

Seasonal variation in the honeydew, invertebrate, fruit and nectar resource for bellbirds in a New Zealand mountain beech forest

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Abstract: To examine the seasonal availability of the major bellbird (*Anthornis melanura*) food sources in a mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest at Craigieburn, the invertebrate, honeydew, and mistletoe (*Peraxilla tetrapetala* and *Alepis flavida*) fruit and nectar resources were sampled over 12 months. The total available food varied 2.6-fold from a low in October (8798 kJ/ha) to a high in December (22,959 kJ/ha) with an annual mean of 15,782 kJ/ha. Invertebrates were available all year and represented 88% of the available food energy. Only 16% of the invertebrate resource was on beech foliage, and beech trunks with honeydew had 60% more invertebrate energy than trunks without honeydew. The energy value of honeydew at Craigieburn (0.9% of the total) was much lower than at lower altitude sites. The relative rankings of honeydew standing crops on 25 permanently marked trees were very constant. On an annual basis mistletoe nectar and fruit made up 6.3% and 4.9%, respectively, of total food energy, but *P. tetrapetala* nectar was 46% of available food in early January, and *P. tetrapetala* fruit was 25% of the total in March. Bellbirds spent less time foraging on invertebrates, and more time on the other foods, than energy values would predict. However, during the peak of its short flowering season, *P. tetrapetala* nectar made up 46% of available energy but only 33% of bellbird foraging observations. At this site *P. tetrapetala* is pollen limited due to insufficient visits from pollinators. This may be because bellbirds require invertebrates for protein, or to feed to nestlings. Therefore the pollination mutualism is faltering, despite high investment in nectar by the plant.

Keywords: *Alepis flavida*; *Anthornis melanura*; bellbird; foraging; honeydew; invertebrate; mistletoe; *Peraxilla tetrapetala*; pollination mutualisms.

Introduction

When anthropogenic changes alter the species found in a community, inter-relationships among organisms, such as mutualisms, may be upset. New Zealand has suffered extensive changes to its fauna and flora: extinctions, range contractions, reduced densities, and introductions of alien species. Only recently has it been appreciated how these changes may alter relationships among species even when all the players are still present.

Bellbirds (*Anthornis melanura*) represent an important example of this process. These widespread endemic honeyeaters (family Meliphagidae) are important pollinators and dispersers of the native flora (Clout and Hay, 1989; Ladley and Kelly, 1996; Ladley *et al.*, 1997). Bellbirds are present throughout the mainland of New Zealand south of about Hamilton, and on many offshore islands (Heather and Robertson, 1996). The two other endemic honeyeaters are also important to pollination and dispersal, but both are

now absent from at least part of the mainland: the tui (*Prothemadera novaeseelandia*) is absent from much of the eastern South Island, and the stitchbird (*Notiomystis cincta*) is now restricted to offshore islands. Because bellbirds are widespread, it was assumed that mutualisms in which they participate would be preserved. However it has recently been shown that several native bird-pollinated plants are suffering pollen limitation, probably due to reduced densities of bellbirds, tui and stitchbirds. The native mistletoe *Peraxilla tetrapetala* (Loranthaceae) is extensively pollen limited at Craigieburn in the central South Island, and other similar sites where tui are absent and bellbirds apparently not common enough (Robertson *et al.*, 1999). *Peraxilla tetrapetala*, along with the closely related mistletoe *Alepis flavida*, may also be disperser limited at Craigieburn (Ladley and Kelly, 1996; Ladley *et al.*, 1997). On Banks Peninsula the scrambling shrub *Fuchsia perscandens* (Onagraceae) is pollen limited and is rarely visited by bellbirds (Montgomery *et al.*, 2001).

To show that such mutualism failures are the result of anthropogenic changes, rather than simply a maladapted plant (for example, offering minimal nectar reward), requires an understanding of what limits the numbers of bellbirds and how these birds select their food sources. Because the Craigieburn study (Robertson *et al.*, 1999) showed pollen limitation in *P. tetrapetala* to be consistent over a number of years, we chose that site to study the diet and food sources available to bellbirds. The first part of this study (Murphy and Kelly, 2001) recorded the diet choice and time budgets of bellbirds at Craigieburn, and the seasonal changes in bellbird density. The conclusion was that bellbirds are annual generalists, eating a wide range of food items, but they specialise seasonally. The principal items of their diet were invertebrates (55% of the annual diet items), honeydew (22%), mistletoe nectar (10%), and mistletoe fruits (10%). Work at other New Zealand sites has also shown these same items to be taken by bellbirds (Gaze and Clout, 1983; Boyd, 1987; O'Donnell and Dilks, 1994; Ladley and Kelly, 1995a, b; 1996). In the present paper, we set out to measure the amount of food available in the Craigieburn environment for birds such as bellbirds.

Bellbirds are an important bird species to study for several reasons, apart from their importance as mutualists. Their wide dietary range means that they may be negatively affected by changes in any one of a number of different food sources, so they may serve as bellweathers of deterioration in many parts of the community. They are also one of the most abundant native birds at Craigieburn and in similar South Island forests, making them numerically important in the food webs. And they are remarkable in being a member of the nectar-feeding Meliphagidae, yet able to persist in the floristically simple, cool temperate, high altitude (900-1300 m) mountain beech (*Nothofagus solandri* var. *cliffortioides*) forests at Craigieburn. Because there are very few nectar-producing plants in high altitude beech forest (Shanks *et al.*, 1990), this habitat must represent a special challenge for a nectar-feeding bird. However, the data on available foods at Craigieburn will also be relevant to most of the other native birds found there, as the food items eaten by bellbirds span most of those eaten by the other birds too.

