

## Diet and impacts of brushtail possum populations across an invasion front in South Westland, New Zealand

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**Abstract:** Impact of the irruptive fluctuation in abundance of brushtail possum populations since their initial colonisation was investigated in the forests of South Westland, New Zealand. Possum abundance, fecundity, and diet, the condition of common possum-palatable tree species, and the abundance of common forest birds were measured at three sites occupied by possums for *c.* 10, 20, and 30 years. Possum densities were highest at the site where possums had been present for *c.* 20 years. Possum fecundity was higher at the site they had recently colonised than at the two sites where they had been present for *c.* 20–30 years. Diet of possums where they had recently colonised was dominated by highly preferred foods (72% of total diet), whereas these same foods contributed just 36% of total diet at the site where possums had been present for more than two decades. Canopy condition of common possum-preferred trees was scored progressively lower in areas with increasing length of possum occupation, especially at the site where the possum population had apparently declined from its maximum density. Native forest bird abundance also declined with increasing length of possum occupation. The implications of these results for management are discussed.

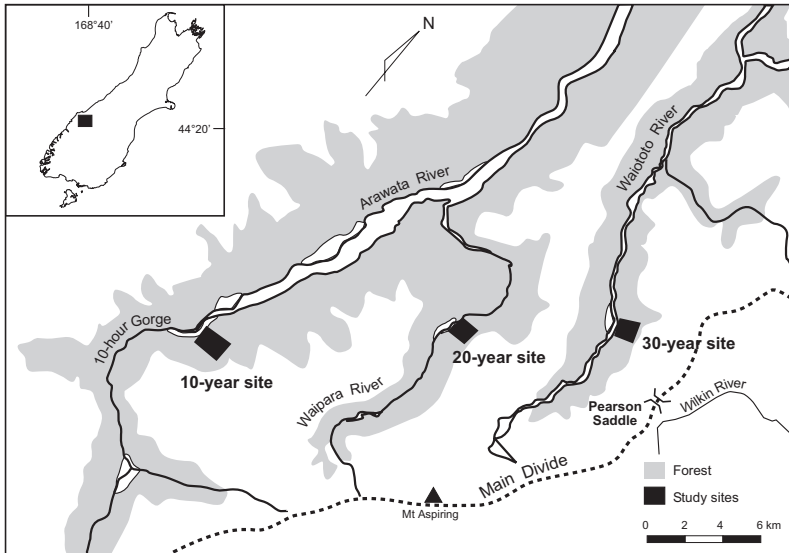
**Keywords:** brushtail possums; colonisation; demography; diet; forest bird abundance; impacts; tree canopy condition; *Trichosurus vulpecula*.

## Introduction

With the exception of some alpine areas and parts of South Westland and Fiordland, brushtail possums (*Trichosurus vulpecula*) occur throughout the main islands of New Zealand, and are generally considered to be a serious conservation pest because of their widespread impact on indigenous ecosystems (Payton, 2000; Sadleir, 2000). The impact of possums on the indigenous vegetation has been the subject of numerous studies, and we now have some appreciation of their impacts on common forest species [see Payton (2000) for a review]. A few studies provide evidence that possums adversely affect indigenous forest birds and other wildlife through predation (Cowan and Moeed, 1987; Pierce and Graham, 1995; Brown *et al.*, 1993, 1996; Innes *et al.*, 1996; McLennan *et al.*, 1996), while others have suggested that forest bird populations may have declined as a consequence of possum-induced forest modification and competition for food (Leathwick *et al.*, 1983; Fitzgerald, 1984; Cowan, 1990b). However, few studies have attempted to quantify these predatory or competitive impacts, particularly for common forest birds. While a few studies have provided some details of varying possum

impacts with increasing length of site occupation (e.g. Pekelharing and Reynolds, 1983; Leutert, 1988; Campbell, 1990; Rose *et al.*, 1993), our knowledge of the sequence, time frame, and magnitude of possum impacts with respect to possum colonisation and length of site occupation is limited. This type of information is of particular interest to forest ecosystem managers who are attempting to mitigate the impact of possums at sites where they have recently become established.

Sites with different lengths of pest-population occupation can be used as a surrogate for time to describe pest impacts and demography over time (Caughley, 1970). Possums are still colonising parts of South Westland (Rose *et al.*, 1993) providing the opportunity to investigate possum impacts during colonisation. In this study three sites with different histories of possum occupation in the Waiaototo, Waipara, and Arawata valleys (Fig. 1) are investigated to infer the impact process during possum colonisation in South Westland. This cross-sectional approach is used instead of a longitudinal study of impact trends through time because the latter would take *c.* 30 years or more to complete (possum populations take some 20–30 years to build up to peak densities following initial colonisation; Pekelharing and Reynolds, 1983;



**Figure 1.** Location of the three study sites in the Arawata and Waiatoto catchments, South Westland.

Pekelharing and Batcheler, 1990; Thomas *et al.*, 1993). With just one site investigated for each of three nominal lengths of possum occupation there is no replication in this study. Cost constraints prevented replication or the inclusion of additional points within the nominal time sequence, and as a consequence the results must be interpreted cautiously.

The study specifically aims to investigate the impact of colonising possum populations on common tree and bird species by measuring relative density and diet of possums, the condition of key tree species palatable to possums, and relative bird densities at the three study sites. The results are interpreted with particular emphasis on the timing of the main impact processes with respect to the length of site occupation by possums.

## Methods

### Colonisation history

Possums were liberated in the Matukituki Valley to the south-east of the Waiatoto Valley in 1916 and in the Wilkin Valley to the east in 1932 (Pracy, 1974). No possum sign was seen during an animal survey of the Arawata, Waipara, and Waiatoto valleys in 1970/71 (Tustin, 1972) but the first reports of possums in the upper Waiatoto date from about this time (Department of Conservation, Hokitika, file note 1.7.2.4). The possums had probably migrated from the Wilkin Valley via Pearson Saddle (Fig. 1). Field inspection by New Zealand Forest Service staff in 1986 revealed high possum numbers in the upper Waiatoto (Department

of Conservation, Hokitika, file note 1.7.2.4). This survey also noted low possum numbers on the east bank of the mid-Waipara, but not elsewhere in that catchment, suggesting they had recently arrived there, probably migrating from the Waiatoto Valley to the west. A faecal-pellet-count survey in 1990 (K. Fraser, Landcare Research, Lincoln, N.Z., *unpubl.*) indicated there were then moderate possum numbers near the confluence of the Waipara and Arawata rivers and that possum numbers on the east bank of the Arawata declined with increasing distance upstream from the Waipara. Near the 10-hour Gorge (Fig. 1) possums were recorded from only the lower forested slopes. A repeat survey in 1991 (K. Fraser, *unpubl.*) revealed that possum numbers were increasing on the east bank of the Arawata, and their altitudinal range was extending near the 10-hour Gorge.

