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FLESHY FRUITS OF INDIGENOUS AND ADVENTIVE PLANTS IN THE DIET OF BIRDS IN FOREST REMNANTS, NELSON, NEW ZEALAND

Summary: The relationship between fleshy-fruited indigenous species and adventive weeds in the diet of 500 mist-netted birds was studied in forest remnants of differing size and degree of modification. Fruit abundance peaked in March and April, and most fruit was either red/orange or purple/black. The physical parameters of adventive and indigenous fruits were not significantly different. Six of the 15 passerine species netted are frugivores, and of those netted 77% had eaten fruit. They were divisible into three groups: endemic (bellbirds, *Anthornis melanura*; tuis, *Prosthemadera novaeseelandiae*), non-endemic but indigenous (silvereyes, *Zosterops lateralis*), and adventive (blackbirds, *Turdus merula*; song thrushes, *T. philomelos*; starlings, *Sturnus vulgaris*).

Bird diets varied between the groups and according to fruit availability as determined by sites and seasons. Endemic birds ate the least adventive fruit; bellbirds ate mainly *Podocarpus hallii* and *Coprosma robusta* fruits at all sites. Tuis had a varied diet, including some adventive fruits. Silvereyes ate the widest range of indigenous and adventive fruits. Blackbirds and, to a smaller extent, song thrushes ate many of the same indigenous fruits as the other bird groups, but their diet included more adventive fruits, e.g., *Berberis glaucocarpa*. Starlings were caught only when they fed on *Sambucus nigra,* but they also ate a few indigenous fruits. There was little seasonal variation in bird numbers caught. Adventive species extended the seasonal availability of fruits into winter, particularly in the forest remnant closest to a town, which had the highest proportion of adventive fruits.

Several weed species distributed mainly by non-endemic and adventive birds are forming new secondary vegetation. Some have large fruit crops which generally offer little food for endemic birds. Where fruiting weeds pre-empt sites that may have been occupied by native species, they create an inferior habitat for endemic birds. However, the non-endemic and adventive birds also disperse indigenous fruits into early successional vegetation, and the importance of their seed rain for conservation of biodiversity will therefore depend on the site.

Keywords: Avian frugivory; fruiting phenology; fruit characteristics; seed dispersal; weeds; endemic birds; adventive birds; forest remnants.

Introduction

Dispersal by birds is the most common mechanism by which adventive weeds invade secondary scrub and damaged indigenous forest of conservation lands in New Zealand (Timmins and Williams, 1987). Which bird species or groups, such as endemic or adventive birds, are primarily responsible for weed dispersal has seldom been investigated in New Zealand. Thomson (1922) considered that European blackbirds (*Turdus merula*)[1] and song thrushes (*Turdus philomelos*) spread introduced plants, McCann (1953) noted how blackbirds spread black nightshade (*Solanum nigrum*)[2], and Allen and Lee (1992) recorded four bird species, including two adventive species, removing *Berberis darwinii* fruit. Burrows (1995), in reviewing the relationships between birds and fleshy fruit dispersal of indigenous plants on Banks Peninsula in Canterbury, emphasised the role of adventive birds in seed dispersal generally. Adventive birds have often been implicated in the spread of adventive plants, e.g., in Australia (Gleadow and Ashton, 1981), Hawaii (LaRosa, 1992), and North America (White and Stiles, 1991).

Once adventive plants have established, their impacts are generally considered from the perspective of the indigenous plants they pre-empt or replace; their interactions with indigenous fauna

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[1] Avian nomenclature follows Turbott (1990).

[2] Botanical nomenclature follows Allan (1961); Webb, Sykes and Garnock-Jones (1988); and Connor and Edgar (1987).

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are rarely studied (e.g., Fraser and Crowe, 1990). Fleshy-fruited weeds can offer additional or alternative food sources for indigenous birds (Date, Ford and Recher, 1991; Sallabanks, 1993), but the effects of any dietary shift can be unpredictable. For example, frugivorous birds which transfer their feeding to adventive species may reduce the dispersal of indigenous species (Knight, 1986; Sallabanks, 1993). In North America the spread of introduced species that hold their fruit longer into the autumn may influence the migration patterns of birds, and ultimately plant distributions (White and Stiles, 1991).

Weeds are most abundant in small forest or scrub reserves close to towns in New Zealand, irrespective of other factors (Timmins and Williams, 1991). We studied three reserves at varying distances from towns, examining the interactions between indigenous and adventive fruiting plants, and three groups of birds. These are: (a) the endemic honeyeaters, bellbirds (*Anthornis melanura*) and tuis (*Prosthemadera novaeseelandiae*); (b) the non-endemic but indigenous silvereyes (*Zosterops lateralis*), self-introduced in the 1850s (Falla, Sibson and Turbott, 1966); and (c) the several species of adventive passerines introduced by European settlers in the period 1850-60 (Falla, Sibson and Turbott, 1966). New Zealand pigeons (*Hemiphaga novaeseelandiae*) are important frugivores because of their large size and dispersal capabilities (Clout and Hay, 1989; Lee, *et al.*, 1991), but we did not attempt to catch these. We were interested primarily in determining the relative contributions of indigenous and adventive fruits to the diets of the three bird groups, and whether this was related to the distance of the forest area from the nearest town.

Methods

Study sites

The study was carried out near the city of Nelson (latitude 41 17', longitude 173 15') (Fig.1, Table 1). We sought forest patches with a range of indigenous and adventive fleshy fruit-bearing woody plant species at varying distances from towns (Table 1) and with sufficient flat areas to permit erection of mist nets. Three small lowland forest remnants were selected which partially satisfied these criteria, but they were of varied composition (Tables 1 and 2).

(1) Eves. This is located in Eves Valley and is the largest (1.50 ha) and most intact of the three patches, although it has been logged and grazed in the past. It is narrow, and follows both sides of a gully between a hill slope and a road. *Nothofagus solandri* var. *solandri* and *Podocarpus hallii* are the main canopy trees

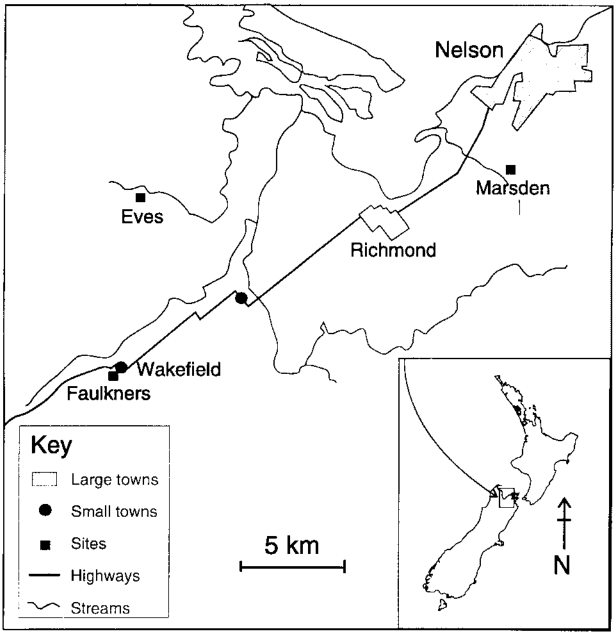

Figure 1: *Location of study sites near Nelson.*

Table 1: *Location and characteristics of study sites near Nelson.*

Name	Grid ref. (NZMS 260)	Altitude (m)	Area (ha)	Distance to town edge (km)	Physiography
Eves	N27 145859	100	1.50	7.5	Low terrace and S-facing toe slopes
Marsden	O27 319867	100	0.18	2.3	Low terrace and S-facing toe slope
Faulkners	N27 133775	90	0.75	0.5	Low terraces and NW-facing scarp

(*P. totara* was not distinguished throughout because of the similarity of its fruit), with emergent *Dacrycarpus dacrydioides*. *N. solandri* var. *solandri* is also common in the understorey, with *Aristotelia fruticosa*, several species of *Coprosma*, *Pseudopanax arboreus*, and other angiosperm trees and shrubs (Table 2). Occasional *Fuchsia excorticata* and *Schefflera digitata* trees are present in the gully. *Berberis glaucocarpa*, *Coprosma rotundifolia*, *C. robusta*, *Crataegus monogyna*, *Leycesteria formosa*, and *Muehlenbeckia australis* are common species on the forest margins or in clearings within the forest. They are also the main fruiting species in the surrounding open countryside, hedges, *Pinus radiata* forest, and orchards.

(2) Marsden. This is located in Marsden Valley and is the smallest (0.18 ha) of the three patches. It occupies a narrow strip between a road and a steep hillside. The forest comprises only a few dozen large trees of mostly *Alectryon excelsus*, with a few *Beilschmiedia tawa*, *Laurelia novae-zelandiae*, *Podocarpus* spp., *Sophora microphylla,* and other angiosperm trees and shrubs. *Melicytus ramiflorus* and *Macropiper excelsum* dominate the understorey. Restoration plantings of *C. robusta* and *Aristotelia fruticosa* occur between the main strip of forest and adjacent hillsides covered with *Pteridium esculentum*, *Ulex europaeus* and scattered *L. formosa*. Within 1 km there are also clumps of *Coriaria arborea*, and species of *Coprosma*, *Berberis glaucocarpa,* and *Crataegus monogyna* scattered through the landscape of farmland, forestry blocks, and regenerating scrub.

