand honeyeaters forage selectively. However, it is known that, at least for some species of plants, tui and bellbirds can differentiate between flowers containing nectar and empty flowers on the basis of age-dependent changes in colour (*Fuchsia excorticata*, Delph and Lively, 1989; *Alepis flavida*, *Peraxilla tetrapetala*, and *P. colensoi*, Ladley *et al.*, 1997). Similarly, bellbirds and tui appear to be able to select between mistletoe (*Peraxilla* spp.) buds for readiness to be opened on the basis of colour changes as the buds mature (Ladley and Kelly, 1995 a, b). Likewise, honeyeaters in Australia and sunbirds in southern Africa use colour changes to determine the availability of nectar in flowers of the Proteaceae family (Collins and Rebelo, 1987). Some nectarivorous birds choose inflorescences with a mixture of open and unopened flowers apparently because the probability of encountering recently opened flowers (i.e. full of nectar) is greater (Collins and Rebelo, 1987). None of the flowers in this study, with the exception of *F. excorticata*, present colour changes related to age. However, we cannot exclude the possibility that the birds could detect less obvious changes in flower morphology or colouration in parts of the spectrum not visible to humans, related to the age of the flower or the nectar content. Foraging behaviour such as selectively visiting inflorescences with open and unopened flowers are likely. Accordingly, we calculated the energetic rewards for birds assuming that the birds were either (a) not selective when foraging on these flowers or that (b) they chose to visit the half of the flowers with the highest energetic rewards. We have also assumed that nectar content and handling time per flower were independent. The nectar reward gained was therefore estimated as the product of flowers visited per unit of time and the average energetic content of each flower.

As each parameter was collected independently, each with its own degree of error, the error associated with the resulting product is compounded. To provide some idea of the possible range of energy obtained whilst feeding, a Monte Carlo randomisation procedure (Manly, 1991) was used. From the range of observed bird feeding rates per minute for each species, one value was randomly chosen (i.e. flowers visited per minute). This value determined the number of energetic values to be chosen from the array of observed data (i.e. each flower was given one value from the observed array of flower energetic values). These energetic values

Table 1: *Comprehensive list of New Zealand native plant species whose flowers are visited by honeyeaters.*