### Study site selection and characteristics

The three sites chosen for study were the Arawata Valley, immediately below the 10-hour Gorge, the mid-Waipara Valley, and the upper Waiatoto Valley (Fig. 1). All three sites were on forested slopes above the eastern banks of these rivers. The available information (above) indicates that possums had recently colonised the 10-hour-Gorge site when this study was undertaken in 1997, had been present on the east bank of the mid-Waipara since the early 1980s, and had been present in the head of the Waiatoto since about the early 1970s. For convenience we name these sites the 10-, 20-, and 30-year sites (Fig. 1), reflecting our best estimates of how long possums had occupied these areas.

The topography of the region is characterised by very steep valley sides with extensive bluff systems and forested boulder fields. The three sites were subjectively selected following field inspection, to ensure that they could be traversed on foot and that other physical and habitat parameters were similar. All three sites were situated on western-facing, lightly dissected faces above unforested river flats. Slopes are moderate (c. 30°) with sampling transects (see below) ranging in altitudes from 80–200 m a.s.l., up to 750–840 m a.s.l.

Forests at the study sites are mixed beech-hardwood forests with a low density of podocarps on lower slopes and silver beech (*Nothofagus menziesii*) forests on upper forested slopes. Silver and red beech (*N. fusca*) dominate the canopies of mature forest on lower slopes at the 10- and 20-year sites, but red beech is absent at the 30-year site where silver beech dominates mature forest at all altitudes. Some localised patches of short-stature forest on old stable surfaces dominated by silver and mountain beech (*N. solandri* var. *cliffortioides*) occur above 600 m at the 10-year site. Kamahi (*Weinmannia racemosa*) is an abundant canopy tree below 600 m at all sites, with occasional southern rata (*Metrosideros umbellata*) and Hall's totara (*Podocarpus hallii*) also present. Beech forest understoreys are a relatively complex mix of woody and fern species, reflecting a high rainfall in this region. All three sites are characterised by abundant and widely scattered patches of seral forest dominated by either mahoe (*Meliccytus ramiflorus*) with pate (*Schefflera digitata*) present, or fuchsia (*Fuchsia excorticata*) with wineberry (*Aristotelia serrata*) and ribbonwood (*Hoheria glabrata*) present. A notable feature of the 30-year site was that most of the fuchsia was dead but standing, presumably recently killed by possums (see Rose *et al.*, 1993; Pekelharing *et al.*, 1998).

### Sampling design

It was not practicable with the resources available to randomly position sampling transects or plots, due to the difficult nature of the terrain at all three sites. Therefore, a single sampling transect was established at each site. Each transect started at the forest margin

on the valley floor, climbed to between 750 and 840 m altitude, traversed the face for about 1 km, then descended back to the valley floor. Sampling stations were systematically established along each transect, but because transect length varied (3–5 km) intervals between stations varied between sites to give 20–21 stations per site. Intervals were 150, 200, and 300 m at the 20-, 30-, and 10-year site, respectively. A consequence of this sampling strategy is that high altitudes (700–840 m a.s.l.) were sampled more heavily than lower altitudes. All sites were visited simultaneously in January, April, and November 1997, when the relative abundances of possums and common bird species were monitored, and vegetation composition and condition were assessed. The sampling strategy used in this study means that we effectively have a sample size of one for each site sampled, although we use sampling stations and individual possums as pseudoreplicates for comparing parameter means among the three sites. We cannot, therefore, directly assess the possibility that all of the differences between sites are related to time since possum colonisation, rather than simply reflecting local differences in ecology. Therefore, only general inferences from major patterns detected can be drawn from the data. Where available, data from similar studies elsewhere are discussed to aid interpretation of the results.

To support our hypothesis that differences between the three sites in possum ecology, vegetation condition and bird abundance were due to length of possum occupation and not inherent site differences, a number of simple, *a priori* predictions of expected outcomes were made (Table 1). The parameters chosen are thought to be largely independent of one another, although some interdependencies may exist (e.g. between diet composition and possum fecundity, or condition of indicator trees and native bird abundance). These predictions are not quantitative, but simply describe rank order (highest to lowest) of each site for each parameter. Results were compared with these predictions.

**Table 1.** Predicted rank order across the three study sites for a range of measured parameters.

Parameter	Rank order		
	10-year site	20-year site	30-year site
Possum abundance	lowest	highest	intermediate
Possum fecundity	highest	lowest or intermediate	lowest or intermediate
High preference foods in possum diet (%)	highest	intermediate	lowest
Condition of indicator trees	good	intermediate	poor
Abundance of native birds	highest	intermediate	lowest

### Vegetation composition

At most (18–20) sampling stations at each site, vegetation composition was described using a plot of about 10-m radius following the RECCE procedures prescribed by Allen (1992), but with species comprising <1% of the ground tier (<0.3 m) ignored. The 58 plots measured were classified into five vegetation types using TWINSPAN (Hall, 1992). A key to these five types was prepared based on the presence of indicator species identified by TWINSPAN and was used to classify the vegetation at each cyanide bait placement (see below). These data enabled the relative abundance of the various forest types along the sampling transect at each study site to be determined.

### Relative possum density and fecundity

Cyanide-paste baits were laid on the ground at 20-m intervals along the sampling transects simultaneously at each study site on one fine night in January, April, and November 1997. Due to high possum numbers at the 20-year site, bait spacing was increased at this site during April and November to reduce the number of possums sampled there. The number of possums killed per 100 bait-nights was calculated for each site and used as a measure of relative possum density. Catch data for the first sampling period (January 1997) provide the most accurate measure of relative possum density as this was the only season where bait spacing was the same at all three sites. However, data from all three sampling periods were used to test for between-site differences in possum density using simple one-way ANOVA.

Stomachs were taken for diet analysis from all possums collected, and the pouch condition (bare or furry) and presence of pouch young noted for adult females. Site differences in adult female pouch status and the frequency of occurrence of pouch young were tested using 3x2 contingency tables.