(3) Faulkners. This is a small (0.75 ha), isolated stand of tall *D. dacrydioides*/*P. hallii* forest set amongst farmland at the margins of the small town of Wakefield. Other canopy trees are scattered individuals of *N. solandri* var. *solandri* and *Prumnopitys taxifolia*. The sparse understorey is dominated by *Coprosma* spp. and *M. ramiflorus*. There are patches of *Ligustrum sinense* and *Lonicera japonica* at one end. The main fruiting plants beyond the sampled forest are further groves of *P. hallii*, while on the adjacent urban sections there is scattered horticultural fleshy-fruited plants, e.g., *Arbutus unedo, Crataegus monogyna,* species of *Cotoneaster*, and *Ilex aquifolium*.

Mist netting

Mist nets with 38 mm mesh were erected on the forest margins, in clearings, or beneath the forest canopy. Rigs were suspended from self-supporting poles 7.5 m tall or from cords 8 m to 10 m above ground in trees in a similar manner to that described by Whitaker (1972). At Eves there were four pole rigs, three 9.1 m long and one 12.8 m long, all in different locations. At Marsden there were three pole rigs, two 9.1 m and one 12.8 m, and one 12.8 m tree rig, all in different locations. At Faulkners there were two 9.1 m pole rigs at one location and 9.1 m and 12.8 m tree rigs at another.

Nets were erected for 1–5 days each month in fine calm weather, with greater emphasis on months with heavy fruiting. Netting was conducted between February 1992 and February 1993 for 33 days at Eves, between February and June 1993 for 19 days at Faulkners, and between December 1993 and June 1994 for 35 days at Marsden. For security reasons the rigs were dismantled every day, which restricted the time they were in position to an average of 5.5 hours per day, mostly between 1000 and 1600 hours. Catches are presented as the number of birds per net effort, which is the number of birds caught (n) divided by the area of each net rig (m^2) multiplied by the hours (t) the net was up, multiplied by 100.

Bird diets

Many birds defecated into sheets suspended below the nets when they were caught in the nets. They were untangled within minutes and placed in small calico bags for 5-10 minutes, during which time they usually defecated. Most birds were banded before being released, to determine whether there were detectable numbers of birds moving between the reserves. Individual faeces were stored in 70% alchohol before being washed in a fine sieve and examined for fruit under a binocular microscope. All whole fruit (used here to include receptacles of

Podocarpaceae and arils), skins, or seeds (all non-fleshy components, including stones) were counted and identified with the aid of a reference collection. The dry weight of pulp eaten was calculated from the dry weight of pulp per seed, per receptacle, or occasionally from the number of fruit skins, whichever was the greater.

Where birds had eaten parts of soft fruits such as apple (*Malus domestica*) this calculation could not be made. The exception was *Alectryon excelsus*, which produces a fleshy aril surrounding much of the seed. This flesh is highly distinctive, and was found in faeces without the seed. In these few instances an estimate was made of the proportion of an individual aril that had been eaten.

Casual observations on a non-systematic basis were made of foraging birds throughout the study.

Fruit

Observations were made at least bimonthly of the abundance and ripeness of fruit of 5-10 individual plants of all accessible fleshy-fruited species along tracks in the forests and on adjacent land. Results are presented as the period when more than half the fruit crop was ripe and the period over which any ripe fruit was present. Abundance of the fruiting species was ranked subjectively as common throughout, common but only in patches, and uncommon or present within 0.25 km of the reserve.

Ripe intact fruits were collected during their period of maximum ripeness from 5–10 bushes and bulked before being split into 3–5 subsamples of equal size. The least diameter was measured on about 25 fruits while for most species a total of *c.* 100 fruits were used for destructive measurements. Each subsample was weighed wet, and then the seeds were extracted by hand from half the sample. Pulp weight was determined by subtraction. All samples were oven-dried to a constant mass at 70°C and reweighed.

Results

Fruit

Eves has the greatest number of fruiting plant species and many of these are present at Marsden (Table 2). The number of species at Faulkners is much lower although several fruiting species are restricted to this site (e.g., *Coprosma crassifolius* and *Ligustrum sinense).* Only a few species have many individuals producing large amounts of fruit throughout the forests or on a high proportion of the forest margins at any of the sites. At Eves these species are *Coprosma robusta*, *C. rotundifolia*, *Muehlenbeckia australis*, *Neomyrtus pedunculata*, *Podocarpus* spp., and *Pseudopanax arboreus*. Several of the adventive species have scattered or patchy distributions in clearings and on the margins, e.g., *Berberis glaucocarpa* and *Leycesteria formosa* (Fig. 2). Neither *Dacrycarpus dacrydioides* nor *Melicytus ramiflorus,* which produce large amounts of fruit in some years, did so during 1992–93.

At Marsden the heaviest-fruiting species are *Alectryon excelsus*, *Aristotelia serrata*, *Coprosma robusta*, *Macropiper excelsum*, *Melicytus ramiflorus*, and the herb *Solanum nigrum* (Fig. 3). *A. excelsus*, *C. robusta*, and *M. ramiflorus* produced particularly large fruit displays.

At Faulkners most fruit was provided by *D. dacrydioides*, *Podocarpus hallii*, *Prumnopitys taxifolia,* and *Ligustrum sinense* (Fig. 4). *M. ramiflorus* was abundant in the forest but produced very little fruit. *Arbutus unedo* and *Ilex aquifolium* were recorded in faeces from trees outside the patch, approximately 0.20 km and 0.25 km away, respectively.

Seasonality of fruit availability was marked, and this was accentuated by the small number of individuals of many species, particularly at Marsden. The main fruiting period was late summer to early autumn at all sites, and there was very little fruit available from late winter through spring and early summer. The only species with large amounts of fruit available in June and July were *Solanum nigrum* and *Ligustrum sinense* at Marsden and Faulkners, respectively (Figs. 3, 4). At Faulkners, several winter-fruiting species were present in adjacent gardens, e.g., *Ilex aquifolium.* These relative fruiting periods of the adventive and indigenous species resulted in a higher percentage of all fruiting species in autumn and winter being adventive species at Marsden and Faulkners (Fig. 5).

Fruit colour of indigenous species (n = 21) covered a wide range, but most fruits were either red/orange (38%) or purple/black (43%) (Table 3). All the adventive fruits (n = 12) were either red/pink (50%) or black (50%) (Table 3). Most are drupes or small berries less than 8 mm in diameter, and therefore available to all birds, including silvereyes (Table 4). Larger fruits include the arils of *Alectryon excelsus* and the berries of *Arbutus unedo* and *Solanum aviculare*. The average water content of pulp was 80.1%, with only a few species below 75%. *Leycesteria formosa* (95.2%) and *Solanum nigrum* (93.7%), both adventive species, have particularly watery flesh (Table 3).

Average flesh (yield) was 50.6% and ranged from a low of only 29–33% in several *Coprosma* species, to 98% in *Arbutus unedo* and *Solanum aviculare*.

Table 2: *Summary of all native and adventive fruiting plants present (P) at Eves, Marsden, and Faulkners, and recorded as being eaten by birds, either from faeces samples (F) or from observations (O).*