| Species | Abundance on Kapiti I.* | Frequency of visitation - Kapiti I. | | | Flower size § | Pollination syndrome # | Record of honeyeater visitation from |
|---|---|---|---|---|---|---|---|
| | | Hihi | Bellbird | Tui | | | |
| **Plants present on Kapiti I.** | | | | | | | |
| *Fuchsia excorticata* | 2 | 3 | 3 | 3 | Large | Ornithophilous (1) | Godley 1979 |
| *Knightia excelsa* | 5, y | 3 | 3 | 3 | Large | Ornithophilous (2) | Godley 1979 |
| *Metrosideros excelsa* | 2 | 3 | 3 | 3 | Large | Ornithophilous (1) | Godley 1979 |
| *Metrosideros fulgens* | 5 | 3 | 3 | 3 | Large | Ornithophilous (1) | Godley 1979 |
| *Metrosideros robusta* | 3 | 3 | 3 | 3 | Large | Ornithophilous (1) | Godley 1979 |
| *Phormium tenax* | 6 | 3 | 3 | 3 | Large | Ornithophilous (1) | Godley 1979 |
| *Sophora* spp. | 2 | 0 | 3 | 0 | Large | Ornithophilous (1) | Godley 1979 |
| *Vitex lucens* | 2 | 3 | 3 | 3 | Large | Ornithophilous (2) | Godley 1979 |
| *Dysoxylum spectabile* | 4 | 3 | 3 | 3 | Medium | Entomophilous (?) | Godley 1979 |
| *Earina autumnalis* | 6 | 1 | 0 | 0 | Medium | Entomophilous (1) | This Study |
| *Elaeocarpus dentatus* | 5 | 3 | 3 | 3 | Medium | Entomophilous (?) | Craig 1981 |
| *Hoheria populnea* | 1 | 3 | 0 | 0 | Medium | Entomophilous (3) | This Study |
| *Metrosideros perforata* | 5 | 3 | 0 | 0 | Medium | Entomophilous (?) | Godley 1979 |
| *Myoporum laetum* | 3 | 3 | 3 | 0 | Medium | Entomophilous (3) | This Study |
| *Passiflora tetranda* | 6 | 2 | 0 | 0 | Medium | Entomophilous (?) | This Study |
| *Pittosporum cornifolium* | 2 | 3 | 3 | 0 | Medium | Entomophilous (?) | This Study |
| *Pittosporum crassifolium* | 1 | 3 | 3 | 3 | Medium | Entomophilous (3) | Godley 1979 |
| *Pittosporum umbellatum* | 2 | 3 | 3 | 3 | Medium | Entomophilous (?) | Godley 1979 |
| *Rhopalostylis sapida* | 6-y | 3 | 0 | 0 | Medium | Entomophilous (3) | This Study |
| *Ripogonum scandens* | 4 | 3 | 0 | 0 | Medium | Entomophilous (?) | This Study |
| *Syzygium maire* | 1 | 3 | 0 | 0 | Medium | Entomophilous (?) | This Study |
| *Aristotelia serrata* | 3, y | 3 | 0 | 0 | Small | Entomophilous (?) | This Study |
| *Geniostoma rupestre* | 4 | 3 | 3 | 3 | Small | Entomophilous (?) | This Study |
| *Kunzea ericoides* | 6 | 0 | 3 | 0 | Small | Entomophilous (?) | This Study |
| *Laurelia novae-zelandiae* | 3,y | 0 | 3 | 0 | Small | Entomophilous (?) | This Study |
| *Melicytus ramiflorus* | 4 | 2 | 0 | 0 | Small | Entomophilous (3) | Godley 1979 |
| *Personia toru* | 5 | 0 | 0 | 0 | Small | Entomophilous (?) | Godley 1979 |
| *Pittosporum eugenioides* | 5-y | 3 | 3 | 3 | Small | Entomophilous (?) | This Study |
| *Pittosporum tenuifolium* | 5 | 3 | 3 | 3 | Small | Entomophilous (3) | This Study |
| *Pseudopanax arboreous* | 4 | 3 | 3 | 3 | Small | Entomophilous (?) | Godley 1979 |
| *Pseudopanax crassifolius* | 3, y | 2 | 0 | 0 | Small | Entomophilous (?) | Godley 1979 |
| *Rubus cissoides* | 4 | 3 | 0 | 0 | Small | Entomophilous (?) | This Study |
| *Shefflera digitata* | 5 | 2 | 0 | 0 | Small | Entomophilous (3) | Godley 1979 |
| *Astelia* spp. | 4 | 1 | 0 | 0 | Minute | Entomophilous (3) | Ths Study |
| *Beilschmiedia tawa* | 6 | 2 | 0 | 0 | Minute | Entomophilous (?) | Craig 1981 |
| *Corynocarpus laevigatus* | 5 | 0 | 2 | 0 | Minute | Entomophilous (3) | Godley 1979 |
| *Cyathodes* spp. | 2 | 0 | 0 | 0 | Minute | Entomophilous (?) | Godley 1979 |
| *Griselinea littoralis* | 2 | 2 | 2 | 2 | Minute | Entomophilous (3) | This Study |
| *Hebe* spp. | 2 | 0 | 0 | 0 | Minute | Entomophilous (3) | Godley 1979 |
| *Myrsine australis* | 5 | 1 | 0 | 0 | Minute | Entomophilous (?) | This Study |
| *Myrsine salicina* | 5 | 2 | 0 | 0 | Minute | Entomophilous (?) | This Study |
| *Nestegis lanceolata* | 3 | 0 | 0 | 0 | Minute | Entomophilous (?) | Godley 1979 |
| *Weinmannia racemosa* | 5 | 3 | 3 | 3 | Minute | Entomophilous (?) | Godley 1979 |
| **Plants not present on Kapiti I.** | | | | | | | |
| *Alepis flavida* | | | | | Medium | Ornithophilous (4) | Ladley 1997 |
| *Clianthus* spp. | | | | | Large | Ornithophilous (1) | Godley 1979 |
| *Metrosideros umbellata* | | | | | Large | Ornithophilous (1) | Godley 1979 |
| *Rhabdothamnus solandri* | | | | | Large | Ornithophilous (2) | Godley 1979 |
| *Peraxilla* spp. | | | | | Large | Ornithophilous (4) | Ladley 1997 |
| *Cordyline* spp. | | | | | Medium | Entomophilous (3) | Craig 1981 |
| *Alseuosmia macrophylla* | | | | | Small | Ornithophilous (1) | Godley 1979 |
| *Dracophyllum* spp. | | | | | Small | Entomophilous (3) | Godley 1979 |

* 1 = very rare; 2 = rare; 3 = occurs; 4 = abundant; 5 = common; 6 = very common (Angher, 1984); y = young plants; 0 = not present.