### Possum diet

Fourteen to 16 possum stomachs were selected from each site each season for diet analysis, giving totals of 45–46 stomachs per site. Stomachs were selected so that equal numbers of male and female possums were assessed from each site and that samples were evenly distributed around the sampling transects. Stomach contents were sorted using the layer separation technique where possible (Sweetapple and Nugent, 1998), but stomachs in which feeding layers were too mixed to separate (18–20% of samples) were sorted by the point-sampling technique (Sweetapple and Nugent, 1998). For each stomach, individual food items were separated and oven-dried at 70°C for 24 hours, weighed, and percent dry weight of total stomach content calculated. Differences between sites in the contribution

to diet of food items that comprised >1% of total diet at any one site were tested using non-parametric Kruskal-Wallis tests.

Preference ratings were calculated (all sites combined) for all foliage foods contributing >1% to total diet at any one site. Preference ratings express the relationship between proportional use of a plant and the proportional abundance of that plant in the habitat. Estimates of the proportional abundance of foliage by species were derived from the RECCE plot data using the methods of Owen and Norton (1995), except that we used standard RECCE plot height-tiers. On these plots, plant species present were given one of seven cover scores (0.0, 0.5, 3.0, 15.0, 37.5, 62.5, or 87.5% of the plot) in each of seven height-tiers (0–0.3, 0.3–2.0, 2.0–5.0, 5.0–12.0, 12.0–20.0 m, emergent, and epiphyte). Cover scores were weighted by the height interval of the tier in which they were recorded (0.3–2.0 tier, 1.7; 2.0–5.0 tier, 3.0; 5.0–12.0 tier, 7.0; 12.0–20.0 tier, 8; emergents, 8.0; epiphytes, 0.5). Weighted cover scores were then summed by species to give estimates of abundance for the whole survey. Proportional abundance of each species was then determined by dividing the estimated abundance of individual species by the combined abundance of all species.

The preference index (PI) used follows that of Nugent (1990), and is calculated as:

$$PI = \frac{\%diet - \%available}{\%diet + \%available}$$

where diet = the percent of total foliar diet (all sites combined).

This produces PI values ranging from +1 (present in stomachs and absent on plots) to -1 (absent in stomachs and present on plots). The PI equals zero when percent in diet equals percent available. Common foliar foods were pooled into groups of very high (PI > 0.67), high (PI = 0.33–0.67), and moderate (PI < 0.33) preference, then the contribution of each group to total diet was compared between sites.

A utilisation index for foliar foods was then calculated for each of the three food preference groups at each site. This index provides a relative measure of the biomass of plant material consumed by possums, compared with the amount available. It differs from the PI in that it takes account of relative possum density, and was calculated by dividing an index of total consumption by possums (percent in diet multiplied by possum catch rate) by their percent abundance (from RECCE plot data). These were then graphed to compare food-preference groups and sites. The highest utilisation indices are interpreted as

predicting when and where the greatest possum impacts are likely to occur.

### Condition of indicator tree species

The condition of eight selected indicator tree species was measured using the Foliar Browse Index (FBI) method (Payton *et al.*, 1999). This method measures foliage cover on a 10-point scale, and crown dieback and possum browse on a 5-point scale. The indicator species selected [Hall's totara, haumakaroa (*Raukaua simplex*), kamahi, mahoe, pate, southern rata, fuchsia, and mountain five-finger (*Pseudopanax colensoi*)] were known to be palatable to possums in Westland (Fitzgerald and Wardle, 1979; Coleman *et al.*, 1985; Owen and Norton, 1995). Up to four trees of each species were measured per sampling station. Additional intermediate sampling stations were established where indicator tree species were encountered along transects when necessary to increase the sample size of each species to 50 individuals per site. At all sampling stations the species and number of standing, dead, indicator trees within 10 m of the sampling-station centre were recorded.

For each species, testing of site differences in foliage cover was by ANOVA with sampling stations located within site. The proportion of trees with crown dieback (scores 1–4) and possum-browsed foliage (scores 1–4) was compared between sites using contingency tables. No scorable mountain five-finger trees were found at the 30-year site and only three were found at the 10-year site, so data for this species were not analysed in detail.

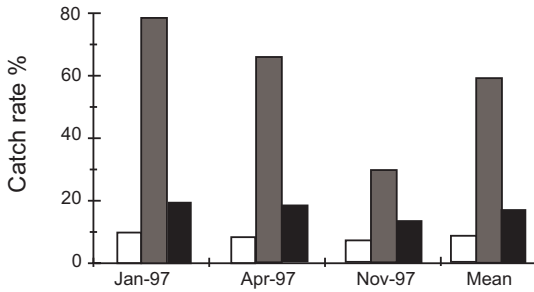
### Relative bird abundance

Relative abundance of forest birds was assessed by standard 5-minute bird counts (Dawson and Bull, 1975) conducted at each sampling station on 2 days during the first two sampling periods, and 1 day in November 1997. Counts were conducted at the same time on the same days at each site by pairs of observers, with one observer working around the sampling transect in the opposite direction from the second observer. The direction of travel of each observer was reversed during the second day of counts when 2 days of counting were undertaken. To minimise observer biases between sites, we attempted to have each of six observers undertake counts at a different site each sampling period (January, April, November). However, two of the original observers were not available for the third sampling period, and were replaced by two new observers. The sampling strategy resulted in 20–42 counts being made by each of six different observers at each site during the study, giving totals of 200–208 counts at each site.

Mean counts per station over the whole study period were calculated for each species, square-root transformed to stabilise residual variance and ensure normality, then analysed using two-way ANOVA with, firstly, vegetation type and, secondly, site as factors. Mean counts in the four vegetation types common to all sites were averaged for graphical presentation of the data. Therefore, site-effect data and analyses are presented, having already accounted for differences in vegetation-type composition.

**Table 2.** Vegetation types identified in this study, and similar types identified by Wardle *et al.* (1973).

Vegetation type	Altitude	Comparable type identified by Wardle <i>et al.</i> (1973)	Percent of cyanide-paste bait points		
			10-year	20-year	30-year
Kamahi-mahoe-pate-fuchsia forest (seral forest with little or no beech present)	100–600 m	D3, D4	11	18	32
Silver beech and/or red beech/kamahi-fuchsia/ <i>Blechnum discolor</i>	100–600 m	B3	25	12	9
Silver beech/ <i>Griselinia littoralis</i> - <i>Carpodetus serratus</i> / <i>Polystichum vestitum</i>	100–800 m	B2	40	66	44
Silver beech/ <i>Griselinia littoralis</i> -haumakaroa- <i>Coprosma pseudocuneata</i>	600–840 m	A4	15	3	15
Mountain beech (sometimes with silver beech)	700–830 m	B1	10	0	0



**Figure 2.** Seasonal and mean possum capture rates at the 10-year (open bars), 20-year (shaded bars) and 30-year (black bars) sites, expressed as a percentage of the number of cyanide bait-nights.