	Location			Endemic birds		Non-endemic birds	Adventive birds				Bird species
	Eves	Marsden	Faulkners	Bellbird	Tui	Silvereye	Blackbird	Chaffinch	Thrush	Starling	(n)
Indigenous fruits											
Alectryon excelsus	P	P			F		F			O	3
Aristotelia fruticosa	P	P		O	F	F	O	F			5
Astelia grandis	P										
Coprosma areolata	P		P								
C. crassifolia			P								
C. grandifolia	P	P		F	O		F				3
C. linariifolia	P										
C. microphylla	P										
C. parviflora	P										
C. propinqua	P										
C. rhamnoides	P					O					1
C. robusta	P	P		F	O	F	F		F		5
C. robusta x *propinqua*	P										
C. rotundifolia	P			F		F					2
C. tenuifolia	P										
Carpodetus serratus	P	P									
Coriaria arborea	P	P		F		F	F				3
Dacrycarpus dacrydioides	P	P	P	O	O	O	O		F	O	6
Fuchsia excorticata	P	P		F		O					2
Hedycarya arborea	P	P									
Ileostylus micranthus	P	P		F	O	F					3
Leucopogon fasciculatus	P					O					1
Macropiper excelsum		P		F	F	F					3
Melicope simplex	P										
Melicytus micranthus			P								
M. ramiflorus	P	P	P	F	F	F	F		F		5
Muehlenbeckia australis	P	P	P	F	F	F	F		F		5
Myoporum laetum		P									
Myrsine australis	P										
Neomyrtus pedunculata	P										
Pennantia corymbosa	P	P				F					1
Pittosporum anomalum	P										
P. eugenioides	P										
P. tenuifolium	P					F					1
Podocarpus hallii	P	P		F	F	F	F	F	F		6
Prumnopitys taxifolia	P	P	P		F	F	F		F	O	5
Pseudopanax arboreus	P	P	P	F	O	F	F				4
Ripogonum scandens	P	P			O						1
Rubus australis	P	P									
Schefflera digitata	P	P				F	F		F		3
Solanum aviculare	P	P				O	O			O	3
Total indigenous fruits	**37**	**22**	**8**	**13**	**13**	**19**	**13**	**2**	**7**	**4**	
Adventive fruits											
Arbutus unedo			P	O		F	O				3
Asparagus asparagoides			P			O					1
Berberis glaucocarpa	P					F	F				2
Cotoneaster franchetii			P				O				1
Crataegus monogyna	P	P	P				F				1
Euonymus europaeus		P	P			O					1
Fragaria vesca		P	P								
Ilex aquifolium		P	P	F							1
Leycesteria formosa	P	P		F	F	F	F		F		5
Ligustrum sinense			P			F	O				2
Lonicera japonica			P			F					1
Passiflora mollissima		P				O	F				2
Prunus avium	P										
Rubus fruticosus			P								
Sambucus nigra	P	P				F				F	2
Solanum nigrum	P	P	P			F	F				2
S. pseudocapsicum			P			O					1
Total adventive fruits	**6**	**8**	**12**	**3**	**1**	**10**	**8**		**1**	**1**	

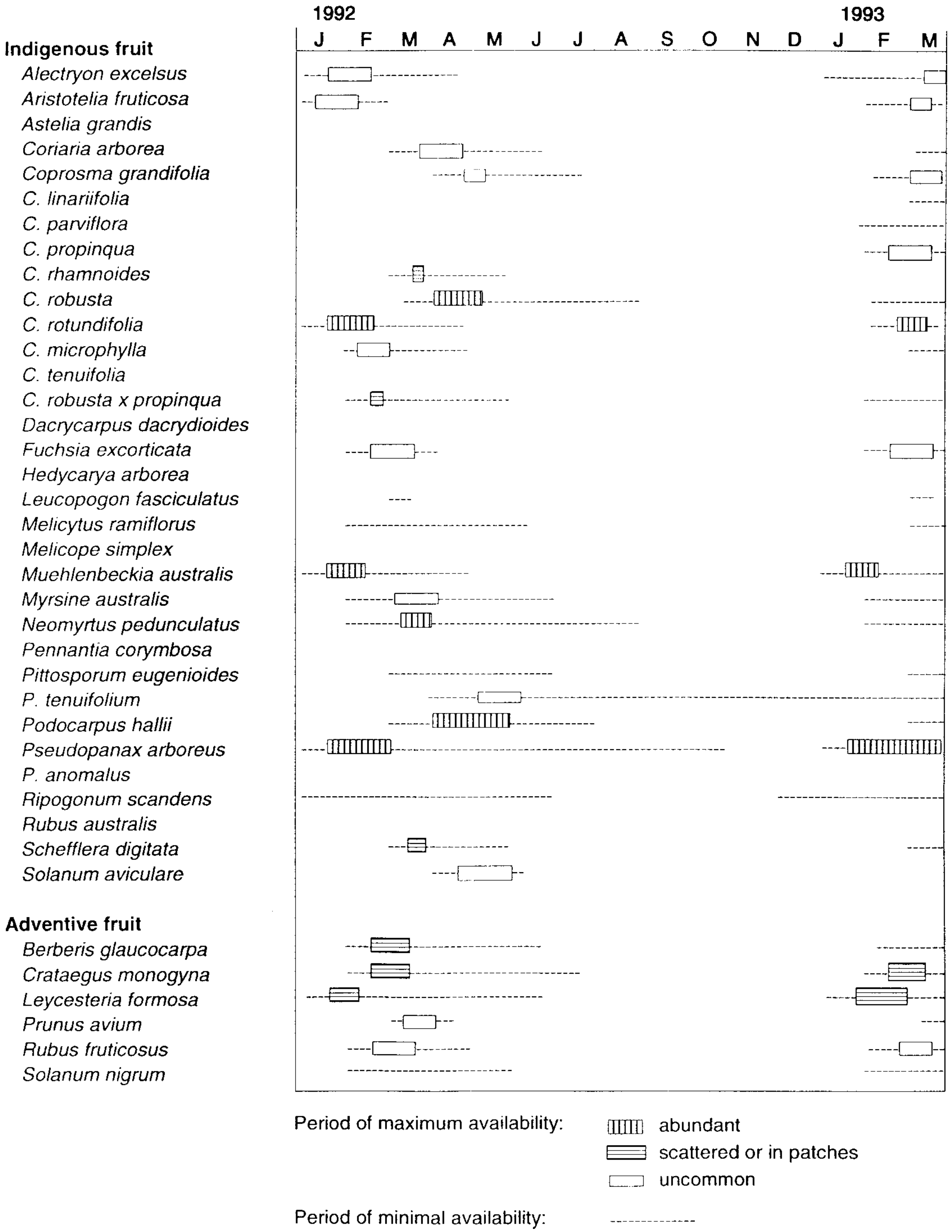

Figure 2: *Availability of ripe indigenous and adventive fruit at Eves, 1992-93.*

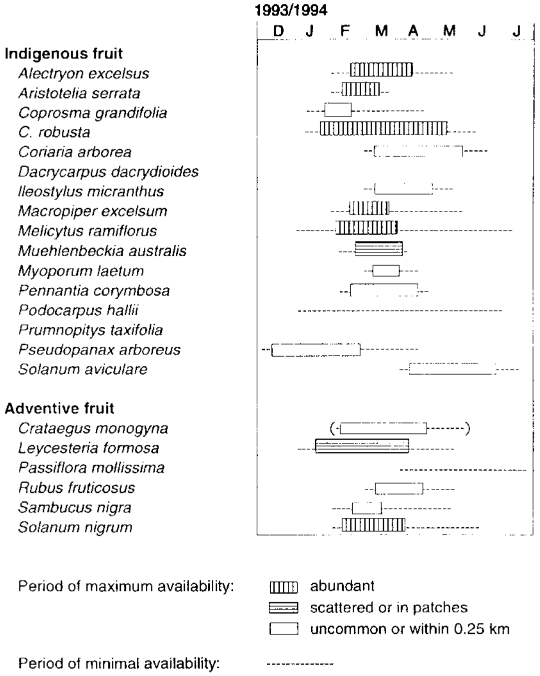

Figure 3: *Availability of ripe indigenous and adventive fruit at Marsden, 1993-94.*

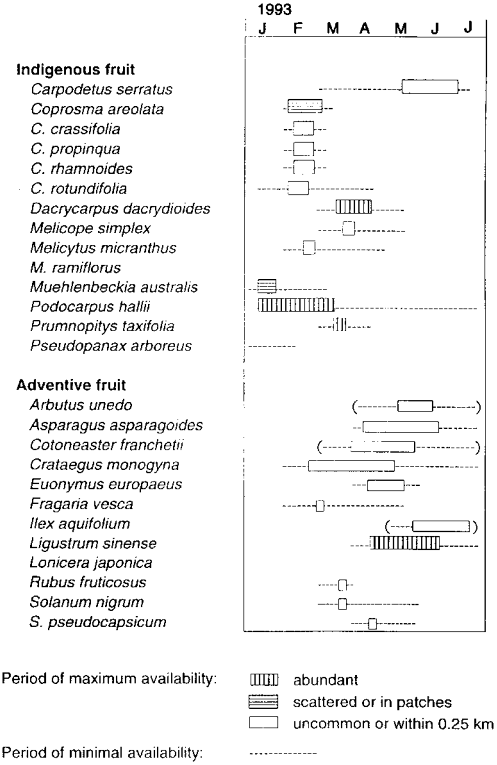

Figure 4: *Availability of ripe indigenous and adventive fruit at Faulkners, 1993.*

There were no significant differences (t test, $P > 0.05$) between fruit characteristics of indigenous and adventive fruits shown in Table 3.

Birds

Six species of frugivorous birds were caught, and these ranged in body weight from 95 g to 12 g, with gapes from 5 mm to 10 mm (Table 4). The relative number of captures per species was: silvereyes > bellbirds > blackbirds > thrushes > tuis > starlings (Table 5). Tuis were relatively more numerous than is indicated by the captures because they frequented mainly higher forest strata, particularly the tall podocarps at Faulkners. They also tended to avoid entanglement more frequently than other birds when they hit the nets. Starlings were rarely seen in the forest at Eves, but frequently flew across the forest. They were common in the podocarps at Faulkners and also in canopy trees of *Alectryon excelsus* at Marsden.

