

Possum (*Trichosurus vulpecula*) diet in a mast and non-mast seed year in a New Zealand *Nothofagus* forest

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Abstract: The annual diet of possums (*Trichosurus vulpecula*) during both a beech (*Nothofagus*) mast fruiting year and a non-mast year in the simple beech forests of the North Branch of the Hurunui Catchment, eastern South Island, New Zealand, was determined by sorting the contents of 270 possum stomachs, collected between December 1999 and December 2001. Beech flowers and seeds contributed 46.1% to annual diet during the mast year, but were not eaten during the non-mast year. Beech foliage and bark made up 13.2% and 45.0% of annual diet in the mast and non-mast years, respectively. Fungi, herbs and grasses together comprised 23.1% and 42.4% of the annual diet in the mast and non-mast years, respectively. Diet varied with altitude and distance down the valley, principally in the relative contributions of foods from the three beech species present, which reflected local canopy composition. Other local food sources such as valley-floor herbs and grasses also contributed significantly to local diet. Although heavily reliant on beech species, possums are unlikely to have a significant impact on beech flower and seed production, or on the health of beech trees because of possums' low abundance and the large beech biomass at this site. Recognised possum-preferred foods such as *Aristotelia serrata*, *Fuchsia excorticata*, *Hoheria glabrata*, *Raukawa simplex*, *Elaeocarpus hookerianus* and mistletoes (*Peraxilla tetrapetala* and *Alepis flavida*) were all strongly preferred by possums but, because of their scarcity in the study area, were only eaten in small quantities.

Keywords: diet; mast fruiting; possum; simple *Nothofagus* forest; *Trichosurus vulpecula*.

Introduction

Beech (*Nothofagus*) species exhibit mast seeding with large quantities of seed ($> 4000.m^{-2}$) produced at intervals averaging *c.* 5 years, with little or no seed produced in many of the intervening years (Wardle, 1984). Partial mast years ($500\text{--}4000$ seeds. m^{-2}) are sometimes observed between full mast years (Wardle, 1984). Beech masting is a significant ecological event in beech forest: heavy flower and seed production triggers eruptions in forest-litter arthropod populations (Alley *et al.*, 2001) and increased breeding activity in some indigenous birds such yellow-crowned parakeet (*Cyanoramphus auriceps*) and kaka (*Nestor meridionalis*) (Elliott *et al.*, 1996; Wilson *et al.*, 1988). Beech mast events also trigger perturbations in the densities of introduced mammalian pests, including house mice (*Mus musculus*) (King, 1982, 1983; Murphy, 1992; Fitzgerald *et al.*, 1996; Alley *et al.*, 2001) and stoats (*Mustela erminea*) (King, 1983). Elevated stoat densities often result in increased predation on indigenous birds (Murphy and Dowding, 1995; Elliott, 1996; Elliott *et al.*, 1996; O'Donnell and Phillipson, 1996; Wilson *et al.*, 1998).

Possums (*Trichosurus vulpecula*) are one of New Zealand's most pervasive mammalian pests, and

threaten indigenous forest ecosystems through their herbivory and predation [see Payton (2000) and Sadleir (2000) for reviews]. In many habitats possums eat large quantities of fruit and seed when these are available (Nugent *et al.*, 2000). Periods of heavy fruit utilisation have been linked with enhanced breeding success in possums (Bell, 1981), and possums have been shown to suppress fruit production in some tree species (Cowan, 1990a; Cowan and Waddington, 1990). Beech masting may, therefore, affect possum diet and fecundity, and possum feeding may affect beech seed production, but these potential interactions have not been quantified. Furthermore, there are no published data on possum diet from the floristically simple beech forests that dominate the indigenous forests east of the Main Divide of the Southern Alps in the South Island and the axial ranges of the North Island (Wardle, 1984). Possum diet has been described from some western South Island beech forests (Owen and Norton, 1985; Cochrane *et al.*, 2003).

The New Zealand Department of Conservation (DOC), Canterbury Conservancy, contracted Landcare Research, Lincoln, New Zealand, to determine possum diet from stomachs collected from the North Branch Hurunui Catchment, eastern South Island in 1999–2001. Seedfall trays in the adjacent South Branch

Hurunui Catchment caught 160.7 kg.ha⁻¹ of beech seed from March to May 2000 (A. Grant, Department of Conservation, Christchurch, N.Z., *unpubl. data*). This equates to *c.* 4000 seeds.m⁻² (Wardle, 1984: p. 256) indicating that the first year of the study was a full beech-mast year. This estimate is likely to underestimate total seedfall as small quantities of seed continue to fall during winter and, for silver beech, spring (Wardle, 1984). The following year, 2001, was a non-mast year with just 0.5 kg.ha⁻¹ of beech seedfall in March to May. The diet study provided the opportunity to compare possum diet in a beech mast and non-mast year, as well as to document possum diet from a simple eastern beech forest and assess variation in diet with altitude, aspect and geographic location. The results of this work are presented in this paper.