‡ 3 = frequent (if every time the flowers were available there were visits by honeyeaters); 2= occasional (if the flowers were visited sometimes only); 1 = rarely (if we rarely saw birds on the flowers); 0 = we have not recorded the birds feeding on such flowers on Kapiti.

§ Large = largest dimension > 20mm; Medium = 10-20 mm; Small = 5.1-9.9 mm; Minute = < 5mm. Sizes from Allan, 1961.

# (1) from Godley 1979; (2) from Petrie 1903 and 1905; (3) from Heine 1938; (4) from Ladley *et al.* 1997; (?) inferred either from data available from members of the same genus with similar characteristics, or from floral morphology.

were summed to give an estimated return to the bird for one minute's foraging (i.e. how many joules a bird might have obtained). This procedure was repeated 1000 times to obtain a range of energetic returns. All energetic values were used when the assumption was that birds did not forage selectively, but only the highest half of the values were selected for assumption (b).

## Results

### Species visited by honeyeaters

A large number of species with small flowers were visited by the honeyeaters on Kapiti Island in addition to the larger-flowered, typical ornithophilous flowers (Table 1). Many of these flowers were visited consistently each year (e.g. *Geniostoma rupestre*, *Pseudopanax arboreus*, *Pittosporum eugenioides*, *Pittosporum crassifolium*, *Pittosporum tenuifolium*, and *Weinmannia racemosa*). Furthermore, all three species of honeyeaters were seen on both male and female flowers of *Pseudopanax arboreus* and *Pittosporum crassifolium*. Some small flowers from species not present on Kapiti Island are also visited by honeyeaters (bottom of Table 1).

### Nectar energetic values

In general, the entomophilous flowers were less rewarding in nectar than the ornithophilous species (Table 2), although there was considerable overlap, particularly for unbagged flowers. There was significantly more nectar in the bagged flowers of *Metrosideros fulgens*, *Dysoxylum spectabile*, *Fuchsia excorticata* and *Pseudopanax arboreus* (males) than in the unbagged flowers. There was also significant variation in nectar production between trees in *Pittosporum crassifolium*. This difference was apparently due to the presence of a female tree in our sample. This tree's flowers had significantly more energy (average 54.6 joules, n=12) than the male trees (26.2 J, 25.8 J, 15.8 J, and 13.0 J; n=11 for each tree).

*Dysoxylum spectabile* flowers sampled later in the season contained more energy than those sampled earlier (Table 2). The number of visitors to the flowers of this species also increased over the season, and observations of kaka (*Nestor meridionalis*), a large omnivorous parrot, feeding on *D. spectabile* only occurred later in the season.

Several of the entomophilous species studied (*Pittosporum crassifolium*, *Pseudopanax arboreus,* and *Pittosporum eugenioides*) had flowers presented simultaneously in compact inflorescences. As a result, the inflorescence as a unit may be a relatively rich source of food accessible from one perch. In general, the energy content of nectar per inflorescence of the entomophilous species was greater than the energetic content per flower of ornithophilous species. However, inflorescences of both entomophilous and ornithophilous species had comparable nectar energetic values (Table 3). This compact flower arrangement allows the rapid processing of flowers by probing birds which often spend less than a second on each flower (Table 4).

Table 2: *Mean standing crops of nectar for bagged and unbagged flowers of selected species used by honeyeaters on Kapiti Island. Generalised linear models were fitted and show the significance of the effects of bagging, tree and the tree x treatment interaction. In the case of Dysoxylum spectabile, we sampled flowers early and late in the season, the significance of the seasonal effect is shown. In three cases where we sampled more than one inflorescence per tree the significance at this level is also shown. NA, not applicable; NS, not significant at P=0.05.*

