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FOODS AND FORAGING OF FOREST BIRDS IN TEMPERATE RAINFOREST, SOUTH WESTLAND, NEW ZEALAND

Summary: Habitat use of a forest bird community was studied in temperate rainforests in South Westland, New Zealand between 1983 and 1985. This paper examines foraging methods, feeding stations and seasonal variations in the availability and use of food types and provides a brief review of the subject. The forest bird community was comprised of a large number of apparently generalist feeders and few dietary specialists. However, the degree of foraging specialisation should not be viewed only in relation to the food types consumed. The 18 species studied differed from each other in the number of plant species used, their preferred feeding stations and method of feeding. Most importantly, the omnivorous birds exhibited varying degrees of sequential specialisation in their diets as they switched between specific food sources from season to season. The information on foraging provides the first step towards predicting the impacts of logging important food trees.

Keywords: Forest birds; bird community; temperate rainforest; New Zealand; foods; foraging; habitat use; nectivory; frugivory; insectivory; feeding specialisation.

Introduction

Today wildlife conservation agencies are required to make predictions about the impacts of forest management practices on bird populations and to make specific recommendations on the size and habitat composition of forest reserves. Some knowledge of habitat use and the degree of habitat specialisation or plasticity of the birds is essential if informed predictions are to be made. In 1981 the New Zealand government placed a moratorium on the logging of 600 000 ha of temperate rainforest in South Westland. We began a study aimed at predicting the impacts of logging on the bird community. We studied forest bird distribution patterns in relation to forest type and habitat use between 1983 and 1985 (O'Donnell and Dilks, 1986, 1989a, 1989b).

Evergreen broad-leaved rainforests are characteristic of the southern hemisphere temperate region (Ovington, 1983). Substantial, relatively unmodified tracts are now confined to Tasmania, Chile and New Zealand. Few studies have been made of habitat use by the whole bird community in New Zealand's rainforests although many have been made in tropical rainforests (e.g., Wolf, 1970; Pearson, 1971; Leck, 1972; Croxall, 1977; Foster, 1978; Beehler, 1983) and in temperate northern hemisphere conifer and hardwood forests (e.g., Hartley, 1953; Gibb, 1960; Morse, 1967, 1968; Jackson, 1970; Maurer and Whitmore, 1981; Saether, 1982, 1983). Most studies in New Zealand have dealt with limited aspects of habitat use by single species or small foraging guilds. Atkinson (1964), Merton (1966), McEwan (1978) and Powlesland (1981) looked at use of feeding stations and food types and Gibb (1961) and Gill (1980) studied use of feeding stations and strata used within the forest. The food and foraging behaviour of only two groups of forest birds, the honeyeaters (Meliphagidae), (e.g., McCann, 1952; Merton, 1966; Gravatt, 1970, 1971; Craig, Stewart and Douglas, 1981; Gaze and Fitzgerald, 1982; Gaze and Clout, 1983; Stewart and Craig, 1985; Bergquist, 1987) and common insectivorous species (e.g., Gibb, 1961; Gill, 1980; Moeed and Fitzgerald, 1982), have been studied. Recently, more detailed studies of the foraging behaviour of single species have been undertaken, for example, Hay (1981), Powlesland (1987) and Best and Bellingham (1990) on kokako (*Callaeas cinerea*), Read (1988a, 1988b) on yellowhead (*Mohoua ochrocephala*), Beggs (1988) and Beggs and Wilson (1987) on kaka (*Nestor meridionalis*) and Clout *et al.* (1986) on New Zealand pigeon (*Hemiphaga novaeseelandiae*).

This paper examines aspects of habitat use by the South Westland bird community by describing foraging methods, strata used within the forest, and seasonal variations in the use of food types, and

discusses the degree of habitat-use specialisation evident in the community and its implications for predicting the impacts of forest logging.

Study area

The study was centred on the Windbag Valley area, South Westland, in the South Island of New Zealand (43° 45'S: 169° 24'E: N.Z. Map Series 1, S77 and S78). The Windbag is an inland montane valley which rises from flats and gentle slopes from 25 m a.s.l. through sloping glacial terraces to 200-500 m and then steep slopes through to the bushline at 1100 m. Rainfall is high, averaging 5280 mm yr^{-1} with up to 6000 mm yr^{-1}, and the climate is mild, mean monthly temperatures ranging between 8 and 18°C through the year.

This area was chosen because it included all major forest types representative of South Westland (O'Donnell and Dilks, 1986). The area is a mosaic of podocarp-hardwood and silver beech (*Nothofagus menziesii*[1]) forests. Kahikatea (*Dacrycarpus dacrydioides*) is common on an outwash plain at the northern end of the valley and as an emergent over silver beech along the valley floor. Forests on the glacial terraces are mixed podocarp-hardwood with a high density of rimu (*Dacrydium cupressinum*). On the lower slopes, kamahi (*Weinmannia racemosa*) is dominant with occasional large emergent rimu. At mid-altitudes the forest consists of southern rata (*Metrosideros umbellata*), and this merges into silver beech at higher altitudes. Silver beech extends to low altitudes along stream sides and alluvial fans.

Methods

Plant phenology

The timing and duration of flowering and fruiting of forest plants was recorded to monitor the seasonal variation in food availability between October 1984 and December 1985 (referred to as 1984-85 in text). Subjective estimates of flowering and fruiting intensity were made:

(1) rare	low intensity, flowering/fruiting on only a few individual plants;
(2) occasional	flowering/fruiting widespread but not heavy; often at the beginning or end of a cycle;
(3) heavy	large amounts of ripe fruit or flowers, usually present on most reproductive individuals.

[1] Plant nomenclature follows Allan (1961), Moore and Edgar (1970), and Connor and Edgar (1987).

Casual observations of flowering and fruiting had been made during the previous year, October 1983-September 1984. Anecdotal information was collected on presence of seeds, seed fall and development of leaf buds and leaf burst.

Habitat use sampling

Observations were made between October 1983 and December 1985. Eight transects, between 1.0 and 2.5 km long, were spaced throughout the study area, and covered the range of forest types, altitudes and landforms. The transects were walked daily for 10 days every two months. Four transects were usually walked each day by one of four different observers. Routes were alternated so that all transects were sampled evenly by all four observers. Habitat use was recorded by instantaneous sampling (Altmann, 1974; O'Donnell and Dilks, 1988). The observers walked slowly (<0.5 km hr^{-1}), searching for birds. When an individual or group was encountered a standardised observation was made that described the activity and precise position of the bird(s) within the forest structure (see below). If the bird could be followed, four further observations were made at one minute intervals, giving a maximum of five observations per bird. Plant species, foraging activity, food type, and level within the forest were recorded as part of each observation. A total of 47 856 observations of birds feeding was collected. Foraging observations were classed according to O'Donnell and Dilks (1988).

Plant species

Eighty-one species of vascular plants and ferns were grouped into 56 plant taxa. The identity of individual plant species was recorded except for the following groups: standing dead trees, windthrown trees, small-leaved *Coprosma* spp., tree ferns, ground ferns, *Rubus* spp., *Astelia* spp., mistletoe (*Peraxilla* spp.), and epiphytic orchids.

Foraging activity

(a) glean	searching for and taking food from the surface of a substrate when the bird is not on the wing;
(b) hawk	searching for and taking food when both prey and bird are in flight;
(c) hover	searching for and taking food when the prey is on the substrate and the bird is in flight;
(d) probe	penetrating into the substrate while searching for prey, most commonly in soil, litter or rotting wood;

(e) rip ripping the substrate and exposing another surface;
(f) scan use of a vantage point to look for prey where the bird stops, looks and flies to another perch if no prey are sighted.

Food type

Foods were classed as flower/nectar, fruit, honey dew, invertebrate (confirmed), invertebrate (probable), leaf/bud, lichen, moss, sap, seed, vertebrate, and wood. A category "unknown food type" was used when foods were not identified definitely.

Level within the forest (stratum)

A measure of the vegetation level the bird was using within the forest: ground, lower understorey, upper understorey, shaded (within) canopy, unshaded (on top of) canopy, in emergent trees, and above canopy in flight. It was not possible to assign specific height ranges to each stratum because the height of each depended on the forest type and structure.

Study species

Observations were collected for all 18 native and seven introduced bird species present in the study area. Results are presented for only 18 species because sample sizes for seven species (N.Z. falcon: *Falco novaeseelandiae*[2], Australasian harrier: *Circus approximans*, morepork: *Ninox novaeseelandiae*, shining cuckoo: *Chrysococcyx lucidus,* long-tailed cuckoo: *Eudynamys taitensis*, dunnock: *Prunella modularis* and song thrush: *Turdus philomelos*), were considered insufficient to analyse.

Analysis

Feeding observations were sorted into frequency tables for each bird species using SAS (registered software of the SAS Institute, North Carolina, U.S.A.). The use of food types was sorted for the entire year and for six sampling periods: February-March, April-May, June-July, August-September, October-November, and December-January. The Chi^2 test of independence was used to identify variability between seasonal foraging patterns where appropriate.

[2] Bird nomenclature follows Turbott (1990).

Results

Phenology of flowering and fruiting

Most plants flowered during spring and summer in 1984-85 (September to March) with a peak from October to December (Fig. 1). Flowers were available for more limited periods than were fruit and seeds, and their nectar represented a huge source of energy. Major nectar sources were kamahi, southern rata, vine rata (*Metrosideros fulgens*) and fuchsia (*Fuchsia excorticata*). Vine rata had the most prolonged flowering period and was the only nectar source available over the whole year, although flowering intensity was greatest between April and September (Fig. 1). Fuchsia had the second longest flowering period of all the species monitored (five months).

Flowering patterns were markedly different during the previous year (October 1983 - September 1984). The intensity and duration of flowering appeared to be greater in many species. For example, southern rata flowered heavily and flowers were found over eight months (October 1983 - May 1984) compared with only three months (December 1984 - February 1985) the following year. Kamahi also flowered between October 1983 and May 1984 compared with only five months the following year. Some shrubs and vines flowered for 1-2 months longer in 1983-84 than 1984-85; e.g., *Pennantia, Rubus, Muehlenbeckia, Clematis, Melicytus*, and *Plagianthus*. A notable exception was the flowering of mistletoes; scarlet mistletoe (*Peraxilla tetrapetala*) did not flower at all in summer 1983-84 and red mistletoe (*P. colensoi*) flowered only lightly. During summer 1984-85 both species flowered heavily with scarlet mistletoe (confined to higher altitudes) peaking about one month before the more widespread red mistletoe.

Most plants carried ripe fruit in autumn and throughout winter in 1984-85 (Fig. 2), with the largest amount of fruit present in April. Three species had fruits available over the whole year; *Coprosma foetidissima, Hedycarya arborea*, and *Ripogonum scandens*.