There has been some previous work on changes in seasonal abundance of most of the food items eaten by bellbirds. Little published work exists on the invertebrate fauna of the Craigieburn Range. However, the invertebrate fauna of a similar mountain beech forest ecosystem at nearby Cass has been described by Johns (1977). In the Cass beech foliage some of the more prominent invertebrates were the chafer beetles (*Odontria halli* and *O. smithii*; Coleoptera: Scarabaeidae), several moth larvae, hemipterans and

flies. The layer of moss, liverwort and lichens that often covers beech trunks was a habitat to some staphylinid species, wetas (*Isoplectron* spp. and *Pleicopectron* spp.), a byrrid and the beetles *Artystona rugiceps* and *Amarotytus edwardsii*. Spiders and cockroaches were found on the bark of rotting wood and the living beech trunk tissue was a microhabitat for a number of wood-boring beetle species.

The only previous study on seasonal changes in abundance of invertebrates in native forest was carried out by Clout and Gaze (1984) in three native forests and three pine plantations in the Nelson region. The native forests were a mixture of *Nothofagus* and podocarps with *Nothofagus truncata* as a major canopy species. An index of active invertebrate biomass was calculated from the amount of falling frass; the results were significantly higher for pine plantations than the native forests, but did not show any monthly pattern in invertebrate abundance for either forest type (Clout and Gaze, 1984).

Honeydew is a sugar-rich fluid produced by the endemic sooty beech scales *Ultracoelostoma assimile* and *U. brittini* (Hemiptera: Margarodidae) which suck the sap of *Nothofagus* spp. (Morales, 1991; Beggs, 2001). Honeydew is eaten by many species including bellbirds, tui, kaka (*Nestor meridionalis*), silvereyes (*Zosterops lateralis*), lizards, wasps, bees and other insects (Kikkawa, 1975; Boyd, 1987; Moller and Tilley, 1989; Moller *et al.*, 1991; Didham, 1993; Markwell *et al.*, 1993; O'Donnell and Dilks, 1994; Beggs, 2001). Honeydew is important in the diets of nectar-feeding bird species in South Island beech forests because so few nectar-producing plants are present (Gaze and Clout, 1983; Clout and Gaze, 1984). Black sooty mould, which is a distinctive feature of honeydew-infested trees, utilizes the sugar in honeydew and provides a microniche for many invertebrates (Didham, 1993).

The harvestable amount of honeydew is measured by the standing crop, which is the quantity present on the surface of beech trees at any one time. At mid altitudes (400 m) on Mt. Oxford, Canterbury, the standing crop from *Ultracoelostoma brittini* on black beech (*Nothofagus solandri* var. *solandri*) peaked after dawn and varied 3.5-fold over a 24 hour period (Kelly *et al.*, 1992). There have been seasonal changes recorded in the production of honeydew in the Nelson region. Gaze and Clout (1983) found the number of honeydew droplets on beech were lowest in February and July and highest in September and June. The sugar concentration also peaked in spring. Boyd (1987) found that the number of honeydew drops, mean drop size, sugar concentration, and hence total energy value, all increased from summer to winter. However, all the above authors point out that honeydew standing crops can vary widely over a few days depending on changes

in rainfall, temperature, humidity, and harvesting rates by animals.

In Craigieburn Forest Park there are few species of plant with bird-pollinated flowers or bird-dispersed fruits (Shanks *et al.*, 1990). By far the most abundant of these are *Peraxilla tetrapetala* and *Alepis flavida*, both parasitising mountain beech at Craigieburn. Unopened flower buds of *P. tetrapetala* provide nectar-feeding birds with an untapped source of nectar as these two species have 'explosive' flowers which do not open until a bird twists the top of the bud (Ladley and Kelly, 1995a, b) although native bees can sometimes open flowers to harvest pollen (Kelly *et al.*, 1996). At Craigieburn the flowering of *P. tetrapetala* extends over three to four weeks, finishing just before *A. flavida* starts flowering (both species flower in January and February: Ladley *et al.*, 1997). At Craigieburn most *A. flavida* fruits ripen in March and April, while most *P. tetrapetala* fruits ripen from April to June with a small number of fruits present on mistletoe until November (Ladley and Kelly, 1996).

There are no other native species of bird-pollinated plant at Craigieburn, although a few plants of the exotic *Salix glaucophylloides* are present and visited by bellbirds (Murphy and Kelly, 2001). The only other bird-dispersed fruiting plants present are several species of *Coprosma* (*C. parviflora* sp. 't', *C. microcarpa* and *C. pseudocuneata*), *Leucopogon fasciculatus* and *Phyllocladus alpinus*, but all are sparse.

We wanted to study the seasonal variation of the bellbird diet in response to the seasonal variation of potential food sources to discover whether any non-mistletoe food sources are dominating the bellbird diet during the mistletoe fruiting and flowering seasons thus reducing the number of bellbird visits to mistletoe plants. Seasonal variation in the relative availability of honeydew, invertebrates, and mistletoe fruit and nectar, could also possibly explain seasonal changes in the bellbird diet and identify months when low energy availability might limit bellbird activity, survival or densities.

To show the seasonal variation between these potential bellbird food sources at Craigieburn we measured the energetic value and variation in honeydew, invertebrates, and fruit and nectar production over a 12 month period. These values were converted to a common scale (energy in kJ per ha) to allow comparisons between the different food sources. Specifically we wanted to know: (1) what is the relative seasonal abundance of the different foods available to bellbirds? (2) are there seasons when total available food supplies are low and may be limiting bellbird population sizes? (3) are there attractive alternative food sources which might monopolise bellbird foraging attention during the mistletoe flowering and fruiting seasons? (4) do bellbirds allocate their time to various

food sources in proportion to the seasonal abundance of the foods?

Methods

Study area

The study area was at Jacks Pass (171° 42.5' E, 43° 9.1' S) which is a forested area within Craigieburn Forest Park, which was described by Shanks *et al.* (1990). The study area is at an altitude of 950 m a.s.l. and is characterised by a cool alpine climate that receives 1500 mm of rain per year. All field work was carried out in mountain beech forest with few other species present in the understorey. The major understorey species are *Coprosma microcarpa*, *C. pseudocuneata*, *C. linariifolia*, *C. parviflora* sp. 't', *Leucopogon fasciculatus* and a few species of ferns. The low woody-species diversity in the area is probably due to the cold, dry climate and the effects of past grazing by deer. Both *Peraxilla tetrapetala* and *Alepis flavida* are common at Jacks Pass.