| | | | | | Significance of effect, P | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Plant species | Unbagged $\bar{x}$ (J)±s.e. | n | Bagged $\bar{x}$ (J)±s.e. | n | Bagging | Tree | Tree x treatment | Season | Inflorescence |
| *G. rupestre* | 1.8 ± 0.2 | 78 | 2.2 ± 0.2 | 74 | NS | NS | NS | NA | NA |
| *D. spectabile* (early) | 3.7 ± 0.8 | 20 | 5.0 ± 0.8 | 37 | < 0.0001 | NS | NS | < 0.0001 | NA |
| *D. spectabile* (late) | 6.7 ± 1.3 | 20 | 14.3 ± 2.5 | 15 | | | | | |
| *P. arboreus* (male) | 1.5 ± 0.2 | 15 | 3.7 ± 0.7 | 19 | < 0.01 | NS | NS | NA | NA |
| *P. eugenioides* | 2.7 ± 0.2 | 130 | 2.5 ± 0.2 | 78 | NS | NS | <0.0001 | NA | NA |
| *P. crassifolium* | 23.0 ± 5.7 | 26 | 34.0 ± 4.9 | 30 | NS | < 0.001 | NS | NA | NS |
| *M. fulgens* | 6.6 ± 1.9 | 22 | 77.5 ± 9.3 | 17 | < 0.0001 | NS | NS | NA | NS |
| *F. excorticata* | 1.8 ± 0.5 | 16 | 8.8 ± 1.2 | 19 | < 0.0001 | NS | NS | NA | NA |
| *M. excelsa* | 22.0 ± 4.6 | 28 | 126.6 ± 19.4 | 12 | * | NS | NA | NA | < 0.01 |

* We did not compare unbagged and bagged flowers for this species because the samples from bagged flowers came from different plants than those from unbagged flowers.

Table 3: *Comparison between the energetic value of nectar in inflorescences of "entomophilous" and "ornithophilous" species. The energetic values of inflorescences were based on observed unbagged standing crops.*

| | Average number of flowers per inflorescence (n) | Energy content (J inflorescence$^{-1}$) |
|---|---|---|
| "Entomophilous" species | | |
| *G. rupestre* | 70 (100) * | 125 |
| *D. spectabile* (early) | 50 (10) | 184 |
| *D. spectabile* (late) | 50 (10) | 336 |
| *P. arboreus* (male) | 300 (10) | 441 |
| *P. eugenioides* | 63 (48) | 170 |
| *P. crassifolium* | 8 (20) | 173 |
| "Ornithophilous" species | | |
| *M. fulgens* | 18 (20) | 116 |
| *F. excorticata* | 7 (100) * | 13 |
| *M. excelsa* | 18 (31) | 385 |

* These plants do not have inflorescences. We counted the number of flowers in ten different branches of ten different plants and averaged them.

## Estimated energetic returns

Whether the birds fed selectively (assumption a) or not (assumption b), the average energetic values of all species of flowers except for *G. rupestre*, when obtained by the birds at the average visitation rate, appeared sufficient to satisfy the estimated energetic requirements of bellbird and hihi (Table 4 and Figure 1). Hihi and bellbird could obtain the energy required when feeding on *G. rupestre* if they forage selectively. With the exception of *G. rupestre* and the early flowers of *D. spectabile*, the energetic values of all species also seemed to fulfil the demands of tui when assuming that tui forage selectively. However, if tui is not selective only the late flowers of *D. spectabile* and *P. crassifolium* fulfil its energetic demands. Honeyeaters feeding on *Pittosporum crassifolium* could be obtaining up to six times the required amount of energy required by an actively foraging honeyeater.

If the birds were leaving behind 30% of the energetic reward of the flowers - as suggested by some of the findings from Australian honeyeaters (Paton and Collins, 1989) - the energy obtained from all species of flowers, except *G. rupestre* would be sufficient, at the average visitation rate, to sustain the energetic needs of the two small honeyeaters, but not that of tui. Assuming 30% of energy is left behind, tui would only be able to satisfy its energetic needs feeding on the flowers of *P. crassifolium* and late-season *D. spectabile*.

