

## Scarce or distracted? Bellbird (*Anthornis melanura*) foraging and diet in an area of inadequate mistletoe pollination

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**Abstract:** Recent work at several central South Island sites has shown that the bird-pollinated mistletoe *Peraxilla tetrapetala* (Loranthaceae) is extensively pollen-limited. We studied the diet, time-budget, and densities of its principal pollinator, bellbirds (*Anthornis melanura*, Meliphagidae), at Craigieburn to find out what aspect of bellbird ecology may be limiting pollination. Direct observations of bellbird diets showed that they are annual generalists on invertebrates (diet range 22 - 85% of food items) and honeydew (diet range 2 - 45%), and concentrate seasonally on mistletoe fruit (18 - 60%) and mistletoe nectar (27 - 58%) when available. The bellbirds at Craigieburn are more insectivorous than New Zealand's other two honeyeaters (tui and stitchbirds). In general, bellbirds are most similar to the short-billed guild of Australian honeyeaters in their beak morphology, foraging behaviour, and diet choice, but with a greater importance of fruit in the bellbird diet. The annual mean number of bellbirds recorded per 5-minute count (1.05) at Craigieburn was relatively low, even compared to other eastern South Island sites, which have lower counts of bellbirds than the western South Island and offshore islands. As mistletoe fruit and nectar were preferred foods when in season, and bellbird counts were low at Craigieburn, we conclude that it is the probable low number of bellbirds in the area, and not their choice of diet, which limits mistletoe pollination and dispersal. The bellbird population at Craigieburn did not appear to be food limited as bellbirds spent less than 20% of their time feeding, and the number of hours per day bellbirds spent feeding and foraging did not change significantly from winter to summer while food resources became more plentiful. Other pressures that limit the bellbird population size, particularly predation from introduced mammals, would appear more likely explanations for poor pollination and disperser services to mistletoes at Craigieburn.

**Keywords:** *Alepis flavida*; *Anthornis melanura*; Bellbirds; frugivory; insectivory; Loranthaceae; Meliphagidae; mistletoe; mutualisms; nectarivory; *Peraxilla tetrapetala*; pollination limitation.

## Introduction

New Zealand has suffered extinctions of many species of native animals and plants in the last 800 years of human occupation, including 32 percent of endemic land and freshwater birds (Taylor and Smith, 1997). Some of the surviving birds are restricted to offshore predator-free islands, or persist on the mainland at lower densities than in pre-human times. Reductions or loss of species can also result in the failure of interspecific interactions which can be critical for the functioning of ecosystems. One example is animal pollination of flowers, which is important in many natural and agricultural ecosystems, and may be threatened by a loss of pollinators (Kearns *et al.*, 1998). In this study we examine the factors limiting numbers

of the bellbird (*Anthornis melanura*<sup>1</sup>), an important widespread bird pollinator in New Zealand. Although not threatened, bellbirds seem to have been reduced in density to the point where pollination mutualisms are failing (Robertson *et al.*, 1999). Such sub-extinction losses from the native fauna and flora may have consequences that have not yet been widely appreciated.

Nectarivory, or birds visiting flowers to feed on nectar, is common in several different bird families (Snow, 1994), including the honeyeaters (Aves: Passeriformes: Meliphagidae). The common name 'honeyeater' arises from the importance of nectar in the diet of most species in this family. Morphological adaptations for nectar feeding are common to all species of the Meliphagidae, including a slender, slightly curved

<sup>1</sup>Bird nomenclature follows Heather *et al.* (1996).

bill and a tube-like, brush-tipped tongue that is used to reach into the base of flowers (McCann, 1964). Bellbirds are one of three species of endemic honeyeaters in New Zealand. The other two members of this family in New Zealand are the tui (*Prothemadera novaeseelandia*) and the stitchbird (*Notiomystis cincta*). As well as nectar, New Zealand honeyeaters also feed on fruit and invertebrates (Merton, 1966; Gravatt, 1969; Craig *et al.*, 1981; Angehr, 1986; Rasch and Craig, 1988; O'Donnell and Dilks, 1994; Castro, 1995; Perrott, 1997). The ecology of bellbirds, like other honeyeaters, is closely associated with the plants on which they feed (Craig and MacMillen, 1985). This interaction between plant and bird is often mutually beneficial, with plants utilizing bellbirds as pollination and seed dispersal agents, and bellbirds using the plants as a source of food. These mutual benefits can lead to co-dependence between the birds and plants, which places both species at risk when mutualistic interactions break down.

Bellbirds are the major pollinator and disperser in the central South Island of two species of endemic mistletoe, *Peraxilla tetrapetala*<sup>2</sup> and *Alepis flavida* (Loranthaceae) (Ladley and Kelly, 1996; Ladley *et al.*, 1997). *Peraxilla tetrapetala* is unusual in having flowers which open only when a bird, or occasionally one of three species of native bee, twists the top of the bud (Ladley and Kelly, 1995a; Kelly *et al.*, 1996). As unopened flowers have very low fruit set, pollinator visits are important for the regeneration of *P. tetrapetala*. In contrast, *A. flavida*, has self-opening flowers which readily self-pollinate so it is much less dependent upon pollinators (Ladley *et al.*, 1997). Previous work in the central South Island at Craigieburn and Lake Ohau has found that *P. tetrapetala* is consistently pollinator limited, and both *P. tetrapetala* and *A. flavida* may be disperser limited (Ladley and Kelly, 1995b, 1996; Robertson *et al.*, 1999). Robertson *et al.* (1999) showed that there were fewer bird visits to mistletoe flowers at Craigieburn and Ohau than in the Nelson region, where *Peraxilla colensoi* was not pollen limited.