Some differences in the intensity and duration of fruiting were observed between the two years. For example, rimu had considerably more fruit in 1983-84 but the crop was available for a shorter period (six months). Ripe miro fruit was present for 12 months between October 1983 and September 1984 compared with nine months the following season when the crop was clearly heavier (*pers. obs.*). Kahikatea did not fruit at all in 1983-84. Almost all shrub hardwoods had fruit in both years. However, in 1983-84 many high altitude shrubs (*Coprosma astonii, C. pseudocuneata, Griselinia*

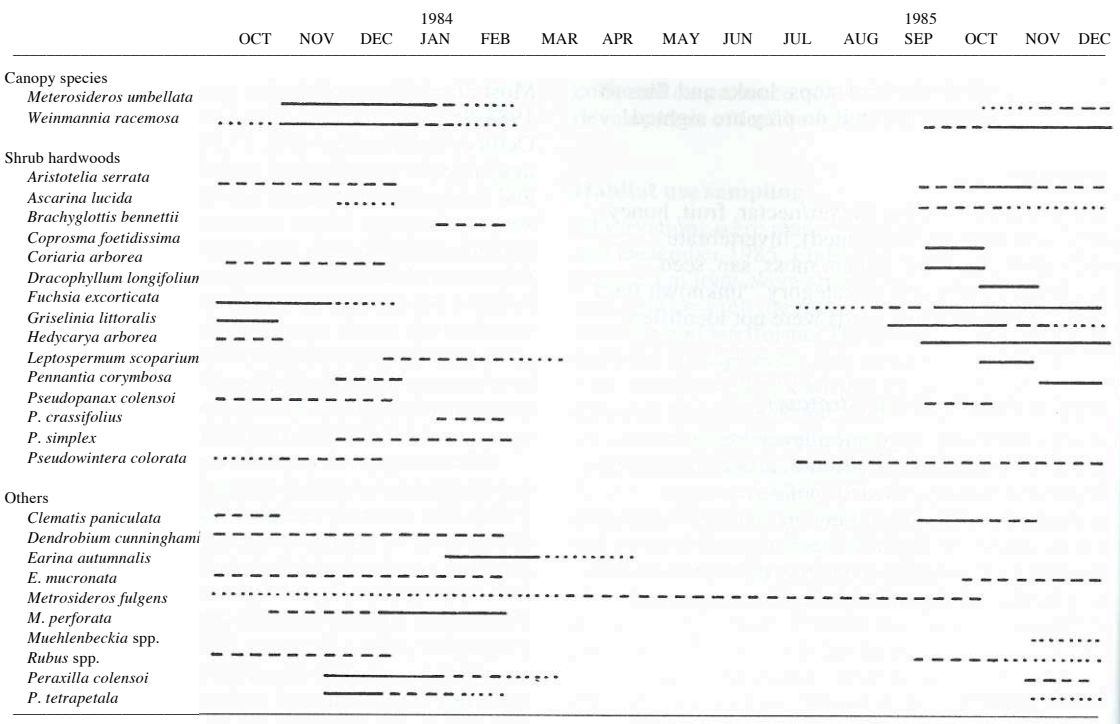

Figure 1. *Duration and intensity of flowering in South Westland forest plants, October 1984-December 1985. Key: rare (•••••••), occasional (— — — —), heavy (————).*

littoralis, Myrsine divaricata, Pseudopanax edgerleyi, P. simplex, P. colensoi, and *Pseudowintera colorata*) had very little fruit compared with the following year.

Several canopy trees retained seeds in the foliage after the fleshy part of the fruits had disappeared. Rimu seed remained attached to foliage tips but the heavier seeds of kahikatea fell. Some of the infertile, brown rimu seeds were still present on trees in December, seven months after the peak crop. Silver beech seeds were present in autumn and winter in 1985 but little seed was present during the previous year. Seeds remained available to birds after they had fallen, either by being caught in moss on large branches, or after dropping to the ground.

Foods and foraging behaviour

Pigeons (Columbidae)

The sole representative of this family, the New Zealand pigeon, primarily ate foliage and fruit. Pigeons fed almost entirely by gleaning in the upper storeys (Figs. 3, 4) in 36 plant species groups (Table 1). Overall, 72% of foods were fruit, 16% of the diet was unidentified, and 10% were leaves and buds (Table 2). Fruit use varied significantly through the year ($P<0.001$). Fruit dominated the diet in all months except October but was most important in autumn and winter (February-August) (Fig. 5). Leaves were eaten in all months but use varied significantly between months ($P<0.001$), increasing in importance from 2% of the diet in June to nearly 20% in August and 75% in October. Leaves became less important again when fuchsia fruits became available in December (Fig. 5).

New Zealand pigeons consumed flowers from five plant species groups (Table 3). Flowers formed a small proportion of the diet, and were swallowed whole rather than used for their nectar (Table 3). They ate fruit from 21 plant groups (Table 4), the most important being canopy and emergent podocarps: rimu (41% of fruit feeding observations), miro (30%) and kahikatea (7%). While some podocarp fruit was available throughout the year it was mostly used between February and July. In winter, once the majority of podocarp fruiting had finished, pigeons moved to higher altitudes to feed on fruit of *Pseudopanax*

Table 1: *Plant species groups used for feeding by forest birds in South Westland (% of total feeding observations for each bird species). Key: - = zero observations; PIG = pigeon; KAK = kaka; KEA = kea; YCP = yellow-crowned parakeet; RIF = rifleman; CRE = brown creeper; WAR = grey warbler; YEL = yellowhead; TIT = tit; FAN = fantail; BLA = blackbird; SIL = silvereye; BEL = bellbird; TUI = tui; GOL = goldfinch; GRE = greenfinch; RED = redpoll; CHA = chaffinch. 1* = Cyathea smithii *and* Dicksonia squarrosa*; 2* = Astelia fragrans, A. grandis *and* A. nervosa*; 3* = Asplenium bulbiferum, Blechnum capense, B. discolor *and* Sticherus cunninghamii*; 4* = Dendrobium cunninghamii, Earina autumnalis *and* E. cunninghamii*; 5* = Peraxilla colensoi *and* P. tetrapetala*; 6* = Rubus cissoides *and* R. schmidelioides.

No. of observations	PIG 2339	KAK 3180	KEA 233	YCP 579	RIF 2078	CRE 2353	WAR 6997	YEL 712	TIT 7109	FAN 5161	BLA 247	SIL 9708	BEL 4270	TUI 695	GOL 987	GRE 79	RED 432	CHA 659
CANOPY SPECIES																		
Dacrydium cupressinum	2.8	14.8	12.0	45.9	1.5	9.6	9.1	-	5.6	8.0	15.8	14.3	10.4	17.7	44.2	15.7	51.9	57.8
Dacrycarpus dacrydioides	5.3	-	0.9	1.7	1.1	3.3	2.7	-	2.0	1.2	2.8	3.7	1.9	2.3	4.4	-	2.5	3.0
Dead tree (various)	-	10.3	20.6	0.2	2.2	0.2	0.3	6.5	5.0	1.8	4.5	0.6	0.6	-	-	0.7	-	0.2
Elaeocarpus hookerianus	-	-	-	0.4	0.1	0.4	0.2	-	0.4	0.2	1.6	0.4	0.3	-	-	-	-	-
Lagarostrobos colensoi	1.2	-	-	1.4	-	0.9	0.2	-	0.5	0.1	-	0.4	0.2	0.1	0.9	-	-	0.8
Libocedrus bidwillii	-	-	-	-	-	-	<0.1	-	0.1	-	-	-	0.1	-	-	-	-	-
Meterosideros umbellata	-	11.5	40.8	3.8	5.9	2.6	1.8	-	1.5	1.9	-	3.3	10.9	16.0	-	-	-	0.5
Nothofagus menziesii	2.6	23.1	13.3	24.0	44.5	47.3	21.4	74.7	15.5	9.2	5.7	11.9	10.0	13.2	37.3	70.9	7.6	13.7
Podocarpus hallii	-	4.2	-	7.1	2.1	1.6	0.9	-	1.1	0.7	2.0	0.6	2.0	0.4	-	-	-	0.2
P. totara	-	-	-	1.4	-	0.9	0.1	-	0.3	0.1	-	0.1	0.1	0.6	-	-	-	-
Prumnopitys ferruginea	23.1	2.4	0.9	1.2	0.4	1.2	4.6	-	3.6	3.2	2.8	2.2	2.2	0.7	-	-	-	1.8
P. taxifolia	0.1	0.1	-	-	-	-	<0.1	-	0.1	-	-	<0.1	0.1	-	-	-	-	-
Weinmannia racemosa	0.4	19.1	1.7	9.2	25.1	19.0	35.2	-	21.9	14.7	3.6	23.3	33.2	11.8	13.0	0.7	2.5	3.2
SHRUB HARDWOODS																		
Aristotelia serrata	0.9	0.2	-	-	-	0.3	0.4	0.6	0.5	0.2	0.8	1.3	0.4	0.4	-	-	-	0.2
Ascarina lucida	-	-	-	1.0	-	<0.1	0.6	-	1.8	1.2	1.2	2.3	2.0	-	-	-	-	-
Carpodetus serratus	0.1	0.1	-	-	-	<0.1	0.3	-	0.2	0.1	2.4	1.0	0.3	2.7	-	-	-	-
Coprosma spp.	0.3	-	-	-	0.9	0.3	1.0	-	2.1	0.4	0.4	0.8	1.0	-	-	-	-	-
C. foetidissima	0.3	0.2	0.4	0.2	0.1	0.1	0.3	-	0.5	0.5	-	0.4	0.9	-	-	-	1.3	0.2
C. lucida	-	-	-	-	0.1	-	<0.1	-	<0.1	<0.1	-	0.1	0.1	0.7	-	-	-	-
C. rotundifolia	0.6	-	0.4	-	-	0.1	0.2	-	0.3	0.1	-	0.5	0.4	-	-	-	-	-
Coriaria arborea	0.4	-	-	-	-	-	<0.1	-	0.1	<0.1	1.6	0.8	0.1	1.4	-	-	-	0.2
Fuchsia excorticata	3.3	2.0	0.9	-	0.4	0.1	0.6	0.8	1.8	0.5	5.7	6.0	9.7	16.7	-	-	-	-
Griselinia littoralis	0.4	0.3	-	-	2.6	2.8	1.2	0.8	1.6	0.5	2.0	2.3	0.8	-	-	0.1	-	-
Hebe spp.	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-
Hedycarya arborea	2.2	1.0	-	-	0.1	0.2	0.7	0.1	0.5	0.5	0.4	0.8	0.3	0.3	-	-	-	-
Hoheria glabrata	0.6	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Leptospermum scoparium	-	-	-	-	-	-	<0.1	-	0.1	-	-	<0.1	-	-	-	-	-	-
Melicytus ramiflorus	0.5	0.2	-	-	0.1	<0.1	0.1	-	0.3	0.2	0.4	1.3	0.2	-	-	-	-	-
Myrsine australis	<0.1	0.2	-	-	0.1	-	0.3	-	0.4	0.2	-	0.3	0.5	0.1	-	-	-	-
M. divaricata	-	-	-	-	0.1	<0.1	0.1	-	0.8	0.2	-	0.5	0.4	-	-	-	-	-
Neomyrtus pedunculata	-	-	-	-	-	<0.1	0.8	-	2.1	0.5	0.4	0.9	0.8	-	-	-	-	-
Olearia spp.	-	-	-	-	0.1	-	<0.1	-	0.1	-	-	0.1	-	-	-	-	-	-
Pennantia corymbosa	0.2	-	-	-	-	-	0.1	-	<0.1	-	-	0.4	0.1	-	-	-	-	-
Phyllocladus aspleniifolius	-	-	-	1.4	-	0.9	1.0	-	1.5	1.0	-	1.2	0.8	-	0.2	-	-	0.3
Pseudopanax colensoi	-	-	-	-	-	0.1	0.1	-	0.1	0.2	0.4	0.2	0.1	-	-	-	-	-
P. crassifolius	2.7	0.9	-	0.7	0.5	2.3	1.0	-	2.4	0.9	2.8	3.5	1.5	0.1	-	-	1.3	1.5
P. edgerleyi	0.9	0.1	-	-	0.5	0.4	0.3	-	0.3	0.4	-	0.4	0.2	1.0	-	-	-	-
P. simplex	3.0	0.1	-	-	2.1	1.9	0.7	0.6	0.9	0.6	2.8	1.5	0.3	0.6	-	-	-	0.2
Pseudowintera colorata	1.5	-	-	-	2.4	1.4	1.7	2.4	2.0	1.0	0.4	0.8	0.7	-	-	-	-	0.2
Shefflera digitata	0.8	0.3	-	-	0.1	-	0.2	-	0.4	0.2	-	1.5	0.3	0.1	-	-	-	-
Treefern spp.[1]	0.2	<0.1	0.4	-	1.1	0.3	4.2	-	9.9	4.0	-	2.7	1.0	-	-	-	-	0.6
OTHERS																		
Astelia spp.[2]	-	-	-	-	-	-	-	-	0.1	<0.1	0.8	<0.1	<0.1	-	-	-	-	-
Cordyline indivisa	-	-	-	-	-	-	-	-	-	-	-	<0.1	-	-	-	-	-	-
Clematis paniculata	-	-	-	-	-	-	-	-	-	-	-	<0.1	-	-	-	-	-	-
Ferns[3]	0.1	0.1	2.2	-	1.4	0.1	0.8	0.6	0.6	0.8	2.4	0.3	0.1	0.3	-	0.2	3.8	0.6
Freycinetia baueriana	-	0.1	-	-	-	0.3	0.2	-	0.5	0.5	0.4	0.8	0.3	-	-	-	-	-
Lichens	-	-	-	-	0.2	-	-	-	<0.1	-	0.4	0.2	-	-	-	0.1	-	0.2
Metrosideros spp.	<0.1	1.4	0.4	1.2	0.1	0.8	3.4	-	2.0	1.7	-	2.3	10.9	6.3	-	0.2	-	0.3
Mosses	0.3	0.4	1.3	0.4	2.3	0.4	0.3	10.0	0.5	1.1	5.3	1.1	0.4	-	-	3.7	13.9	3.0
Muehlenbeckia australis	1.9	0.2	-	-	-	<0.1	0.1	-	0.2	0.2	-	0.1	<0.1	0.1	-	-	-	-
Nertera sp.	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Orchids[4]	1.0	0.4	-	-	-	<0.1	0.1	-	0.1	0.1	-	0.2	0.1	-	-	-	-	-
Parsonsia sp.	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Peraxilla spp.[5]	0.1	6.0	-	-	-	0.2	<0.1	2.0	0.1	-	1.6	2.9	0.6	1.2	-	7.5	-	0.8
Phormium tenax	-	-	-	-	-	-	-	-	-	<0.1	-	-	-	-	-	-	-	-
Ripogonum scandens	1.0	0.2	-	-	0.1	0.1	1.0	-	3.6	1.9	0.8	1.0	0.7	0.3	-	-	-	0.3
Rubus spp.[6]	<0.1	0.2	-	-	0.1	<0.1	0.3	-	0.6	0.4	-	0.8	0.1	-	-	-	-	-
Uncinia	-	-	-	-	-	-	<0.1	-	<0.1	-	-	<0.1	-	-	-	-	-	-
NOT IN PLANTS																		
Ground feeding	0.4	0.1	3.9	1.0	1.0	0.2	0.2	1.4	2.1	1.7	28.3	0.3	0.2	-	-	6.5	7.6	10.5
Aerial feeding	<0.1	<0.1	-	-	0.1	-	1.8	-	1.1	38.0	-	<0.1	1.5	4.6	0.6	5.1	-	-