Methods

Study area

The study area consisted of the forested parts of the upper North Branch Hurunui Catchment, North Canterbury, New Zealand, from Harper Pass on the Main Divide of the Southern Alps to Mackenzie Stream, 14 km east of the Main Divide (Fig. 1). The valley floor is characterised by broad river flats at 600–700 m a.s.l., much of which are open grasslands dominated by exotic species. The valley sides are almost entirely forested by beech up to *c.* 1300 m a.s.l. Red beech (*Nothofagus fusca*) occurs on the lower and mid-altitudes slopes, with silver beech (*N. menziesii*) present

throughout, but dominating the canopy at high altitudes and in wetter western parts of the study area. Mountain beech (*N. solandri* var. *cliffortioides*) is common in the drier eastern parts of the study area, particularly at high altitudes. In total, beech species comprise 82% of the estimated total plant biomass in the study area: 21%, 27% and 34% for mountain, red and silver beech, respectively [data derived from the National Vegetation Survey (NVS) databank]. The sparse non-beech components of these forests are dominated by small-leaved *Coprosma* species, *Griselinia littoralis*, *Phyllocladus alpinus* and *Myrsine divaricata*. Possum-preferred tree species are uncommon or rare, ranging from about 0.5% [*Raukawa simplex* (Mitchell *et al.*, 1997), *Hoheria glabrata*] to less than 0.05% (*Aristotelia serrata*, *Fuchsia excorticata*) of estimated plant biomass (NVS databank). Subalpine and alpine shrublands, grasslands and herbfields are present above the upper limit of forest.

Possums have been present in the study area since at least 1963 (Cowan, 1990b) and leg-hold trap-catch rates of 8–16 possums per 100 trap-nights during the study period (A. Grant, Department of Conservation, Christchurch, N.Z., *unpubl. data*) indicate a low-density possum population (*c.* 1–2 possums.ha⁻¹: B. Warburton, Landcare Research, Lincoln, N.Z., *pers. comm.*).

Possum stomach collection

Stomachs were taken from possums caught on the same six transects during each sampling trip. Transects were subjectively located to sample the north and south sides of the valley, and the western, middle and

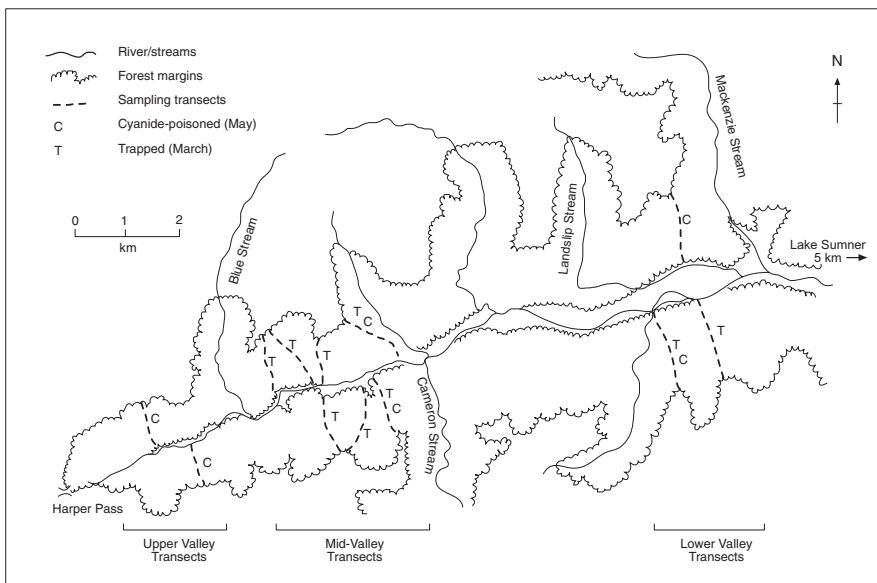


Figure 1. The North Branch Hurunui study area and location of sampling transects.

eastern parts of the study area (Fig. 1). They ran from the forest-grassland margin on the valley floor to the upper altitudinal limit of tall forest. Between 13 and 25 sampling stations were established at approximately 25-m vertical intervals along each transect. Cyanide baits (Feratox®, Feral Control, Auckland) were laid in bait stations at each sampling station for about 4 days (range: 2–5 days), in December, February/March, May/June, and September, in each of the two years. A total of 360 possum stomachs were collected during the study. Of these, 270 were sorted and analysed (30 in February/March in both years and 35 for all other collections). When more than 35 stomachs were collected in the same sampling period, those sorted had been randomly selected from the whole sample.

Each possum sampled was allocated to three strata: altitude, geographic location, and the side of the valley (aspect). These strata were defined as low (600–800 m), mid (800–1100 m), and high (1100–1300 m) for ‘altitude’; upper, mid, and lower valley for ‘geographic location’ (Fig. 1); and north and south side for ‘side of valley’. The sampling strategy resulted in varying numbers of stomachs analysed per stratum, reflecting the relative availability of each stratum and relative possum density in each. The resulting total diet data therefore are weighted toward those strata where most possums were caught and, hence, are an unbiased measure of the mean per-capita diet.

Relative possum density was compared among strata by calculating the capture rate (expressed as a percentage of bait nights) for each stratum on each line every sampling period. However, data for low and high altitudes in the upper-valley stratum were excluded because there were less than four bait stations in each stratum. Mean capture rates and 95% confidence intervals were calculated for each stratum.