Bellbird limitation of mistletoe pollination and dispersal could result from either bird distraction or bird scarcity. Distraction would occur if bellbirds present during mistletoe flowering or fruiting were instead choosing other, perhaps energetically more valuable, food sources. This would result in a low proportion of mistletoe fruit and nectar in the bellbird diet during the mistletoe flowering and fruiting seasons. Previous work on the diet of bellbirds shows that they have a flexible omnivorous diet (Merton, 1966; Gravatt, 1969; Angehr, 1986; Boyd, 1987; Rasch and Craig, 1988; O'Donnell and Dilks, 1994). Bellbirds concentrate on

high carbohydrate sources, such as nectar, but this is limited by geographical and seasonal availability of such foods, and by competitive pressures from other birds, especially tui (Craig, 1985; Rasch and Craig, 1988). Bellbirds are more insectivorous where there are fewer flowering and fruiting species, and honeydew is an important carbohydrate source where it is available.

The only previous work that has looked at the change in bellbird feeding in relation to a single food source has been with honeydew, which is a sugar-rich fluid produced by *Ultracoelostoma assimile*, *U. brittini*, and *U. dracophylli* (Hemiptera: Margarodidae), a genus of endemic scale insects living on southern beech (*Nothofagus* spp) trees (Morales, 1991). In forest near Nelson, where bellbirds spent more time feeding on honeydew than on insects and fruit, the percentage of time spent feeding on honeydew increased significantly in February and March when the sugar concentration of honeydew was low (Gaze and Clout, 1983). As honeydew, like nectar, is a high source of energy, this suggests that these bellbirds could be energy limited in certain months. In another nearby study area the proportion of foraging for honeydew by male bellbirds remained relatively stable and the proportion of foraging for honeydew by female bellbirds fell, even though honeydew concentration and standing crop increased over the interval (Boyd, 1987). The failure of bellbirds to increase the proportion of honeydew in the diet with increasing production of honeydew may be due to competition from tui and/or wasps and the differences between the sexes caused by males dominating females (Boyd, 1987). Intraspecific aggression was also observed in bellbirds by Craig and Douglas (1986) where diet and spatial behaviour changed in relation to energy rewards. Therefore, if bellbirds are not competitively excluded from them, and there are few other high energy food sources, a seasonal change in the bellbird diet to concentrate on mistletoe nectar and fruit would be expected.

Alternatively, bellbird limitation of mistletoe may be the result of bird scarcity: a low density of bellbirds in the area. Even if individual bellbirds in season ate solely mistletoe nectar and fruit, a low density of bellbirds would limit their effectiveness as pollinators and dispersers. Low bird densities in New Zealand forests have been previously suggested as possible limiting factors for fruiting and flowering plant species (Ladley and Kelly, 1996; Anderson, 1997; Castro and Robertson, 1997; McNutt, 1998; Robertson *et al.*, 1999). Estimates of bellbird density using 5-minute counts have suggested that bellbirds occur in higher numbers in habitats of more diverse vegetation (Onley, 1980, 1983; McCallum, 1982; Clout and Gaze, 1984), at medium to high altitudes (Dawson *et al.*, 1978; Gill, 1980; Wilson *et al.*, 1988), and during particular seasons in each area (Gill, 1980; Wilson *et al.*, 1988).

<sup>2</sup>Plant nomenclature follows Allan (1961), Barlow (1966) and Webb *et al.* (1988).

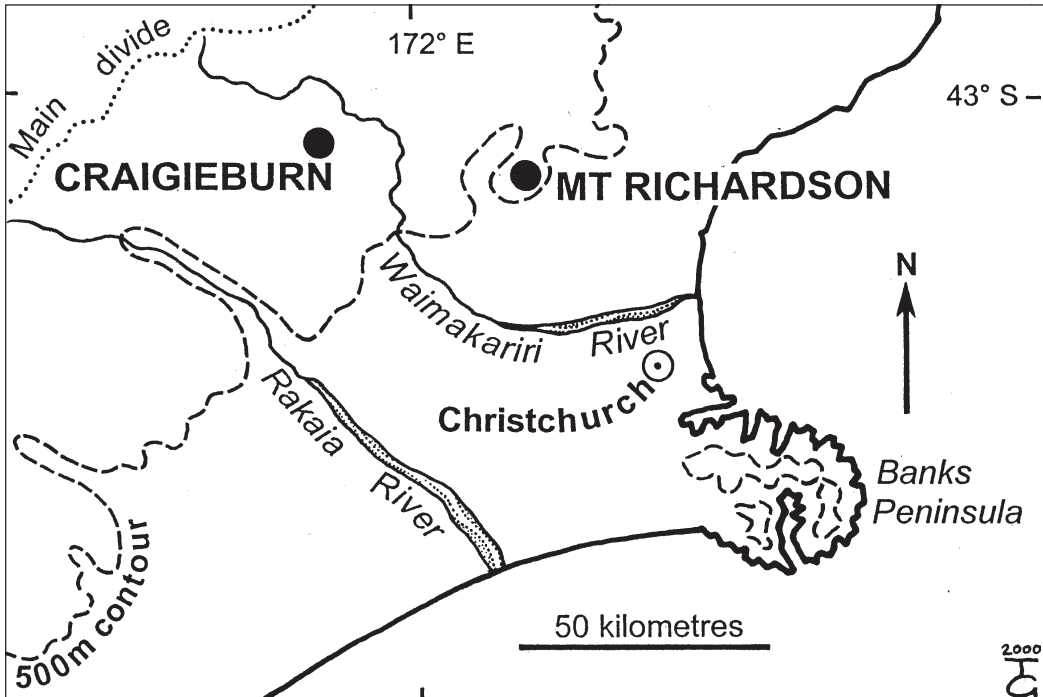


Figure 1. Location of study areas in Canterbury, South Island, New Zealand.