Bird abundance and foraging

Native birds that are present at Craigieburn in the beech forest are the bellbird, silvereye, South Island tomtit (*Petroica macrocephala*), fantail (*Rhipidura fuliginosa*), rifleman (*Acanthisitta chloris*), brown creeper (*Mohoua novaeseelandiae*), grey warbler (*Gerygone igata*), kea (*Nestor notabilis*), morepork (*Ninox novaeseelandiae*), yellow-crowned parakeet (*Cyanoramphus auriceps*) and occasionally New Zealand falcon (*Falco novaeseelandiae*). The long-tailed cuckoo (*Eudynamis taitensis*) and shining cuckoo (*Chrysococcyx lucidus*) arrive in the summer to breed. The most important introduced birds in the area are the chaffinch (*Fringilla coelebs*), blackbird (*Turdus merula*), redpoll (*Carduelis flammea*), and dunnock (*Prunella modularis*), with lower numbers of song thrush (*Turdus philomelos*), greenfinch (*Carduelis chloris*), and goldfinch (*Carduelis carduelis*). Of these species the bellbird is by far the most important visitor to mistletoe flowers and fruit (Ladley and Kelly, 1996; Ladley *et al.*, 1997).

During the timing of this study bellbirds were recorded at relatively low numbers during 5-minute counts, ranging from 2.76 per count in March to 0.46 in November (Murphy and Kelly, 2001), but other species of birds were not recorded. Another series of 5-minute bird counts including all bird species were performed in May and September 1999 and January 2000. On each occasion, counts were done at 15 stations twice per day for three days.

To determine which part of the beech forest was used by bellbirds for foraging, records were kept of the

height tier used by the bellbirds whenever they were observed feeding during the diet sampling described by Murphy and Kelly (2001).

Honeydew

Honeydew standing crop was measured on the trunks of 25 randomly chosen, permanently marked mountain beech trees at Jacks Pass. The sampling quadrat was a permanent 50 cm high cylindrical area of each beech tree trunk at breast height. Each month honeydew droplets were gathered with a micro-pipette and the number of drops, and the total volume of all the drops, were recorded for each tree. The combined volume from each tree was then stored on filter paper so sugar quantities could be analyzed in the laboratory. Beech trees were sampled only following 48 hours of dry weather because of the potential for precipitation to remove or dilute honeydew droplets. Honeydew sampling was carried out in the morning so as to avoid warm conditions that cause evaporation, making droplets more viscous, and preventing the measuring of volume (Kelly *et al.*, 1992). In certain months viscous honeydew was unavoidable and volume could not be measured on some trees. However, for these trees the honeydew was still collected for sugar analysis. No sampling was possible in June and August 1997 due to persistent rain that washed away honeydew.

The amount of honeydew sugar (mg of sucrose/quadrat) was measured using an antherone colourmetric assay of the redissolved sugar from the filter paper (McKenna and Thompson, 1988). The energy value of honeydew from quadrats was calculated assuming that 1 mg sucrose = 16 J (Grant and Beggs, 1989). The mean honeydew volume/m² of bark, number of drops/m², sugar concentration % weight/volume, and total standing crop of sugar for each month was calculated from all 25 beech trees, including those with no honeydew.

Constancy over time in the rank order of the 25 trees by total honeydew standing crop (J/m²) was examined by calculating the Spearman rank correlation coefficient for each pairwise comparison among months. To see whether the strength of this correlation changed with time interval, a linear regression of rank correlation coefficient against interval between the pair of samples was calculated.

The honeydew J/m² were converted to J/hectare using measurements of tree d.b.h. (diameter at breast height) and total height for all beech trees in sixteen 20 m x 20 m plots at Jacks Pass. Bark area per tree was calculated as the mean of two simple models (Kelly, 1990). The first model treated each tree as a cone, which tapered from the d.b.h. measurement at the bottom to zero at the top. The second model treated each tree as a cylinder (to allow for branches). As the

true bark area probably lies between the two model estimates, the mean of the two values was used. Bark area was then summed for all trees in each plot and converted to m²/ha; the mean from the 16 plots was 8316 ± 1577 m²/ha (± 95% CI). For each honeydew tree in each month the J/m² was then converted to kJ/hectare. The kJ/ha for all trees was then averaged in each month to give a monthly mean honeydew kJ/ha.

Invertebrates

Since bellbirds at Craigieburn mainly forage for invertebrates by gleaning the bark and foliage of beech trees (Murphy and Kelly, 2001), invertebrate samples were gathered from mountain beech trees in the study area. Fifteen invertebrate samples were gathered from quadrats on randomly selected beech trees each month. Five samples were taken from foliage, 5 from 'honeydew' bark (distinguished by a coating of sooty mould that grows on honeydew), and the other 5 from 'normal' bark (not coated with sooty mould). For consistency, samples were collected in the afternoon on days when there had been no rain.

Bark samples were collected using a step ladder placed against the northern aspect of each tree trunk. A 29 x 16 cm quadrat was marked at a standard height of 3 metres. This height was chosen as bellbirds were often seen feeding at this height and it was within reach of a ladder. The quadrat was given three quick sprays of pyrethrum, which increases invertebrate activity (driving them out of their refuges), and left for one minute. The quadrat was then scraped with a wire brush with samples being caught in a collection tray. The sample was placed in an individual container filled with 70% alcohol.

Foliage samples were also collected at a height of 3 metres on the northern aspect of the tree. A 100 g (wet weight) sample of foliage was collected and placed in a plastic bag on a spring balance. The bag was then sealed and shaken vigorously for one minute. The foliage was removed and the remaining contents of the bag were placed in a container with 70% alcohol.