## Results

### Vegetation composition

Five different forest types were identified, and related to types identified in the same area by Wardle *et al.* (1973) (Table 2). Although there was a broadly similar mix of forest types recorded at all three sites, some differences were apparent. Mountain beech forest, which occurred on old, stable surfaces, was only recorded at the 10-year site, and seral forests were more common at the 20-year, and particularly the 30-year sites, than at the 10-year site (Table 2). Red beech was absent from the 30-year site but the silver/red beech forest type was still recorded there, although it was less abundant than at the other two sites (Table 2).

### Relative possum density and fecundity

Possum density varied among the three sites. Possum catch rate in January 1997 at the 10-year site was only 9.8 possums caught per 100 bait-nights. This was about half that recorded at the 30-year site and just

**Table 3.** Mean percent dry weight of items comprising more than 1% of total possum diet (all seasons pooled) at any one of three sites in South Westland with different lengths of possum occupation (10-, 20-, 30-year sites). Foods are ranked in order of average importance to total diet across the three sites. Chi-square ( $\chi^2_2$ ) and *P*-values (\* = significant at the 95% level) for Kruskal-Wallis tests comparing the proportion of total diet at the three sites are given for each food item. Preference indices (PI) are provided for foliar foods.

Food item	Percent of total diet			PI	$\chi^2_2$	<i>P</i> -value
	10-year	20-year	30-year			
<i>Fuchsia excorticata</i> foliage	7.6	40.2	9.3	0.63	50.0	<0.001*
<i>Weinmannia racemosa</i> foliage	13.2	6.7	21.2	0.19	11.3	0.004*
<i>Aristolelia serrata</i> foliage	18.1	12.5	8.7	0.78	9.6	0.008*
<i>Muehlenbeckia australis</i> foliage	21.1	12.4	5.3	0.98	43.9	<0.001*
<i>Polystichum vestitum</i>	5.7	9.1	1.8	0.51	11.1	0.004*
<i>Weinmannia racemosa</i> flowers	1.0	0.7	6.7	–	9.6	0.008*
<i>Meliclytus ramiflorus</i> foliage	1.1	1.6	4.6	-0.20	1.6	0.45
<i>Coprosma foetidissima</i> foliage	0.0	0.5	6.5	0.42	37.2	<0.001*
Dicotyledonous herbs	0.7	3.6	2.0	0.93	1.2	0.58
<i>Raukahu simplex</i> foliage	0.5	2.5	1.8	-0.25	0.7	0.70
<i>Pennantia corymbosa</i> fruit	0.3	0.6	3.5	–	1.0	0.61
Mistletoe foliage	4.1	0.0	0.0	1.0	6.3	0.043*
<i>Rubus cissoides</i> foliage	1.5	0.5	2.2	0.28	0.6	0.76
<i>Blechnum</i> spp.	<0.1	0.2	3.8	0.27	12.1	0.002*
<i>Raukahu simplex</i> fruit	2.9	1.1	0.0	–	8.7	0.013*
<i>Podocarpus hallii</i> foliage	1.7	0.8	1.3	0.17	3.1	0.22
<i>Hoheria glabrata</i> foliage	0.0	0.1	3.2	0.08	25.9	<0.001*
<i>Fuchsia excorticata</i> flowers	2.3	0.3	0.0	–	5.7	0.06
<i>Rubus cissoides</i> fruit	3.0	0.0	0.0	–	6.3	0.043*
<i>Coprosma rotundifolia</i> foliage	0.5	0.1	2.3	0.81	8.8	0.012*
<i>Phymatosorus pustulatum</i>	0.0	0.0	2.2	0.94	16.3	<0.001*
Fungi	0.0	<0.1	1.6	–	23.7	<0.001*
Others (54 items)	15.2	6.5	12.6	–	–	–
Total fruits	6.9	2.7	5.2	–	0.9	0.64
Total flowers	3.5	1.6	9.3	–	15.5	<0.001*
Invertebrates	<0.1	<0.1	<0.1	–	0.4	0.83

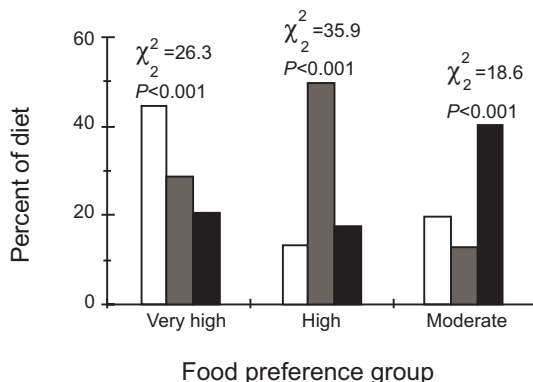
12.4% of that recorded at the 20-year site (Fig. 2). Site differences in mean catch rate over the three seasons were significant ( $F_{2,6} = 11.4$ ,  $P = 0.009$ ). The rank order of the three sites for possum density conforms to our *a priori* prediction (Table 1).

Possum fecundity differed between the three sites, with 39, 3, and 2 percent of adult females with pouch young at the 10-, 20-, and 30-year sites respectively ( $\chi^2_2 = 44.0$ ,  $P < 0.001$ ). The low overall percentage of females with pouch young resulted from possum sampling being undertaken outside of the main breeding season of late autumn to early winter (Cowan, 1990a). Of the adult females captured in November and January, 53, 0, and 3 percent were carrying spring-born young at the 10-, 20-, and 30-year sites respectively. The percentage of adult females with bare (not furry) pouches, indicating they were currently or had previously carried pouch young, dropped from a high of 94 at the 10-year site to a low of 46 at the 30-year site ( $\chi^2_2 = 20.1$ ,  $P < 0.001$ ). The percentage of adult females with bare pouches at the 20-year site (62%) was not significantly different from that recorded at the 30-year site ( $\chi^2_1 = 3.6$ ,  $P > 0.05$ ).