In this paper we attempt to establish which of the two hypotheses (distraction or scarcity) can best explain why bellbirds are limiting mistletoe pollination and possibly dispersal. Three questions were examined: (1) During the mistletoe flowering and fruiting seasons, are bellbirds concentrating on non-mistletoe foods? (2) Are bellbird densities at Craigieburn lower than in other parts of New Zealand? (3) Is the bellbird population at Craigieburn food-limited, in one season or overall? To answer these questions, the bellbird diet, time budget, and numbers were sampled over a twelve month period.

## Methods

### Study area

The Craigieburn study area (NZMS 260 K34 050831) was at Jack's Pass in the centre of Craigieburn Forest Park (Fig. 1). The area is at 950 m altitude and is characterised by a cool alpine climate with 1500 mm of rain per year (Shanks *et al.*, 1990). All field work was carried out in mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest which is the sole canopy tree in the area. There are few other plant species

present; the major understorey species are occasional *Coprosma microcarpa*, *C. pseudocuneata*, *C. linaifolia*, *C. parviflora* sp. 't', and *Leucopogon fasciculatus*. The beech trees are hosts to the hemiparasitic mistletoes, *Peraxilla tetrapetala* and *Alepis flavida*. Both are locally common (Robertson *et al.*, 1999) and the mistletoes are the only native bird-pollinated plants in the area.

A range of native and introduced birds are present at Craigieburn (Shanks *et al.*, 1990), but only bellbirds, silvereyes (*Zosterops lateralis*), and chaffinches (*Fringilla coelebs*) are previously reported to visit mistletoe flowers (Ladley *et al.*, 1997), and we have twice recently observed kea (*Nestor notabilis*) visiting the flowers of *P. tetrapetala* at Craigieburn. Tui are not present in the Craigieburn area. All mammals in the beech forest are introduced, including two important bird predators, stoats (*Mustela erminea*) and brushtailed possums (*Trichosurus vulpecula*), but ship rats (*Rattus rattus*) are not present (King, 1983).

### Bellbird diet

Foraging observations were carried out monthly from March 1997 to February 1998, except for June 1997 when snow prevented access to the study area. Two

trips were made to gather foraging data in January as *P. tetrapetala* flowers in early January while *A. flavida* flowers in mid January. The timing of this study split the annual cycle of *P. tetrapetala* and *A. flavida*, by recording fruit dispersal in 1997 and flower pollination in 1998, but the two years were similar in mistletoe flowering densities (379 flowers/m<sup>2</sup> in 1997 and 422 flowers/m<sup>2</sup> in 1998), overall levels of natural pollination in *P. tetrapetala* (44.9% natural fruit set in 1997 and 35.3% natural fruit set in 1998), and overall levels of fruit dispersal (Robertson *et al.*, 1999 and unpublished). Therefore we believe the two summers were similar; in any case, the 12 months represent a complete sample of bellbird diet over a one year time period.

Data on bellbird diet was collected using direct observations gathered along four 500 m long transects on paths in different parts of the study area. All observations were made using Nikon 8x23 binoculars. Each transect was traversed in both directions in the morning and afternoon per monthly trip. Transects were walked at a constant pace of 1 km/h and were not walked in adverse weather such as rain or high winds when bellbird conspicuousness would be reduced (Dawson, 1981).

When a bellbird was encountered the first foraging event in each 30 second time period was recorded until visual contact with the bellbird was lost up to a maximum of 5 observations. This method and time interval were chosen as it separated foraging observations into discrete events but still allowed us to gather enough data given the low number of bellbirds encountered. For every feeding event the following food categories were recorded: (1) nectar (plant species noted), (2) fruit (plant species noted), (3) definite invertebrate (where the invertebrate could be seen), (4) probable invertebrate (where the food item could not be seen but where the beak movement and foraging behaviour was consistent with invertebrate foraging), and (5) honeydew.

### Bellbird time budget

Time budget observations were collected simultaneously with diet observations during the second half of the study from July 1997 to February 1998, using instantaneous sampling. Time budget data were not collected during the first part of the study, but the data do span the period from midwinter to midsummer, ie from when bellbird food sources were expected to be scarce (winter) until they should be plentiful (summer). Also, these data covered the critical period for mistletoes, which is the flowering period where pollination is limited, whereas fruit dispersal is not so limiting (Robertson *et al.*, 1999).

At the start of each 30 second observational sampling period, when the bellbird was visible, its activity was placed in one the following activity

categories: (1) feeding, which included gleaning, hawking and probing for invertebrates, gleaning honeydew drops, flower visitation and frugivory; (2) locomotion, including flying, walking or hopping; (3) calling; (4) rest; (5) preening; and (6) social interaction, including aggression and any other social contact between bellbirds.

The foraging hours per day were also calculated, because any decrease in the percentage of foraging time from winter to summer may be the result of the same amount of foraging hours per day between seasons, spread over increased daylength in summer. This was achieved by multiplying the daylength for the middle date of each monthly field trip (Marsden, 1998) by the proportion of the bellbird time spent feeding or foraging (defined as feeding plus locomotion) on that field trip. Daylength was defined as the time from sunrise to sunset.

### Bellbird counts

Five-minute bird counts were used as an index of bellbird density between March 1997 and February 1998, employing the methods described by Dawson and Bull (1975). This technique was chosen as it was quick and efficient, and bellbirds are thought to not vary greatly in conspicuousness among seasons (Wilson *et al.*, 1988; Gibb, 1996). Counts were carried out at three count stations, 200 metres apart, on each of the four transects used for diet observations.

To minimize the effects of factors that could influence the detectability of bellbirds we used the same observer on all counts, all count stations were in the same vegetation type (mountain beech forest), and counts were not carried out in adverse weather conditions that could affect the conspicuousness of bellbirds. Bellbird counts were recorded in the morning and again in the afternoon of the same day to avoid any bias due to diel variation of bellbird numbers and/or conspicuousness (Dawson, 1981).