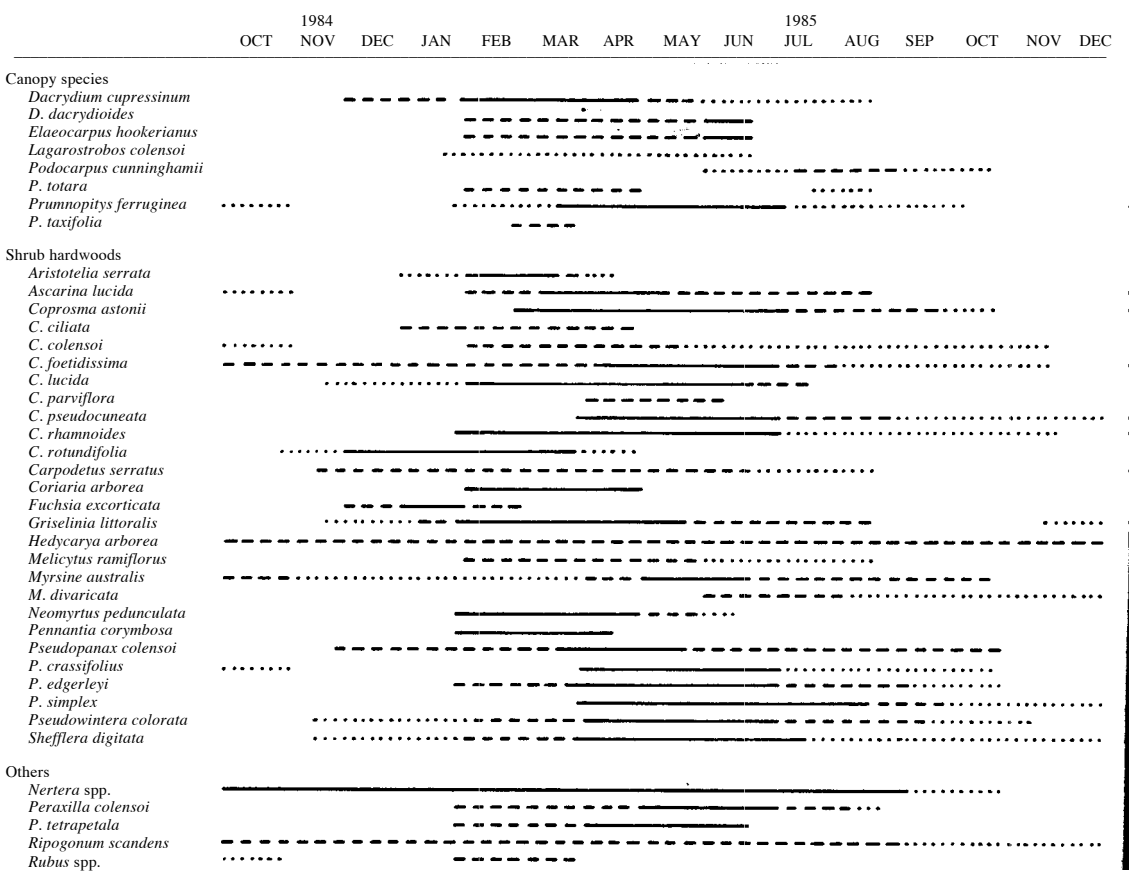

Figure 2. *Duration and intensity of fruiting in South Westland forest plants, October 1984-December 1985. Key: rare (•••••••), occasional (— — — —), heavy (————).*

spp. and horopito (*Pseudowintera colorata*). Supplejack (*Ripogonum scandens*) and pigeonwood (*Hedycarya arborea*) were used heavily throughout the year as was fuchsia in the summer.

Leaves were eaten from 20 species of both canopy and understorey plants (Table 5) mainly when new growth was available. The most important species were rimu (28% of leaf feeding observations), *Muehlenbeckia* spp. (19%), *Pseudopanax* spp. (11%), silver beech (9%), *Coprosma rotundifolia* (7%) and *Plagianthus betulinus* (6%). Other minor elements in the diet included developing rimu seeds and the fruiting bodies of galls (*Cyttaria*) from silver beech (Table 2).

Parrots (Psittacidae)

Parrots were represented in the study area by two large species, the kaka and kea (*Nestor notabilis*), and the smaller yellow-crowned parakeet (*Cyanoramphus auriceps*). These parrots used a variety of foraging techniques (Fig. 3) while feeding mainly in the upper forest storeys (Fig. 4). Most notable was their specialised ripping behaviour, in which they ripped bark from branches and trunks exposing galleries of larval beetles. Kaka also made sap-feeding holes in tree trunks by using their lower mandible to prise a "trapdoor" through the outer bark and to gouge tiny holes into the superficial layer of the cambium (O'Donnell and Dilks, 1989a). Kaka and kea used different methods of nectar gleaning; while kaka took nectar with the aid of a specialised "brush tongue" and left the flower intact, the kea crushed the flower, presumably to obtain the nectar.

