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DIET OF BRUSHTAIL POSSUMS OVER A PASTURE-ALPINE GRADIENT IN WESTLAND, NEW ZEALAND

Summary: The diet of brushtail possums *(Trichosurus vulpecula* Kerr) in mixed hardwood forests on a central Westland hillside is described from analysis of plant cuticle fragments and seeds in their faeces. Faeces were collected monthly for 2.25 years from animals live-trapped from low altitude forest/ pasture margins through to high altitude alpine shrublands. The diet included forest and pasture foliage, buds, and fruits of over 100 species, although most were eaten infrequently. Foliage was taken most often from woody forest species (88%), with three canopy species, kamahi *(Weinmannia racemosa),* southern rata *(Metrosideros umbellata),* and mahoe *(Melicytus ramiflorus),* providing 69% of the leaf intake. Pasture species formed 12% of the diet of possums living within 300 m of the forest edge, with 90% of this being clovers *(Trifolium* spp.) and grasses. Fruit was taken from a wide range of forest species.

Diet varied with sex, season, and altitude. Males ate more pasture foliage and less ferns than females and differed significantly in their use of many of the major woody species. Woody species were favoured most in winter and spring, ferns and fruits in autumn and winter, and pasture species in autumn. Pasture species were eaten only by possums denning within 1000 m of the forest/pasture margin, and high-altitude species by possums denning nearby.

Only 15 forest species were eaten as much as or more than expected from their relative abundance. Ten of these species were frequently eaten, and the remainder infrequently, being locally rare. Preferred species showed clear evidence of possum browse and were often represented by many dead stems. This demonstrated the adverse effects of possums in such mixed hardwood forests.

Keywords: Trichosurus vulpecula; brushtail possum; Phalangeridae; diet patterns; food preference; rata; Metrosideros umbellata; kamahi; Weinmannia racemosa; hardwood forests; pasture; forest damage; Westland, New Zealand.

Introduction

Brushtail possums *(Trichosurus vulpecula* Kerr) occur over an extremely wide range of habitats in both Australia and New Zealand. As a consequence, possum diet is extremely diverse and has been the subject of 77 published papers (Morgan and Sinclair, 1983).

Possums are common throughout most of New Zealand below 1200 m a.s.l., and reach their highest densities in indigenous mixed hardwood forests, where evidence of their browsing is often marked. The severity of modification by possums of the mixed hardwood stands in central North Island and Westland has stimulated local possum control and studies of possum diet in these habitats, e.g., Kean and Pracy (1953), Mason (1958), Gilmore (1967), Fitzgerald (1976), Fitzgerald and Wardle (1979), and Leathwick, Hay and Fitzgerald (1983).

The effect of possums grazing on native or introduced grasslands has been less studied (Gilmore, 1965a, b; Harvie, 1973; Jolly, 1976), although farmer organisations in the 1960s suggested that the selective grazing of pasture species by possums was limiting stock numbers (Quinn, 1968). More recently, bovine tuberculosis has been identified in possums feeding on pasture amongst stock, so putting them at risk to the disease. This has resulted in the extension of possum control programmes from heavily browsed upland forests to low-altitude farmlands (Coleman, 1981).

A broad study of the population dynamics and movements of possums gave us the opportunity to study both the changes in possum diet over an altitudinal gradient from forest / pasture margin to alpine shrubland, and to determine the impact of possums on a range of forest and pasture species. The vegetation patterns, possum densities, and overt browse patterns in this area were described by Coleman, Gillman, and Green (1980), and possum movement patterns by Green and Coleman (1981). The present paper describes the possums' diet according to season, sex, and altitude, compares the frequency of pasture species taken by animals living within different altitudinal strata, and lists dietary preferences for major foods. The impact of possums on New Zealand's mixed hardwood forests is discussed.

Study Area

The study area was described by Coleman et al. (1980). Briefly, it comprised a 1.5 km wide strip of altitudinally-stratified indigenous forest on the nonhern flank of Mt Bryan O'Lynn (42°37'S, 171 °43' E) in central Westland, and extended from improved pasture at 250 m a.s.1. to alpine shrubland at 1200 m a.s.1. The pastures were dominated by rye grass *(Lolium perenne)* and clovers *(Trifolium* spp.), the low level, selectively-felled terrace lands by kamahi *(Weinmannia racemosa)* and *Cyathea smithii*, and the clear-felled terrace lands by shrub hardwoods such as horopito *(Pseudowintera colorata),* wineberry *(Aristotelia serrata),* and *Coprosma* spp. The mid-altitudinal faces were dominated by kamahi and *Quintinia acutifolia,* the mid-altitudinal ridges by southern rata *(Metrosideros umbellata)* and kamahi, the high forests by broadleaf *(Griselinia littoralis),* cedar *(Libocedrus bidwillii),* southern rata, and kamahi, and the alpine shrublands by shrub hardwoods, e.g., *Olearia* and *Dracophyllum* spp. *

Possums colonised the study area in the 1940s and attained their highest densities in the early 1960s (L. Pracy, pers. comm.). Densities during this study were determined by extinction-trapping (Coleman et al., 1980), and were average to high compared with populations in other New Zealand forests, i.e., 10.4/ha, varying from 25/ha on the forest/pasture margin to 1.9/ha within high-altitude forests.