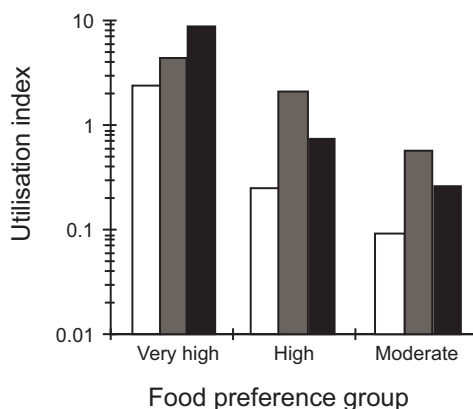
### Possum diet

Foods or food groups that comprised >1% of total possum diet at one or more of the three sites are shown in Table 3. Possum diet across the three sites was dominated by kamahi (*W. racemosa*) and the foliage of three soft-leaved, deciduous, seral species [fuchsia, wineberry (*A. serrata*), and pohuehue (*Muehlenbeckia australis*)], although the proportions of each species varied significantly between sites (Table 3). Consumption of wineberry and pohuehue, two of the most highly preferred foods in this study, was greatest at the 10-year site, and lowest at the 30-year site. Consumption of fuchsia was greatest at the 20-year site and of kamahi at the 30-year site. Of the smaller dietary components, some foods were eaten in moderate quantities at the 10-year site [e.g. mistletoe (*Peraxilla colensoi*, *P. tetrapetala* and *Alepis flavida*) foliage, fuchsia flowers, bush lawyer (*Rubus cissoides*) fruit] but rarely or never eaten at the other sites. Other, generally moderate-preference (as indicated by PI values) foods were of moderate importance to possum diet at the 30-year site, but rarely or never eaten at the other sites; examples include mahoe (*M. ramiflorus*) foliage, *Blechnum* spp., stinkwood (*Coprosma foetidissima*) foliage, fungi, ribbonwood (*H. glabrata*) foliage. This pattern of declining importance of the most preferred foods and increasing importance of moderate-preference foods with increasing length of possum occupation (summarised in Fig. 3) conforms to the predicted pattern of diet composition (Table 1).

Utilisation of very-high-preference foods was high at all three sites, but was greatest at the 30-year site



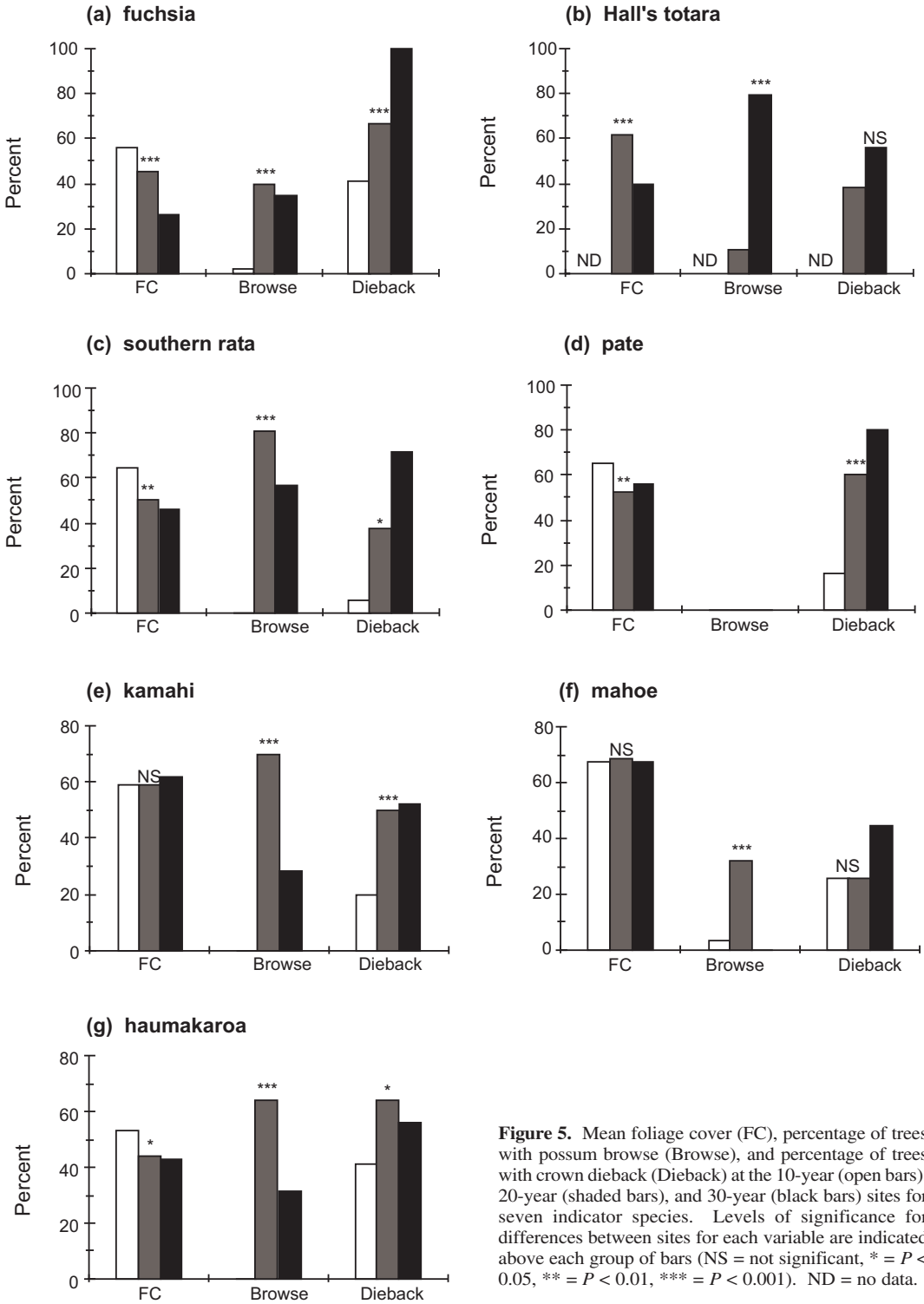
**Figure 3.** Mean percent of total possum diet for very highly, highly, and moderately preferred food-groups at the 10-year (open bars), 20-year (shaded bars), and 30-year (black bars) sites. Kruskal-Wallis test statistics comparing study sites are given for each food group.



**Figure 4.** Utilisation indices (consumption by possums/availability) for three food-preference groups at 10-year (open bars), 20-year (shaded bars), and 30-year (black bars) sites.

(Fig. 4). As expected, utilisation of high- and moderate-preference foods was less than for very-high-preference foods at all sites, but in contrast to very-high-preference foods, their utilisation was highest at the 20-year site, reflecting the high possum densities there. Utilisation of high- and moderate-preference foods declined to low levels at the 20- and 30-year sites, suggesting that possum impact on these food groups was low at these sites.

Southern rata made up just 0.3% of total possum diet (all sites combined) and two of the other selected indicator tree species, pate and mountain five-finger, were not recorded in stomachs from any of the three sites. The apparent lack of importance of these recognised possum-preferred foods (Fitzgerald and



**Figure 5.** Mean foliage cover (FC), percentage of trees with possum browse (Browse), and percentage of trees with crown dieback (Dieback) at the 10-year (open bars), 20-year (shaded bars), and 30-year (black bars) sites for seven indicator species. Levels of significance for differences between sites for each variable are indicated above each group of bars (NS = not significant, \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ ). ND = no data.