To see if seasonal changes in bellbird numbers at Craigieburn were also found at lower elevation sites in Canterbury, we performed 5-minute bird counts at Mt Richardson forest (NZMS 260 L34 468805) on the edges of the Canterbury Plains, 35 km from Craigieburn (Fig. 1). Counts were carried out on two adjacent walking tracks (Mt Richardson and Blowhard) with 20 and 16 count stations, respectively, at 200 m spacings over an elevation range from 400 to 1050 m.

Bellbird count data from Craigieburn and Mt Richardson were compared to data from 117 other sites throughout New Zealand collated by A.W. Robertson (Massey University, Palmerston North, N.Z., *pers. comm.*). Counts at a number of stations per site and in some instances over several seasons were averaged into a single mean per site. Sites were grouped into

predator-free or -reduced (Little Barrier Island, Kapiti Island, Mapara Reserve); North Island (north and south of Auckland separately); and South Island (east and west of the main divide separately).

### Analysis

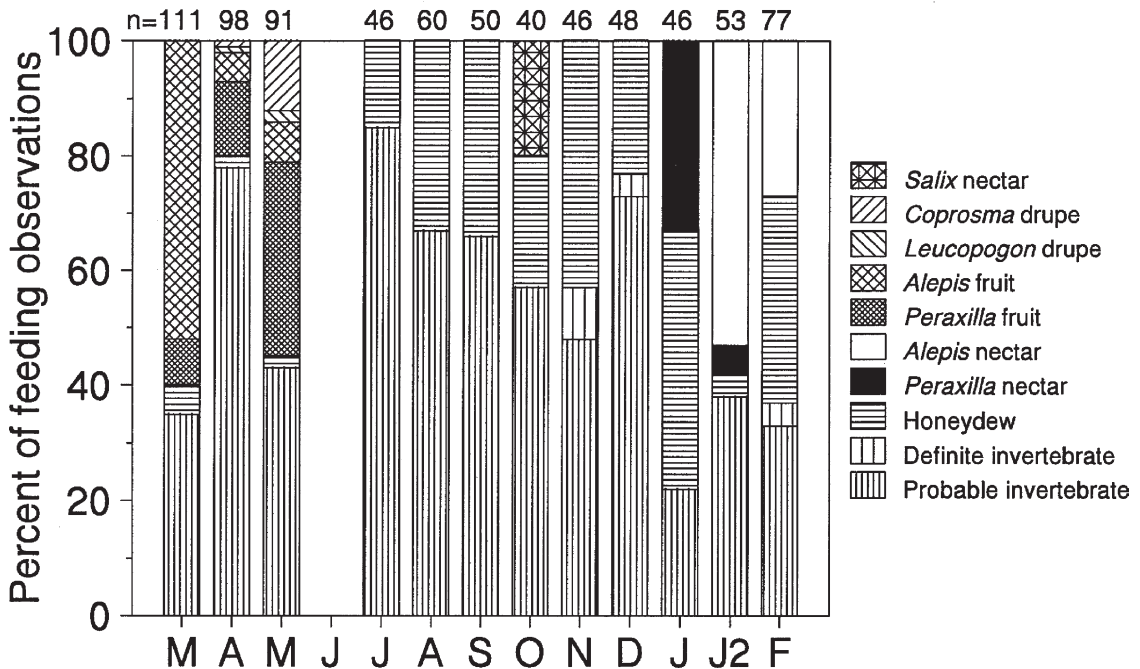
Chi-square tests were used to test for significant differences in bellbird diet between months. The expected value for each food category each month was the annual average percent dietary composition multiplied by the number of feeding observations made in that month. Because of low expected Chi-square values in certain food categories we lumped together definite invertebrates and probable invertebrates; and *Peraxilla tetrapetala* flowers and fruit and *Alepis flavida* flowers and fruit.

For bellbird time budgets, a Chi-square test of independence was used to identify any differences in the relative number of feeding observations between months. Expected values were again based on annual

averages. To test for changes from winter into summer in the time bellbirds spent feeding and in locomotion, both the proportions of time, and hours per day, for both feeding and foraging (feeding plus locomotion) were plotted seasonally and tested separately with linear regressions.

A Chi-square test of independence was used to test for any differences in the number of calling observations in the bellbird time budget between months. This was to examine if bellbird conspicuousness varied between seasons.

As bellbird counts were not normally distributed a Kruskal-Wallis test was used to identify any significant differences in the mean 5-minute counts at Craigieburn between months. Poisson ANOVAs were used to compare overall counts between Craigieburn and the Mt Richardson area separately for each counting date. National comparisons of 5-minute count data used a one way analysis of variance, with Northland excluded since bellbirds were not present at any of the 7 sites.



**Figure 2.** Observed bellbird diet (% of dietary items) at Craigieburn from March 1997 to February 1998. Samples were monthly, except for two in January (early = J and mid = J2), and none in June when sampling was prevented by bad weather. The number of observations at each date is given at the top. Plant species involved were *Salix glaucophylloides*, *Coprosma parviflora*, *Leucopogon fasciculatus*, *Alepis flavida*, and *Peraxilla tetrapetala*.

## Results

### Bellbird diet

A large percentage of the bellbird diet (22 - 85% of observed food items) was comprised of probable invertebrates (Fig. 2). This component of the bellbird diet had peaks in April, July and December before dropping below 40% for the rest of the summer. In November, December and February a small number of definite invertebrate foraging events were also observed (Fig. 2). The total number of invertebrate observations (probable invertebrate plus definite invertebrate) in the bellbird diet varied significantly between months ( $\chi^2 = 51.8$ ,  $df = 11$ ,  $P < 0.001$ ).