Methods

Sampling

The foods eaten were evaluated by a study of leaf cuticle and seed fragments present in possum faeces. Each month from February 1976 to April 1978, one faecal pellet was collected from each of 60-120 possums captured during the first of three nights of live-trapping, using permanently stationed box traps spread throughout the forest and adjacent farmland. In all, 1725 pellets were collected, with sample sizes from each altitudinal stratum directly reflecting local possum abundance. Pellets were subsequently grouped according to season (autumn = February-April), sex, and altitudinal home zone of the possums sampled; home zones were assigned after studying the records of live-trapping and den sites. Altogether, eight zones, each 100 altitudinal metres wide, were delineated in the study area, although sufficient pellets for interzonal comparisons were collected from only six.

Identification of species eaten

Techniques used to prepare pellets for identification of cuticles broadly followed those of Dunnet, Harvie, and Smit (1973). Samples of 10-40 pellets were broken up in water and a sub-sample of 10-20 ml searched for small seeds under x20 magnification using a dissecting microscope. The reconstituted sample was washed over two "Endecott" sieves (212 _m and 1.4 mm) and large seeds removed. All solids in the lower sieve were broken up in a 'Sorval' blender for 30 seconds, then cleared by cooking in a solution of chromic and nitric acids until all cellular leaf tissue had dissolved, leaving behind the more acid-resistant, embossed leaf cuticles. Each cleared sample was examined under x200 magnification, and the first 400 fragments of cuticle located during a systematic search were identified. This sample size gave a sampling error of 3-5% (see Yamane, 1964; p. 257), which was considered satisfactory. The maximum horizontal width of each fragment encountered, as first seen in the viewing field, was measured in arbitrary units with an eyepiece graticule, and fragment widths totalled for each species to quantify and compare major foods.

Most of the plant foliage commonly eaten could be identified to species level. However, the cuticles of some conspecifics were too similar to be separated, in particular, small-leaved *Coprosma* spp. (*C. parviflora, C. colensoi, C. rhamnoides, C. pseudocuneata,* and *C. ciliata); Metrosideros* lianes *(M. perforata* and M. *diffusa);* some *Pseudopanax* spp. *(P. edgerleyi, P. crassifolium,* and *P. lineare);* and pasture grasses.

Cuticles were identified from reference photographs and slides of cuticles from over 160 vascular plants collected on Mt Bryan O'Lynn. Each reference specimen was prepared by 'cooking' in nitric acid at concentrations and for periods of boiling appropriate to its fragility, then dehydrated in alcohols and stained with carbyl fuchsin. Specimens were photographed to provide a punch card recall system founded on the epidermal cell characteristics impressed into adaxial and abaxial leaf cuticles.

Determining digestive indices

The proportions of different leaf cuticles found in faeces did not accurately reflect the proportions ingested because rates of digestion vary for different plant species (Dunnet et al., 1973). All plant species

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* Nomenclature follows Allan (J 961) and Parham and Healey (1976).

recorded at 1 % or more by width in seasonal diet samples, plus a few species frequently eaten but in smaller quantities, were used in feeding trials to establish correction factors for different rates of digestion. In each trial, 20 acclimatised, separately-housed possums were fed daily for one week on a 'cake' of bread, sugar, honey and equal quantities by weight of freshly chopped, mature canopy leaves of four to eight species. Faeces were collected daily from each possum from day three onwards, and comparisons made of ingested and egested cuticle fragment frequency and size.

The calculation of an index of digestion (I.D.) was based on the known intakes of cuticle for each species. However, as leaves varied in their weight per unit surface area according to species, so did the area of cuticle ingested in each trial. Leaf surface area/weight ratios were determined from 50 leaves of each species using an image-processing system based on a solid-state array sensor (Cady and Hodgson, 1980). Digestive indices were then calculated for each trial food, as described by Dunnet et al. (1973), by standardising each species against kamahi, locally the most frequent food (Table 1).

A comparison of the proportions of woody species in the diet of possums with the occurrence of those species in the forest was used to indicate food preferences. Food preference ratios were derived from the corrected proportions of woody species eaten and species' basal areas generated from 304 descriptive vegetation plots established on Mt Bryan O'Lynn (summarised in Coleman et al., 1980). It is assumed that stem basal areas usefully (though only approximately) reflect leaf biomass.