Overall catch rates were highest at Eves, at better than 1.0 bird per net effort in most months. However, the distribution of fruit within the forest structure differed at the three sites, and hence bird activity with respect to the heights of the mist nets also differed. This precludes the data from being a useful measure of the relative number of birds at the three sites. Variability in catch rate between months was attributable mostly to variation in the number of silvereyes (Table 5). Over the summer period January-March there was noticeably lower bird activity during February (Table 5).

Seasonality of diets

The number of fruit species recorded from faeces per month at Eves ranged from 5–11 in autumn (March-May) to 0–4 in winter (June-August) (Table 6). *Podocarpus hallii* was the most frequent species, recorded from October, when it comprised 100% of the records, through to June, when it comprised 54%. During summer and autumn the next most frequent indigenous species were *Pseudopanax arboreus* (7–30%) and *Muehlenbeckia australis* (4–29%); during early winter the main species were *Coprosma robusta* (0–23%) and *P. arboreus* (15%).

Table 3: *Fruit colour, size, number of seeds per fruit, fruit weight, seed weight, flesh weight, and water content of indigenous and adventive fruits eaten by passerine birds. († pur/blck = purple to black).*

	Colour of ripe exocarp	Diameter (mm)		Seeds per fruit		Fruit wet wt (mg)		Flesh dry wt (mg)		Seeds dry wt (mg)		Percent flesh (dry wt)	Flesh water (% fresh)
		$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.		
Indigenous fruits													
Alectryon excelsus	red	13.5	1.1	1.0	-	1100.1	290.1	132.30	14.10	164.6	13.5	44.6	84.0
Aristotelia serrata	pur/blck†	5.0	0.7	4.9	2.1	101.2	3.5	12.53	2.50	19.7	1.7	38.9	80.6
Coprosma areolata	pur/blck	4.0	0.4	4.0	-	52.2	6.9	5.10	0.07	5.6	1.1	47.7	87.3
C. grandifolia	orange	6.5	0.8	4.0	-	195.0	8.0	14.20	2.50	28.0	10.0	33.6	89.9
C. propinqua	blue	5.0	0.7	4.0	-	89.5	5.6	9.20	1.00	6.9	0.4	57.1	88.0
C. robusta	orange	4.6	0.5	4.0	-	82.5	2.1	6.80	1.00	11.9	1.0	36.4	89.0
C. rotundifolia	orange	3.2	0.4	4.0	-	51.0	5.2	4.67	0.58	11.4	1.4	29.0	83.9
Coriaria arborea	black	3.6	0.4	5.1	0.6	26.6	3.0	5.00	0.31	5.8	0.2	46.3	75.9
Dacrycarpus dacrydioides	red	6.6	1.0	1.5	0.3	155.0	11.0	24.67	2.87	27.8	0.3	47.0	76.0
Fuchsia excorticata	pur/blck	6.8	0.6	260.0	-	326.0	80.0	-	-	-	-		-
Ileostylus micranthus	yellow	4.1	0.3	1.0	-	61.5	6.5	5.83	0.60	10.7	1.5	35.3	82.0
Macropiper excelsum	orange	5.5	0.8	127.2	16.2	1706.7	166.6	159.00	4.50	215.5	17.6	42.5	87.5
Melicytus ramiflorus	pur/blck	5.2	0.8	6.5	0.8	59.9	1.8	7.85	0.78	8.8	0.9	47.1	80.9
Muehlenbeckia australis	white	3.7	0.6	1.0	-	21.6	2.0	2.33	0.19	3.2	0.0	42.4	86.4
Pennantia corymbosa	pur/blck	6.3	0.4	1.0	-	201.1	6.2	30.67	1.53	26.6	1.5	53.6	79.5
Peraxilla colensoi	yellow	6.3	0.4	1.0	-	190.7	3.3	42.80	4.00	20.5	4.5	67.6	71.0
Podocarpus hallii	red	5.3	0.8	1.0	-	112.3	13.0	9.90	1.00	8.0	0.9	55.3	89.7
Prumnopitys taxifolia	black	9.5	0.3	1.0	-	558.9	26.1	46.40	5.06	202.6	6.8	18.6	81.0
Pseudopanax arboreus	black	4.7	0.2	2.0	-	22.6	0.2	3.05	0.30	4.7	0.4	39.3	77.3
Schefflera digitata	purple	3.5	0.2	8.3	0.5	23.9	1.8	4.23	0.50	4.2	0.5	50.4	73.0
Solanum aviculare	orange	182.0	19.1	266.0	32.0	5070.0	736.0	1059.27	158.85	15.7	1.1	98.5	77.0
Mean ± S.D.		**14.1**	**8.2**	**33.7**	**17.2**	**486.0**	**240.0**	**75.5**	**48.8**	**38.2**	**14.1**	**46.5** **± 3.5**	**82.0** **± 5.6**
Adventive fruits													
Arbutus unedo	red	300.3	60.1	7.0	2.3	1923.0	200.9	800.00	110.00	14.1	2.2	98.3	42.0
Berberis glaucocarpa	black	7.6	0.4	3.7	0.9	359.5	18.8	50.80	4.70	42.2	4.3	54.6	83.4
Cotoneaster franchetii	red	7.6	0.2	2.0	-	190.0	12.6	31.00	2.10	13.4	1.6	69.8	82.0
Crataegus monogyna	red	9.9	0.5	1.0	-	520.0	19.0	88.30	4.00	78.5	3.3	52.9	75.1
Euonymus europaeus	pink	10.7	1.0	2.2	0.1	297.4	30.6	68.00	1.00	50.2	1.6	57.5	65.0
Ilex aquifolium	red	9.7	0.3	4.0	-	506.0	89.0	74.00	2.00	124.0	14.9	37.4	77.0
Leycesteria formosa	black	8.7	0.7	71.0	9.1	336.5	5.0	14.70	0.20	16.5	0.3	47.1	95.2
Ligustrum sinense	black	5.3	0.3	1.0	-	42.9	1.9	5.70	0.25	8.4	0.4	40.4	72.0
Lonicera japonica	black	5.1	1.0	6.1	3.4	87.0	4.0	12.10	1.33	6.7	1.1	64.4	84.0
Sambucus nigra	black	5.7	0.4	3.2	0.4	117.0	14.0	13.92	-	7.3	0.6	65.8	86.5
Solanum nigrum	black	6.0	0.5	36.2	6.6	146.1	13.2	7.70	1.50	10.1	1.0	43.3	93.7
S. pseudocapsicum	red	11.4	-	37.4	-	802.0	-	173.6	-	135.8	15.3	56.1	68.4
Mean ± S.D.		**32.3**	**23.3**	**14.5**	**6.1**	**443.9**	**132.2**	**111.6**	**61.4**	**42.2**	**12.8**	**57.3** **± 4.5**	**77.0** **13.8**

Table 4: *Mean body weight and gape size of primarily fruit-eating passerines, Nelson study sites.*

Common name	Weight (g) $\bar{x}$	S.D.	n	Gape (mm)
Bellbird	29.2	4.4	54	6
Blackbird	95.6	6.4	31	9
Song thrush	68.0	4.6	12	10
Starling	77.7	-	2	9
Tui	93.3	14.0	6	9
Silvereye	12.3	1.4	311	5

Coprosma rotundifolia and *Neomyrtus pedunculata* were abundant (Fig. 2), particularly on the forest margins, but were rarely recorded in faeces. The most frequent adventive species was *Leycesteria formosa* (8–30%), present continually in the faeces for 6 months from summer to winter. *Berberis glaucocarpa* (6–11%) and *Crataegus monogyna* (2–4%) were recorded during autumn.

At Marsden the number of fruit species recorded from faeces ranged from two in early summer to 14 in autumn (Table 7). There was no sampling in winter when fruit availability was very low (Fig. 3). *Melicytus ramiflorus* (15–39%) was the most frequent species from mid summer to late autumn, followed by *P. arboreus* (4–32%). *Coprosma robusta* (3–23%) and *Macropiper excelsum* (6–14%) were most frequent in late summer and autumn. Several other indigenous species were recorded for short periods at low frequency, partly because they were uncommon at the site (Fig. 3), e.g., *Aristotelia serrata* (2–9%) and *Schefflera digitata* (4–11%). *Podocarpus hallii* (1–8%) was recorded from summer to autumn despite the very low abundance of fruit (Fig. 3).

The most frequent adventive species were *L. formosa* (2–18%), which was present from summer to late autumn, and the herb *Solanum nigrum* (3–22%).