Diet analysis

Stomachs with layered contents were sorted using the ‘layer separation’ technique (Sweetapple and Nugent, 1998), where discrete layers of single food items within the stomach are separated, oven dried at 70°C for 24 hours, and weighed. For the 1.8% of whole or part stomachs without discernable food layers, contents were sorted by sieving through a 2-mm mesh, then identifying, drying, and weighing 100 fragments systematically selected from the material retained in the sieve (Sweetapple and Nugent, 1998).

Stomach contents were identified by species and food type (foliage, fruit, flower, bark, and seed) for woody species and ferns, but herbaceous material from the valley-floor grasslands was pooled, as was herbaceous material from the forest floor, and all fungi. Beech seed was identified to species by seed size, seed wing characteristics, and beech foliage traces or small foliage layers found within the seed layers.

The percent dry weight for each food item identified was calculated for each stomach. The mean percent dry weight (all stomachs) for each collection was then calculated for each food item, and the annual means were calculated by averaging the collection means. Differences between years in the contribution to diet of food items that comprised more than 0.5% of annual diet in either year were tested using Kruskal-Wallis tests. Because the sampling regime was balanced (strata were sampled in proportion to their size, with the same lines sampled each season, and the same seasons sampled each year) there was no need to account for stratum and seasonal effects to obtain an unbiased estimate of mean annual possum diet. Statistical analyses were performed using the Systat (version 6) statistical package.

Preference and utilisation indices

Preference ratings express the relationship between proportional use of a plant and its proportional abundance. They were calculated for foliage and bark (combined) of forest plant species identified in stomach samples. Relative foliage biomass can be quickly and relatively accurately estimated from cover scores (Spurr and Warburton, 1991). Therefore, plant availability was estimated from cover scores on RECCE plots (Allen, 1992), using similar methods to Owen and Norton (1995). Sixty five RECCE plots, one at every second sampling station along all six transects, were measured in 2000/2001 (NVS databank). On these plots, plant species present were given one of six cover scores (<1%, 1–5%, 5–25%, 25–50%, 50–75%, >75% of the plot area) in each of seven tiers (0–0.3, 0.3–2.0, 2.0–5.0, 5.0–12.0, 12.0–20.0 m above ground, emergent, and epiphyte). Cover scores were then weighted by their mid points (e.g. the 5–25% cover class was weighted by 15) and by the vertical intervals of the tiers in which they were recorded (e.g. the 2.0–5.0-m tier was weighted by 3.0, with emergents weighted by 8.0, the same as for canopy trees, and epiphytes weighted by 0.5). Weighted cover scores were then summed by species to give estimates of relative availability for each plot. Mean proportional availability was then determined for each species over all plots by dividing the total availability of each species by the total availability of all species.

The preference index (PI) used was the forage ratio (Loehle and Rittenhouse, 1982) and is calculated as:

$$PI = \frac{\% \text{diet}}{\% \text{abundance}}$$

where % diet = the percentage of total foliar diet.

Preference index values below 0.5 indicate low preferences and PI values above 2.0 indicate high preferences. For forest plants recorded in possum diet

but not on RECCE plots, a minimum PI was calculated by using the minimum possible abundance score of 0.15 (one occurrence in the 0–0.3-m tier with a cover score of 1).

If possum densities vary markedly between statistical strata, then PIs are of limited use for comparing relative browse pressure between strata. Therefore, a utilisation index (UI) was calculated for each stratum for high preference foods as follows:

$$UI = D_a \left(\frac{\% \text{diet}_a}{\% \text{abundance}_a} \right)$$

where D_a = possum capture rate in stratum a, $\% \text{diet}_a$ = percentage of total diet in stratum a, and $\% \text{abundance}_a$ = percentage of abundance in stratum a.

Table 1. Possum sampling effort, possum catch-rate (possums caught/100 bait-nights \pm 95% confidence limits) and the number of stomach samples analysed for each stratum in the North Branch Hurunui Catchment.

Stratum	Bait stations	Bait-nights	Possums caught	Catch-rate	Stomachs analysed
Altitude					
Low (600–800 m)	33	1169	166	14 \pm 3	126
Mid (800–1100 m)	74	2554	163	6 \pm 2	119
High (1100–1300 m)	21	738	33	4 \pm 2	25
Side of valley					
North	65	2227	156	7 \pm 2	131
South	63	2234	206	9 \pm 2	139
Geographic location					
Lower valley	50	1825	152	8 \pm 1	112
Mid valley	50	1725	140	8 \pm 2	103
Upper valley	28	911	70	8 \pm 4	55
Total	128	4461	362	8 \pm 1	270

Table 2. Mean percent dry weight of food items in a beech-mast (1999–2000) and non-mast (2001) year. Kruskal-Wallis test statistics (H) and P values for the comparison of importance of each diet item between the two years are shown. Significant results at the 95% confidence level are indicated (*). Preference indices (PI) are given for foliage categories (includes bark for beech species) for foods occurring within the forest. Minor foods (< 0.5% in both years) are listed at the bottom of the table together with their percent contribution to total diet (both years combined) and their preference indices (in brackets).