Fruits in possum diet were assessed by using reference collections to identify seeds recovered from faeces. No attempt was made to estimate the numbers of fruits eaten. Not only are the exo- and mesocarp remains of fruit in faeces hard to identify and quantify, but also the endocarp (seed), which is more resistant to digestive processes and so taxonomically more useful, often varies numerically within species. In addition, possums reject an unknown proportion of the seeds of many large-seeded species, e.g. miro *(Podocarpus ferrugineus)* and matai *(P. spicatus)*.

Results

Foods eaten

Possums on Mt Bryan O'Lynn mostly ate the foliage from woody forest species (88.1 %), with ferns, forest herbs, and introduced pasture species being of lesser importance (Table 2). The woody species browsed came from 23 angiosperm and two gymnosperm families. However, only seven species and three foods identified to generic level comprised 1 % or more of all foliage eaten. Sixty-nine percent of all foliage eaten came from only three species, kamahi (33.2%), southern rata (24.2%), and mahoe *(Melicytus ramiflorus,* 11.6%). The other major contributors were *Pseudopanax* spp. (4.2%), *Coprosma foetidissima* (3.2%), *Neopanax simplex* (2.0%), wineberry (1.9%), cedar (1.9%), other *Metrosideros* spp. (1.3%), and other *Coprosma* spp. (1.3%). Together, these foods included at least three from the forest canopy, four from the sub-canopy, two from the understorey, and lianes from all tiers.

Of the minor contributions to the diet, 2.2% were Pteridophyta, and included 11 fern species, each from a different family. Most were ground ferns, although the consumption of tree ferns *(Cyathea smithii* and *Dicksonia squarrosa)* and of epiphytic Polypodiaceae reflected the wide range of feeding sites used by possums. Only one fern, *Asplenium bulbiferum,* was eaten frequently (1.9%).

Introduced pasture species comprised 2.9% of all foliage eaten, with about 90% of this being unidentified grasses (Gramineae) and clovers. Other pasture foods comprised 20 species from nine families, including Compositae (7 spp.), Plantaginaceae (2 spp.), and Ranunculaceae (2 spp.), all of little consequence (0.1 % in total). Other minor foods included 14 species of indigenous forest herbs and grasses, and two species of exotic trees. Together, they formed less than 0.2% of all foliage eaten.

About 6% of all foliage eaten could not be identified. The fraction was similar within different samples, and did not bias the results towards any particular diet group.

A small but diverse group of miscellaneous items eaten (0.4%) included pteridophyte rhizomes and sporangia, insect and arachnid cuticles, flower petals, and bark. Although bark was undoubtedly eaten deliberately, the rarity of other items in this group indicated accidental ingestion.

The fruits eaten by possums came from at least 19 woody forest species, three forest herbs, and five pasture species (Table 3). Most seeds recovered (80%) came from putaputaweta *(Carpodetus serratus),* horopito, *Coprosma* spp., *Nertera* spp., and the family Gramineae. Other fruits eaten frequently but in small numbers included those of

Table 1: *Digestive indices for common possum foods established from feeding trials. Data are from four trials with* Weinmannia racemosa *as the standard in each trial. Index of digestion (I.D.) = {total egested cuticle area of species/total egested cuticle area of* W. racemosa] / *[ingested fresh weight of species/ingested fresh weight of* W. racemosa].

Plant species	Total area of cuticle recovered from faeces (arbitrary units, width x 2)	Leaf area of adaxial and abaxial surfaces / g fresh weight (cm^2)	Index of digestion (I.D.)
TRIAL 1			
Weinmannia racemosa	24527	77	1.0
Metrosideros umbellata	12088	56	0.4
M. diffusa/perforata	7302	96	0.4
Aristotelia serrata	15782	134	1.1
Rubus spp.	62331	113	3.7
Dracophyllum traversii	38794	40	0.8
Podocarpus hallii	25677	34	0.5
Quintinia acutifolia	8624	78	0.3
TRIAL 2			
Weinmannia racemosa	13079	77	1.0
Cyathea smithii	36324	133	4.8
Dicksonia squarrosa	43380	182	7.8
Libocedrus bidwillii	14971	24	0.3
Podocarpus ferrungineus	21655	65	1.5
Myrsine divaricata	12251	70	0.8
Histiopteris incisa	31736	117	3.7
Hebe salicifolia	5888	89	0.5
TRIAL 3			
Weinmannia racemosa	16720	77	1.0
Melicytus ramiflorus	6978	92	0.5
Coprosma foetidissima	10019	84	0.6
Pseudopanax colensoi	35540	43	1.2
Trifolium ambiguum	1719	134	0.2
Asplenium bulbiferum	4016	72	0.2
Gramineae	3871	118	0.3
TRIAL 4			
Weinmannia racemosa	19727	77	1.0
Neopanax simplex	5496	134	0.5
Coprosma rotundifolia	11505	97	0.7
Griselinia littoralis	19500	60	0.8