In the laboratory invertebrates were removed from the alcohol solution by flotation and sorted into taxonomic orders. Invertebrates were not identified further than orders as the focus of the study was on the estimated energy of the invertebrate resource. Larvae could not be classified into orders and were just grouped under the label 'Larvae'. Each invertebrate was then measured for total body length and the data were arranged in size classes of 1 mm before estimating dry weight from body length. Estimates of dry weight from body dimensions have been successfully used in past studies of terrestrial and aquatic invertebrates (Huxley, 1924; Englemann, 1961; Breyermeier, 1967; Tilbrook and Block, 1972; Rogers *et al.*, 1976; Meyer,

1989; Towers *et al.*, 1994). Such estimates have the advantage of being quick and are not affected by possible weight loss of specimens that have been stored in alcohol (Meyer, 1989).

We used the equation of Rogers *et al.* (1976), which is a generalised regression equation that estimates the dry weight of terrestrial insects from their body length:

$$W = 0.0305 L^{2.62} \quad (1)$$

where *W* is weight in mg and *L* is body length in mm. This equation was chosen because it was derived from insect orders similar to those at Craigieburn.

The estimated energetic value of invertebrates per quadrat was calculated from the weight assuming 1 g = 24.2 kJ (Bell, 1990). This value was chosen as it covered a wide variety of insect orders, similar to those at Craigieburn, and included energy values of adults and larvae. A similar value was also reported by Cummins and Wuycheck (1967).

To estimate the kJ/ha of foliage invertebrates each month the estimated invertebrate kJ per sample (100 g wet weight) was corrected for the estimated dry weight of each sample and the total beech foliage dry weight per hectare. The dry weight/wet weight conversion factor was derived by collecting 10 samples of mountain beech foliage, each weighing 100 g, removing the leaves from the twigs, drying the leaves, and reweighing. The total dry weight of mountain beech foliage per ha has been estimated as 12.8 tonnes (Wardle, 1984; p. 322).

The estimated kJ/ha for bark invertebrates was calculated from the estimated energy value of each sample, divided by the area of the quadrat, times the total bark area of that type per hectare. A separate survey of 57 randomly selected trees in this area indicated that 49% of trees are infested with honeydew, giving (8316 × 0.49) m² of honeydew bark and (8316 × 0.51) m² of normal bark per hectare. This then gave a kJ/ha for each of the 5 monthly replicates for 'honeydew' and 'normal' bark.

The invertebrate kJ/ha value for each of the 5 monthly replicates in each of the three habitat categories ('honeydew' bark, 'normal' bark, and foliage) were averaged to give a monthly mean energy value for each category. The replicates within each month were used to test for month to month changes within each habitat category. Overall energy values in the three habitats were compared using a one way anova on the monthly means for each category. The values for the three categories were summed to give overall invertebrate abundance.

Mistletoe fruit and nectar

The energy value of *Peraxilla tetrapetala* and *Alepis flavida* fruit and nectar was measured on permanently tagged plants at Craigieburn. Mistletoe data were gathered only in the months fruit and nectar appeared in the bellbird diet, which were March, April and May 1997 for mistletoe fruit (the 1 April sample in Table 4 was categorised as 'March' to match honeydew and invertebrate samples taken at the end of March); and early January, late January and early February 1998 for mistletoe nectar (Murphy and Kelly, 2001).

Mistletoe fruit-sugar was calculated from (1) the number of ripe fruits present on tagged plants at the time of bellbird feeding observations; (2) sugar content per fruit; (3) mean fruit per m³ of mistletoe; and (4) mean m³ of mistletoe/ha in six 20 m x 20 m permanent plots at Jacks Pass.

Mistletoe nectar-sugar was more difficult to estimate because the mistletoe flower ripening rate (kJ/ha present in flowers ripening on that day) would give a lower limit to nectar availability, because it excludes flowers ripened on previous days which may still have some remaining nectar. The total number of open flowers present on that day would give an upper limit to nectar availability, as it assumes all open flowers are full with nectar whereas some will have had the nectar removed. Here, we have used the latter estimate (upper limit) for the time of bellbird feeding observations. This will probably only slightly overestimate nectar availability: relatively few flowers are visited by birds, so nectar harvesting rates at Craigieburn are thought to be rather low (Robertson *et al.*, 1999) and open flowers frequently still contained abundant nectar.

The energy value of mistletoe fruit and nectar was approximated using 1 mg of sugar = 16 J, the same as used for honeydew. The drupes of *Coprosma parviflora* sp. 't' and *Leucopogon fasciculatus* were not sampled as both species were uncommon and they made up only 1.1 % and 0.3 % of the annual bellbird diet respectively (Murphy and Kelly, 2001).

Relative preference ratings for bellbirds

The overall abundance of each food (% of the total available each month) was compared to how frequently bellbirds were seen feeding on that food (% of foraging time on the food that month), as recorded by Murphy and Kelly (2001) at the same site. A preference rating >1 indicates that the food is used more often than its abundance would predict, and a rating of <1 indicates the converse.

Results

Bird species present and bellbird foraging

From May 1999 to January 2000, bellbirds were the species noted most often at Craigieburn in 5-minute bird counts (Table 1). Introduced finches (redpolls, chaffinches, and unidentified finches) and silvereyes were the other most common species. Most of the birds present at Craigieburn rely wholly or principally on the foods surveyed here, although some species also eat major components of plant seeds (redpoll, goldfinch, greenfinch), ground dwelling invertebrates (blackbird, song thrush), or meat (kea).

Table 1. Mean number of birds seen or heard per 5-minute count at Craigieburn on three occasions in 1999-2000. On each occasion 90 counts were done (15 stations x twice per day x 3 days). For scientific names of birds see text.