Food item	Mast year (%)	Non-mast year (%)	H	P	PI
<i>Nothofagus</i> pooled by food type					
Beech foliage	10.6	35.6	51.7	< 0.001*	
Beech seed	37.1	0.0	109.5	< 0.001*	
Beech bark	2.6	9.4	4.8	0.028*	
Beech flowers	9.0	0.0	18.5	< 0.001*	
<i>Nothofagus</i> pooled by species					
Red beech	23.2	30.7	7.0	0.008*	1.7
Mountain beech	25.4	12.5	6.5	0.011*	0.9
Silver beech	10.6	1.8	7.1	0.008*	0.1
Total <i>Nothofagus</i> species	59.3	45.0	11.2	0.001*	
Other foods					
Fungi	8.6	18.3	2.9	0.090	-
Valley-floor herbs and grasses	10.3	17.7	3.6	0.051	-
Forest-floor herbs	5.3	6.7	0.1	0.777	6.1
<i>Raukaua simplex</i> foliage	2.4	2.2	0.6	0.439	5.1
<i>Muehlenbeckia axillaris</i> foliage	0.9	2.6	2.3	0.138	-
<i>Hoheria glabrata</i> foliage	1.4	1.8	0.8	0.373	18.0
<i>Polystichum vestitum</i>	2.2	0.3	0.9	0.351	13.5
Small-leaved <i>Coprosma</i> foliage	1.0	0.9	< 0.1	0.878	0.4
<i>Coprosma foetidissima</i> foliage	0.6	0.8	0.3	0.582	1.13
<i>Aristolotelia serrata</i> foliage	0.1	1.0	2.9	0.091	> 120.0
<i>Rubus</i> spp. foliage	0.9	0.2	0.9	0.335	4.4
<i>Podocarpus nivalis</i> fruit	0.9	0.0	2.2	0.155	-
<i>Blechnum</i> spp.	0.3	0.5	0.1	0.751	10.0
<i>Podocarpus nivalis</i> foliage	0.7	< 0.1	3.5	0.063	1.6
Mistletoe spp. foliage	0.5	0.0	3.9	0.048*	> 60.0
Other items pooled	4.6	2.2			-

Foods < 0.5% in both years: moss/litter/soil, 0.26; *Rubus* spp. flowers, 0.25; unidentified bark and wood, 0.25; *Gaultheria depressa* fruit, 0.21; *Fuchsia excorticata* foliage, 0.18, (46); unidentified foliage, 0.09; *Elaeocarpus hookerianus* foliage, 0.08, (> 16); *Pseudopanax crassifolius* foliage, 0.07, (0.2); *Gaultheria antipoda/depressa* foliage, 0.04, (0.3); *Myrsine divaricata* foliage, 0.03, (0.1); *Aristolotelia fruticosa* foliage, 0.02, (> 4); Invertebrates, 0.13; *Hebe* species foliage, 0.01, (< 0.01); *Muehlenbeckia axillaris* fruit, 0.01; *Hypolepis* species, < 0.01, (0.1); *Raukaua anomalous* foliage, < 0.01, (0.5).

Results

Possum density and distribution

The mean possum capture rate throughout the study was 8 ± 1 (95% confidence limits) possums per 100 cyanide bait-nights. The capture rate was identical in both years indicating that repeated sampling of the transects did not reduce possum abundance. Possums were evenly distributed along the length of the catchment and on both its north and south sides, but were more abundant on the lower forested slopes (Table 1).

Possum diet

Foods from beech species (pooled) were the most significant contributors to possum diet, totalling 59% and 45% of annual diet during the mast and non-mast years, respectively (Table 2). Substantial quantities of all three beech species present were eaten, with red beech, followed by mountain beech, the most important beech food species, while foliage then seed were the most important beech food types (Table 2).

Food type composition of the beech component of annual diet varied markedly between the two years (Table 2, Fig. 2). Seeds and flowers contributed 46% to total diet during the mast year but were not eaten during the non-mast year (Table 2). Beech seed was almost exclusively foraged from within beech canopies in all seasons, as seed food layers often contained traces of green beech foliage but no litter, fungi or herbs as would be expected if seed was eaten while possums foraged on the ground. Possums were feeding heavily on beech seed (45% of diet) before it was ripe in February 2000, and were still eating large quantities of it (37% of diet) in September 2000 (Fig. 2). Beech flowers were only eaten in December 1999, they appeared to be mainly the anthers of male flowers, and were largely from mountain beech at high altitude sites.

The absence of beech seed and flowers in the non-mast year was largely compensated for by a greater than threefold increase in the consumption of beech foliage and bark in that year (Table 2, Fig. 2). Red beech dominated the beech foliage food group in the non-mast year, particularly in early summer (December) when it contributed 46% to possum diet (Table 3) and was comprised exclusively of soft new foliage. Beech bark eaten was thin, often green, and included some woody material, clearly sourced from small-diameter branches. Bark was sometimes eaten in large quantities. It made up more than 50% of contents in 7% of stomachs. Although beech foliage and bark were important components of possum diet, the large biomass of these species in the study area meant these foods did not gain high preference indices (Table 2).