Rubus schmidelioides, Pennantia corymbosa, Pittosporum colensoi, Myrsine spp., *Pseudopanax* spp., and to a lesser extent *Dacrydium bidwillii,* pate *(Schefflera digitata),* and mahoe. A limited range of seeds was recovered from species with non-fleshy pericarps, presumably ingested accidentally, e.g., *Hoheria lyallii, Ranunculus repens,* southern rata, *Uncinia* sp., clover sp., *Juncus* sp., and foxglove *(Digitalis purpurea).*

Variations in diet

Seasonal variation

The relative proportions of major groupings of foliage eaten by possums (woody species, ferns, pasture species, and unknowns) varied seasonally (Fig. 1A), with the broad patterns identified in 1976 repeated in 1977 and 1978. When the data for the three years were lumped, the total width of fragments identified for woody species (χ^2 = 134.49), ferns (χ^2 = 270.00), and pasture species (χ^2 = 187.93) all varied seasonally ($p<0.001$). Woody forest species were browsed most often in Winter and spring, ferns in autumn and winter, and pasture species in autumn. Lesser groups (forest herbs, woody exotics, and miscellaneous) showed similar variation, but their absence from one or more seasons limited analyses.

Varying patterns of use were also found for individual food species (Fig. 2A). For the common foods, use of southern rata and mahoe was most

Table 2: *The percent occurrence of major foliate foods of possums (based on the summed width of cuticle fragments) on Mt Bryan O'Lynn in each season (only species occurring at 0.1% or greater in total intake included; autumn = February-March; T = trace).*

	Seasonal intake (%)				
Species eaten	Autumn 1976-78	Winter 1976-77	Spring 1976-77	Summer 1976-78	Annual intake (%)
INDIGENOUS WOODY SPECIES					
Libocedrus bidwillii	1.3	2.8	3.0	0.7	1.9
Podocarpus ferrugineus	0.1	T	T	0.2	0.1
P. *hallii*	1.4	0.8	0.1	1.0	0.8
Rhipogonum scandens	0.1	0.0	0.1	0.1	0.1
Melicytus ramiflorus	7.3	13.8	16.5	9.5	11.6
Fuchsia excorticata	0.1	T	0.1	T	0.1
Pittosporum eugenioides	0.1	T	T	0.1	0.1
Metrosideros umbellata	15.2	28.9	29.0	26.4	24.2
Metrosideros spp.	2.8	0.5	0.1	1.2	1.3
Aristotelia serrata	1.8	1.7	1.5	2.5	1.9
Weinmannia racemosa	37.7	32.2	34.5	25.3	33.2
Quintinia acutifolia	0.1	0.1	0.2	0.4	0.2
Rubus spp.	1.1	0.1	0.1	0.4	0.5
Pennantia corymbosa	0.1	0.1	0.2	0.1	0.1
Schefflera digitata	T	0.1	T	0.1	0.1
Neopanax simplex	2.6	3.3	1.6	0.1	2.0
Pseudopanax spp.	4.3	4.2	3.0	5.5	4.2
Griselinia littoralis	0.1	0.5	0.1	0.3	0.2
Dracophyllum traversii	0.0	0.0	0.1	1.1	0.2
Myrsine divaricata	0.2	0.3	0.2	0.2	0.2
Coprosma foetidissima	3.8	1.4	2.4	5.6	3.2
C. *rotundifolia*	0.3	0.1	0.2	0.4	0.2
Coprosma spp.	2.0	0.4	0.7	2.4	1.3
Hebe spp.	T	T	T	0.2	0.1
Other	T	T	T	T	0.3
Total for all species	83.1	91.7	93.5	84.2	88.1
INDIGENOUS FERNS					
Histiopteris incisa	T	0.1	0.1	T	0.1
Asplenium bulbiferum	2.1	3.5	1.1	0.9	1.9
Blechnum spp.	0.1	0.1	T	T	0.1
Other	T	0.3	T	T	0.1
Total for all species	2.3	4.0	1.4	1.1	2.2
INTRODUCED HERBS AND GRASSES					
Brassica rapa	T	0.2	T	T	0.1
Trifolium spp.	0.8	0.8	0.9	1.3	0.9
'Pasture grasses'	3.2	0.9	1.1	1.0	1.7
Hieracium pilosella	0.1	0.1	T	T	0.1
Other	T	0.1	T	T	0.1
Total for all species	4.4	2.1	2.1	2.5	2.9
FOREST HERBS AND MISCELLANEOUS					
Total for all species	1.6	0.1	0.2	0.4	0.7
UNKNOWNS					
Total for all species	8.6	2.1	2.7	11.7	6.1

Table 3; *Fruits eaten by possums on Mt Bryan O'Lynn (as indicated by seeds in their faeces; autumn = February-March).*