The largest identified components of the kaka diet were invertebrates (15%), nectar (12%), fruits (8%), seeds (6%) and sap (3%). Food types varied

Table 2: *Food types of forest birds in South Westland (percent of observed diet). Key: n = number of feeding observations; - = zero observations; Inv = invertebrate; Inv? = probable invertebrate.*

	n	Inv	Inv?	Nectar	Honey-dew	Sap	Fruit	Leaf/ Bud	Seed	Moss	Lichen	Wood	Gall	Unknown
Pigeon	2339	-	-	1.3	-	-	72.3	10.0	0.3	-	-	-	0.2	15.5
Kaka	3180	14.7	54.3	12.1	0.1	2.8	7.6	1.1	6.0	0.2	<0.1	0.4	-	-
Kea	233	12.5	32.2	37.8	-	-	-	4.3	9.4	3.4	-	0.4	-	-
Parakeet	579	-	-	-	-	-	11.4	1.7	13.5	-	-	-	-	72.7
Rifleman	2073	18.4	80.6	-	-	-	0.7	-	-	-	-	-	-	-
Brown creeper	2353	17.2	80.7	<0.1	-	-	0.5	-	-	-	-	-	-	-
Grey warbler	6997	12.1	86.5	-	-	-	0.2	-	-	-	-	-	-	-
Yellowhead	712	16.7	81.6	0.8	-	-	0.4	-	-	-	-	-	-	-
Tit	7109	9.1	89.1	-	-	-	0.3	-	-	-	-	-	-	-
Fantail	5161	13.1	85.4	<0.1	-	-	0.3	-	-	-	-	-	-	-
Blackbird	247	1.6	-	-	-	-	25.5	-	-	-	-	-	-	72.1
Silvereye	9708	8.1	73.2	7.6	<0.1	-	10.5	<0.1	0.1	<0.1	<0.1	-	-	-
Bellbird	4270	10.2	64.6	14.7	3.5	-	6.5	<0.1	-	-	-	-	-	-
Tui	695	5.3	-	41.3	3.2	-	14.1	-	-	-	-	-	-	35.1
Goldfinch	987	7.1	-	-	-	-	-	-	6.2	-	-	-	-	86.6
Greenfinch	79	17.7	-	-	-	-	-	-	21.5	-	-	-	-	60.8
Redpoll	432	-	-	-	-	-	2.1	-	8.6	-	-	-	-	87.5
Chaffinch	659	6.7	-	-	-	-	2.0	-	33.7	-	-	-	-	56.8

Table 3: *Plant species groups used for flower feeding by forest birds in South Westland (% of total flower feeding observations for each bird species). Key: - = zero observations. 1* = Metrosideros fulgens, M. perforata *and* M. diffusa*; 2* = Peraxilla colensoi *and* P. tetrapetala*; 3* = Rubus cissoides *and* R. schmidelioides.

	Pigeon	Kaka	Kea	Brown Creeper	Yellow-head	Fantail	Silvereye	Bellbird	Tui
Number of observations	31	385	88	1	6	2	735	605	287
Canopy species									
Dacrydium cupressinum	-	-	-	-	-	-	1.4	-	-
Metrosideros umbellata	-	28.1	97.7	-	-	-	24.4	25.1	32.8
Nothofagus menziesii	-	2.3	-	-	-	-	1.4	-	-
Podocarpus hallii	-	2.3	-	-	-	-	-	-	-
Weinmannia racemosa	-	2.9	-	-	-	-	6.8	1.3	3.8
Shrub hardwoods									
Coprosma foetidissima	6.5	-	-	-	-	-	0.3	-	-
C. rotundifolia	-	-	-	-	-	50.0	-	-	-
Coriaria arborea	-	-	-	-	-	-	-	-	3.5
Fuchsia excorticata	36.6	13.3	2.3	-	-	50.0	53.3	54.7	40.4
Hedycarya arborea	-	-	-	-	-	-	-	-	0.4
Melicytus ramiflorus	-	-	-	-	-	-	0.5	-	-
Pennantia corymbosa	-	-	-	-	-	-	0.1	-	-
Pseudopanax colensoi	-	-	-	-	-	-	1.1	-	-
P. crassifolius	-	-	-	-	-	-	1.6	2.0	2.1
P. simplex	-	-	-	100.0	-	-	-	0.2	-
Pseudowintera colorata	-	-	-	-	-	-	-	0.2	-
Shefflera digitata	-	-	-	-	-	-	-	0.7	-
Others									
Clematis paniculata	-	-	-	-	-	-	0.5	-	-
Earina autumnalis		45.2	1.3	-	-	-	-	0.5	- -
Freycinetia baueriana	-	-	-	-	-	-	-	0.7	-
Metrosideros spp.[1]	-	3.1	-	-	-	-	6.8	11.9	13.9
Peraxilla spp.[2]	9.7	46.0	-	-	100.0	-	1.2	3.3	2.8
Rubus spp.[3]	3.2	-	-	-	-	-	-	-	-

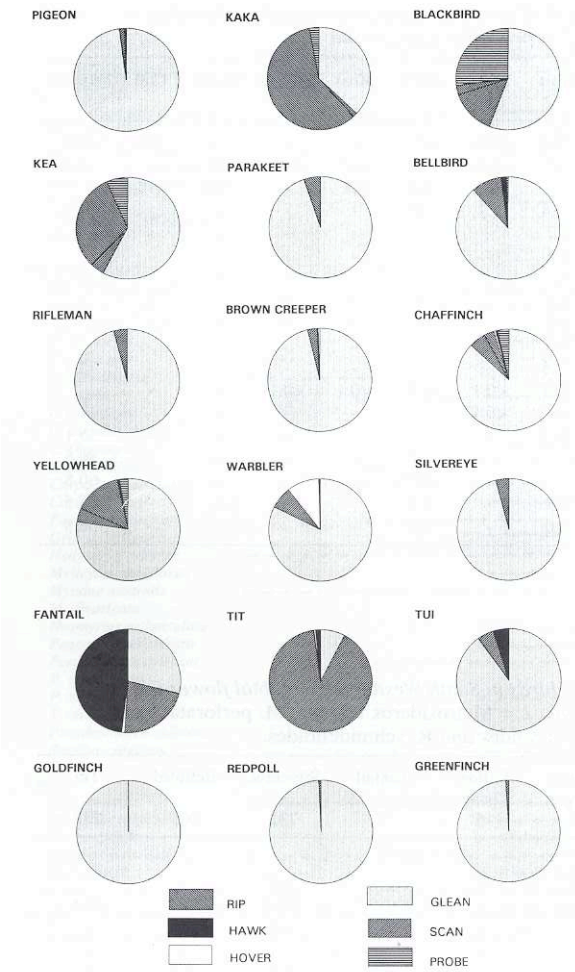

Figure 3. *Foraging methods of South Westland forest birds (for sample sizes see Table 1).*

markedly from season to season (Fig. 5). Use of fruit and seeds (P<0.001) and invertebrates and leaves (P<0.005) varied significantly through the year. Nectar was most important during spring and summer (October-February) and represented *c*. 25% of the diet in December, but no kaka were seen consuming nectar in the April-May and August-September sampling periods. Fruit was important in autumn and winter, being most prominent in April (*c*. 20%). Seeds were taken in all months except October and were most important in winter (June-August). Kaka fed on sap mainly in late winter-early spring with most observations in August. The minor items, honeydew, wood, leaf, lichen and moss, were consumed in most sampling periods. Kaka fed on honeydew from kamahi and rata. They ate wood on standing dead trees, taking soft, moist white decaying wood, possibly because of the food value of fungal mycelia or fruiting bodies. Much of the surface gleaning by kaka was for invertebrates, but in some cases it was possible that birds were feeding on other foods such as fungus, honeydew or seeds which had been caught in bark or moss.

Kaka used 29 plant species groups, 19 as sites for feeding on invertebrates, 10 for fruit, six for leaves and eight for nectar (Tables 1-6). Nearly 95% of kaka observations were on only six canopy species (rimu, southern rata, silver beech, Hall's totara: *Podocarpus hallii*, miro: *Prumnopitys ferruginea*, kamahi) and dead trees, and on parasitic mistletoes growing on silver beech and fuchsia (Table 1). In January 1984 *c*. 70% of feeding observations were on red and scarlet mistletoes and overall they provided 46% of nectar foods (Table 3). Seasonal use of plant species changed as food availability changed. Silver beech and kamahi were the most important species providing a wide range of foods throughout the year. Rimu was of secondary importance overall, but was vital during autumn and winter, providing 51% of fruit foods and 82% of seeds. *Metrosideros* spp. were the major nectar sources (31% overall) and provided 60% of observed foods in summer 1983-84.

Important foods for kea in the forest were nectar (38%), invertebrates (13%) and seeds (9%) (Table 2). However, too few food items were identified in autumn and winter to make definitive statements about how the diet varied with season (Fig. 5). The few kea observations in some seasons probably resulted from the birds moving out of the forest and into the alpine zone to feed (*pers. obs.*), rather than from their being inconspicuous in those months. In the forest nectar-feeding was important in December and February when it represented *c*. 45% and 60% of the diet respectively. Leaves and moss were important items in April and October, and seeds were eaten in December. Like kaka, kea fed on soft decaying wood tissues.

Kea fed from 14 plant species groups, the most important overall being southern rata (41% of feeding observations), silver beech (13%), rimu (12%) and standing dead and wind-thrown trees (21%) (Table 1). Shrubs were used seasonally for leaves and flowers. Rata was important for its nectar, representing the source of 98% of nectar-feeding observations in summer. The only seeds eaten were rimu. Dead trees were important for invertebrates (site of 53% of confirmed observations of feeding on invertebrates).