Apart from invertebrates the only other food source that was observed in the bellbird diet in every month was honeydew (Fig. 2). The proportion of honeydew in the bellbird diet also varied significantly between months ( $\chi^2 = 80.6$ ,  $df = 11$ ,  $P < 0.001$ ), with a range from 2 - 46% of the observed diet.

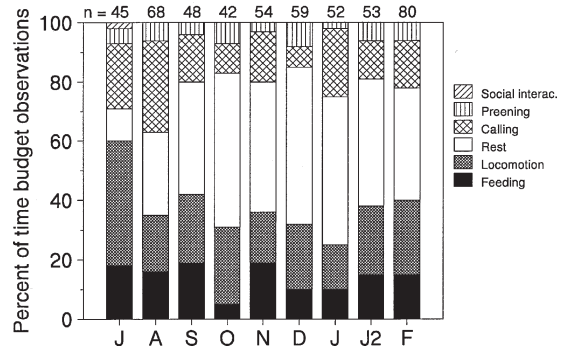
Mistletoe fruits were present in the bellbird diet only in the months of March to May (Fig. 2). The proportion of *Peraxilla tetrapetala* fruit in the bellbird diet increased from 8% of all feeding observations in March to peak at 34% in May (Fig. 2). After May no further *P. tetrapetala* fruit was seen being eaten by bellbirds, even though small numbers of fruit remained on *P. tetrapetala* until December. Similarly, bellbirds were only observed feeding on *Alepis flavida* fruit from March (when it made up 52% of all feeding observations) until May (7%; Fig. 2). With *A. flavida* eaten especially in March and *P. tetrapetala* more in April and May, there was a substantial proportion of mistletoe spp fruit in the bellbird diet throughout autumn.

The timing of nectar production also overlapped between the two mistletoe species, with bellbirds feeding on *P. tetrapetala* nectar in early and late January and *A. flavida* nectar taken in late January and in February (Fig. 2). *P. tetrapetala* flowers made up 33% of the diet in early January, while *A. flavida* nectar was 53% of bellbird diet in late January and still made up 27% of feeding observations in February.

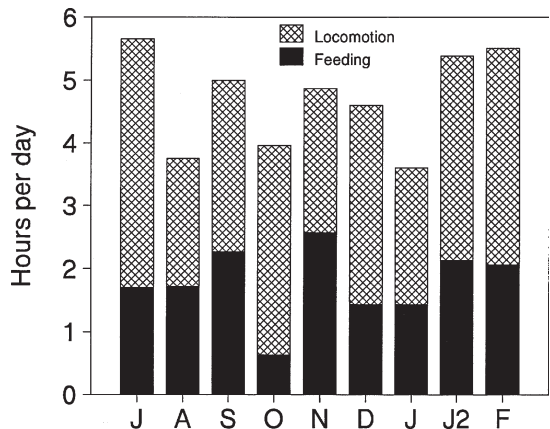
The only other food sources observed in the bellbird diet were small proportions of the drupes of *Leucopogon fasciculatus* and *Coprosma parviflora* sp. 't' in April and May, and bellbirds visiting the flowers of an introduced willow species, *Salix glaucophylloides*, in October which could have been feeding on nectar, pollen, or insects.

### Bellbird time budget

Between July and February, bellbirds at Craigieburn spent between 5 and 19% of their total time feeding



**Figure 3.** Observed bellbird time budgets (% of time spent) at Craigieburn from July 1997 to February 1998. The number of observations at each date is given at the top. In January samples were taken early (J) and in the middle of the month (J2). *Social interac.* = social interactions.



**Figure 4.** Hours per day that bellbirds spent feeding and in locomotion at Craigieburn from July 1997 to February 1998. Based on time budgets in Fig. 3 multiplied by hours of daylight at the time of each sample.

(Fig. 3). The proportion of feeding observations did not change significantly between months ( $\chi^2 = 5.6$ ,  $df = 8$ ,  $P = 0.69$ ). However, the proportion of time spent feeding only reflects the result of successful foraging events. Another major cost of foraging is search time. To provide a maximum estimate of searching time we assumed that all the time spent in locomotion was in search of food. This assumption was made as we observed few other purposes for bellbird locomotion at Craigieburn, with contact between bellbirds only being recorded once in the time budget, and few

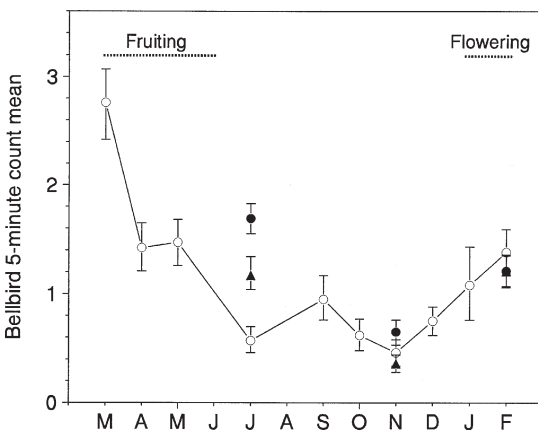
bellbirds being observed feeding fledglings. Nonetheless, the number of locomotion observations also did not change significantly between months ( $\chi^2 = 11.9$ ,  $df = 8$ ,  $P = 0.16$ ).

When we used the change in day length between July and February to convert the data into hours spent per day in feeding and in locomotion (Fig. 4), and tested these over time with a linear regression, there was no significant trend either for hours spent feeding ( $F = 0.09$ ,  $P = 0.77$ ), hours in locomotion ( $F = 0.004$ ,  $P = 0.95$ ), or total foraging hours (feeding plus locomotion;  $F = 0.03$ ,  $P = 0.87$ ). The number of calling observations in the bellbird time budget did not change significantly ( $\chi^2 = 14.96$ ,  $df = 8$ ,  $P = 0.059$ ), although it was close to the 0.05 threshold. Social interactions were rare as only one was observed in July (Fig. 3).