	Seasonal intake of seeds (total numbers)				
Species eaten	Autumn 1976-78	Winter 1976-77	Spring 1976-77	Summer 1976-78	Total
INDIGENOUS WOODY SPECIES					
Podocarpus ferrugineus	10	4			14
P. spicatus	8				8
Dacrydium bidwillii	16				16
Phylocladus alpinus	2				2
Pseudowintera colorata	179	17			196
Melicytus ramiflorus	46				46
Pittosporum colensoi	2	32	13		47
Metrosideros umbellata				4	4
Neomyrtus pedunculata	5				5
Pla1ianthus betulinus	1				1
Hoeria lyallii		8			8
Carpodetus serratus	102	223	238	26	589
Rubus schmidelioides	30	2		11	43
Urtica ferox	2	6	2		10
Pennantia corymbosa	52				52
Schefflera digitata	19				19
Pseudopanax spp.	10	19			29
Myrsine spp.	23	48	16		87
Coprosma spp.	504	60		86	650
HERBACEOUS SPECIES AND GRASSES					
Uncinia sp.	1				1
Nertera spp.	101	89	63	37	290
Juncus sp.	2		1		3
Carex sp.	3				3
Ranunculus repens	19	9			28
Triticum vulgare			2		2
Digitalis purpurea	1				1
Trifolium sp.	1				1
Grainineae	384	3	2	3	392
OTHERS					
Indeterminate	93	8	6	3	110
Total No. seeds recovered	1616	528	343	170	2657

sharply seasonal in winter and spring. Although less clearly seasonal, kamahi was eaten mostly in autumn, winter, and spring; *Coprosma foetidissima* in summer and autumn; and both *Asplenium bulbiferum* and 'grass' in autumn and winter.

The number of species eaten comprising more than 1 % of the diet did not vary significantly from season-to-season. However, the total number of species eaten varied from 87 in autumn to 69 in summer, 62 in winter, and 57 in spring ($\chi^2 = 6.99$, $0.1 > p > 0.05$).

Ingestion of fruit, as indicated by seeds, was markedly seasonal ($\chi^2 = 709.6$, $p < 0.001$, Table 3) and followed the fruiting cycle of forest and grassland species. Most fruits of most species were eaten in autumn, fewer in winter, and fewest in spring-summer. Fruits of putaputaweta and *Nertera* spp. were eaten throughout the year. The number of 'species' eaten, using data from complete years only (February 1976-January 1978), was also greatest in autumn and least in spring-summer ($\chi^2 = 7.57$, $p > 0.05$), reflecting the sharp seasonality of most fruiting cycles.

Altitudinal variation

The intake of major food groups reflected their altitudinal distribution (Fig. 1B). Woody species comprised about 90% of the diet of mid- to high-forest possums (zones 3 to 8) but less than 80% for low-altitude, forest-edge possums (zones 1 and 2). Conversely, ferns and pasture foods were eaten most frequently by possums from zones 1 and 2 (6.2 and 8.2% of all foliage eaten respectively) and infrequently by those at higher levels ($p < 0.001$). Forest herbs and unidentified foliage were taken equally at all altitudes.

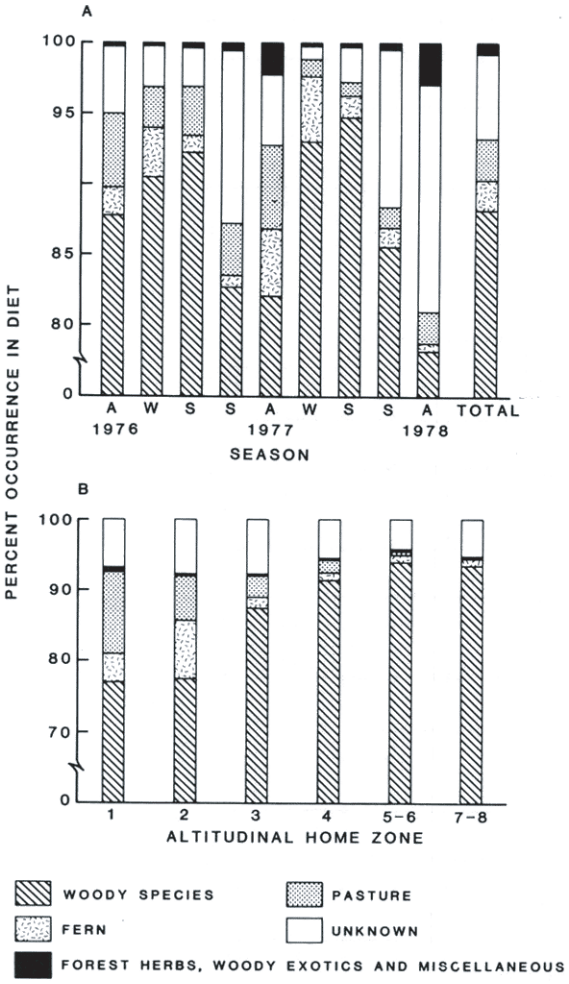

Figure 1: *Seasonal and altitudinal variations in the percent occurrence of the major groupings of foliage eaten by possums. For the seasons (A, W,S,S), autumn (A) = February-April. Altitudinal zones were defined as intervals of 100 m from zone* 1 *(200-300 m a.s.l.) to zone* 8 *(900-1000 m a.s.I.).*