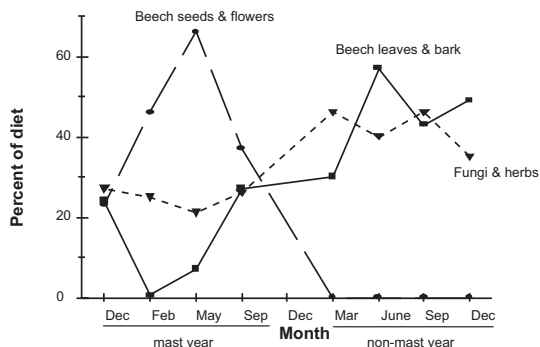


Figure 2. Contribution to possum diet of beech seeds and flowers (circles), beech leaves and bark (squares) and fungi and herbs (triangles) during each collection period, in the North Branch Hurunui. Mast year 1999–2000, non-mast year 2001.

In total there was a significant but modest decline in consumption of all beech foods from the mast to the non-mast year (Table 2). This difference was possibly made up for by increases in fungi and valley-floor herbs, although statistical tests were non-significant (Table 2). These two foods were the next most important food items after beech in both years, each contributing between 8.6 and 18.0% to annual diet (Table 2). Fungal material mainly consisted of basidiomycete sporocarps (mushrooms), and was eaten year round but particularly from February to June (Table 3). Valley-floor herbs and grasses were also eaten year round, with consumption greatest in September and December (Table 3). This food group was dominated by clover (*Trifolium* species) and fine grasses (Gramineae). They contributed 24.1% of annual diet at low altitudes but < 6.0% at higher altitudes. One possum travelled over 1 km and at least 550 m vertically after feeding on the valley-floor grasslands.

Forest-floor herbs were the only other food to exceed 3.0% of annual diet in either year (Table 2). Prominent components of this group included *Nertera villosa*, *Viola cunninghamii*, *Gunnera monoica* and *Pratia angulata*.

Recognised possum-preferred forest species such as haumakaroa (*Raukaua simplex*), ribbonwood (*Hoheria glabrata*), wineberry (*Aristotelia serrata*), mistletoe (*Alepis flavida* and/or *Peraxilla tetrapetala*), fuchsia (*Fuchsia excorticata*) and pokaka (*Elaeocarpus hookerianus*) were all small contributors to total diet in both years. However, they were all strongly sought after, having high preference indices (Table 2), which indicates that low levels of consumption were a consequence of low abundance of these species in these forests, some of which (e.g. mistletoe, pokaka,

Table 3. Mean seasonal and annual possum diet (December 1999–December 2001) in the North Branch Hurunui Catchment.

Food Item	Feb–March	May–June	September	December	Annual
Main food groups					
Foliage (woody species)	18.5	30.0	35.4	47.0	32.6
Foliage (herbaceous species)	19.9	8.9	34.0	21.6	21.1
Fruit and seeds	26.6	33.0	18.3	< 0.1	19.5
Fungi	20.5	21.5	2.6	10.0	13.7
Bark	10.7	5.6	8.4	< 0.1	6.2
Flowers	0.0	0.0	0.0	19.2	4.8
Ferns	3.1	0.7	0.7	2.0	1.6
Other foods	0.7	0.3	0.6	0.2	0.5
Individual food items					
<i>Nothofagus fusca</i> foliage	2.6	17.8	11.1	35.8	16.8
Valley floor herbs and grasses	10.8	6.0	22.9	18.2	14.5
Fungi	20.5	21.5	2.6	9.9	13.6
<i>Nothofagus fusca</i> seed	5.4	8.0	14.9	0.0	7.1
<i>Nothofagus solandri</i> var. <i>cliffortioides</i> seed	11.7	13.4	3.2	0.0	7.1
Forest floor herbs	8.3	2.9	9.2	3.5	6.0
<i>Nothofagus solandri</i> var. <i>cliffortioides</i> foliage	2.3	8.1	9.6	0.1	5.0
<i>Nothofagus menziesii</i> seed	5.9	11.6	0.2	0.0	4.4
<i>Nothofagus solandri</i> var. <i>cliffortioides</i> flowers	0.0	0.0	0.0	16.9	4.2
<i>Nothofagus fusca</i> bark	2.5	2.4	6.4	< 0.1	2.8
<i>Nothofagus solandri</i> var. <i>cliffortioides</i> bark	7.3	2.3	0.5	0.0	2.5
<i>Raukaua simplex</i> foliage	2.1	1.5	5.4	< 0.1	2.3
<i>Muehlenbeckia axillaris</i> foliage	3.5	0.1	0.0	3.3	1.7
<i>Hoheria glabrata</i> foliage	3.7	0.1	0.0	2.6	1.6
<i>Polystichum vestitum</i>	3.1	0.7	0.7	0.6	1.3
<i>Nothofagus menziesii</i> foliage	< 0.1	0.7	4.0	0.0	1.2
Small leaved <i>Coprosma</i> spp. foliage	1.4	< 0.1	0.9	1.6	1.0
<i>Coprosma foetidissima</i> foliage	1.4	0.4	0.4	0.6	0.7
<i>Aristolelia serrata</i> foliage	0.4	0.0	1.8	0.0	0.6
<i>Nothofagus fusca</i> flowers	0.0	0.0	0.0	2.2	0.6
<i>Nothofagus menziesii</i> bark	0.0	0.7	1.5	0.0	0.6
<i>Rubus</i> spp. foliage	0.4	0.0	0.0	1.9	0.6
<i>Podocarpus nivalis</i> fruit	1.8	0.0	0.0	0.0	0.5
<i>Blechnum</i> spp.	0.0	0.0	0.0	1.5	0.4
<i>Podocarpus nivalis</i> foliage	0.1	0.3	1.0	0.0	0.4
Mistletoe foliage	< 0.1	1.0	< 0.1	0.0	0.3
<i>Rubus</i> spp. flowers	0.0	0.0	0.0	1.0	0.3
Other foods	4.9	0.5	3.7	0.3	2.7

wineberry) were not recorded on any of the RECCE plots.