### Bellbird 5-minute counts

As 5-minute counts are strictly a measure of conspicuousness and not reliable measures of density, because of the difficulties comparing between different sites, seasons, and observers, we acknowledge that count results can only be used as an index of density.

At Craigieburn there were seasonal changes in the mean number of bellbirds counted per count station between March 1997 and February 1998 (Fig. 5). The difference in the mean count for the ten months sampled, where  $n = 24$  in each month, was statistically significant (Kruskal-Wallis ANOVA,  $F = 8.25$ ,  $df = 9$ ,  $P < 0.001$ ).



**Figure 5.** Bellbird density (mean number per 5-minute count  $\pm$  S.E.) from March 1997 to February 1998 at Craigieburn (950 m altitude, hollow circles) and at Mt Richardson forest (400 - 1050 m) on Richardson track (filled circles) and Blowhard track (filled triangles). The timing of mistletoe fruiting and flowering at Craigieburn is shown at the top.

**Table 1.** Bellbird densities from 5-minute counts in various regions of New Zealand. "Islands & protected" includes Little Barrier Island, Kapiti Island, and Mapara Reserve. Published and unpublished data collated by A.W. Robertson (*pers. comm.*).

Region	Mean bellbirds/count	No of sites
Islands & protected	2.00	3
South Island (west)	1.82	44
South Island (east)	1.36	33
North Island south of Auckland	0.63	32
Northland	0	7

The highest counts were in March; counts decreased markedly through the winter with lows in July, October, and November followed by an increase through summer again.

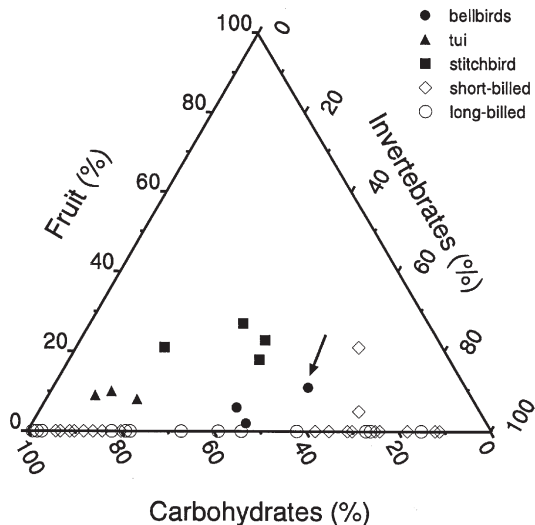
Bellbird counts at Mt Richardson showed a similar pattern of declining until late spring and then increasing again (Fig. 5). 5-minute counts were significantly higher than at Craigieburn in July (change in deviance = 13.02, d.f. = 1,  $P < 0.001$ ), but not significantly different in November ( $P = 0.68$ ) or February ( $P = 0.84$ ).

Bellbird counts from a range of sites in New Zealand (Table 1) varied significantly among regions, even with Northland excluded from the analysis ( $F = 12.64$ ,  $df = 3$ , 108,  $P < 0.001$ ). The highest numbers of bellbirds were counted where protected from predators. Of the mainland sites, the western side of the South Island had the highest counts, and the North Island the lowest. Annual average 5-minute counts at Craigieburn (1.05 birds per count) were relatively low even within the eastern South Island, being 14th lowest of the 33 sites. Of the sites with lower averages, most were based on counts only in spring (when bird densities are at a minimum), and only three eastern South Island sites had samples throughout the year and lower mean counts than Craigieburn.

## Discussion

### The diet of bellbirds compared to other honeyeaters

Different honeyeater species vary in their relative use of the three major food groups (carbohydrates, invertebrates, and fruit; Fig. 6) in studies where annual diet data were available (Gravatt, 1969; Ford, 1976; Ford and Paton, 1976a, 1977; Keast, 1976; Crome, 1978; Paton, 1980, 1982; Collins and Briffa, 1982; Bergquist, 1985; Angehr, 1986; Castro, 1995; Perrott, 1997). The 'carbohydrate' category included nectar



**Figure 6.** Annual mean diet composition of different New Zealand (solid symbols) and Australian (open symbols) Meliphagidae species. Each point on the graph represents the annual mean diet for a species from a single study or site, comprised of the annual mean percentages of the three major Meliphagidae food groups: invertebrates, fruit, and carbohydrates (nectar, honeydew, lerp and manna). Australian species are classified as long-billed or short-billed to distinguish between the two main feeding guilds in the Australian Meliphagidae. The Craigieburn bellbird data are marked with an arrow.

and other carbohydrate sources such as honeydew, lerp (the protective covering of certain Australian Hemipterans), and manna (sugary plant sap). The previously reported differences between the New Zealand species (tui more nectarivorous, bellbirds more insectivorous, and stitchbirds more frugivorous: Gravatt, 1969; Craig *et al.*, 1981; Angehr, 1986), are well illustrated in Fig. 6. The reduced carbohydrate intake of bellbirds, stitchbirds, and some short-billed Australian honeyeaters, can be partially explained by larger territorial honeyeaters such as tui excluding them from concentrated nectar resources (Craig, 1985; Rasch and Craig, 1988; Collins *et al.*, 1990). Where there is less competition because of a different assemblage of species, or seasonally abundant or spatially diffuse carbohydrate resources, these honeyeaters have a larger proportion of their diet made up of carbohydrates (Gravatt, 1969; Wykes, 1985; Noske, 1996; Franklin, 1997). The Craigieburn bellbird data show one extreme end of the New Zealand honeyeater dietary niche: highly

insectivorous due to the limited carbohydrate resources in the area, despite the lack of competition from other honeyeaters.