Species	May-99	Sep-99	Jan-00	Mean
Bellbird	3.24	1.83	1.98	2.35
Redpoll*	0.21	2.47	1.39	1.36
Silvereye	1.06	0.62	0.90	0.86
Chaffinch*	1.09	1.07	0.41	0.86
Fantail	0.29	0.68	0.17	0.38
Brown creeper	0.13	0.90	0.08	0.37
Tomtit	0.31	0.22	0.31	0.28
Rifleman	0.13	0.11	0.31	0.19
Greenfinch*	0.19	0.23	0.00	0.14
Blackbird*	0.16	0.16	0.10	0.14
Song thrush*	0.00	0.39	0.02	0.14
Grey warbler	0.01	0.07	0.16	0.08
Kea	0.01	0.14	0.07	0.07
Dunnock*	0.07	0.01	0.01	0.03
Goldfinch*	0.04	0.00	0.00	0.01
Parakeet	0.00	0.00	0.01	0.004
Finch*	3.37	2.23	1.23	2.28
Unidentified	0.00	0.00	0.16	0.05

* exotic species

Direct observation of 763 bellbird feeding locations showed that the majority of their feeding time was spent in the middle layers of the forest. Overall, 0.5% of feeding observations were in the tops of the tree canopies, 12.8% just below the canopy, 77.6% were in the upper or middle levels of the trees, 4.9% near the ground and 4.2% on the ground itself.

Honeydew

We found a wide range of levels of *Ultracoelostoma* infestation in the 25 beech trees sampled. Three trees never had any honeydew droplets present, while four trees had honeydew drops on every sampling occasion. The other 18 trees varied from month to month in whether honeydew drops were present, with the lowest total number of trees carrying droplets in May and July (Table 2). The rank order of honeydew standing crop (J/m^2) on the 25 trees was highly constant, with all but one of 45 pairwise Spearman correlations being significant at $P < 0.05$ and most at $P < 0.001$. There was no significant effect of the time interval between samples on the size of the correlation coefficient (Figure 1), showing that trees were consistently high or low honeydew producers over the whole study period.

The mean volume of honeydew ($\mu l/m^2$), and the mean number of drops/ m^2 had their lowest values in winter (Table 2). This resulted in the mean energetic value (kJ/ha) of honeydew fluctuating seasonally from a low in July 1997 to a peak in January 1998, when sugar concentrations were particularly high. The overall level of honeydew energy was relatively low, with an annual average of 145 kJ/ha.

Invertebrates

The more common families in our samples included Entomoboyidae in the Collembola (springtails), the genus *Celatoblatta* from the Blattodea (cockroaches), Staphylinidae and Colydiidae in the Coleoptera

Table 2. The mean honeydew abundance for each month at Craigieburn between March 1997 and February 1998 (per m^2 of bark and per hectare). Based on means of all 25 trees; the number of non-zero trees in each month is also shown. Wet weather prevented data collection in June and August.

Month	Volume $\mu l/m^2$	Number of drops/ m^2	Energy value J/m^2	kJ/ha (mean \pm 95% CI)	No. trees with drops
March	7.62	17.11	3.52	30.7 \pm 17.1	17
April	5.84	7.18	2.72	23.7 \pm 17.5	17
May	1.17	5.97	0.64	5.6 \pm 3.4	9
July	0.64	2.44	0.33	2.9 \pm 2.2	7
September	5.85	10.51	3.27	28.6 \pm 22.9	14
October	13.80	12.81	11.84	103.4 \pm 87.6	15
November	11.10	15.23	7.39	64.5 \pm 36.4	18
December	10.73	12.69	9.48	82.8 \pm 49.3	16
January	5.44	5.27	91.57	799.6 \pm 579.4	12
February	7.72	9.19	4.52	39.4 \pm 26.0	15

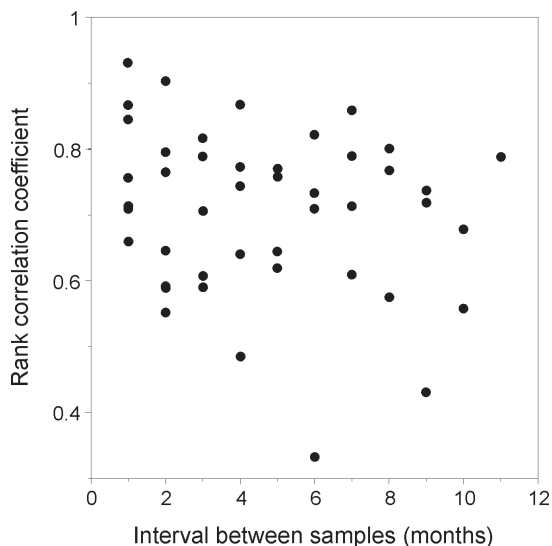


Figure 1. Constancy of ranking of the 25 honeydew trees by honeydew standing crop (J/m^2) among months, against time interval between each pair of months. The regression was non-significant ($n = 45$, $R^2 = 0.03$, $F_{1,43} = 1.54$, $P = 0.22$).

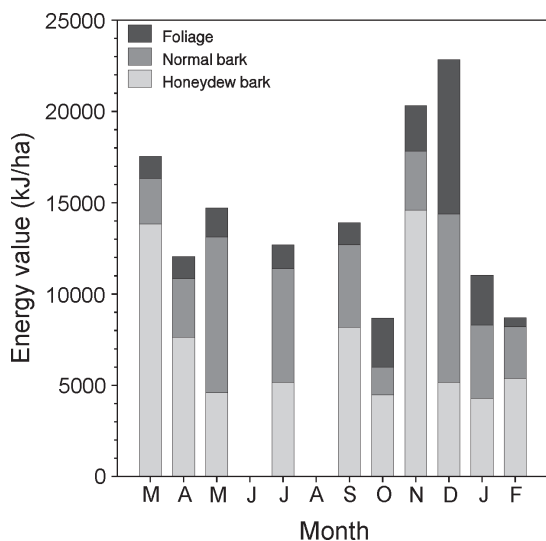


Figure 2. The mean energy value for invertebrates in the three beech habitats at Craigieburn, between March 1997 and February 1998. Bad weather prevented sampling in June and August. For statistical testing among months within each habitat, see text.

Table 3. The overall percentage of individuals in different invertebrate orders collected in the three beech tree habitats at Craigieburn, between March 1997 and February 1998. Larvae could not be identified to order and were grouped together. For each habitat, $n = 5$ replicates \times 10 months (excluding June and August).