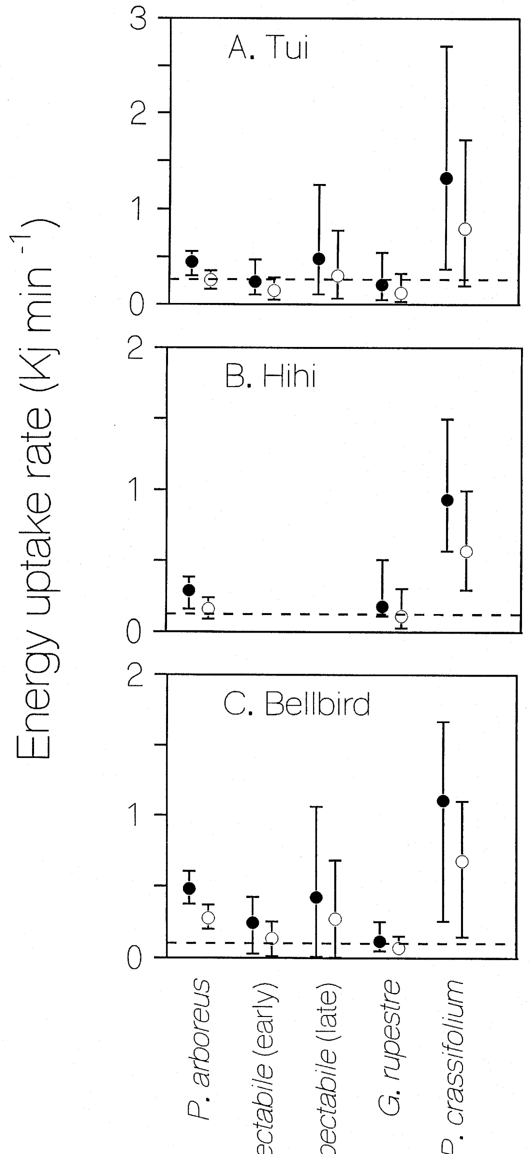

Figure 1: *Estimated energy intake (kJ min$^{-1}$) by birds foraging at selected species of flowers on Kapiti I. Filled circles indicate energy intake by birds foraging selectively on the half of the flowers containing the largest energetic values. Open circles indicate median energy intake by non-selectively foraging birds. Bars at either side of the median indicate 95% confidence intervals as determined by a Monte Carlo randomisation procedure (see text for details). Dashed line indicates the estimated amount of energy required per minute by each honeyeater species. Note Y-axis scale varies.*

Table 4: *Average number of flowers (mean±s.e.) visited by individual honeyeaters while foraging for one minute with total time of observations.*

| Plant | Bellbird (flowers min $^{-1}$) | n | Obs. time (min) | Hihi (flowers min $^{-1}$) | n | Obs.time time (min) | Tui (flowers min $^{-1}$) | n | Obs. time (min) |
|---|---|---|---|---|---|---|---|---|---|
| *G. rupestre* | 47.4±6.29 | 8 | 10.2 | 70.4±8.35 | 5 | 17.3 | 72.4±12.61 | 8 | 10.2 |
| *D. spectabile* early | 37.2±5.35 | 1 | 6.0 | - | - | - | 41.3± 8.49 | 5 | 2.6 |
| *D. spectabile* late | 42.0±5.84 | 1 | 8.6 | - | - | - | 43.1± 5.11 | 2 | 12.7 |
| *P. arboreus* (male*) | 85.6±3.27 | 5 | 3.1 | 48.5±9.13 | 2 | 1.4 | 79.1± 5.97 | 4 | 3.8 |
| *P. crassifolium* | 28.5±3.35 | 8 | 17.5 | 25.9±5.30 | 2 | 2.9 | 38.0± 9.08 | 5 | 25.3 |

* No data are available for female flowers.

# Discussion

Variability in the availability of pollinators or plants may limit the evolution of specificity in pollination systems (Baker and Hurd, 1968; Stebbins, 1970). This lack of specialisation is particularly important on islands where isolation may limit the number of species present and therefore the number of potential interactions between species. We suggest that some New Zealand flowers might be structurally simple in order to permit pollination by both insects and birds. It is clear from Table 1 that New Zealand honeyeaters were investigating small flowers as a regular foraging activity. This could be due to the evolution of these bird species in an island environment with few pollinators, where plants had evolved unspecialised small flowers that could be pollinated by a large array of species.

Although in many cases it appears that the honeyeaters were obtaining sufficient energy from the nectar to justify their visits to these small flowers, the importance of other components of the nectar that satisfy other dietary needs cannot be discounted. Honeyeaters could also be foraging for small insects or pollen when visiting these small flowers. The last two possibilities could explain the persistence of tui on *Geniostoma rupestre* and the flowers of *Dysoxylum spectabile* early in the season, which seemingly did not fulfil their energetic demands. Moreover, the birds may potentially forage when flowers have the greatest amount of nectar e.g. in the early morning or they may selectively forage on the richest flowers. The Monte Carlo simulation suggested that if only the best half of the flowers were visited, all three honeyeaters would be gaining surplus energy with the exception of tui on *Dysoxylum* early in the season and on *Geniostoma*.