At Faulkners very few (2–5) fruit species were recorded from faeces per month and *P. hallii*

Table 5: *Numbers of primarily fruit-eating birds and other birds caught at three Nelson sites, and overall capture rate per net effort (defined as 100 h per 1 m^2 of net).*

Eves		1992								1993
Bird species	Species total	Feb	Mar	Apr	May	Jun	Aug	Oct	Nov	Jan
Bellbird	36	2	5	10		5	2	5		7
Blackbird	16	2	5	4	1	2		1		1
Silvereye	107	11	21	9	9	9	20	10	3	15
Thrush	5			2		1		2		
Tui	3				1				1	1
Others	39	14	2	6	5	2	4	1		5
Net effort		28.9	13.3	23.9	8.6	17.2	17.2	17.2	13.5	21.9
Birds per net effort		1.0	2.5	1.3	1.9	1.1	1.5	1.1	0.3	1.4

Faulkners		1993				
Bird species	Species total	Feb	Mar	Apr	May	Jul
Bellbird	7		1	5	1	
Blackbird	6	2	2		1	1
Silvereye	78	2	23	25	7	21
Thrush	2			2		
Others	15		2	8	4	1
Net effort		40.1	41.0	75.2	51.0	46.7
Birds per net effort		0.1	0.7	0.5	0.3	0.5

Marsden		1993/1994						
Bird species	Species total	Dec	Jan	Feb	Mar	Apr	May	Jun
Bellbird	20	3	5		7	2	3	
Blackbird	7			2		2	3	
Silvereye	165	5	58	22	60	10	8	2
Starling	2			2				
Thrush	5		2	1			2	
Tui	5		1	3	1			
Others	84	7	19	8	4	5	21	20
Net effort		41.1	63.7	62.7	66.7	57.3	31.0	15.1
Birds per net effort		0.4	1.4	0.6	1.1	0.3	1.2	1.5

Table 6: *Monthly relative frequency of occurrence of fruits in all birds (1992-93) at Eves. Values are the number of occurrences of individual species as a percentage of all occurrences in all birds. (* = adventive).*

	Oct	Jan	Feb	Mar	Apr	May	Jun	Aug
Occurrences (n):	18	30	27	35	35	14	18	16
Fruit species								
Aristotelia serrata			3.7					
*Berberis glaucocarpa**				11.1	6.0			
Coprosma grandifolia				2.2	4.5			
C. robusta				4.4	10.4		23.1	
C. rotundifolia		10.7						
*Crataegus monogyna**				2.2	4.5			
*Leycesteria formosa**		25.0	29.6	6.7	11.9	26.7	7.7	
Melicytus ramiflorus				8.9	4.5	6.7		
Muehlenbeckia australis		17.9	29.6	4.4	6.0			
Podocarpus hallii	100	17.9	7.4	31.1	25.4	53.3	53.8	
Pseudopanax arboreus		28.6	29.6	28.9	14.9	6.7	15.4	
*Rubus fruticosus**					3.0			
Schefflera digitata					9.0	6.7		
No. of fruit species:	**1**	**5**	**5**	**9**	**11**	**5**	**4**	**0**

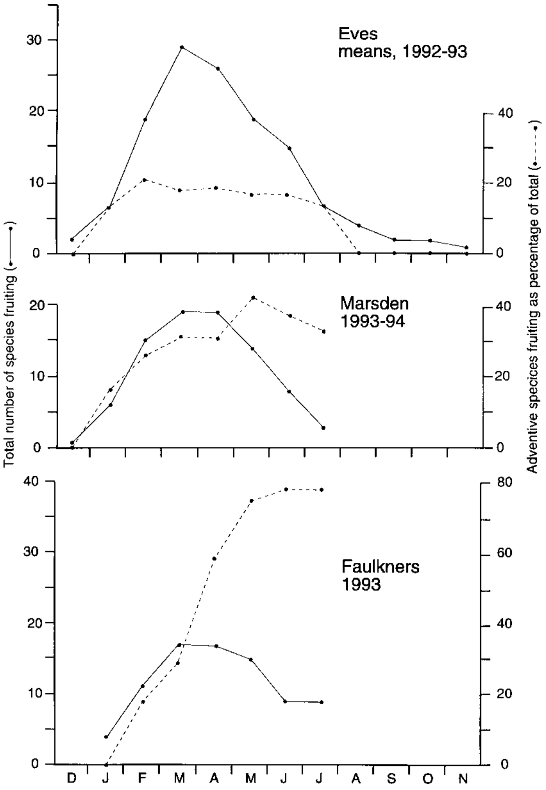

Figure 5: *Total number of species fruiting, and adventive species fruiting as a percentage of the total at Eves, Marsden, and Faulkners.*

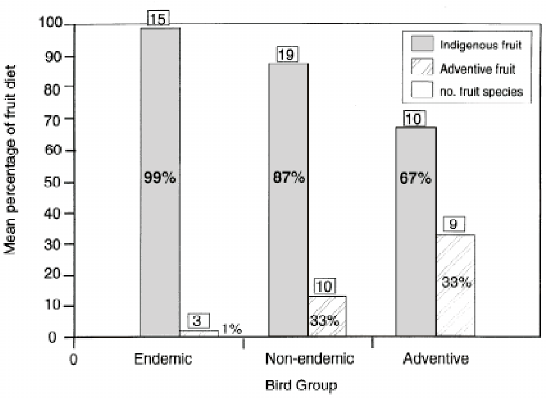

Figure 6: *Relative importance of indigenous and adventive fruits in the diet of endemic, non-endemic, and adventive birds, Nelson area.*

(27–83%) was dominant throughout the limited sampling period (Table 8). *Prumnopitys taxifolia* (17–67%) and *Dacrycarpus dacrydioides* (7–28%) would be under-represented because of the difficulty of catching birds feeding in the forest canopy. Two adventive species, *Arbutus unedo* (18–35%) and *Ligustrum sinense* (3–27%), were most frequent in winter.

Diet of endemic birds

Fruit was present in 66–100% of bellbird faeces at all sites. It was predominantly *Podocarpus hallii* (Tables 9–11), with *C. robusta* at Eves and Marsden. The only adventive fruits recorded in faeces were a small percentage of *Leycesteria formosa* at Eves (Table 9) and one record of *Ilex aquifolium* at Faulkners (Table 11). Many bellbirds caught at Eves voided liquid faeces, and this was probably mainly honeydew from the margarodid scale insect *Ultracoelostoma brittini* on *Nothofagus solandri.*

Insufficient tuis were caught to draw conclusions as to their diet from the faeces, although 66–100% contained fruit (Tables 9–11). Field observations at Eves and Faulkners indicate that their fruit diets were dominated by *D. dacrydioides, P. hallii*, and *Prumnopitys taxifolia.* At Marsden, where there was little podocarp fruit, their diets comprised an assortment of other indigenous fruits. The only record of adventive fruit was a small amount of *Leycesteria formosa* at Eves (Table 9).

Diet of non-endemic and adventive birds

Fruit was present in the faeces of most (78–86%) silvereyes. The main indigenous fruits at Eves and Faulkners on a frequency or dry weight basis were *P. hallii* and *Pseudopanax arboreus*, whereas no single species dominated at Marsden. The faeces contained a wide range of adventive fruits at the three sites. *Leycesteria formosa* (15%) and *Ligustrum sinense* (14%) were the third most frequent fruits in faeces at Eves and Faulkners respectively. Several fruits recorded in the faeces have a mean diameter almost twice the 5 mm gape of silvereyes (*Crataegus monogyna*, *L. formosa*, and *Prumnopitys taxifolia*, Table 3).

Fruit was present in 50–71% of blackbird faeces at the three sites. *L. formosa* was the most frequent fruit at Eves, and together with *Berberis glaucocarpa* and *Crataegus monogyna* adventive species comprised 70% of the fruit dry weight (Table 9). *P. hallii* was the main indigenous species at Eves and *Prumnopitys taxifolia* at Faulkners (Table 11). Several other indigenous fruits contributed to blackbird diets at Marsden, particularly *Alectryon excelsus* arils

Table 7: *Monthly relative frequency of occurrence of fruits in all birds (1993-94) at Marsden. Values are the number of occurrences of individual species as a percentage of all occurrences in all birds. (* = adventive).*

	Dec	Jan	Feb	Mar	Apr	May
Occurrences (n):	8	47	30	69	17	19
Fruit species						
Alectryon excelsus			3.0	1.8		
Aristotelia serrata		1.7	9.1			
Coprosma grandifolia				1.8		
C. robusta			3.0	8.9	23.1	14.3
Cordyline australis						3.6
Coriaria arborea	50.0	5.1		1.0	3.8	3.6
Fuchsia excorticata	50.0	1.7				
Ileostylus micranthus						7.1
*Leycesteria formosa**		11.9	18.2	1.8	3.8	14.3
Macropiper excelsum			6.1	14.3	11.5	7.1
Melicytus ramiflorus		39.0	24.2	27.7	15.4	17.9
Muehlenbeckia australis		6.8	9.1	1.8		
*Passiflora mollissima**						3.6
Pennantia corymbosa				2.7		
Pittosporum tenuifolium					3.8	
Podocarpus hallii		1.7		8.0	7.7	3.6
Prumnopitys taxifolia				0.9		
Pseudopanax arboreus		32.2	15.2	3.6	11.5	
*Sambucus nigra**			3.0	3.6		7.1
Schefflera digitata					11.5	3.6
*Solanum nigrum**			3.0	22.2	7.7	14.3
Unidentified pulp*			6.1			
No. of fruit species:	**2**	**8**	**11**	**14**	**10**	**12**