With the exception of mistletoe, all minor foods (maximum annual consumption = 0.5–3.0%) were eaten in similar quantities in both years (Table 2). Mistletoe foliage was recorded from four stomachs during the mast year. For each record, mistletoe was closely associated with beech seed food layers. Mistletoe was not recorded in possum stomachs during the non-mast year.

Other minor foods with high preference indices were the ferns *Polystichum vestitum* and *Blechnum* species (*B. procerum* and *B. penna-marina* pooled), and foliage of *Rubus* species (Table 2). Foliage from small-leaved *Coprosma* species and *Coprosma foetidissima* was also regularly eaten in small quantities

but these foods had low to moderate preference indices (Table 2).

Invertebrates made up just 0.1% of total diet, although this included several hundred lepidopteran larvae, mainly eaten on the valley-floor grasslands in September 2001.

Dracophyllum longifolium, *Griselinia littoralis*, *Olearia lacunosa*, *Phyllocladus alpinus* and *Pseudopanax crassifolius* each accounted for $\geq 0.5\%$ of total plant biomass within the study area (NVS databank) but were not recorded in possum diet.

Comparison of utilisation indices across strata

Utilisation indices for high preference foods ranged from very high (> 100) to low (< 10) across different strata for different foods. These differences (Table 4)

Table 4. Utilisation indices for the main high preference food groups in the eight altitude and valley zone strata. Missing data indicate that the food item was not recorded on RECCE plots in that strata.

Food item	Altitude strata			Location within valley			Side of valley	
	low	mid-	high	upper	mid-	lower	north	south
Forest-floor herbs	32	34	30	28	32	41	32	46
<i>Raukaua simplex</i> foliage	42	10	7	16	13	22	23	12
<i>Hoheria glabrata</i> foliage	0	66	–	38	429	–	49	837
<i>Polystichum vestitum</i>	34	34	144	33	23	108	39	87
<i>Rubus</i> spp. foliage	19	13	–	1	208	11	15	60
<i>Blechnum</i> spp.	33	40	7	4	91	0	28	28

did not correspond to possum-density patterns across the study area. Very high utilisation was recorded at mid-valley sites for ribbonwood, *Rubus* species and *Blechnum* species, at south-side sites for ribbonwood and at high altitude sites for *Polystichum vestitum*, yet the utilisation of these foods was usually low or moderate (10–50) in other strata (Table 4). Utilisation of ribbonwood, *Rubus* species and *Polystichum vestitum* was markedly greater on the south (north facing) side than on the north side of the study area (Table 4). This reflects the relative abundance of these species on each side of the catchment, with all three least abundant on the south side (NVS databank).

Discussion

Beech flowers and seed in possum diet

The mast seeding of beech during the study had a marked effect on the feeding activity of possums in the study area. Beech seeds and flowers featured prominently in possum diet during the beech-mast year, but were not eaten at all during the second year of the study. This was not unexpected, as possums elsewhere feed heavily on most fruits and many flowers when they are available (Nugent *et al.*, 2000), and possums have been recorded travelling several hundred metres from their usual home ranges to feed on beech flowers (Ward, 1978).

An approximate beech seed preference index for the mast year can be calculated from data presented here and in the literature as follows. Annual foliage production for montane red-silver beech forest is *c.* 2500 kg ha⁻¹ (Sweetapple and Fraser, 1992). The biomass of beech flowers produced is similar to the subsequent seed crop (161 kg ha⁻¹ in 2000) (Alley *et al.*, 2001), so *c.* 2820 kg ha⁻¹ of foliage, flowers and seed were produced by woody forest vegetation in the study area during the mast year, of which 5.7% was beech seed. Beech seed made up 59% of all foods from woody forest vegetation (excluding bark), eaten by

possums during the mast year (Table 2). The resultant high preference index of 10.2 (59%/5.7%) clearly demonstrates that possums actively foraged for beech seed during the mast year.

Assuming there is a mean possum density of about 1–2 ha⁻¹ in the study area and that wild possums consume about 160 g (dry weight) of food per night (Fitzgerald *et al.*, 1981), possums ate *c.* 22–44 kg ha⁻¹ of beech seed during the mast year. This equates to about 14–27% of the assumed March–May seedfall in the study area, and indicates that possums probably caused only a modest reduction in total seedfall. The proportion of the total seed crop eaten by possums is likely to be less than this because some beech seed continues to fall during winter and spring (Wardle, 1984).