The dietary importance of the common food species in each zone largely reflected their altitudinal distribution (Fig. 2B). Thus wineberry, *Asplenium bulbiferum,* clover spp., and grasses were taken most frequently by low-altitude, forest-edge possums (zones 1 and 2); mahoe and kamahi by low-to mid-altitude possums (zones 1 to 4); southern rata and *Coprosma foetidissima* by mid- to high-altitude possums (zones 4 to 8); and cedar and *Neopanax simplex* only by possums at the highest altitude.

Possums ate a similar number of species in each altitudinal zone. At low altitudes (zones 1 and 2), pasture species comprised about 30% of all species eaten; those were replaced at higher altitudes by a variety of woody and herbaceous forest species.

The species of fruit eaten by possums also followed the altitudinal distribution of parent plants. Possums living near the forest / pasture margins ate fruit from low-altitude podocarps such as miro and matai, low-altitude hardwoods (pate and mahoe), and some pasture species. Conversely, possums living at high altitudes ate fruit from such high-altitude species as *Dacrydium bidwillii, Pittosporum colensoi,* and *Carex* sp. Possums living at mid altitudes ate the widest variety of fruits, from species characteristic of both high- and low-altitudes.

Sexual variation

The relative proportions of all major foods eaten by male and female possums varied significantly (Table 4A). Possums of both sexes consumed similar proportions of the foliage of woody species (88.1 % of the total intake) and 'other' foods (6.7%, comprising miscellaneous, woody exotics, and unknowns). However, females ate significantly greater proportions of ferns than males, and males ate significantly greater proportions of forest herbs and pasture species than females. Although these foods together comprised only 5.2% of the total diet, these differences between the sexes were great enough to produce a difference over the whole diet.

The seasonal intake of all major food groups except forest herbs was different for male and female possums (Table 4B). Females ate significantly more foliage from woody species in summer than males. Females also ate more ferns than males in most seasons, while males ate significantly more pasture foods than females in all seasons. Among 'other' foods, the pattern was less clear, with males eating more than females in winter, spring, and summer and less in autumn.

Altitudinal differences were found between male and female food intake for all major diet groups