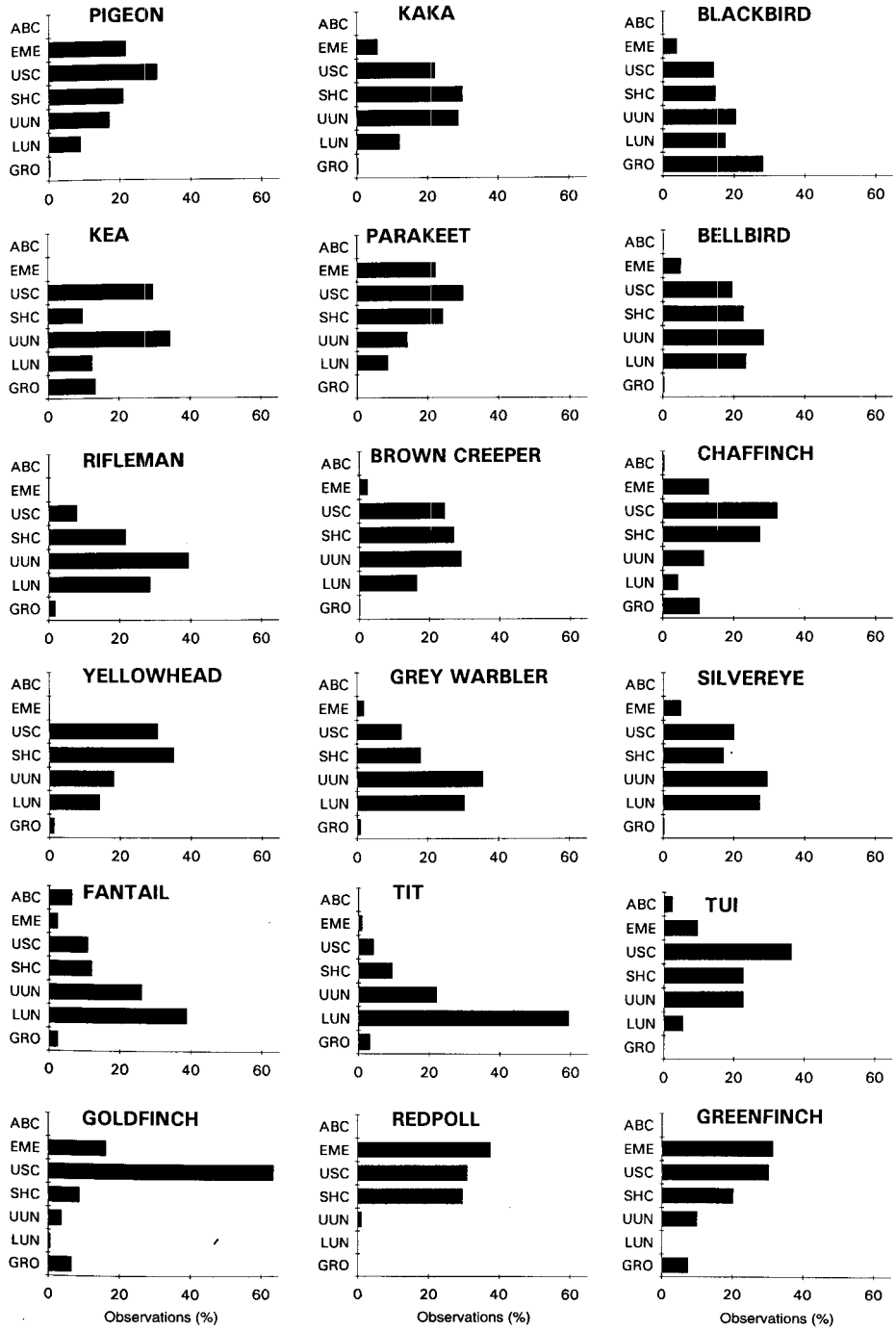

Figure 4. *Foraging levels utilised by South Westland forest birds (for sample sizes see Table 1). Foraging levels: ABC = above canopy, EME = emergent leaves, USC = unshaded canopy, SHC = shaded canopy, UUN = upper understorey, LUN = lower understorey, GRO = ground.*

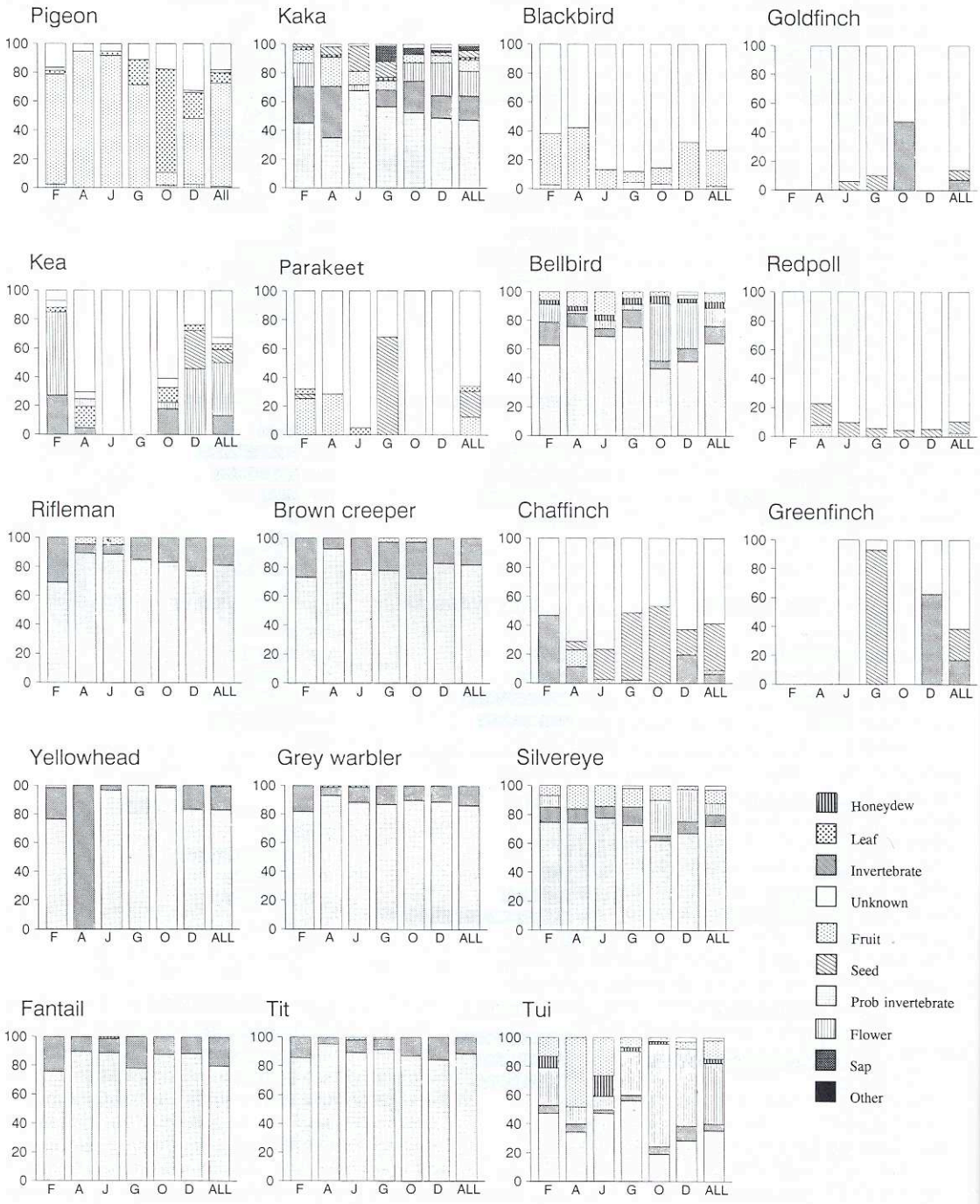

Figure 5. *Seasonal variation in the observed diets of forest birds in South Westland, 1983-1985. (Sample sizes given above each bar. F=February-March, A=April-May, J=June-July, G=August-September, O=October-November, D=December-January, All=Sum of all months combined).*

Table 4: *Plant species groups used for fruit feeding by forest birds in South Westland (% of total fruit feeding observations for each bird species). Key: - = zero observations; PIG = pigeon; KAK = kaka; YCP = yellow-crowned parakeet; RIF = rifleman; CRE = brown creeper; WAR = grey warbler; YEL = yellowhead; TIT = tit; FAN = fantail; BLA = blackbird; SIL = silvereye; BEL = bellbird; TUI = tui; RED = redpoll; CHA = chaffinch; 1* = Coprosma astonii, C. pseudocuneata *and* C. rhamnoides*; 2* = Peraxilla colensoi *and* P. tetrapetala*; 3* = Rubus cissoides *and* R. schmidelioides.

Number of observations	PIG 1691	KAK 243	YCP 66	RIF 14	CRE 12	WAR 17	YEL 3	TIT 22	FAN 13	BLA 63	SIL 1019	BEL 278	TUI 98	RED 9	CHA 13
CANOPY SPECIES															
Dacrydium cupressinum	40.7	50.6	80.3	-	-	5.9	-	4.6	-	23.8	17.2	30.9	63.3	100.0	15.4
Dacrycarpus dacrydioides	6.2	-	-	-	16.7	-	-	-	-	-	2.7	3.6	4.1	-	-
Elaeocarpus hookerianus	-	-	-	-	-	-	-	-	-	-	-	2.2	-	-	-
Podocarpus hallii	-	17.7	18.2	-	-	-	-	-	-	-	0.2	0.7	-	-	-
P. totara	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-
Prumnopitys ferruginea	30.3	9.9	-	-	-	-	-	-	-	7.9	-	1.1	2.0	-	-
P. taxifolia	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SHRUB HARDWOODS															
Aristotelia serrata	1.2	-	-	-	-	-	-	-	-	3.2	4.5	1.4	-	-	-
Ascarina lucida	-	-	-	-	-	-	-	31.8	61.5	-	12.5	6.8	-	-	-
Carpodetus serratus	-	0.8	-	-	-	-	-	-	-	7.9	0.6	0.3	17.4	-	-
Coprosma spp.[1]	0.3	-	-	-	8.3	-	-	4.6	-	-	2.5	9.4	-	-	-
C. foetidissima	0.3	2.9	1.5	-	-	-	-	-	7.7	-	0.8	7.9	-	-	-
C. lucida	-	-	-	-	-	-	-	-	-	-	-	0.4	5.1	-	-
C. rotundifolia	-	-	-	-	-	-	-	-	-	-	1.0	4.0	-	-	-
Coriaria arborea	0.6	-	-	-	-	-	-	-	-	3.2	2.9	0.7	-	-	-
Fuchsia excorticata	3.1	-	-	-	-	-	-	-	15.4	22.2	1.1	1.4	-	-	-
Griselinia littoralis	0.3	-	-	-	-	5.9	100.0	-	-	3.2	22.0	0.7	-	-	-
Hedycarya arborea	3.1	4.9	-	-	-	-	-	-	-	-	-	0.4	-	-	-
Myrsine australis	0.1	-	-	-	-	-	-	-	-	-	0.7	3.2	1.0	-	-
M. divaricata	-	-	-	-	-	-	-	-	-	-	1.0	2.9	-	-	-
Neomyrtus pedunculata	-	-	-	-	-	-	-	-	-	-	2.1	6.1	-	-	-
Pennantia corymbosa	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pseudopanax colensoi	-	-	-	-	-	-	-	-	-	-	0.7	-	-	-	-
P. crassifolius	3.4	7.4	-	-	41.7	47.1	-	45.5	-	11.1	18.4	7.9	-	-	76.9
P. edgerleyi	-	1.2	-	57.1	-	-	-	4.6	15.4	-	2.0	1.1	4.1	-	-
P. simplex	4.1	-	-	42.9	33.3	35.3	-	4.6	-	11.1	10.8	0.4	-	-	7.7
Pseudowintera colorata	2.1	-	-	-	-	-	-	-	-	-	1.0	2.5	-	-	-
Shefflera digitata	1.1	-	-	-	-	-	-	-	-	-	8.6	-	1.0	-	-
OTHERS															
Nertera sp.	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Peraxilla[2]	-	1.2	-	-	-	-	-	-	-	6.4	0.9	0.4	-	-	-
Ripogonum scandens	1.4	0.4	-	-	-	-	-	-	-	-	0.1	2.9	2.0	-	-
Rubus[3]	-	-	-	-	-	-	-	-	-	-	1.2	-	-	-	-

A large proportion of the diet of parakeets was unidentified but many observations were probably of feeding on invertebrates. Fruit feeding was confirmed on three species: rimu, Hall's totara and hupiro (*Coprosma foetidissima*) (Table 4). Rimu fruit was important in autumn (February-April), and in August rimu seeds made up nearly 70% of the diet (Fig. 5). The new leaves and buds of silver beech were eaten. Parakeets were not seen feeding on flowers or nectar. They fed on 17 plant species groups, mainly rimu (46%), silver beech (24%), Hall's totara (7%), and southern rata (4%) (Table 1).