Wardle, 1979; Coleman *et al.*, 1985) might be a result of possum diet not being assessed during winter in this study. Possums mainly ate pate and mountain five-finger during winter months elsewhere in South Westland (Fitzgerald and Wardle, 1979), and consumption of southern rata was high in winter in northern Westland (Coleman *et al.*, 1985). Beech species, which made up 25–50% of the estimated total foliar biomass at the three sites, were also not recorded in possum diet during the study.

Total fruit consumption was similar at all three sites and averaged just 4.9% of total diet, but the use of flowers [mainly kamahi (*W. racemosa*)] peaked at 9.3% of diet at the 30-year site (Table 3). Invertebrates were unimportant (<0.1%) dietary items at all three sites.

### Condition of indicator tree species

Little or no possum browse was recorded for any of the indicator species at the 10-year site (Fig. 5). Consistent with this, mean foliage cover scores at the 10-year site were similar to, or higher than, the other two sites, and the proportion of trees with dieback at the 10-year site was similar to, or lower than, the other two sites.

With the exception of Hall's totara and pate, possum browse on indicator trees peaked at the 20-year site with browse frequencies ranging between 32% and 81% of scored trees, reflecting the greater abundance of possums at this site (Fig. 5). Although 32% of mahoe trees at the 20-year site were browsed, no possum browse was recorded on this species at the 30-year site. No recent (January 1997) possum browse was recorded on pate at any site, but high frequencies of dieback and "hedging" at both the 20- and 30-year sites (field observations) suggest that possums browsed pate heavily in other seasons or years at these two sites. For Hall's totara, possum browse was light (10% of trees) at the 20-year site but heavy (79% of trees) at the 30-year site.

Trends in foliage cover for indicator species followed one of three patterns. For kamahi and mahoe,

foliage covers were high (59–69%) at all sites despite high frequencies of possum browse at the 20-year site. For southern rata, pate, and haumakaroa, mean foliage cover scores were highest at the 10-year site (53–65%), and about 20% lower at the 20- and 30-year sites. Finally, foliage covers for fuchsia and Hall's totara were lower (36–43%) at the 30-year site than at the 20-year site (Fig. 5).

Twenty scorable mountain five-finger trees were located at the 20-year site but just three trees were found at the 10-year site and none at the 30-year site, although the presence of seedlings of this species was noted at all three sites. Condition of the 20-year-site trees was poor, with a mean foliage cover of just 31%, compared with a mean of 58% for the three 10-year-site trees. Eighty percent of the 20-year-site trees were possum browsed and 90% had some, mainly light, crown dieback, whereas no dieback or possum browse were recorded at the 10-year site.

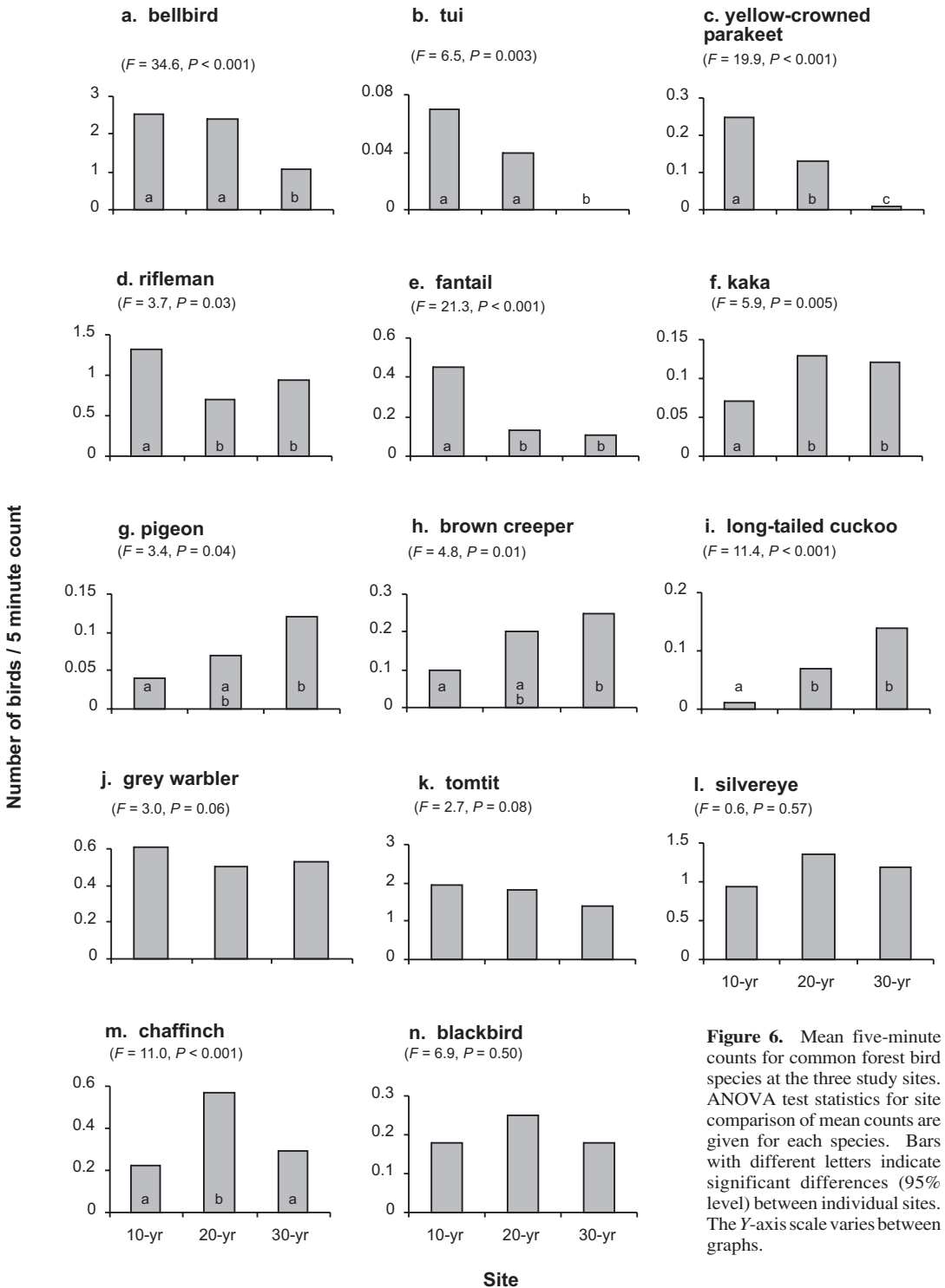
Canopy dieback frequencies at the 20- and 30-year sites were similar to, or higher than, those at the 10-year site for all indicator species (Fig. 5). In most cases the frequency of recorded dieback was also higher at the 30- than the 20-year site.