The presence of fruit in the diet of the New Zealand honeyeaters is the major dietary feature which divides the New Zealand and Australian honeyeaters (Gravatt 1969; Craig *et al.*, 1981). The Australian species have traditionally been divided into short-billed or long-billed morphological and feeding guilds. Short-billed genera, such as *Meliphaga*, *Conopophila*, *Manorina*, *Plectorhyncha*, and *Melithreptus*, are supposedly chiefly insectivorous, while long-billed genera, such as *Anthochaera*, *Acanthorhynchus*, *Philemon*, *Myzomela*, *Entomyzon*, and *Phylidonyris*, are more nectarivorous (Ford and Paton, 1977, 1985; Pyke, 1980; Tullis *et al.*, 1982; Recher *et al.*, 1985). However, this division is not apparent in Fig. 6. The lack of distinction between the short-billed and long-billed guilds can be explained by a degree of flexibility in the foraging behaviour of species in both guilds (McFarland and Ford, 1991), and also by some short-billed species which specialise on non-nectar carbohydrate sources (Paton, 1980). Short-billed species forage by gleaning, which is an energetically inexpensive method for foraging on non-clumped resources such as invertebrates, honeydew, manna, and lerp.

Bellbirds are similar to short-billed Australian honeyeaters in their beak morphology (Ford and Paton, 1985; Bartle and Sagar, 1987), and their use of gleaning (Ford and Paton, 1976b; Tullis *et al.*, 1982). As a result the diet of bellbirds is most similar to that of the short-billed Australian honeyeaters with a large degree of insectivory.

#### Are bellbirds distracted during mistletoe flowering and fruiting seasons?

Our data show that bellbirds at Craigieburn are annual generalists, with invertebrates, and to a lesser extent honeydew, making up a large proportion of the diet; and seasonal specialists on mistletoe fruit and mistletoe nectar when they are available. During the mistletoe flowering and fruiting seasons, bellbirds forage most often on mistletoe but continue to include other food sources. This broad diet is perhaps a key feature that enables them to inhabit the Craigieburn high altitude beech forest throughout the year despite the very simple vegetation and shortage of flowering and fruiting plants.

This broad generalist diet is similar to the diets of bellbirds observed elsewhere in New Zealand (Merton, 1966; Gravatt, 1969; Gaze and Fitzgerald, 1982; Angehr, 1986; Boyd, 1987; Rasch and Craig, 1988; O'Donnell and Dilks, 1994). The major difference in the bellbird diet between our study and that in other



habitats is the lesser importance of carbohydrates, presumably as a result of the scarcity of nectar bearing plant species at Craigieburn. Because nectar is only abundant for about 6 weeks at Craigieburn, honeydew is an important carbohydrate source. This supports the prediction of Paton (1980) that honeydew can be an effective substitute for nectar in the diet of nectarivorous birds.

The energy value of mistletoe fruit and nectar was only a small proportion of the total food energy available in most months (Murphy, 1998). There was no evidence that mistletoes were getting less attention than other food sources at the same time; in fact mistletoe fruit and nectar were usually a greater percentage of the observed diet (18 - 60%) than they were of the available energy sources in kJ/ha (4 - 42%; Murphy, 1998). If anything, this shows that bellbirds were concentrating on mistletoes at the expense of honeydew and invertebrates, both of which are less spatially concentrated and may be harder to collect. Birds may have a higher net energy gain on localised foods like mistletoe nectar than on dispersed foods like invertebrates which involve more searching time and movement.

No other birds have been seen visiting mistletoe flowers over three seasons at Craigieburn (Ladley *et al.*, 1997), even though silvereyes and occasionally blackbirds are present there. Similarly, silvereyes and blackbirds have been recorded eating *Peraxilla tetrapetala* fruit (O'Donnell and Dilks, 1994; Ladley and Kelly, 1996) but in several seasons of work at Craigieburn the only observed dispersers are bellbirds (Robertson *et al.*, 1999). Therefore mistletoe pollination and dispersal at Craigieburn rely almost totally on bellbirds.

*Peraxilla tetrapetala* and *Alepis flavida* are taken in relatively large proportions when available, compared to bellbird diet in other habitats which have a larger number of nectar-bearing species. Although effective dispersal and pollination is not just determined by the visitation of an animal vector (Whelan and Goldingay, 1989; Schupp, 1993), the large proportion of mistletoe in the bellbird diet suggests that bellbirds are concentrating on mistletoe fruits and flowers at Craigieburn. This, and the scarcity of other pollinators and dispersers in the area, makes them a key pollinator and disperser of *P. tetrapetala* and *A. flavida* at Craigieburn.

### Are bellbirds scarce at Craigieburn?

At Craigieburn 5-minute counts of bellbirds were highest in early autumn and lowest in spring. This seasonal variation is consistent with either a change in bellbird numbers, or seasonal variation in bellbird conspicuousness, or both. Lower bellbird

conspicuousness in winter has been suggested by Dawson *et al.* (1978) and Gill (1980). However in the Orongorongo Valley, Wellington, Gibb (1996) stated that bellbirds have a high frequency of calling and singing throughout the year with little seasonal variation in conspicuousness. The bellbird time budget at Craigieburn showed that there was no significant change in the proportion of time spent calling between July 1997 and February 1998, a time period that includes the breeding season. Our results therefore suggest that there is little seasonal variation in bellbird conspicuousness at Craigieburn. The only exception may be during *A. flavida* fruiting in March, when time budget data were not collected, but calling and social interaction seemed to be especially common. This could increase conspicuousness and contribute to the peak in 5-minute bellbird counts in March. However, the March peak may also result from local movement of bellbirds into the immediate study area to feed on *A. flavida* fruits, which were patchily distributed within Craigieburn forest. Overall, it seems likely that the seasonal variation of bellbird counts at Craigieburn is largely the result of actual changes in local bellbird density.