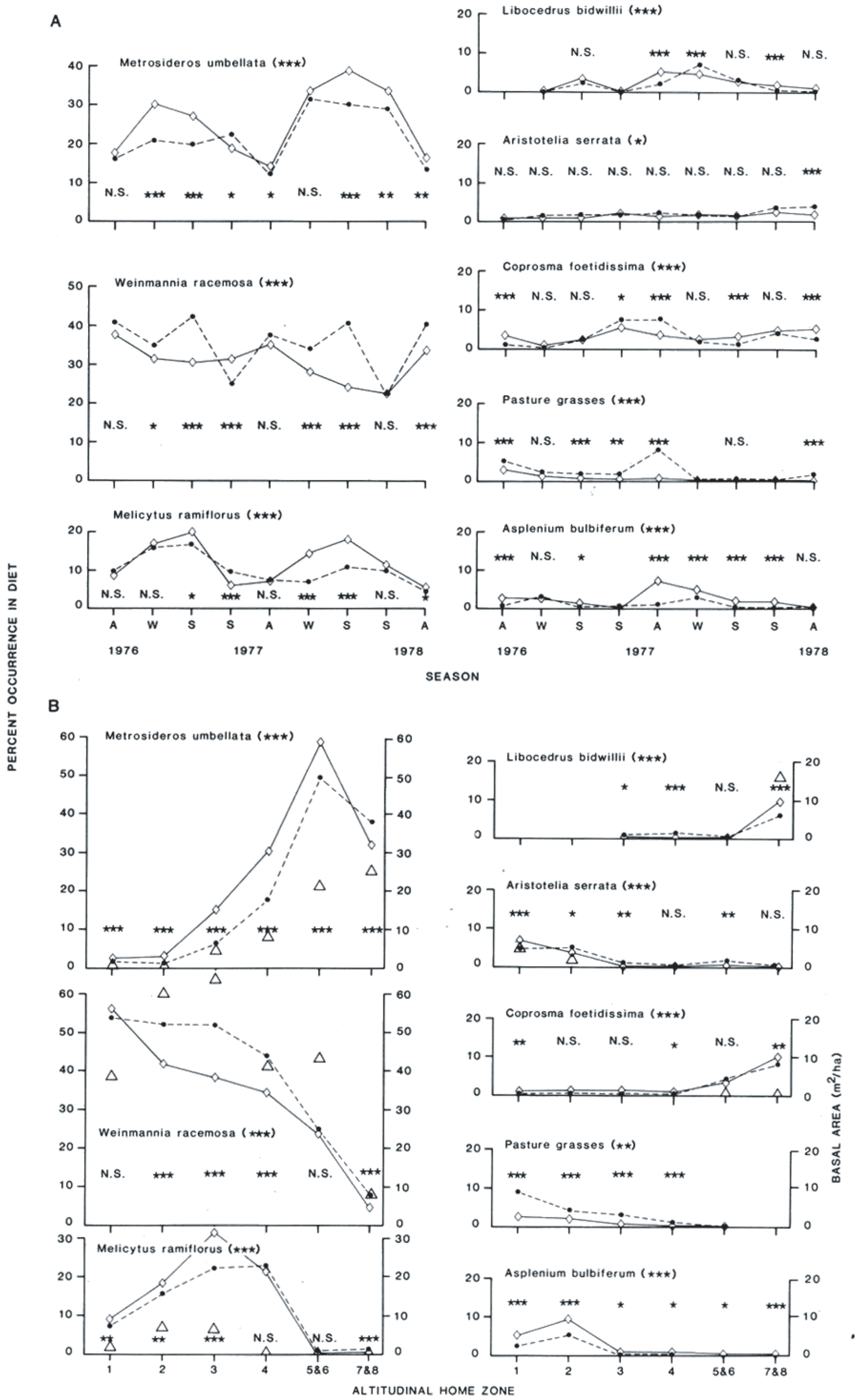

Figure 2: *Seasonal and altitudinal variations in percent occurrence of some common foods in the diet of male (•- - - - •) and female (◊—◊) possums. For the seasons (A,W,S,S), autumn (A) = February-April. Altitudinal zones were defined as intervals of 100 m from zone 1 (200-300 m a.s.l.) to zone 8 (900-1000 m a.s.l.). Statistical significance of differences in amounts eaten by males and females* is *shown for each season (Fig. 2A) and each zone (Fig. 2B), and for all seasons or zones lumped (in parenthesis). Levels of significance are indicated by N.S. = p>0.05,* = p 0.05, ** = p 0.01, *** = p 0.001. Basal areas shown in Fig. 2B (Δ) were determined from 304 vegetation plots scattered over the study site.*

(Table 4C). Females ate more foliage from woody species than males in zone 1, and males ate more foliage from woody species than females in zone 2. No significant differences were found for woody foliage in other zones. Females consumed significantly more fern than males in most zones but less pasture foods in all except the highest zones. Differences in male and female diet were less consistent amongst infrequently eaten forest herbs and the 'other' food grouping.

Male and female possums ate different proportions of the most favoured species across both seasonal and altitudinal gradients (Fig. 2A and B). Females ate more southern rata and mahoe than males in all except the highest altitudinal zones and in most seasons. Conversely, males ate more kamahi than females at most altitudes and in most seasons. Of the lesser species, *Asplenium bulbiferum* was preferred by females at all altitudes and in most seasons, and 'grasses' by males at all altitudes and seasons.

The range of fruits eaten by males and females was generally similar. About 80% of all seeds (and hence fruit) eaten both by males and females came from the five most often eaten species.

Table 4: *The total width (in arbitrary units) of all cuticle fragments identified in major food groups, season, and altitudinal zone for male and female possums (corrected for differential digestion). The seasonal data include three autumn samples (autumn = February-April), and two winter, spring, and summer samples. Altitudinal zones were defined as intervals of 100 m from zone* 1 *(200-300 m a.s.l) to zone* 8 *(900-1000 m a.s.l). The 'goodness of fit' test compares male and female intake within each food, season or zone, while the 'test of independence' examines the dependence of the intake from all food, season, and zone categories upon the sexes (NS = $p > 0.05$, * = p 0.05, ** = p 0.01, *** p 0.001).*

A. MAJOR FOOD GROUPS	*Total width of cuticle fragments*						
	Woody	*Fern*	*Herb. forest*	*Pasture*	*Other*	*Fragment total*	χ *test of independence*
Male	18878	346	43	886	1469	21622	
Female	19180	626	22	389	1404	21621	285.04
χ *(Goodness of fit)*	2.40	80.66	6.15	193.73	1.38	0.0	
Significance	NS	***	*	***	NS	NS	***

B. SEASONAL VARIATION	*Season*				All seasons
(1) *Woody Species*	Autumn	Winter	Spring	Summer	χ^2
Male	6026	4392	4430	5890	
Female	5947	4406	4541	6235	8.08
χ^2	0.52	0.02	1.37	9.82	
Significance	NS	NS	NS	**	*
(2) *Ferns*					
Male	72	173	38	58	
Female	266	211	96	94	48.37
χ^2	111.35	3.76	24.24	8.05	
Significance	***	NS	***	**	***
(3) *Pasture Species*					
Male	504	115	134	223	
Female	137	86	75	137	51.68
χ^2	210.12	4.18	16.66	20.54	
Significance	***	*	***	***	***
(4) *Herbaceous Forest Species*					
Male	22	5	0	22	
Female	14	5	0	7	2.74
χ^2	1.36	0.0	0.0	6.76	
Significance	NS	NS	NS	**	NS
(5) "*Others*"					
Male	583	115	197	1001	
Female	842	86	91	727	127.76
χ^2	47.07	4.18	39.01	43.45	
Significance	***	*	***	***	***