Flowering in beech starts at low altitudes in mid-spring and progresses up-slope at about 300 m per month, and lasts about 2 weeks at any one location (Wardle, 1984). The observation that most possums that ate beech flowers were caught at high altitudes probably reflects this variable timing of flowering at different altitudes. Flowering may have largely finished at lower altitudes when the December 1999 sample was taken. Possum feeding on beech flowers is likely to have had a negligible effect on seed set given that flowering was probably prolific and of short duration, that possums apparently targeted male flowers, and that beech flowers are wind pollinated (Wardle, 1984).

The consumption of beech seeds and, in particular, flowers highlights the plasticity of possum feeding behaviour, with large and rapid shifts in feeding activity enabling possums to utilise new and ephemeral food sources.

The heavy and prolonged (at least 8 months) consumption of beech seed by possums during a beech mast year potentially adds another dimension to the perturbations in mammalian pest numbers in beech forests known to occur during and after beech mast years (e.g. King, 1983). In years when quality food resources, such as fruits, are abundant, adult female

possum body condition (weight) is higher than average, promoting earlier breeding, higher pouch young survival (Bell, 1981), and spring breeding (Cowan, 1990b). This may raise possum densities above the long-term average, which can result in increased browsing pressure on, or even death of, preferred tree species (e.g. Cowan *et al.*, 1997). Masting in beech species, particularly if mast years occur consecutively, may drive such possum population increases. Indeed, possum trap-catch rates in the study area were stable between 1995 and 1999 but nearly doubled between 1999 and 2001 (A. Grant, *unpubl. data*). The effect of beech mast events on possum fecundity and juvenile survival warrant investigation.

Beech foliage and bark in possum diet

When beech flowers and seed were absent during the non-mast year, possums ate large quantities of beech foliage and bark. These items have previously been shown to be virtually absent from possum diet in other beech forests. They made up just 1.5% of annual diet in a mixed silver beech-hardwood forest in South Westland (Owen and Norton, 1995), and were unrecorded in the diet of possums in two other mixed beech forests in Westland (Cochrane *et al.*, 2003; Sweetapple *et al.*, 2004). While bark of non-beech species is sometimes taken as food (Kean, 1967), it has not been recorded as exceeding 1% of total diet in previous possum diet studies (Nugent *et al.*, 2000).

The consumption of beech bark in this study is even more surprising given that bark from *Nothofagus* species has a high tannin (antifeedant secondary metabolites) content, to the extent that it provided the source of tannin for a leather-tanning industry in New Zealand in the late 19th century (Cooper and Cambie, 1991). Possums may have eaten bark for the simple sugar content of the inner bark (phloem). The extensive bark consumption in this study may be a consequence of the limited range and quantity of preferred foods available to possums in non-mast years within the

study area. Unless the nutritional properties of beech species differ markedly from area to area, the results of the current and other diet studies demonstrate that beech foliage and bark are in fact palatable, and despite being of low preference to possums (they are not eaten at all in some beech forests) these foods sometimes contribute significantly to annual possum diet in the absence of abundant sources of more preferred foods.

Although moderate preference indices were recorded for red and mountain beech (foliage and bark combined), this feeding is unlikely to have a significant impact on beech canopies at the population level because of the vast annual production of foliage and relatively low possum densities in the study area. Using the foliage production data from Sweetapple and Fraser (1992) and food consumption data from Fitzgerald *et al.* (1981), possums ate just 0.3% of annual beech foliage production in the current study area. However, heavy impact on individual trees is possible if possum browsing was concentrated on a few individuals.

Bark chewing could potentially be far more damaging than the modest quantities involved would suggest. Ring barking could lead to death of small- to moderate-sized branches, particularly where possums were most abundant along the lower forest margin. Indeed, heavy possum browsing damage to mountain beech was observed by the author along a valley-floor forest margin near the Mounds of Misery (Arthur's Pass National Park, South Island, New Zealand). In October 2001 *c.* 50% of the trees on this forest margin along a 1-km front exhibited some recent crown dieback (dead leaves still attached). Possums had stripped much of the bark from all dead branches, with branches up to 5 cm in diameter affected. Dieback exceeded 50% of the crown in a few individuals, but was not apparent on trees more than a few metres back from the forest margin. The dieback episode appeared to have been of short duration as all affected branches had been dead for a similar length of time. Bark chewing

Table 5. Mean percent dry weight of beech foods in possum diet from central and eastern South Island, New Zealand. The number of possum stomachs analysed in each sample is given (*n*).

Area/Forest type	<i>n</i>	Foliage	Bark	Seed	Flowers	Total
Arthur's Pass National Park - mountain beech forest ¹	46	9	0	0	0	9
Kaikoura - mountain beech/ <i>Kunzea</i> forest ²	101	13	0	23	0	36
Craigieburn Forest Park - mountain beech forest ³	27	< 1	3	24	2	29
Maruia Valley - red/silver beech forest ¹	30	< 1	0	75	0	75
Tutaki Valley - red/silver beech forest ⁴	27	3	5	35	0	43
Nelson Lakes National Park - red/silver beech forest ⁴	9	0	0	40	0	40

¹A. Byrom and P. Sweetapple *unpubl. data*

²G. Nugent and P. Sweetapple *unpubl. data*

³P. Sweetapple *unpubl. data*

⁴A. Byrom, Landcare Research, Lincoln, *unpubl. data*

by possums on beech trees has also been reported to cause death of branches in the North Island's Ruahine Range (Grant, 1956). Possum impacts on beech crowns at high-use sites, such as forest-pasture margins in simple eastern and central beech forest warrant investigation.