As bellbirds take large proportions of mistletoe fruit and nectar in their diet when they are available, the mistletoe plants should be receiving adequate pollination and dispersal if there are enough bellbirds present. Since pollination is not adequate (Robertson *et al.*, 1999), we conclude that there is a relative shortage of bellbirds in the area. This could arise either because bellbird numbers are too low, or mistletoe numbers too high (if mistletoes have recently increased to unusually high densities). However, historical data generally show that New Zealand's endemic mistletoes have declined over the last century (Robertson *et al.*, 1999). The idea that bellbird numbers are too low is supported by the relatively low 5-minute bellbird counts at Craigieburn compared to other sites in New Zealand (Table 1). The eastern South Island had lower mean counts than the western South Island and predator-free islands, but even within the eastern South Island, Craigieburn was one of the lowest. The mean number of birds per count at Craigieburn was around half the regional mean for the best regions.

A low number of bellbirds at Craigieburn could result in mistletoe pollination limitation. This effect may be particularly marked in the eastern South Island since this area has low densities of bellbirds and also has few or no tui, which are a competent alternative pollinator for *Peraxilla* spp. (Ladley *et al.*, 1997). We conclude that mistletoe pollination at Craigieburn is poor because tui are absent and bellbirds are scarce, not because bellbirds are distracted by other foods during flowering.

### What is limiting the number of bellbirds at Craigieburn?

If a low density of bellbirds at Craigieburn is a likely factor limiting mistletoe pollination, and possibly dispersal, then this poses the question of why the area cannot sustain a higher number of bellbirds. Is the bellbird population limited by food, by predation, by disease, by shortage of nest sites, or by some other factor?

Our data argue against food limitation in the montane beech forest, despite the high altitude and simple vegetation. If bellbirds were food limited in part of the year at Craigieburn then individuals should spend a greater proportion of their time foraging when food resources are scarce. This difference in bellbird foraging time should be seen between winter and summer at Craigieburn, where the mean total food energy available increased by 36% from a low in July to a high in December (Murphy, 1998). However, the time budget data showed that there was no significant change between winter and summer in the feeding or foraging (feeding plus locomotion) percentages of the bellbird time budget, and also no change in the number of hours spent foraging per day. Alternatively, it may be argued that bellbirds were short of food in all seasons. This also seems unlikely as they never spent more than 20% of their time feeding, and often spent much more of their time at rest or preening. Overall these data suggest that bellbirds at Craigieburn are able to fill their dietary needs in <20% of their time in both winter and summer, and that the population seems to not be food limited. In pure food supply terms the area could sustain a higher number of bellbirds.

If food is not limiting bellbirds, they must be limited by another factor such as territoriality, a lack of nest sites, disease, or predation (Gill, 1995). The rarity of aggressive encounters seen between bellbirds at Craigieburn argues against territoriality as a limit and shows that food resources are either not scarce enough to fight over, or too dispersed to defend. Nest sites are unlikely to be limiting as bellbirds at Craigieburn nest in the forks of beech trees (D.J. Murphy and T. Ward-Smith, *unpubl.*) which are abundant. Introduced bird pox and malaria decimated lowland populations of the Hawaiian honeycreepers in the nineteenth century (Warner, 1968). Island bird populations may be more vulnerable to introduced diseases because their immune system has been isolated from mainland diseases (Gill, 1995). However, no specific evidence for disease has been recorded in bellbirds.

The most likely limiting factor on the bellbird population is predation by introduced mammals such as stoats and possums, which are both present at Craigieburn. Ship rats are important bird predators in New Zealand, but they are at extremely low densities

at Craigieburn (King, 1983). Introduced mammalian predators have decimated the New Zealand avifauna (Diamond and Veitch, 1981; Clout and Saunders, 1995). The stoat has been identified as a serious nest predator that threatens the survival of bird species on the mainland including the kereru (*Hemiphaga novaeseelandiae*: Pierce, 1993), kaka (*Nestor meridionalis*: Wilson *et al.*, 1998), mohua (*Mohua ochrocephala*: Elliott, 1996; O'Donnell, 1996), and possibly the yellow-crowned parakeet (*Cyanoramphus auriceps*: Elliott *et al.*, 1996). Possums eat eggs, chicks, and adults of at least 6 species of native bird (Innes, 1995). Almost all native birds are much more abundant on predator-free offshore islands, as shown for bellbirds in Table 1. On the mainland, where there has been pest control of introduced mammals, native birds such as kokako, tui, kereru, bellbirds, fernbirds, and silvereyes have increased in numbers (Bradfield and Flux, 1996).

We therefore conclude that mistletoe pollination is inadequate at Craigieburn (and, by analogy, at other eastern South Island sites), because of predation by introduced mammals leading to reduced densities of bellbirds, the principal pollinator. To test this hypothesis, supplementary food could be provided to bellbirds, or the densities of predators such as stoats could be reduced, to see whether either treatment results in an increase in bellbird numbers and an increase in the success of mistletoe pollination. Such an experiment involving predator trapping is currently under way at Craigieburn.

Conservation programmes in New Zealand have largely focused on management of rare species (Taylor and Smith, 1997). However, nationally widespread and "common" species that are important for key ecosystem processes like pollination, but which could be facing population pressures, need to be recognised to avert future threats to native biodiversity.

## Acknowledgements

Many thanks to Jim Briskie, Colin McLay, Ian McLean, and Colin O'Donnell for help with experimental design and analysis; Alastair Robertson for his unpublished collation of bellbird count data; Sandra Anderson for helpful comments on a draft; and the Department of Conservation (Arthur's Pass) for permission to work at Craigieburn.

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