Order	Honeydew bark	Normal bark	Foliage	Mean
Acarina	31	65	30	42.0
"Larvae"	28	6	19	17.7
Coleoptera	14	7	5	8.7
Hemiptera	3	2	16	7.0
Pseudo-				
scorpionoidea	10	6	0	5.3
Collembola	6	5	4	5.0
Aranea	3	3	5	3.7
Hymenoptera	< 1	< 1	8	3.0
Blattodea	3	4	0	2.3
Diptera	< 1	< 1	6	2.3
Thysanoptera	< 1	< 1	3	1.3
Gastropoda	< 1	< 1	2	1.0
Psocoptera	< 1	< 1	2	1.0
Total	100	100	100	100

(beetles), and Coccoidea in the Hemiptera. The very numerous small mites (Acarina) could not be identified to family.

There were some general differences between the community structure of invertebrates collected from the foliage and invertebrates collected from bark (Table 3). From the foliage samples there was a higher proportion of dipterans, hymenopterans and thysanopterans than those samples collected from bark. There was also a smaller proportion of mites, coleopterans, and no blattodeans and pseudoscorpionoids collected from foliage. There was very little difference in the proportion of different invertebrate orders within samples between the two bark types. For all three beech habitats Acarina was the most abundant Order.

Although larger invertebrates were rare, their greater size meant they still contributed significantly to the overall weights and energy values. Over all months combined, 89% of the individuals were between 0.1 and 3.0 mm contributing 27% of the energy values, 9% of the individuals were 3.1-6.0 mm contributing 43% of energy, and the 1.3% between 6.1 and 11.0 mm contributed 25% of the energy.

Changes over months in invertebrate energy values are shown in Fig. 2. To test whether the mean invertebrate energy value (kJ/ha) varied significantly between months for each of the three beech habitat types (foliage, 'honeydew' bark and 'normal' bark), we used one-way ANOVAs with the 5 samples in each month as replicates. The invertebrate energy value in foliage varied highly significantly between months

($F_{9,40} = 4.01$, $P = 0.001$) with a peak in December 1997. However, the invertebrate energy value in 'honeydew' bark ($F_{9,40} = 1.31$, $P = 0.26$) and 'normal' bark ($F_{9,40} = 0.56$, $P = 0.82$) did not vary significantly between months.

The overall mean invertebrate energy available at Craigieburn was greatest for those samples collected from bark (Fig. 2), and differences among the three habitat types were highly significant ($F_{2,27} = 6.97$, $P = 0.004$). The invertebrates collected from foliage, 'honeydew' bark and 'normal' bark had monthly mean values of 2344, 7336, and 4576 kJ/ha respectively. Invertebrates in the foliage made up a large proportion of the total invertebrate energy only when foliage invertebrates peaked in December.

Mistletoe fruit and nectar

The available energy value (kJ/ha) of *Peraxilla tetrapetala* fruit increased from March to May 1997 (Table 4), driven by the increased ripening of fruits later in the season. The opposite trend was seen in *Alepis flavida* fruit which ripened mainly in March. The maximum monthly energy value of *Peraxilla tetrapetala* fruit was more than twice as high as that of *Alepis flavida* because of the higher sugar content of *P. tetrapetala* fruit (Table 4).

For *Peraxilla tetrapetala* flowers the mean energy value for nectar decreased sharply from early January to February 1998, reflecting the short duration of the *P. tetrapetala* flowering season. The proportion of flowers open for *Alepis flavida* increased over this same time.

However, the much lower amount of nectar per flower meant that the total energy value of *A. flavida* nectar was an order of magnitude less than for *P. tetrapetala* nectar (Table 4).

Overall energy resources

The total estimated energy per hectare in the surveyed foods was dominated by invertebrates (Fig. 3), which across all months averaged 87.8% of the total, and in winter made up over 99%. The only other food available all year was honeydew but this averaged only 0.9% of the total, with a maximum of just under 4% of all food energy in January. Fruit and nectar were only available seasonally, but *P. tetrapetala* nectar represented 46% of the available energy per hectare in early January. The monthly total energy value varied 2.6-fold from a low in October (8798 kJ/ha) to a high in December (22,959 kJ/ha).

Bellbird foraging behaviour was compared to the relative amounts of each food available each month (Table 5). Although invertebrates made up the largest diet category for bellbirds in most months (Murphy and Kelly 2001), invertebrates were eaten less often than their abundance would suggest (mean preference rating = 0.59), and other foods (especially honeydew) usually had preference ratings greater than one. When mistletoe fruit and nectar were available, they were usually foraged on more frequently than their abundance would predict, except for flowers very early (*P. tetrapetala* and *Alepis*) or late (*P. tetrapetala*) in the season.

Table 4. Energy value of fruit and nectar of *Peraxilla tetrapetala* and *Alepis flavida* at Craigieburn (mean \pm 95% CI). Fruit data are for the 1997 fruiting season and flowering data for the 1998 flowering season.

Measurement	<i>P. tetrapetala</i>	<i>A. flavida</i>
Overall mistletoe m ³ per ha	518 \pm 351	464 \pm 408
Number of fruit per m ³ of mistletoe, 1997	137	207 \pm 83
Sugar per fruit (mg sucrose)	14 \pm 10	9 \pm 3
Total fruit kJ/ha/year	15,328	9568
Percent of fruits ripe on 1 April 1997	0	21
Percent of fruits ripe on 22 April 1997	5	7
Percent of fruits ripe on 25 May 1997	32	3
Number of flowers per m ³ of mistletoe in 1998	464 \pm 164	226 \pm 44
Nectar volume per flower (μ l)	36 \pm 6	4 \pm 2
Sugar concentration of nectar (%)	12 \pm 3	13 \pm 2
Sugar per flower (mg sucrose)	5 \pm 0.1	0.6 \pm 0.3
Total flower kJ/ha/year	17,840	976
Percent of flowers open, 3-6 Jan 1998	56	1
Percent of flowers open, 18 Jan 1998	2	5
Percent of flowers open, 2 Feb 1998	1	35

Table 5. Relative preference ratings for bellbirds foraging on different food items at Craigieburn in 1997-98. The preference rating is the percentage of foraging time spent on that item, divided by the percentage of available food represented by that item at the time. A blank means that the food item was not available in that month; a zero means the food was available but bellbirds were not seen to forage on it. Data were not collected in June and August due to wet weather. P. tet = *Peraxilla tetrapetala*, A. flav = *Alepis flavida*.