Recent unpublished studies of possum diet in central and eastern South Island indicate that high levels of beech-food consumption are not unique to the Hurunui study site. Possum diet was measured at six sites with beech forest during 2000–2001 and foods from beech species contributed 9–75% to total diet at all sites at the times the samples were taken (Table 5).

Ground-level feeding

The ability of possums to utilise large quantities of low quality foods is not surprising given that their natural habitats include sclerophyll *Eucalyptus* forests in Australia, where their diet is dominated by low quality, highly defended *Eucalyptus* foliage (Freeland and Winter, 1975). However, there appear to be limits to how much *Eucalyptus* foliage can be eaten: Possums supplement their diet by foraging for herbs on the forest floor, even though this means increased exposure to predators and increased foraging effort (Freeland and Winter, 1975). This feeding strategy parallels that seen in the North Branch Hurunui during the non-mast year.

The importance of forest floor fungi is another notable feature of Hurunui possum diet. Fungi are often recorded in possum diet (Nugent *et al.*, 2000), but are usually only a minor component of total diet (< 1%). In the North Branch Hurunui most possums had eaten some fungi, and it contributed 8.6–18.3% to annual diet. Given the scattered distribution of fungi within forest, and the large quantities of fungi sometimes seen in stomachs, possums clearly actively foraged for fungi at this site. It is likely that this foraging behaviour reflects an increased relative preference for fungi due to the paucity of other preferred-food sources in this low-diversity forest, because although fungi are common in all beech forests (P. Johnston, Landcare Research, Auckland, N.Z., *pers. comm.*), they constitute < 1% of total diet in the more floristically diverse mixed beech forests in Westland (Owen and Norton, 1995; Cochrane *et al.*, 2003; Sweetapple *et al.*, 2004). The consumption of fungi in all areas may be due to their relatively high concentrations of most macronutrients and low carbon-to-nitrogen ratios (Clinton *et al.*, 1999), which probably make them easily digested, rich sources of nutrients.

The other foods eaten by ground-foraging possums were herbs, both from within and outside the limits of tall forest, and ferns such as *Blechnum* species and *Polystichum vestitum*. Similar species and quantities of herbaceous ground foods have been recorded in the diet of possums from forest adjacent to pasture

(Coleman *et al.*, 1985), with, as in this study, some possums travelling over 1 km through forest to feed on pasture (Green and Coleman, 1986).

Most of the few invertebrates eaten by possums in this study were also obtained while possums foraged on the ground. The lepidopteran larvae that dominated this food category were usually encountered within valley-floor grassland food layers within the possum stomachs. Owen and Norton (1995) reported that dipteran larvae made up 28% of the winter diet of possums from a mixed silver beech-hardwood forest in South Westland, but dipteran larvae were not recorded in the current study or other studies of possum diet in beech forests.

Potential possum impacts

Considerable possum impacts in beech forests have been recorded previously (James, 1974; Rose *et al.*, 1993; Pekelharing *et al.*, 1998; Sweetapple *et al.*, 2004). These predominantly involve the collapse of seral forests, particularly those dominated by fuchsia, and the dieback of some other non-beech species including southern rata (*Metrosideros umbellata*), kamahi (*Weinmannia racemosa*) and Hall's totara (*Podocarpus hallii*) (Rose *et al.*, 1993; Sweetapple *et al.*, 2004).

Similar patterns of possum impact are likely in the Hurunui Catchment. Beech species account for 82% of the forest biomass within the study area and these species are unlikely to be significantly affected by possum browsing, at least at the population level. Possum impacts on less common plants are likely to be significant. Woody seral species are heavily targeted by possums in the study area. Wineberry, ribbonwood and fuchsia have some of the highest preference or utilisation indices in this study. Other plants with high preference or at least high local utilisation indices are mistletoe, pokaka, *Polystichum vestitum*, *Blechnum procerum*/*B. penna-marina*, forest-floor herbs, haumakaroa and the lianes *Rubus cissoides* and *R. schmidelioides*. These plants would be the most useful candidates for monitoring programmes aimed at assessing possum impacts in this forest. Utilisation of some preferred plants varied enormously between sites within this study area (Table 4), therefore, possum impacts will be variable in space and any monitoring programme would have to be extensive, or targeted to the sites of highest utilisation for the species of interest.

Possum impacts on mistletoe at this site appear to be greatest during beech mast events. Consumption of mistletoe was significantly greater in the mast year compared with the non-mast year. This may be a consequence of more extensive foraging in beech canopies by possums during mast years, particularly in mountain beech (Table 2), the main host species for *Alepis flavida* and *Peraxilla tetrapetala*. A concurrent,

marked decline in mistletoe health was recorded during the mast year in the study area, but not in a nearby area where possums had been controlled (A. Grant, *unpubl. data*). More intensive possum control may therefore be required during mast years compared with non-mast years to protect beech mistletoes in some areas.

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