New Zealand wrens (Acanthisittidae)

The rifleman (*Acanthisitta chloris*) fed mainly by gleaning insects throughout the forest strata (Figs. 3, 4; Table 2). Riflemen were, however, seen feeding on fruits of *Pseudopanax* spp. in April-May and June-July (Fig. 5, Table 4). While fruit represented 4.3% and 2.6% of the diet in these months, over a whole year fruits contributed less than 1% of the feeding observations. Rifleman used 33 plant species groups (Table 1); 18 groups were confirmed for invertebrate foraging, the most important being silver beech (34%) and kamahi (26%) (Table 6). Of lesser importance were the understorey shrubs associated with beech and kamahi forest, *Pseudopanax* spp. (3%), broadleaf (*Griselinia littoralis*) (3%), horopito (2%), and high altitude canopy species (rata 6%; Hall's totara 2%).

Table 5: *Plant species groups used for leaf/bud feeding by forest birds in South Westland (% of total leaf/bud feeding observations for each bird species). Key: - = zero observations; 1* = Coprosma astonii, C. pseudocuneata *and* C. rhamnoides*; 2* = Asplenium bulbiferum*; 3* = Dendrobium cunninghamii, *E*arina autumnalis *and* E. mucronata*; 4* = Rubus cissoides *and* R. schmidelioides.

	Pigeon	Kaka	Kea	Yellow-crowned parakeet	Silvereye	Bellbird
Number of observations	228	34	10	4	1	1
Canopy Species						
Dacrydium cupressinum	28.1	-	-	-	-	-
Meterosideros umbellata	-	11.8	-	-	-	-
Nothofagus menziesii	9.2	32.4	20.0	100.0	-	-
Prumnopitys ferruginea	0.4	-	-	-	-	-
Weinmannia racemosa	0.9	23.5	20.0	-	-	100.0
Shrub hardwoods						
Aristotelia serrata	0.4	-	-	-	-	-
Carpodetus serratus	1.3	-	-	-	-	-
Coprosma spp.[1]	0.9	-	-	-	-	-
C. rotundifolia	6.6	-	10.0	-	-	-
Cyathea smithii	-	-	10.0	-	-	-
Fuchsia excorticata	2.6	-	-	-	-	-
Griselinia littoralis	1.8	-	-	-	-	-
Hoheria glabrata	6.1	-	-	-	-	-
Melicytus ramiflorus	2.2	-	-	-	-	-
Pseudopanax crassifolius	2.2	-	-	-	-	-
P. edgerleyi	8.8	-	-	-	-	-
P. simplex	-	-	-	-	100.0	-
Others						
Asplenium bulbiferum	0.9	-	40.0	-	-	-
Muehlenbeckia australis	18.9	2.9	-	-	-	-
Orchids[2]	2.6	17.7	-	-	-	-
Parsonsia sp.	3.5	-	-	-	-	-
Rubus[3]	-	8.8	-	-	-	-

Warblers and flycatchers (Muscicapidae)

This group comprised six species, five native species that were almost entirely insectivorous: brown creeper (*Mohoua novaeseelandiae*), yellowhead, grey warbler (*Gerygone igata*), fantail (*Rhipidura fuliginosa*) and yellow-breasted tit (*Petroica macrocephala*); and the introduced blackbird (*Turdus merula*) (Table 2).

The native insectivorous species used most forest plant groups (43-53 groups, Table 1) except for the yellowhead, which used only 11 plant species. Yellowheads foraged almost exclusively on silver beech (75% of observations) and in plants associated with beech: moss (10%), dead trees (7%) and mistletoe (2%). The brown creeper, grey warbler, fantail and tit frequently used silver beech (9-47% of observations) and kamahi (15-35%) (Table 1). A wide range of shrubs and understorey species were used, with broadleaf, horopito, *Pseudopanax* spp. and tree ferns being most important. A large proportion of fantail observations (38%) were not on plants at all but of birds hawking in the air (Table 1). Fruit, mainly from *Pseudopanax, Coprosma* and broadleaf, was of minor importance to these species (Table 2).

The native insectivorous species mainly fed by gleaning (Fig. 3). The yellowhead, brown creeper and grey warbler gleaned predominantly on foliage and twigs, but nearly half of fantail feeding was by hawking and 90% of tit foraging was by scanning. Only the yellowhead fed by ripping dead wood and only the grey warbler by hovering at foliage tips (Fig. 3). Yellowheads fed mainly in upper forest strata while brown creepers fed more evenly through all levels in the forest. Grey warbler, fantail and tit fed mainly in the understorey (Fig. 4).

Blackbirds fed on both invertebrates and fruit, but 72% of the sources were unidentified. A large number of observations were of birds on the ground (28%, Table 1) but most birds were disturbed before food types could be identified. They fed on fruit throughout the year but this was most important in late summer and autumn when it contributed to over 40% of the blackbird's observed diet (Fig. 5). Blackbirds fed in 30 plant species groups in addition to ground feeding. The most important plants were rimu (16%), silver beech (6%), fuchsia (6%), standing dead trees (4%) and kamahi (4%). A wide range of shrubs were used, many of which were associated with forest

edges and canopy gaps, e.g., tutu (*Coriaria arborea*), wineberry (*Aristotelia serrata*) and fuchsia, and 9% of observations were on epiphytes.

Silvereyes (Zosteropidae)

The silvereye (*Zosterops lateralis*) used a diverse range of foods (Table 2) from most plant species groups available to them (Table 1). Silvereyes fed in all levels of the forest usually by gleaning (Figs. 3, 4). The use of all food types varied significantly through the year ($P<0.001$). Although over 80% of the diet was comprised of invertebrates, during spring and summer nectar was important (8-26% during October-February, Fig. 5). Fruit was consumed in all months, particularly between April and August (12-18% of observations) but other foods contributed to less than 1% of the diet (Table 2).

Silvereyes fed from 52 plant species groups, and the common tree species (kamahi, silver beech and rimu) were visited most frequently (Table 1). Nectar was taken from 14 species, mainly fuchsia (53%), various rata species (31%) and kamahi (7%) (Table 3). Twenty-six plant species provided fruit, with the most important being haumakaroa (*Pseudopanax simplex*, 29%), rimu (17%), tutu (13%) and pate (*Shefflera digitata*, 9%) (Table 4). Invertebrates were taken from at least 35 species, the most important being kamahi (22%), silver beech (20%), rimu (10%), kahikatea (8%) and toatoa *Phyllocladus aspleniifolius* var. *alpinus* (6%) (Table 6).

Honeyeaters (Meliphagidae)

Two honeyeaters, tui (*Prosthemadera novaeseelandiae*) and bellbird (*Anthornis melanura*), inhabit South Westland forests. Invertebrates, fruit and nectar were major components in the diets of both species but nectar was considerably more important for tui (Table 2). Both honeyeaters fed mainly by gleaning (Fig. 3) but their feeding was concentrated in different forest strata (Fig. 4). Tui concentrated in the upper levels, particularly the unshaded canopy, while bellbirds were observed throughout all levels to the lower understorey.

The use of all food types, except use of honeydew by bellbirds, varied significantly with season ($P<0.001$). Tui fed on nectar throughout the year but the proportion in the observed diet increased from *c.* 10% in April and June to 32% in August and a peak of 73% in October, dropping off again to 54% in December and 28% in February (Fig. 5). Nectar feeding by bellbirds showed a similar pattern, with a peak in October (41% of observations). Honeydew was taken by both species in most months (Fig. 5), representing up to 13% of the tui's observed diet (mid-winter) and 2-5% of the bellbird's observed diet. Both species used 8-10 plant groups for nectar feeding (Table 3), mainly rata species and fuchsia. Overall, 37% of bellbird and 46% of tui nectar-feeding observations were on rata species while 55% of observations for bellbird and 40% for tui were on fuchsia. Most honeydew was taken from kamahi, with the remainder from southern rata.

The amount of fruit in the observed diets of both tui and bellbird also varied seasonally and peaked in April for tui (48%) and June for bellbird (16%) (Fig. 5). Tui took fruit from nine plants (Table 4), with rimu (63%) and marbleleaf (*Carpodetus serratus*) (17%) being the most important species. Although fruit formed less of the total observed diet of bellbirds than of tui, bellbirds used a much wider range of plant species (25 groups, Table 4). Rimu was again the most important food species, contributing to 31% of fruit feeding observed in bellbirds. Other notable species that bellbirds took fruit from were *Coprosma* spp. (22%), *Pseudopanax* spp. (12%), tutu (6%) and rohutu (*Neomyrtus pedunculata*, 6%).

Tui used only four tree species when foraging for invertebrates (silver beech, kamahi, kahikatea and mountain totara). Over half of the observations of tui feeding on invertebrates were of birds catching insects on the wing. Bellbirds used 28 plant species groups, which included canopy, understorey and epiphyte plants (Table 6). Invertebrate foods were most important in August when they represented nearly 90% of the bellbird feeding observations and 60% of the tui observations (Fig. 5).

Finches (Fringillidae)

Four species of introduced finches were found in South Westland forests: chaffinch (*Fringilla coelebs*), greenfinch (*Carduelis chloris*), goldfinch (*C. carduelis*), and redpoll (*C. flammea*). Feeding observations of the goldfinch and greenfinch were limited because the birds were only common in the forests in winter. We had difficulty identifying the foods of finches when they fed in the uppermost levels of the forest and most foods were unidentified (Table 2, Fig. 5). Chaffinches fed on invertebrates, fruit and seeds, goldfinch and greenfinch on seeds and invertebrates, and redpolls on fruit and seeds. Seeds were probably the major part of the diet of all four species in winter; most fruit was eaten in April and invertebrates in summer (Fig. 5). Almost all foraging by finches was gleaning (Fig. 3).

Table 6: *Plant species groups used for invertebrate feeding by forest birds in South Westland (% of total invertebrate feeding observations for each bird species). Key: - = zero observations; KAK = kaka; KEA = kea; RIF = rifleman; CRE = brown creeper; WAR = grey warbler; YEL = yellowhead; TIT = tit; FAN = fantail; BLA = blackbird; SIL = silvereye; BEL = bellbird; TUI = tui; GRE = greenfinch; RED = redpoll; CHA = chaffinch; 1* = Coprosma astonii, C. pseudocuneata *and* C. rhamnoides*; 2* = Astelia fragrans, A. grandis *and* A. nervosa*; 3* = Asplenium bulbiferum, Blechnum capense, B. discolor *and* Sticherus cunninghamii*; 4* = Metrosideros fulgens, M. perforata *and* M. diffusa*; 5* = Peraxilla colensoi *and* P. tetrapetala*; 6* = Rubus cissoides *and* R. schmidelioides*; 7* = Cyathea smithii *and* Dicksonia squarrosa.