Month	Invertebrates	Honeydew	P. tet fruit	A. flav fruit	P. tet nectar	A. flav nectar
March	0.39	31.87		5.06		
April	0.88	11.40	2.34	0.95		
May	0.58	71.31	1.39	4.95		
July	0.85	655.33				
September	0.66	166.02				
October	0.58	19.57				
November	0.57	136.17				
December	0.77	63.81				
January (early)	0.44	12.33			0.72	0
January (late)	0.41	1.02			1.50	128.82
February	0.39	84.42			0	7.24
Mean	0.59	113.93	1.87	3.65	0.74	45.35

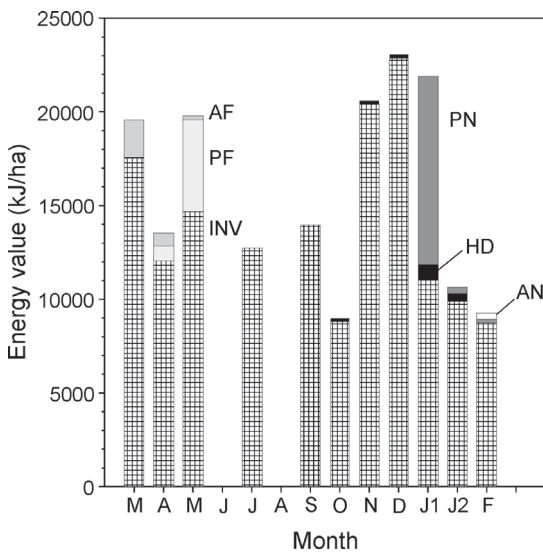


Figure 3. The mean energy value (kJ/ha) of the major bellbird food sources at Craigieburn in 1997-98. Because mistletoe nectar was sampled in late January (“J2”), but invertebrates and honeydew were not, the J2 values for the latter two variables are interpolated by averaging the early January and early February samples. AF, *Alepis* fruit; PF, *Peraxilla* fruit; INV, invertebrates; PN, *Peraxilla* nectar; AN, *Alepis* nectar; HD, honeydew.

Discussion

Bird abundance

While bellbirds were the species most often recorded in 5-minute counts, this does not necessarily mean they were present at the highest density. Species that are

very conspicuous will be over-represented in 5-minute counts compared with more cryptic species. However, many of the other birds at Craigieburn are also quite conspicuous (chaffinches, blackbirds, silvereyes, parakeets), others are attracted to humans (tomtits, kea), and only the dunnoek could be truly described as cryptic. Therefore we feel confident that bellbirds are one of the most abundant birds at the study site.

Honeydew

The only previously published work on the constancy over time of honeydew standing crops on different trees was over a 4-month interval at a lower altitude site in Canterbury. Kelly *et al.* (1992) showed that there was a significant correlation between standing crops in August and December. Our results from Craigieburn reinforce and extend this conclusion, and show that honeydew density on particular trees is very stable over periods of up to a year. This is longer than the presumed lifespan of individual *Ultracoelostoma* insects (Morales 1991).

The seasonal pattern of honeydew standing crop at Craigieburn is consistent with previous results (Gaze and Clout, 1983; Boyd, 1987) that indicated there is a peak in the honeydew standing crop in spring. The main difference from previous studies is the decrease in honeydew standing crop energy value for Craigieburn over autumn to winter while there was an increase in honeydew at this time in Nelson (Boyd, 1987). Such changes may be dependent on rainfall and harvesting in the few days prior to each set of sampling.

At Craigieburn honeydew had a very low energy per unit area value in comparison to invertebrates and mistletoe fruit and nectar: in Fig. 3 the honeydew value can hardly be seen for most months. The overall annual mean energy value was 145 kJ/ha, equivalent to 18 J/m² of bark. Much higher values have been reported

for other sites at lower altitudes (cf. Craigieburn at 950 m a.s.l.). For a 390 m altitude site in Canterbury, the data in Kelly *et al.* (1992) are equivalent to 125–447 J/m² through one day (assuming average honeydew sugar concentration of 25% w/v). Moller *et al.* (1991, 1996) show standing crops of around 2800 to 8600 J/m² at sites near Nelson. However, there are two obvious reasons for the differences among these values. The first is the high elevation of the Craigieburn site. Honeydew decreases at higher altitudes; Beggs (2001) notes that the insect becomes uncommon above 800 m. The second is that our data are based on randomly selected trees, whereas all other published studies to date use trees selected for carrying honeydew. The most productive individual of our 25 trees had an annual mean standing crop of 83 J/m², nearly five times higher than the mean across all trees.

Although the honeydew energy values at Craigieburn were low, honeydew is still the only carbohydrate source available year round in this montane beech forest and its importance as a bellbird food source should not be underestimated. It is also noteworthy that 'honeydew' bark supports 60% more J/m² of invertebrates than 'normal' bark, so honeydew also increases food supplies for birds indirectly.

Invertebrates

Our estimates of invertebrate abundance were based on samples taken on trunks and foliage at 3 m height. Of course, birds forage at a range of heights including those higher in the canopy, and no single sampling method can replicate the methods that birds use to find invertebrates. However, bellbirds spent the vast majority of their feeding time in these middle levels of the forest which we sampled. Therefore these data do give an indication of potential invertebrate food in the area searched by bellbirds, and seasonal variation in this based on a standardised sampling method.

These results show that invertebrates are a potentially highly valuable food source, especially on bark. Overall, the mean invertebrate energy appeared relatively stable between seasons (Fig. 3), which is similar to the stable seasonal invertebrate abundance described by Clout and Gaze (1984).