Table 8: *Monthly relative frequency of occurrence of fruits in all birds (1993) at Faulkners. Values are the number of occurrences of individual species as a percentage of occurrences in all birds. († = faeces with both seeds and pulp, and only pulp; * = adventive)*

	Feb	Mar	Apr	May	Jun
Occurrences (n):	4	29	35	19	22
Fruit species					
Arbutus unedo†				18.5	35.0
Dacrycarpus dacrydioides			28.0	7.4	
*Ilex aquifolium**			2.9		
Ileostylus micranthus			2.9		
*Ligustrum sinense**			2.9	14.8	27.5
*Lonicera japonica**					10.0
Podocarpus hallii	33.3	83.3	66.0	59.3	27.5
Prumnopitys taxifolia	66.6	16.7			
*Solanum nigrum**					2.9
No. of fruit species:	**2**	**2**	**5**	**4**	**5**

which comprised an estimated 58% of fruit dry weight (Table 10). Some of this is taken from fallen fruit on the ground. Adventive species were infrequent in blackbird faeces at Marsden and Faulkners, although at the latter site they were observed eating *Ligustrum sinense* and *Arbutus unedo*.

Thrushes had the lowest presence of fruit in their faeces overall (14–100%) at the three sites. The small number of samples is sufficient only to indicate that their faeces contain fruit of both indigenous and adventive species, including *L. sinense* at Faulkners.

Starlings were frequently observed eating podocarp fruit at Faulkners, but they rarely descended to the level of even the tall nets except at Marsden, where two were caught feeding on *Sambucus nigra* (Table 10).

Several other bird species were caught (Table 13), but only chaffinch faeces contained fruit. Of the 44 caught, 32 faeces were examined and 6 contained

Table 9: *Composition of fruit component of bird diet at Eves. († = not determined)*

	Bellbird (n = 36)		Silvereye (n = 108)		Tui (n = 3)		Blackbird (n = 16)		Thrush (n = 5)	
	% presence	% dry wt	% presence	% dry wt	% presence	% dry wt	% presence	% dry wt	% presence	% dry wt
Indigenous fruit										
Coprosma grandifolia	2.8	1.1	1.9	0.2			6.3	1.8		
C. robusta	13.9	9.6	3.7	1.0			18.8	0.8		
C. rotundifolia	2.8	0.4	0.9	0.4						
Melicytus ramiflorus			5.6	5.9			12.5			
Muehlenbeckia australis	8.3	0.9	10.3	6.6			18.8	0.6		
Podocarpus hallii	44.4	85.9	25.2	66.6	100	99.0	25.0	23.3	20.0	17.0
Pseudopanax arboreus	8.3	1.1	29.0	12.2			18.8	0.6		
Schefflera digitata			3.7	0.7			12.5	2.8	20.0	83.0
Adventive fruit										
Berberis glaucocarpa			1.9	2.1			31.3	23.7		
Crataegus monogyna			1.9	0.2			12.5	43.6		
Leycesteria formosa	2.8	1.0	15.0	3.9	30.0	1.0	50.0	2.6		
Rubus fruticosus			1.9	†						
% presence of fruit	**74.0**		**86.0**		**66.6**		**71.0**		**14.0**	
Fruit species per defecation (x̄ ±S.D.)	**1.3 ± 0.6**		**1.6 ± 1.1**		**1.0**		**2.0 ± 0.8**		**1.0**	

Table 10: *Composition of fruit component of bird diet at Marsden. († = not determined; ‡ = estimated from mean values)*

	Bellbird (n = 20)		Silvereye (n = 106)		Tui (n = 4)		Blackbird (n = 11)		Starling (n = 2)		Thrush (n = 5)	
	% presence	% dry wt	% presence	% dry wt	% presence	% dry wt	% presence	% dry wt	% presence	% dry wt	% presence	% dry wt
Indigenous fruit												
Alectryon excelsus							18.2	57.8				
Aristotelia serrata			4.2	2.0	50.0	14.0						
Coprosma grandifolia	5.0	8.4	3.0	1.8								
C. robusta	25.0	25.5	10.3	11.3			9.1	0.8			50.0	91.0
Cordyline australis			2.4	†								
Coriaria arborea	5.0	0.1	2.4	0.5			18.2	2.9				
Fuchsia excorticata	5.0	0.2										
Ileostylus micranthus	5.0	2.8	3.0	1.5								
Macropiper excelsum			13.9	6.1	50.0	42.0						
Melicytus ramiflorus	20.0	5.4	40.0	19.3	75.0	26.8	27.3	17.4			50.0	8.0
Muehlenbeckia australis	5.0	0.5	6.1	3.4	25.0	2.2					20.0	0.6
Pennantia corymbosa			4.2	23.5								
Pittosporum tenuifolium			2.4	†								
Podocarpus hallii	35.0	55.3	4.8	10.1			18.2	6.6				
Prumnopitys taxifolia					50.0	15.0						
Pseudopanax arboreus	10.0	2.0	18.8	11.7			9.1	0.3				
Schefflera digitata			4.8	0.5								
Adventive fruit												
Leycesteria formosa			13.9	1.0							20.0	0.1
Sambucus nigra			5.5	5.5					100	100		
Solanum nigrum			24.2	1.9			9.1	3.1				
Passiflora mollissima							9.1	11.1‡				
Unidentified fruit pulp							9.1				20.0	†
% presence of fruit	**66.6**		**78.0**		**100.0**		**50.0**		**100**		**60.0**	
Fruit species per defecation (x̄ ±S.D.)	**1.6 ± 0.7**		**1.6 ± 0.8**		**2.0 ± 0.7**		**1.8 ± 0.3**		**1.0**		**2.3 ± 0.4**	

fruit; one contained a *P. hallii* seed and five contained *L. formosa* seeds (mean 13, range 2–56). One contained *Aristotelia serrata* pulp without seeds.

Some individual seeds were examined microscopically, but there was very little sign of broken or damaged seeds from the frugivorous birds, even of relatively soft seeds such as those of *Solanum nigrum*. In contrast, the faeces of seed-eating finches were always a finely ground mush of vegetative matter without whole seeds, although seed parts and occasionally whole seeds were sometimes detectable in chaffinch faeces.

Discussion

The three sites studied had different vegetation structure and composition, and were sampled in

Table 11: *Composition of the fruit component of the diet at Faulkners. († = faeces with seeds amongst the pulp; ‡ = faeces with no seeds in the pulp; n.d. = not determined)*

	Bellbird (n = 7)		Silvereye (n = 106)		Blackbird (n = 8)		Thrush (n = 3)	
	% presence	% dry wt	% presence	% dry wt	% presence	% dry wt	% presence	% dry wt
Indigenous fruit								
Dacrycarpus dacrydioides			10.5	9.7				
Ileostylus micranthus	12.0	1.0	0.8	0.1				
Podocarpus hallii	86.0	96.0	60.1	51.9			33.3	6.8
Prumnopitys taxifolia			4.8	14.7	100	100	33.3	43.5
Adventive fruit								
Arbutus unedo (seeds)†			4.0	9.1				
A. unedo (pulp)‡			13.8	n.d.				
Ilex aquifolium	12.0	3.0						
Ligustrum sinense			13.8	14.1			33.3	49.7
Lonicera japonica			3.2	0.3				
Solanum nigrum			0.8	0.1				
Unidentified pulp			2.4	n.d.				
% presence of fruit	**100**		**78.0**		**66.6**		**100**	
Fruit species per defecation ($\bar{x}$ ± S.D.)	**1.1 ± 0.3**		**1.4 ± 0.9**		**1.0**		**1.0**	

Table 12: *Rank order of the three most important dispersers of some of the fruiting plants in England that are weeds in New Zealand. (from Snow and Snow, 1988)*

	Hedera helix	*Crataegus monogyna*	*Ligustrum* spp.	*Ilex aquifolium*	*Sambucus nigra*
Birds in New Zealand					
Blackbird	1	1	1	1=	2=
Song thrush	2		3		2=
Starling	3		2=		1
Birds not in New Zealand		2, 3	2=	1=, 2	

different years and partly in different seasons, yet present a similar picture as to the relationships between the endemic, non-endemic, and adventive birds and the native and adventive fruits. The relationship for the two endemic birds, bellbirds and tuis (family Meliphagidae), is particularly important in evaluating the impact of weeds on biodiversity conservation.