Overall, canopy condition of our indicator species conforms to the *a priori* prediction that canopy condition would be highest at the 10-year site, intermediate at the 20-year site and lowest at the 30-year site.

Recent mortality of indicator trees, as measured by frequency of standing dead trees (absence of live tissue under bark) at sampling stations, appears to differ markedly between sites. No dead trees were recorded at the 10-year site, and only one dead fuchsia tree was recorded at the 20-year site. In marked contrast, dead trees of all indicator species except mountain five-finger were recorded on at least one plot at the 30-year site, with dead fuchsia found on the majority of plots where the presence of this species was recorded as live or standing dead trees (Table 4). These records are supported by aerial observations that

**Table 4.** The number of sampling stations (*n*) with either live or standing dead trees, and the percentage of these (%) with standing dead trees, for the eight indicator species at each study site.

Indicator species	10-year site		20-year site		30-year site	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Fuchsia ( <i>Fuchsia excorticata</i> )	21	0	29	3	17	83
Southern rata ( <i>Metrosideros umbellata</i> )	4	0	15	0	5	40
Kamahi ( <i>Weinmannia racemosa</i> )	21	0	23	0	19	16
Hall's totara ( <i>Podocarpus Hallii</i> )	0	–	19	0	14	7
Pate ( <i>Schefflera digitata</i> )	22	0	25	0	17	6
Haumakaroa ( <i>Raukaua simplex</i> )	19	0	19	0	15	6
Mahoe ( <i>Melicytus ramiflorus</i> )	14	0	18	0	18	0
Mountain five-finger ( <i>Pseudopanax colensoi</i> )	3	0	8	0	0	–



**Figure 6.** Mean five-minute counts for common forest bird species at the three study sites. ANOVA test statistics for site comparison of mean counts are given for each species. Bars with different letters indicate significant differences (95% level) between individual sites. The Y-axis scale varies between graphs.

crown mortality of indicator species was negligible at the 10- and 20-year sites, but the forest canopy at the 30-year site was peppered with dead fuchsia, southern rata, kamahi and Hall's totara crowns (field observation).

### Relative bird abundance

Common native birds exhibited mixed relationships between their relative abundance and length of site occupation by possums (Fig. 6). Counts of five species [bellbird (*Anthornis melanura*), tui (*Prothemadera novaeseelandiae*), yellow-crowned parakeet (*Cyanoramphus auriceps*), rifleman (*Acanthisitta chloris*) and fantail (*Rhipidura fuliginosa*)] declined significantly from the 10- to the 30-year site (Fig. 6a–e). The means for two other species [grey warbler (*Gerygone igata*), tomtit (*Petroica macrocephala*)] were also greatest at the 10-year site, although not significantly so. If the data for long-tailed cuckoo (*Eudynamis tailensis*) are ignored [because their numbers are likely to simply reflect those of brown creeper (*Mohoua novaeseelandiae*), whose nests they parasitise (Heather and Robertson, 1996)], then the numbers of three species increased significantly from the 10- to the 30-year site [kaka (*Nestor meridionalis*), pigeon (*Hemiphaga novaeseelandiae*), brown creeper] (Fig 6f–h). Because the numbers of more species of birds declined than increased from the 10- to the 30-year site, these data provide weak support for our *a priori* hypothesis that native bird numbers would decrease with increasing length of possum occupation.

Mean counts of exotic chaffinch (*Fringilla coelebs*) and blackbird (*Turdus merula*) and the self-introduced silvereye (*Zosterops lateralis*) were all highest at the 20-year site, but only significantly so for chaffinches (Fig. 6l–n).

Four other forest-dwelling bird species [song thrush (*Turdus philomelos*), dunnock (*Prunella modularis*), shining cuckoo (*Chrysococcyx lucidus*), falcon (*Falco novaeseelandiae*)] were recorded on five-minute counts during the study, but only in very low numbers (<0.05/count) and with no significant trend evident between sites.

These mixed trends in bird abundance across the three study sites were also observed within feeding-ecology groups. There were species with positive and negative abundance trends within nectar and fruit (bellbird, tui, pigeon), insect (rifleman, fantail, grey warbler, tomtit, brown creeper, long-tailed cuckoo) and mixed (yellow-crowned parakeet, kaka, silvereye, blackbird) feeding groups (Fig. 6).

## Discussion

### Sampling design

Without replication, this study can only provide weak evidence of the quantitative changes in possum density, fecundity, diet, indicator-tree-species canopy condition, and forest bird abundance with increasing time since possum colonisation. The alternative hypothesis is that the observed patterns reflect characteristics of the selected sites unrelated to the possums. Vegetation composition and demography potentially offer an explanation for differing possum densities and impacts across the three sites. Young populations of some tree species are more tolerant of possum browsing than older populations (Stewart and Veblen, 1982; Payton, 1983). Seral forests were more abundant at the 20- and 30-year site than at the 10-year site, which suggests that the forests of the 20- and 30-year sites are more frequently disturbed, resulting in younger structures, than the 10-year site. Yet it was the 10-year site that had the lightest possum impacts. Furthermore, the possum population at the 10-year site was evidently not constrained by the relative paucity of possum-preferred seral species (Nugent *et al.*, 2000), because possum fecundity was highest there. Therefore, while vegetation composition differed between the three areas, it is unable to explain key between-area differences for the parameters studied.

Our five *a priori* predictions of the site rank order for various parameters (Table 1) were all supported by our results and, therefore, support the hypothesis that observed differences between sites are indeed due to differences in time since possum colonisation. Thus, while we accept that any conclusions about the magnitude of differences between sites with different histories of possum colonisation can only ever be conditional, we conclude that in the absence of an obvious alternative explanation, the differences between sites are primarily possum-colonisation effects.