Mistletoe fruit and nectar

The energy value of *Peraxilla tetrapetala* fruit and nectar was much greater than for *Alepis flavida* (Fig. 3) due to the higher energy value of *P. tetrapetala* fruits and flowers. On an annual basis the energy value of mistletoe fruit and nectar was generally low, being less than 4% of the total food energy. However, this was mainly due to the limited seasons when these foods were available. In early January, when *P. tetrapetala* nectar was at its peak, it represented 46% of the total

food energy available, but the *P. tetrapetala* flowering season is concentrated into only three weeks of the year. Fortunately for birds, the sequential flowering and fruiting times of the two mistletoe species means that either nectar or fruit are available in varying amounts from early January into June.

Overall comparison of food resources

At first glance the Craigieburn beech forest appears to be a relatively food-impooverished region for bellbirds. The standing crop of honeydew is much smaller than at lower altitudes, there are almost no nectar or fruit sources apart from mistletoe, and, except for the peak in mistletoe nectar in early January, the mistletoe fruit and nectar kJ/ha available is also low. However, it is the abundance of invertebrates, the overlap of the different food resources, and the annual stability of certain foods, that probably contributes to a continued bellbird presence at Craigieburn. The seasonal change in total available food from summer to winter was surprisingly small.

Invertebrates and honeydew are the two food sources that are available throughout the year, and these are potentially key foods for bellbirds. Invertebrates are important because they are present all year and dominate the available food energy, averaging 88% of the total. Honeydew is a key food source because, even though it was a relatively small amount of the total available energy (kJ/ha) for each month, it was the only pure carbohydrate source available for most of the year. Previous studies on bellbird diet have always observed a pure carbohydrate component to the diet (Murphy and Kelly, 2001, and references therein). As in other Meliphagidae this component is usually nectar, but Paton (1980) predicted that a carbohydrate source such as honeydew could be an effective substitute for nectar because of its chemical similarity. This prediction is supported for bellbirds in another beech-dominated habitat (in Nelson) where the only pure carbohydrate component of the bellbird diet was honeydew (Boyd, 1987). At Craigieburn honeydew makes up 22.1% of the annual bellbird diet (Murphy and Kelly, 2001). If bellbirds require a certain amount of pure carbohydrate in their diet then the importance of honeydew at Craigieburn is strengthened: without it a bellbird population might not be sustainable. Moreover, honeydew also apparently increases the available invertebrate food resource.

If energy is the primary determinant of bellbird diet choice, we would expect diet to track the abundance of foods, and the relative preference ratings in Table 5 should be close to one. This is based on the key premise of optimal foraging theory, that an animal's foraging behaviour is determined by energy maximization (Hughes, 1993), within the constraints of nutrient

demands and food availability (Stephens and Krebs, 1986), and other internal and external variables that make up the animal's state (Houston, 1993). In fact, honeydew appeared to be eaten more often, and invertebrates less often, than the measured abundances would predict. However, there are several possible reasons for this. Firstly, invertebrates do not want to be eaten so they are hidden, whereas all the other foods are in plain view. This means that the searching time, prey capture, and perhaps prey handling time would be higher for invertebrates, reducing their value in terms of energy gain per minute foraging. Secondly, the simple sugars in nectar, fruits and honeydew all have high assimilation efficiencies (close to 100%) in a bird's gut, whereas the assimilation efficiency of invertebrates is probably only around 71% (Bell, 1990).

There is another factor that could cause honeydew to be eaten more often than its energy value would suggest. The invertebrate data show that 'honeydew' tree trunks are rich in invertebrates. By moving over tree trunks, bellbirds could simultaneously search for invertebrates and harvest honeydew drops. This combined foraging approach may make it energetically feasible to gather honeydew even when the honeydew is relatively sparse.

In general, mistletoe nectar and fruit were also eaten more often than would be predicted from their relative contributions to total available food (Table 5). Broadly, this could again be partly due to the relative discounting of invertebrates through searching time and lower assimilation efficiency. Mistletoes also differ from both invertebrates and honeydew in being more spatially clumped: the nectar and fruits are held in a few concentrated places. Therefore, bellbird foraging could be more efficient on mistletoe foods once the bird reaches a mistletoe plant. This may also increase their proportion of the bellbird diet when mistletoe fruit and nectar are available.

The time that bellbirds spend foraging on *P. tetrapetala* flowers during the flowering season is also of particular interest for its effects on the pollination success of the mistletoe. In this regard, the data for early January, when the vast majority of *P. tetrapetala* flowers ripen over only a three week period, are of some concern. At this time *P. tetrapetala* nectar makes up 46% of the available food, but only 33% of bellbird foraging observations (Murphy and Kelly, 2001). The birds are spending a lot of time on *P. tetrapetala* flowers, but not enough to provide adequate pollination: Robertson *et al.* (1999) documented pollen limitation at Craigieburn from 1994/95 to 1996/97, and unpublished observations for the 1997/98 season show continuing pollen limitation there. It is not clear why bellbirds spend so much time collecting honeydew even when it is sparse, yet do not devote more attention to *P. tetrapetala* flowers (which must be far more

energetically rewarding) in early January. It may be that many of the bellbirds are collecting invertebrates to feed to nestlings, as breeding at Craigieburn runs from early November into mid February. Another possible factor is that birds need a mixed diet of both carbohydrate for energy, and invertebrates for protein, and the birds may be able to meet their carbohydrate needs in a short time without visiting all flowers. The diet data at first seem to argue against both these hypotheses, because in early January bellbirds were seen to spend 45% of their time on honeydew and only 22% on invertebrates (Murphy and Kelly 2001). However, if the honeydew was collected incidentally while searching for invertebrates, these hypotheses could still be valid. Since in early January *P. tetrapetala* nectar is twelve times more abundant than honeydew, and is also more spatially clumped, it is hard to believe that it would make sense to forage on honeydew simply for the sugar.

Finally, Figure 3 emphasises the short-term character of the *P. tetrapetala* nectar energy resource: although large, it comes like a sudden spike and is gone almost as rapidly. Before human arrival, bird densities were higher, and the *P. tetrapetala* flowers presumably got greater pollination service despite the short season. Now that pollinating birds are less abundant on the mainland, the *P. tetrapetala* flowering season may be too short for the remaining birds to adequately service, and the mutualism is faltering.

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