Bird diets

The relative importance of nectar (including honeydew), fruit, and invertebrates in the diet of bellbirds and tuis has been debated (Craig, Stewart and Douglas, 1981). This is partly because the study

Table 13: *Numbers of non-frugivorous bird faeces examined and the presence of seeds. († =* Leycesteria formosa *(5),* Podocarpus hallii *(1))*

Common name	Site Eves	Marsden	Faulkners	With seeds
Chaffinch	16	22	6	6†
Fantail	2	7	5	0
Goldfinch	5	7	-	0
Greenfinch	7	4	1	0
Grey warbler	-	12	2	0
House sparrow	-	1	-	0
Hedge sparrow	3	4	1	0
Kingfisher	-	1	-	0
Shining cuckoo	-	3	-	0
Yellowhammer	-	1	-	0

methods used, including our own, have not determined the absolute importance of these items in their diet. Two previous studies in the South Island based on direct observations of bird behaviour (Gaze and Clout, 1983; O'Donnell and Dilks, 1994) emphasised the greater importance of invertebrates and nectar or honeydew as compared with fruit, for both tuis and bellbirds. Our data for different forest types show that fruit is a major component of the diet of bellbirds for much of the summer and autumn. The importance of fruit was possibly related to competition for honeydew from wasps (*Vespula* spp.) at Eves (Moller and Tilley, 1989), where there was a noticeable increase in the frequency of watery faeces lacking fruit in May, after a sharp decline in wasps with the onset of wet, cold weather. This sharp switch back to honeydew foraging was convincingly demonstrated for kaka (*Nestor meridionalis*) by Beggs and Wilson (1991). At Faulkners there was negligible honeydew because of the absence of *Nothofagus* species, and few flowering species to provide nectar (Table 2).

Bellbirds showed a preference for fruit of *Coprosma robusta*, and especially *P. hallii*, as they do elswhere in New Zealand (Beveridge, 1964; Warburton *et al*., 1992; O'Donnell and Dilks, 1994). The latter is reflected in their preference for the upper canopy layers of podocarp/angiosperm forest (Fitzgerald, Robertson and Whitaker, 1989; Spurr, Warburton and Drew, 1992). The high consumption by bellbirds of *P. hallii* fruits in our study, despite the abundant fruit of other species in clearings and on forest edges, may therefore reflect a preference for foraging in the forest canopy, rather than any compelling preference for this fruit or any evolutionary linkage with *P. hallii*. Even so, the high consumption by bellbirds of *P. hallii* and their virtual neglect of most other species calls for an explanation in view of their potentially broad diet (Craig, Stewart and Douglas, 1981), as reflected in their ability to live in a wide range of vegetation types with and without abundant fruit (Clout and Gaze, 1984; Craig, Stewart and Douglas, 1981; Moffat and Minot, 1994), and the large number of fruit species they are known to consume (Burrows, 1995; O'Donnell and Dilks, 1994). In contrast, bellbirds clearly ignore the adventive fruits encountered in this study, just as they did the abundant fruit of the adventive *Berberis darwinii* in Dunedin (Allen and Lee, 1992).

Our limited faecal samples and casual field observations suggest that tuis consume a similar range of indigenous fruit to bellbirds, but with the inclusion of larger fruits in accordance with their larger size and gape, e.g., *Alectryon excelsus* and *P. taxifolia*. Their ability to consume these larger fruits possibly makes them less selective for *P. hallii* than bellbirds where there is a limited diversity of tall trees. Tuis appear to eat very little adventive fruit in these forest patches, with the exception of *Leycesteria formosa,* which they have also been observed consuming in other forest patches in the Nelson region (J. Tilley, *pers. comm.*, Landcare Research, Nelson). Like bellbirds, tuis never visited the large displays of *Ligustrum sinense* fruit at Faulkners. In Auckland, where tuis are common in and around urban areas, they use indigenous fruits and those of the adventive *Ligustrum lucidum* and *L. sinense* extensively in autumn (Bergquist, 1987).

The relative unimportance of adventive fruits in the diets of tuis and bellbirds may simply reflect their unwillingness to descend to the generally lower heights of these fruit, but this appears unlikely because of the consumption of *C. robusta* by bellbirds and some *Leycesteria formosa* by tuis, two shrubs that are no taller than the abundant adventive species they largely ignore, e.g., *Berberis glaucocarpa* at Eves.

Silvereyes have the most varied fruit diet, with 29 indigenous species and 10 adventive species recorded in their faeces or by observation of their feeding (Table 2) in just these three forest patches. They also eat a very wide range of invertebrates in the Nelson area (Moeed, 1979). A similarly highly varied fruit diet has been noted in South Westland (O'Donnell and Dilks, 1994) and in Australia, involving both indigenous fruits (French, Dowd and Lill, 1992) and adventive fruits (Cleland, 1952). Silvereyes have only a 5 mm gape, but at least three fruit species identified from their faeces have a mean diameter well in excess of 5 mm. *Leycesteria formosa* fruits (8.7 mm ± 0.7) are exceptionally watery and soft, and are eaten either by pecking the drupes or swallowing them but only smaller fruits of *P. taxifolia* (9.5 mm ± 0.3) and *C. monogyna* (9.9 mm ± 0.3) could be swallowed by silvereyes. When deriving theoretical dispersal abilities for extinct birds and the ecological consequences of their demise (e.g., Clout and Hay, 1989), a very liberal interpretation of a bird's ability to swallow fruits of a particular size should be considered.

Blackbirds and thrushes consume similar proportions of indigenous and adventive fruit species but blackbirds consume fruit more frequently, as they do in Europe (Herrera, 1984a; Snow and Snow, 1988). Blackbirds in particular consume large quantities of several adventive species, including *Berberis glaucocarpa* and *Crataegus monogyna,* which are largely ignored by endemic birds.

Starlings appeared to consume large quantities of podocarp fruit, as they do in the North Island (Beveridge, 1964). Otherwise their fruit diet in the three forest patches appears to be limited in comparison with thrushes or blackbirds, and likewise Burrows (1995) listed only four species of indigenous plants eaten by starlings. They appear to be attracted mainly to species with heavy crops such as the podocarps, *Cordyline australis*, and *Fuchsia excorticata* on Banks Peninsula (C. Burrows, *pers. comm.*, University of Canterbury, Christchurch). In this study starlings were netted only in the vicinity of a single heavily fruiting *Sambucus nigra* bush which provides them with a large food source on some parts of Banks Peninsula (Williams, 1983). The preference of starlings for large fruit displays may be partially explained by morphological limitations, such as wing shape, which limits the ways in which they can take fruit (Snow and Snow, 1988), and their tendency to feed on fruit during autumn, when they form large flocks, as they do in Britain (Snow and Snow, 1988), North America (White and Stiles, 1991; Holthuijzen and Sharik, 1984) and Australia (Cleland, 1952).

Chaffinches are often mentioned as eating fruit (e.g., Williams, 1969) but our results show that fruit forms a negligible component of their diet. However, the presence of small numbers of *L. formosa* seed in several faeces (Table 13) is further evidence of the wide acceptability of this adventive plant. There is no evidence from our results that most of the other small introduced passerines such as goldfinches (*Carduelis carduelis*) or greenfinches (*Chloris chloris*) consume fruit, although the latter have been recorded consuming large quantities of *Lycium ferocissimum* in Hawkes Bay (MacMillan, 1981). The few house sparrows (*Passer domesticus*) caught never had fruit in their faeces, but they have been regularly observed consuming *Solanum laciniatum* pulp presumably containing the small and closely intermixed seeds (P.A.W., *pers. obs.*).

Numerous studies have attempted to relate fruit characteristics to diet choice in frugivorous birds, particularly blackbirds amongst those studied here (Herrera, 1984a; Sorensen, 1981; Snow and Snow, 1988). The relationships are highly complex and include many factors, as listed by Stiles (1993). Fruit chemical composition has received most attention, but proximal nutrient analysis has been largely unsuccessful because it ignores the complexities of bird digestion (Martinez del Rio and Restrepo, 1993). Starlings, for example, have a lower glucose uptake but a faster amino acid uptake than some other frugivores, which places their digestive system nearer to that of a carnivore (Obst, 1991). Their lack of sucrase activity also limits the range of fruits they are able to fully utilise to those with low sucrose : glucose ratios (Martinez del Rio and Stevens, 1989). These relationships may restrict the number of adventive and indigenous New Zealand fruit species they consume.

Despite the truism concerning the failure of proximal analysis (Martinez del Rio and Restrepo, 1993), fruits with high lipids (greater than 10%) are the dominant and/or preferred food of most highly frugivorous birds (Stiles, 1993). The Podocarpaceae have a high oil content in many tissues (Cambie, 1976), but the receptacles of *P. hallii* - which are important to many birds, as shown by this study and others (Beveridge, 1964) - have less than 2% lipids (P.A.W., *unpubl. data*). The adventive fruits in this study are similarly low in lipids, with the exception of *Hedera helix* and *Euonymus europaeus* (Debussche, Cortez and Rimbault, 1987).