Ornithophilous flowers were clearly visited regularly as shown by the large and significant difference between bagged and unbagged standing crops of nectar (Table 2). The lack of difference between the nectar content of bagged and unbagged flowers of *Pittosporum eugenioides*, *Geniostoma rupestre*, and *Pittosporum crassifolium* may be due to either a low visitation rate to these flowers or to the plant continuing to produce nectar as it is cropped by visitors (Pyke, 1991). The mechanisms and timing of nectar production for most New Zealand plants are unknown and more research in this area is necessary.

The flowers of some plants might have evolved alternative mechanisms, other than a large corolla size or specific calyx shape, to ensure pollination by birds. Our observations show that the nectar on female *Pseudopanax arboreus* flowers is spread over the surface of the flower in such a way that to obtain it the flower has to be licked. Licking the flowers is time-consuming and in the process the birds' head or beak contacts the stigma of the flower. This "lolly-pop" syndrome is shared by the entire inflorescences of *Pittosporum eugenioides*. Nectar collects on top of the flowers and the birds appear to lick the nectar from the surface of the inflorescence rather than from individual flowers. However, this may promote self-pollination through the transfer of pollen to adjacent stigmas (geitonogamy). Thus, if there is no self-incompatibility mechanism and inbreeding depression is high, selection for this mode of pollination may be limited.

New Zealand's generally windy conditions may make large flowers with wide petals susceptible to damage by wind (Coulter, 1975). Smaller flowers arranged in inflorescences could produce a similar visual impact and still provide a large reward (Table 3), while better resisting the effects of wind. Dense inflorescences could also make it easy for birds to brush their heads against flowers and be covered by pollen while still allowing insect visitation. Tui have been observed brushing their white neck feathers and lower breast against *Pseudopanax arboreus* flowers while feeding on them and a female hihi captured in an area of *Pseudopanax arboreus* was carrying this species' pollen on her forehead. We have also collected *Geniostoma rupestre* pollen from the foreheads of hihi.

Temperatures and general weather conditions during winter and spring can favour bird activity over insect activity. For instance, Anna hummingbirds (*Calypte anna*) in California (Stiles, 1971; 1973), as well as many other birds living at high elevation in the tropics (Cruden, 1972), are active during unfavourable weather conditions, and are important pollinators when insects are inactive. New Zealand weather is unpredictable and cold spells are common, especially during spring when many plants flower. Several of the plant species investigated here flower in the cooler months. *Pseudopanax arboreus* (July-December) and *Dysoxylum spectabile* (May-July) flower in late autumn and winter while *Pittosporum eugenioides* (October), *Geniostoma rupestre* (August-November) and *Pittosporum crassifolium* (September-October), flower in spring. The flowering periods of these species span a short time (four or five weeks) and if unfavourable weather occurs during this time, pollination could be severely affected. Therefore, winter and spring-flowering New Zealand plants may benefit from being visited by both birds and insects, particularly during cold spells.

Honeyeaters tend to feed in discrete areas of forest and, because they have similar feeding interests, it is common to find the three species feeding together. The larger, more dominant tui (Craig, 1984; Rasch, 1985; Ladley *et al.*, 1997; Castro, *pers. obs.*) can defend a whole tree and visit most flowers in it, whereas bellbirds and hihi are often displaced and move from tree to tree more frequently, increasing the possibility of cross pollination. The aggressive behaviour of tui tends to displace bellbirds and hihi to plant species with smaller flowers (Craig, 1984; Rasch, 1985). Thus, small flowers may be only used when honeyeater densities are high. The use of several trees per feeding bout induced by such agonistic behaviour may provide higher quality pollination than that achieved by insect visitors (Stephenson, 1982).

This study demonstrates the value of small flowers to honeyeaters as complements to the larger “ornithophilous flowers”. To say that honeyeater visits to New Zealand’s small flowers are incidental does not seem to be justified; rather, these flowers form an important component of the honeyeater diet. More research is needed on the relationship between New Zealand honeyeaters, insects, and the plants they use, specifically to measure the effectiveness of birds as pollen vectors, and to compare the efficiency of insects and birds as pollinators. Flowers such as *Corynocarpus laevigatus* and *Griselinia littoralis*, which are not visited intensively, might not be actively pollinated by birds, but the possibility should be studied. Comparative mainland and island studies could help us to understand the importance of pollination by birds. The possibility that the unspecialised flowers of the New Zealand bush may have allowed introduced insects, such as bees, to carry on pollination, alleviating the effects of reduced bird abundance should also be investigated. The results of such studies will help the understanding of forest dynamics and will be important for the management of natural areas.

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