Number of observations	KAK 466	KEA 29	RIF 381	CRE 405	WAR 846	YEL 119	TIT 647	FAN 677	BLA 4	SIL 784	BEL 436	TUI 27	GRE 14	RED 70	CHA 14
Canopy species															
Dacrydium cupressinum	13.3	-	2.4	12.4	7.6	-	5.1	6.4	-	10.2	7.6	-	-	-	20.5
Dacrycarpus dacrydioides	-	-	1.8	2.0	2.5	-	1.9	1.2	-	8.4	3.7	5.4	14.3	-	-
Dead tree (various)	26.0	51.7	1.6	-	-	-	4.4	1.0	-	0.7	0.7	-	-	-	-
Elaeocarpus hookerianus	-	-	-	-	0.1	-	0.3	0.6	-	1.7	-	-	-	-	-
Lagarostrobos colensoi	-	-	-	2.7	0.5	-	0.2	0.4	-	1.4	1.4	-	-	-	4.6
Meterosideros umbellata	6.0	20.7	13.1	0.5	2.0	-	1.6	1.5	-	0.3	7.6	-	-	-	-
Nothofagus menziesii	15.7	13.8	34.1	57.5	22.3	96.6	19.8	10.6	-	20.0	13.3	29.7	42.9	100.0	45.5
Podocarpus hallii	1.1	-	1.3	1.2	0.2	-	0.6	0.3	-	-	3.0	2.7	-	-	-
P. totara	-	-	-	0.5	-	-	0.2	-	-	-	-	-	-	-	-
Prumnopitys ferruginea	2.2	-	1.1	1.2	3.0	-	1.9	1.5	-	1.7	1.4	-	-	-	-
P. taxifolia	0.6	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-
Weinmannia racemosa	30.0	-	26.5	13.8	36.5	-	17.6	10.0	-	22.1	37.4	8.1	-	-	-
Shrub hardwoods															
Aristotelia serrata	1.1	-	-	0.3	0.2	-	0.9	-	-	1.4	-	-	-	-	-
Ascarina lucida	-	-	-	-	0.4	-	1.1	-	-	1.7	0.5	-	-	-	-
Brachyglottis spp.	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-
Carpodetus serratus	-	-	-	-	0.6	-	-	-	-	0.8	-	-	-	-	-
Coprosma spp.[1]	-	-	0.8	0.7	1.2	-	3.6	0.4	-	0.6	1.2	-	-	-	-
C. foetidissima	-	-	-	-	0.4	-	-	0.3	-	-	-	-	-	-	-
C. rotundifolia	-	-	-	-	0.1	-	0.3	-	-	0.3	-	-	-	-	-
Coriaria arborea	-	-	-	-	-	-	-	-	-	1.1	0.5	-	-	-	-
Fuchsia excorticata	0.9	-	1.1	-	1.4	-	2.2	0.7	-	0.1	2.5	-	-	-	-
Griselinia littoralis	0.6	-	3.4	1.7	1.0	0.8	1.6	0.4	-	4.2	1.6	-	-	-	-
Hedycarya arborea	0.2	-	-	-	0.7	-	0.3	0.4	-	1.0	-	-	-	-	-
Lepidothamnus intermedius	0.2	-	-	-	-	-	-	0.2	-	-	-	-	-	-	9.1
Melicytus ramiflorus	-	-	-	-	-	-	0.5	0.2	-	0.8	0.2	-	-	-	-
Myrsine australis	0.4	-	-	-	0.4	-	0.3	0.3	-	-	-	-	-	-	-
M. divaricata	-	-	-	-	0.1	-	0.2	0.7	-	0.1	0.2	-	-	-	-
Neomyrtus pedunculata	-	-	-	-	0.4	-	0.3	-	-	0.6	-	-	-	-	-
Pennantia corymbosa	-	-	-	-	0.5	-	-	-	-	1.8	-	-	-	-	-
Phyllocladus aspleniifolius	-	-	-	0.7	0.8	-	0.9	1.0	-	6.1	0.7	-	-	-	2.3
Pseudopanax colensoi	-	-	-	0.5	-	-	-	-	-	0.3	10.1	-	-	-	-
P. crassifolius	0.2	-	1.6	2.2	1.8	-	1.4	1.2	-	1.2	1.6	-	-	-	-
P. edgerleyi	-	-	-	-	-	-	0.2	-	-	0.4	-	-	-	-	-
P. simplex	-	-	1.8	1.0	0.2	0.8	0.8	0.2	-	0.3	0.2	-	-	-	-
Pseudowintera colorata	-	-	2.4	0.7	2.0	-	1.2	0.2	-	0.1	0.7	-	-	-	-
Shefflera digitata	0.9	-	-	-	0.2	-	0.9	0.3	-	0.1	0.7	-	-	-	-
Others															
Astelia spp.[2]	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-
Ferns[3]	-	-	-	-	0.5	0.8	0.3	0.6	-	0.1	-	-	-	-	-
Freycinetia baueriana	-	-	-	-	0.4	-	0.3	0.2	-	-	-	-	-	-	-
Lichens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.3
Metrosideros spp.[4]	0.2	-	0.5	-	1.4	-	0.6	0.4	-	3.6	1.4	-	-	-	-
Mosses	0.2	-	-	-	-	0.8	0.5	0.2	25.0	1.3	0.9	-	-	-	9.1
Muehlenbeckia australis	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-
Peraxilla[5]	0.2	-	1.3	-	-	-	-	-	-	-	-	-	42.9	-	-
Ripogonum scandens	-	-	-	-	1.4	-	2.5	0.7	-	1.8	0.5	-	-	-	2.3
Rubus[6]	0.2	-	0.5	-	0.1	-	0.3	0.3	-	0.4	0.2	-	-	-	-
Treeferns[7]	-	-	3.9	-	4.9	-	11.3	1.8	-	1.7	0.3	-	-	-	4.6
Not in plants															
Ground/air	-	10.3	0.8	-	3.7	-	11.8	54.8	75.0	0.1	-	54.0	-	-	-

Overall, chaffinch used the widest range of plant species groups (23), with goldfinch, greenfinch and redpoll using 10, nine, and six species respectively (Table 1). Rimu was the most important plant for all the finches. Over 50% of chaffinch observations from August to October were of feeding on rimu seed. All seed foraging by greenfinches was in rimu as was 51% of goldfinch foraging and 89% of redpoll foraging. Goldfinches also took considerable amounts of silver beech seed (49% of seed feeding observations) and redpolls took kamahi seed (11%). Rimu and silver beech were also the most important sources of invertebrate foods (Table 6). A relatively high proportion of finch feeding was on the ground (Table 1). Fruit appeared to be a minor component of the diet of chaffinch and redpoll, representing only 2% of the feeding observations (Table 2).

Discussion

Foraging strategies of South Westland forest birds

South Westland forests support most bird species now characteristic of mainland New Zealand forests. Of the 18 species studied all except the New Zealand pigeon (which ate foliage and fruit) fed on combinations of invertebrates, nectar, fruit, seeds and sap. The three parrot species, two honeyeaters and the silvereye had broad omnivorous diets which varied considerably between seasons. The flycatchers, warblers and rifleman were almost entirely insectivorous. Large proportions of the diets of the finches were not identified but we suspect they had mixed seed and invertebrate diets, as recorded elsewhere (Reader's Digest, 1985). Therefore the bird community apparently comprised a large number of generalist feeders and few dietary specialists. Although fruit and nectar were important dietary components there were no wholly fruit or nectar feeders, as are present in tropical rainforest communities (Foster, 1978; Bell, 1982; Beehler, 1983).

This apparent lack of specialisation in food types may be a characteristic of some temperate island systems. Islands long isolated from sources of faunal invasion have low diversity in their forest-bird fauna. It has been hypothesised that temperate forest birds are mainly habitat generalists resulting from broad ecological niches, low bird species richness, and abundant resources (Kikkawa, 1966, 1975; Orians, 1969; Diamond, 1970; Bull and Whitaker, 1975). However, foraging patterns of New Zealand forest birds have probably been influenced by changes in the composition of the bird community over the last thousand years or so through a large number of extinctions (Williams, 1962; Cassels, 1984; Holdaway, 1989). Introductions of European bird species which have become established in forests (O'Donnell and Dilks, 1986), extensive reduction in forest area through logging and clearing for agriculture (Stidolph, 1933; Flux, 1977), and the introduction of browsing animals (deer, *Cervus*[3] spp.; goats, *Capra hircus*; possums, *Trichosurus vulpecula*) which have altered the composition of plant species present in forests (Veblen and Stewart, 1982) have also influenced foraging opportunities. With the extinction of 40-50% of the terrestrial New Zealand avifauna we suspect that more specialist than generalist species have disappeared because the specialists (e.g., huia: *Heteralocha acutirostris*) were least able to adapt to changes associated with the arrival of Polynesians and then Europeans. One factor contributing to the survival of some of the endemic bird genera in forests today (e.g., kokako: *Callaeas cinerea*, parrots: *Cyanoramphus* spp., *Nestor* spp.) may be their widely omnivorous diets.

However, the degree of foraging specialisation should not be viewed only in relation to the food types consumed. The 18 species studied differed from each other in the number of plant species used, their preferred feeding stations and method of feeding. Most importantly the omnivorous birds exhibited varying degrees of sequential specialisation in their diets as they switched between specific food sources from season to season. Body size, energetics, social factors, interspecific interactions, sex and breeding behaviour of birds (Craig *et al*., 1981; Foster, 1987) can also mean that seemingly generalist feeding strategies are more specialised than is first apparent. Thus, contrary to some views (e.g., Morse, 1981) the species which ate the widest variety of foods, the parrots and honeyeaters, had some of the most complex feeding strategies. For example, kaka, which had the most diverse repertoire of foraging techniques and ate a wide variety of foods, moved from one food source to another during their annual cycle. Kaka appeared to be mobile in response to changing availability of food sources and used foods at different altitudes and in coastal or inland sites at different times of the year (e.g., rata, fuchsia). Their behaviour also indicated that they selected specific invertebrate foods, for example, by excavating the deep galleries of cerambycid beetle larvae in standing dead trees and surface galleries in Hall's totara

[3] Mammal nomenclature follows King (1990).

trees in late winter, in similar fashion to that already described for kanuka (*Kunzea ericoides*) by Beggs and Wilson (1987). Sap-feeding by the kaka was highly specialised and was carried out mainly in late winter and early spring when very few nectar sources were available, energy demands were high and sap flow was increasing (O'Donnell and Dilks, 1989a). Their feeding on fungal bodies embedded in decaying wood was also specialised and has not been recorded elsewhere to our knowledge.

South Westland *Nothofagus* forests are not as depauperate in nectar and, particularly, in fruit supplies as has often been suggested. While it may be generally true that *Nothofagus* trees provide few resources for birds (Kikkawa, 1975; Craig *et al*., 1981; Wardle, 1984; Lee *et al*., 1991), in South Westland the silver beech associations have a significant shrub and epiphyte flora which provide a wide range of foods. Important nectar sources come from mistletoes, horopito, orchids (*Dendrobium, Earina*), *Pseudopanax* spp., and probably *Astelia* spp. Fruit bearing plants particularly horopito, *Pseudopanax* spp., *Coprosma* spp. and *Myrsine* spp., were common throughout, not just on stream edges as in other areas (Craig *et al*., 1981). Such diversity may result from high rainfall, as *Nothofagus* forests on the drier east coast of New Zealand have a much simpler structure (Wardle, 1984) or because possums, which selectively browse some of the fruit-bearing species (e.g., Wilson, 1984), are only recent colonists to southern South Westland and have yet to reduce plant diversity.