The relative contribution of indigenous and adventive fruits to the diets of endemic, non-endemic, and adventive birds in this study can be summarised as follows (Table 1, Fig. 6). Endemic birds, especially bellbirds, use little adventive fruit apart from *Leycesteria formosa*, but they consume large quantities of indigenous fruit. Non-endemic birds, in this context only silvereyes, consume virtually any fruits they are capable of swallowing from both fruit groups, with the result that adventive fruits are important in their diet. Adventive birds consume a wide range of indigenous and adventive fruits.

From the perspective of the indigenous honeyeaters, which are the only widespread endemic fruit-eating birds apart from New Zealand pigeons, the adventive weed species studied here represent an inferior food source in as much as the fruits they bear are largely ignored. Thus, it can be inferred that where adventive fruiting trees and shrubs pre-empt sites or replace indigenous species, they create an inferior habitat for indigenous frugivores, at least during the life of the adventive vegetation.

Adventive fruits extend the period of fruit availability into winter, when there are few indigenous fruits available in these small northern South Island forest remnants (Figs 2, 3). In the New Zealand (Southern Hemisphere) context these relative fruiting times have arisen because most woody weeds were introduced for horticulture (Timmins and Williams, 1987), and specifically to provide colour in winter gardens. Many of the more successful invasive species such as *Crataegus monogyna*, *Hedera helix*, *Ilex aquifolium*, and *Ligustrum* spp. are from the Northern Hemisphere (Webb, Sykes and Garnock-Jones, 1988), where fruiting coincides with abundant late autumn and winter migratory birds (e.g., Snow and Snow, 1988). In one study the number of species fruiting increased slightly from 12 in late summer to 15 in winter (Snow and Snow, 1988, Fig. 1). In New Zealand, where bird migrations are mainly local, the numbers of indigenous fruits available in winter are reduced, as shown in our small forest patches in Nelson, and at a regional scale on Banks Peninsula (from 29 to 17; Burrows, 1995), or in several central North Island forests (from 19 to 11; Leathwick, 1984).

The main bird species to benefit from the winter availability of the adventive fruits in the Nelson area are silvereyes and blackbirds. McCann (1953) also recorded blackbirds as being the main species eating *Solanum nigrum* during winter in the North Island. This relative benefit may not apply in different bioclimatic zones of New Zealand, for example in urban Auckland, where tuis selectively consumed *Ligustrum* spp. fruit during winter, even when indigenous fruits (*Pseudopanax arboreus*, *Prumnopitys taxifolia*) were available (Bergquist, 1987, table 2). These relationships have similarities to those reported from North America, where adventive species extended the seasonal availability of fruits (Sallabanks, 1993; White and Stiles, 1991).

Birds as weed dispersers

The effectiveness of seed dispersal is the contribution a disperser makes to the future reproduction of a plant (Herrera and Jordano, 1981; Schupp, 1993). Several aspects of the dispersers' behaviour and physiology contribute to their effectiveness, of which the quantity of fruit consumed is a major component. In this respect the colonists brought to New Zealand the primary dispersers (blackbirds, thrushes, and starlings) of a range of European woody fruiting plants (Snow and Snow, 1988) that have since become weeds of conservation land (Williams and Timmins, 1990). Foremost among these dispersers is the blackbird, which rapidly penetrated indigenous forest (Philpott, 1918; Beveridge, 1964) and which is now especially abundant on forest margins (Moffat and Minot, 1994) as well as in urban areas. Blackbirds are versatile and efficient fruit handlers and consumers that defecate most of the seeds they consume (Herrera and Jordano, 1981; Snow and Snow, 1988). However, the presence of *Alectryon excelsum* and *Prumnopitys taxifolia* pulp or skins in their faeces, and the absence of seeds, suggests that they are occasionally pulp predators (*sensu* Howe, 1977; Courtney and Sallabanks, 1992), or they regurgitate the seeds, or else they process the large seeds more quickly, leaving the pulp in the gut to be digested (e.g., Courtney and Sallabanks, 1992). Whatever their mode of feeding, there is possibly a reduction in the volume or efficiency of seed dispersal. Blackbirds are known to regurgitate *Crataegus monogyna* seeds in the field and in the laboratory (Sorensen, 1981, 1984), but these seeds are most frequently defecated (Snow and Snow, 1988). *Alectryon excelsum* seedlings appear in a wide range of garden and other sites frequented by blackbirds in Nelson city, indirect evidence suggesting that blackbirds are partly responsible for seed dispersal, whatever the manner in which they handle the seeds.

Swallowed fruits take approximately 30 minutes to be defecated from blackbirds (Barnea, Yom-tov and Friedman, 1991; Sorensen, 1984), and enhanced germination relative to hand-cleaned seeds has been reported (Barnea, Yom-tov and Friedman, 1991; Holthuijzen and Sharik, 1984). The post-foraging behaviour of birds can be an important component of their dispersal efficiency (Izhaki, Walton and Safriel, 1991; Herrera and Jordano, 1981; Herrera, 1984a; Schupp, 1993), and the behaviour of blackbirds, thrushes, and starlings appears to be superior to that of endemic frugivorous passerines as far as weed dispersal is concerned. These birds not only frequent urban areas where many weeds originate (Timmins and Williams, 1991), but in the Nelson area they also move between such areas and a wide range of urban and rural vegetation types more frequently and in greater numbers than endemic birds. Frequent movements between different kinds of vegetation - for example, from stands of moderately tall woody vegetation with weeds to shorter vegetation where weeds are likely to become established - also facilitate weed invasions (P.A. Williams and B.J. Karl, *pers. obs.*). Non-endemic silvereyes behave similarly, but are less likely to introduce woody weeds to areas of herbaceous vegetation because they seldom forage on the ground, and because some species, such as *Crataegus monogyna* and *Prunus* spp., have fruits mostly too large for silvereyes. However, silvereyes are the most important indigenous disperser of a very wide range of weeds, and their tendency to spend only a short period on any individual bush (French, O'Dowd and Lill, 1992) will assist this process. New Zealand pigeons are known dispersers of several weeds, but low local densities limit their impact.

Flocking behaviour and the timing and distance of seasonal movements have an influence on the seed dispersal efficiency of birds because these factors are likely to increase the number of dispersers at critical times (French, 1992; Herrera, 1984a, b; Schupp, 1993; Snow and Snow, 1988). Bellbirds, tuis, and silvereyes are known to move seasonally between montane and lowland zones (Wilson, Taylor and Thomas, 1988). In this study, the few autumn and winter months sampled produced a similar number of birds per net effort to the summer months, especially in the most intact forest remnant at Eves. This minimal seasonal variation in bird numbers and indigenous fruit abundance, albeit from very small forest patches, has stronger similarities to some Australian forests (Forde, 1986; French, 1992) than to Europe, where both maximum fruit abundance and bird numbers correspond to autumn and winter (e.g., Stiles, 1980; Herrera, 1984a). Apart from the behaviour of starlings mentioned above, juvenile blackbirds disperse over several kilometres in autumn (Bull, 1953, and *pers. comm.*), and silvereyes undertake local migrations to urban areas, particularly in autumn and winter (Kikkawa, 1962). Indication of their potential for movement within the overall study area was a bird banded at Faulkners being caught at Marsden, 22 km away, the following year. This local movement brings them in contact with adventive fruit when it is relatively more abundant than indigenous fruit, as discussed above, and hence more likely to be consumed and dispersed, e.g., *Ligustrum sinense* and *Arbutus unedo* at Faulkners. The latter was one of only two species of weed seed in faeces that did not originate from inside the forest patches. This illustrates a propensity for weed dispersal into reserves closest to towns, as is Faulkners of the three studied here, having the highest number of weeds, irrespective of other characteristics such as reserve size and shape (Timmins and Williams, 1991).

An important result of the interaction primarily between adventive birds, particularly blackbirds, and silvereyes with weed species is the development of extensive new habitats, e.g., *Berberis darwinii* scrub (Allen and Lee, 1992), *Crataegus monogyna* scrub (Williams and Buxton, 1986), *Chrysanthemoides monilifera* shrublands (Partridge, 1994), and *Ribes sanguineum* shrublands (Williams, 1984). Our results suggest that these habitats offer more suitable fruit to the adventive and non-endemic birds primarily responsible for their formation than to endemic birds. In contrast, where there are few indigenous shrubs or birds, such as in extensive areas of *Ulex europaeus* (Lee, Allen and Johnson, 1986) or *Cytisus scoparius* (Williams, 1983), adventive birds and silvereyes will play a critical role in the dissemination of the initially colonising indigenous fruiting plants (*Coprosma*, *Melicytus*, *Pseudopanax*), and hence in habitat creation for indigenous birds. The outcome for biodiversity conservation of the seed rain from adventive birds, and the recently self-established silvereye, depends on their seed loads and the nature of the receiving vegetation.

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