### Possum demographics

Possum populations, like those of other invading species, have commonly been assumed to undergo some form of irruptive cycle, where initial population expansion is rapid until densities attain a "peak" (maximum density) that exceeds the sustainable long-term carrying capacity of the environment, before declining to lower "post-peak" levels (Bamford, 1972; Fraser, 1979; Pekelharig, 1979; Thomas *et al.*, 1993). Fecundity of ungulate and possum populations varies at different stages of a population irruption following colonisation. Fecundity is highest during the population-building phase, and lowest when populations are declining (Caughley, 1970; Pracy, 1975; Fraser, 1979). High fecundity, particularly the

high incidence of spring breeding at the 10-year site, suggests that the possum population was probably rapidly increasing there. The fecundity and relative-possum-density patterns suggest that the 10-, 20-, and 30-year sites were at pre-peak, near-peak, and post-peak stages, respectively, of an irruptive oscillation. It is unlikely that the 20-year possum population had already entered a post-peak population decline phase. If it had we would have expected fecundity there to be lower than at the 30-year site (Caughley, 1970).

### Possum diet and impacts on vegetation

Diet of possums in the study sites shifted from being dominated by highly-preferred species at the 10-year site to being dominated by less-preferred species at the 30-year site. These shifts in diet composition reflect declining availability of the most-preferred foods with time, at least on a per capita basis. Recent mortality of preferred species, particularly fuchsia, at the 30-year site also suggests an absolute decline in the abundance of these species.

Similar changes in the diet of possums with increasing length of site occupation have been recorded in podocarp-hardwood forests of the Orongorongo Valley, lower North Island, (Green, 1984; Brockie, 1992). Some highly-preferred foods important to total diet in 1946–47 (e.g. fuchsia) were largely absent from their diet by 1963, with a few species eventually becoming locally extinct (Campbell, 1990). Further small shifts toward greater consumption of formerly minor foods were recorded by 1989 (Allen *et al.*, 1997).

These changes in possum diet and vegetation structure following colonisation support the conclusions of Riney (1964) and Caughley (1970) that mammal population irruptions following liberations are driven by food supply, and that post-peak population declines are the result of food supply depletion by the colonising populations.

Dietary shifts were also associated with declining condition of live trees. For all species monitored, possum impacts appeared negligible at the 10-year site. Although browse frequencies were generally highest at the 20-year site, which corresponds with the high possum densities at that site, crown condition, measured by foliage cover and frequency of dieback, was usually poorest at the 30-year site. The record of dead but standing indicator trees at sampling stations indicates low rates of tree death until about or after the time possum numbers peaked. In summary, possum impacts on common possum-preferred tree species within the study sites were relatively light prior to the peaking of possum populations, but for some species were considerable thereafter.

Several other Westland studies also report that possum-induced dieback is only conspicuous once

colonising possum populations are at near-peak or in post-peak phases (Pekelharing, 1979; Pekelharing and Reynolds, 1983; Leutert, 1988; Pekelharing and Batcheler, 1990; Rose *et al.*, 1992, 1993). In at least some cases conspicuous dieback occurs rapidly, within 2–3 years, once initiated (Pekelharing and Batcheler, 1990; Rose *et al.*, 1992). After canopy dieback is conspicuous it becomes progressively less apparent over time (Pekelharing and Reynolds, 1983; Rose *et al.*, 1992) as dead trees eventually collapse. This indicates that the rate of canopy death declines with increasing length of time, once an initial dieback pulse has passed.

Our plant utilisation data also suggest that for some species possum impacts decline following the post-peak decline in possum numbers. Utilisation of high- and moderate-preference species declined from the 20- to the 30-year site. In contrast though, utilisation of very-high-preference species was highest at the 30-year site; therefore, possum impacts on these foods are likely to remain high once possum numbers peak.

The degree of post-peak possum-induced decline in condition of palatable species also varies between species of similar palatability, and may be related to their relative abundance, with the most severe possum impacts occurring on the least common species. In our study kamahi and mahoe, the most abundant of possum-preferred species monitored at the 30-year site, are the least affected, while Hall's totara, pate, haumakaroa, and southern rata are all relatively scarce and in poor condition compared with kamahi and mahoe. In the Orongorongo Valley, gradual but continuing declines of possum-palatable plants have been recorded long after possum populations peaked, with these long-term declines largely confined to the less abundant possum food species (Campbell, 1990; Brockie, 1992).

The key management implication of this is that in order to preserve the physiologically dominant components of South Westland forests where possums are still colonising, possum populations should be controlled before they peak. This strategy is currently being implemented by the New Zealand Department of Conservation in South Westland sites with pre-peak possum populations. The strategy might be used successfully in areas where seral fuchsia forests are common, by monitoring fuchsia, and controlling possums once high frequencies of possum browse (c. 50% of trees browsed) are recorded.

Pekelharing *et al.* (1998) found that possums killed fuchsia in South Westland within 2 years of their trap-catch index exceeding about 25%, but caution needs to be exercised when using a possum-density threshold for triggering management intervention across a wide area. The possum-density/plant-condition relationship is likely to be site specific and related to the abundance of the plants to be protected and the

abundance and relative palatability of other foods.

A possum control strategy aimed at protecting the physiologically dominant components of the forest is unlikely to provide adequate protection of the most highly favoured, low-biomass possum foods, such as mistletoe species and pohuehue. These species were not monitored during this study, but the high initial and subsequent declining importance in possum diet, and the very high utilisation indices, even at the 10-year site, for this group of species suggests that browsing by possums has considerable negative effects on these species even when possum numbers are quite low. Data from other studies indicate that holding possum densities below 5% trap-catch is sometimes necessary to protect low-biomass palatable species such as mistletoes (Wilson, 1984; Sweetapple *et al.*, 2002).

### Possum impacts on forest birds

Overall the abundance of native birds declined with increasing length of possum occupation within the study area, but numbers of kaka, pigeon and brown creeper increased. Despite these data, kaka and pigeons are unlikely to have benefited from possum invasion of the study area because in South Westland both rely heavily on foods preferred by possums (O'Donnell and Dilks, 1994; Nugent *et al.*, 2000). Furthermore, numbers of both species approximately doubled following possum removal on Kapiti Island (H. Robertson, Department of Conservation, Wellington, N.Z., *unpubl.*). Therefore, the mixed abundance-trends observed across the study area indicate that factors other than time since possum colonisation were having a strong influence on native bird abundance within the study area. This means we are unable to draw any firm conclusions about which species were affected by possums, the magnitude of these effects, or the relative importance of possum predatory and competitive pressures.

Possum control was initiated at the 10- and 20-year sites in 1998, immediately after our study. Repeating the bird survey at all three sites while possum numbers remain low at the two controlled sites would help determine which bird species are affected by possums, and to what extent. Replication of this study would also be valuable to confirm the impact patterns described in this study, particularly for birds. However, the potential for such replication is diminishing as possums continue to invade the few remaining possum-free areas on mainland New Zealand.

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