Only the New Zealand pigeon fed predominantly on fruit. In the tropics frugivory can be advantageous because of the low energetic cost involved in fruit feeding compared with the high demands of constantly searching for invertebrates. Sources of fruit are said to be relatively predictable in tropical forests, fixed in space and to offer nutritional rewards usually available only from arthropods (Beehler, 1983). Under a tropical forest canopy the microclimate is relatively stable (Barry, 1984). In contrast the climatic conditions in South Westland vary considerably during the day, season and year (*pers. obs*.), contributing to substantial variability in phenological events. However, given the degree of diversity in forest composition and a tendency for birds to move seasonally, some degree of frugivory is possible in most bird species. Fruit is scarce in spring and summer, but birds move between highland and lowland food sources (O'Donnell and Dilks, 1986) and from canopy trees to lower understorey shrubs (O'Donnell and Dilks, *pers. obs*.).

In years when fruit is scarce, foliage may be an important food for the New Zealand pigeon. While leaves and buds contributed to only 10% of the pigeon's overall diet in this study, in October they comprised over 70%, a fact also recorded in other studies (McEwan, 1978; Clout *et al*., 1986). The recognised high mobility of pigeons (Clout *et al*., 1986) in early spring may be in response to other fresh foliage sources at that time of year.

Many bird species, particularly the small passerines, were largely insectivorous. Given the abundance and diversity of insects generally (Morse, 1980) and their diversity in New Zealand forests (e.g., Hoy, 1958, Moeed and Meads, 1984) compared with the relative paucity of fruit- and nectar-bearing plants, it is not surprising that most bird species are insectivorous. While insect populations in South Westland undergo marked seasonal fluctuations (Robertson *et al*., 1986) they still provide an all-year food source. In *Nothofagus*-dominated associations, a major component of forests in South Westland, insectivory is the most reliable feeding strategy because of the changing availability of other food types.

Fruit constituted less than 1% of the observed foods of six passerine species (rifleman, brown creeper, yellowhead, grey warbler, fantail, yellow-breasted tit) and was mainly eaten in winter and at higher altitudes. However, these passerines are still properly described as insectivorous because fruit constitutes such a small proportion of their diet (O'Donnell and Dilks, 1989b). Moeed and Fitzgerald (1982) thought fruit could make an important contribution to the energy budget of insectivorous birds in autumn and winter. This may be true in South Westland because invertebrate numbers in winter are six or seven times lower than in summer (Robertson *et al*., 1986), at a time when fruit is still widely available (Fig. 2).

Predictability of fruit and flower food sources in South Westland

The marked irregularity of flowering and fruiting of individual plant species in South Westland makes them somewhat unpredictable food sources. Podocarps and beech trees have irregular intervals between good flowering, fruiting or seeding years (Hinds and Reid, 1957; Beveridge, 1964; Wardle, 1984; Allen and Platt, 1990; Burrows and Allen, 1991). There may be a few good fruiting years in succession in podocarp forests, but more often there are 3-5 year intervals between good crops. Kahikatea is the heaviest fruiting species of all the podocarps; a single tree may bear over 800 kg of

fruit (Beveridge, 1964). It also has the longest intervals between fruiting years, sometimes as long as seven years (*pers. obs.*). During our study kahikatea fruited only once (autumn 1985) and then not heavily. While many shrub species fruit annually to some extent, the bulk of fruit biomass comes from the emergent podocarps. The importance of heavy flowering of mistletoes in summer 1984-85 compared with its virtual absence in summer 1983-84 and 1985-86 was reflected by the high use of these species by kaka (77% of kaka feeding observations) in December-January 1984-85. While mistletoe nectar was virtually absent in the other years, rata flowered heavily in summer 1983-84, and contributed to the bulk of nectar feeding that year. Only pigeonwood, supplejack and vine rata (*Metrosideros fulgens*) had flowers or fruit present throughout the year. Most other species had flowers present for 3-6 months and fruit for 6-9 months.

Intensity and duration of flowering and fruiting also vary with latitude and topography. Plants at higher altitudes usually flower later than those in coastal and lowland situations. Fruiting of podocarps can be heavy in one area and light in another. For example, rimu did not produce fruit in the 1983-84 season at Hunt's Beach, 30 km north of the study area (P. Gaze, *pers. comm.*), but fruited heavily in the study area.

Although the intensity and regularity of phenological events is somewhat unpredictable, given the diversity of forest plants available it is possible that some species will flower and fruit heavily in any given year. Thus, overall, some food is always available for forest birds despite considerable variations for individual plant species. The birds which have a large component of plant foods in their diets are also the larger and more mobile species (New Zealand pigeon, tui, kaka, kea, parakeets), which sometimes travel long distances to feed on short-lived food patches (Gravatt, 1970, 1971; Clout *et al.,* 1986; Craig *et al.*, 1981; H.A. Robertson, *pers. comm.*; P.R. Wilson, *pers. comm.*; G.P. Elliott, *pers. comm.*). However, while the amount of food available each year may be sufficient to maintain bird populations, some species may require full mast events to initiate widespread successful breeding, for example in kaka (R. Moorhouse; J.R. Beggs, *pers. comm.*) and parakeets (*pers. obs.*).

Role of South Westland forest birds as pollinators and seed dispersers.

It is widely accepted that indigenous forest birds in New Zealand play a key role in pollination and seed dispersal and that there has been ample opportunity for the development of bird-adapted seed dispersal systems (McCann, 1952; Beveridge, 1964; Clout and Hay, 1989; Lee *et al.*, 1991). However, just because a bird feeds on nectar or fruit does not necessarily mean it is an effective pollinator or disperser. Birds may be flower-robbers, taking nectar but not picking up pollen, or they may not disperse seeds very far from the parent tree. Our data suggests that four bird species (kaka, tui, bellbird, silvereye) play important roles in pollinating some forest plants. Kaka and tui have specialised brush tongues suited to gathering nectar, while the tongue of the kea is more simple (Garrod, 1872; McCann, 1963). Many kea fed destructively on flowers. When feeding on fuchsia, rata and mistletoe, they completely crushed the flowers to extract the nectar.

At least five bird species (New Zealand pigeon, tui, bellbird, silvereye and the introduced blackbird) are probably important seed dispersers through fruit feeding. The introduced song thrush and dunnock also ate fruits (*pers. obs.*), but we were unable to determine their likely role in seed dispersal. The role of kaka, kea and parakeets and the introduced finches as seed dispersers is unclear. All species act primarily as seed destroyers but occasionally they eat fruits. For example, at times kaka consume 50-60 seeds per minute when feeding on rimu and feeding bouts can last over 60 minutes, but when feeding on larger miro fruits they sometimes peel and eat the fleshy tissue and then drop the seed to the ground (*pers. obs.*). However, Beveridge (1964) found that kaka also cracked miro seeds and ate the contents. Kaka eat fuchsia fruits whole and probably disperse their seeds. Therefore, despite occasionally eating fruits, it is likely that the New Zealand parrots contribute little to overall seed dispersal in New Zealand forests.

Impacts of logging on forest birds

The two primary criteria for selecting trees for logging are species and trunk diameter. In South Westland forests, large diameter, mature and recently dead specimens of rimu, kahikatea and silver beech, would be the main targets for logging. The information on foraging provides the first step towards predicting the impacts of logging these trees. The removal of any plant species used by birds would have a potential impact on them if the resource was limited. The degree of impact will depend on the level of extraction and whether or not the birds can switch to alternative food sources. The impact of removing plants which are used in

specific seasons and represent specialised food sources is likely to be high, because alternative food sources are probably rare. This study indicated that the bird species which were usually obligate forest dwellers spent a large proportion of their time feeding on merchantible tree species. For example, kahikatea was important for N.Z. pigeon, rimu for N.Z. pigeon, kaka, kea, yellow-crowned parakeet and tui, silver beech for yellowhead, kaka, kea, yellow-crowned parakeet, rifleman and brown creeper, and dead trees for kaka, kea and yellowhead. Usually birds used the largest diameter trees in the forest (O'Donnell and Dilks, 1986). We predict that removing them would have a major impact on these bird species. Spurr, Warburton and Drew (1992) and Warburton *et al*. (1992) made similar predictions for N.Z. pigeon, bellbird and tui in Okarito forests which may be subject to either selective or coupe logging of mature and old rimu. The situation in South Westland is harder to predict because of the more diverse forest types and presence of threatened bird species.

A review of studies of the effects of logging on threatened forest birds in New Zealand (O'Donnell, 1991) suggests that most of these bird species would not switch to alternative food sources. This is particularly so for kaka, yellow-crowned parakeet and yellowhead which have disappeared from almost all forests where beech and podocarps were the main logging targets. These threatened birds were probably limited either by the food supplies or nest sites provided by these trees. It is most likely that in the absence of any other factors which may be more limiting in logged forest, a combination of both food supply and nest site limitation is important. Almost all feeding and nesting of yellowheads occurs in large, old beech trees (Read, 1988a; Elliott, 1990). In South Westland, yellowheads were never seen feeding in nearby forest types or other tree species within the beech forest (O'Donnell and Dilks, 1986). There is little information available on the relative importance of major food-producing trees as nest sites for kaka and parakeets.

Moorhouse (1991) hypothesised that variations in breeding intensity of North Island kaka (*Nestor meridionalis septentrionalis*) of Kapiti Island were related to variations in food supply. Likewise, Beggs and Wilson (1991) found that of 31 radio-tagged kaka only two pairs attempted to breed in six years, and their data suggested a link between lack of energy sources and low reproductive rate. Like kaka, breeding of yellow-crowned parakeets in Fiordland is largely confined to years when beech trees seed heavily, and food is abundant (G. Elliott, C. O'Donnell, P. Dilks, *unpubl. data*). While New Zealand parrots may breed more frequently if food were more abundant (Beggs and Wilson, 1991; Moorhouse, 1991; Powlesland and Lloyd, 1994), if extreme natural variability in food supply limits populations, then extracting preferred food trees from the forest by logging would further limit productivity. We were unable to explore the relationship between annual variability in food supply and productivity because no attempt was made to monitor breeding activity during the study.

The next step in predicting the impacts of logging will be to show, to what degree, the important food trees are "preferred" by birds in South Westland, by comparing degree of use with the availability of tree species, and sizes of trees, in different seasons, and determining if their removal would have a critical impact on the birds if removed. More information on the food limitation hypothesis, particularly its influence on threatened species, is also required. This will be the subject of future work.

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