Table 4: *Continued*

C. *ALTITUDINAL VARIATION*

	Altitudinal zone						All zones
	1	2	3	4	5-6	7-8	
(1) *Woody Species*							
Male	2621	2876	3132	3298	3316	3384	
Female	2927	2711	3193	3290	3452	3366	22.54
χ^2	16.88	4.87	0.59	0.01	2.73	0.05	
Significance	***	*	NS	NS	NS	NS	***
(2) *Ferns*							
Male	97	209	22	22	32	14	
Female	205	385	36	43	18	40	21.70
χ^2	38.63	52.15	2.91	6.15	3.38	11.57	
Significance	***	***	NS	*	NS	***	***
(3) *Pasture Species*							
Male	540	238	166	76	8		
Female	266	140	40	18	4		26.88
χ^2	93.15	25.41	77.07	34.56	0.75		
Significance	***	***	***	***	NS		***
(4) *Herbaceous Forest Species*							
Male	7		7		21		
Female	11		8		7		6.89
χ^2	0.50		0.0		6.76		
Significance	NS		NS		**		**
(5) *Other Foods (unknown, exotic woody, misc.)*							
Male	331	277	277	205	238	191	
Female	191	364	324	241	122	191	90.89
χ^2	37.55	11.81	3.68	2.91	37.38	0.0	
Significance	***	***	NS	NS	***	NS	***

Diet choice

The food preference ratios calculated for woody species in Table 5 can be used to assess the relative importance of these species to possums. A ratio of 1.0 implies that possums eat the expected quantity of the species relative to its abundance; a ratio greater than 1.0 implies that possums eat more than expected, and a ratio of less than 1.0, less than expected. Trace foods contributing less than 0.1 % to the diet are not listed.

Only 15 'species' were eaten in expected or more than expected quantities. Nine of these were commonly eaten *(Coprosma foetidissima, Pseudopanax* spp., *Neopanax simplex,* mahoe, southern rata, wineberry, other *Coprosma* spp., kamahi, and cedar); others *(Rubus* spp., *Fuchsia excorticata,* Hall's totara *(Podocarpus hallii), Metrosideros perforata,* pate, and *Myrsine divaricata)* were so rare that they contributed little to the diet. Species which were relatively common in the forest but were eaten less often than expected included miro, horopito, putaputaweta, broadleaf, and *Quintinia acutifolia*. Many trace species were rare in the forest.

Even among the most common foods, possums showed varying preference (Table 5). Southern rata and mahoe, although less common than kamahi, were taken proportionately more frequently. Similarly, *Neopanax simplex,* '*Pseudopanax* spp.' and *Coprosma foetidissima* appeared to be eaten more frequently than cedar, wineberry, and other *Coprosma* spp., which were more common in the forest.

The effect of such preferences by possums on some

Table 5: *Dead stem basal areas and preference ratios (% occurrence in diet/% of total basal area) of woody forest species eaten by possums.* (1 = *Assessment methods described in Coleman et al. (1980);* 2 = *Includes* R. schmidelioides *and* R. australis; 3 = *Includes* P. crassifolium, P. edgerleyi *and* P. lineare; 4 = *A liane - basal area unknown;* 5 = *A lumping of* 11 *commonly occurring* Coprosma *species).*

Species eaten	*Percent occurrence of species in woody diet (based on total width of cuticle fragments)*	*Species % in total basal area of forest*	*Mean basal area of dead stems (m/ha) from 304 plots*	*Food preference ratio*
Rubus spp.[2]	0.57	0.01	0.0	57.0
Fuchsia excorticata	0.11	0.002	0.0	55.0
Coprosma foetidissima	3.63	0.08	0.0	45.4
Pseudopanax spp.[3]	4.31	0.11	0.0	39.2
Neopanax simp ex	2.27	0.19	0.0	11.9
Podocarpus hallii	0.90	0.21	0.76	4.3
Melicytus ramiflorus	13.20	3.33	0.01	4.0
Metrosideros perforata'	1.50	-	0.0	-
Metrosideros umbellata	27.50	10.53	1.77	2.6
Schefflera digitata	0.11	0.08	0.0	1.4
Aristotelia serrata	2.16	2.05	0.04	1.0
Coprosma spp.	1.48	1.72	0.002	0.9
Weinmannia racemosa	37.68	45.64	1.67	0.8
Myrsine divaricata	0.23	0.28	0.01	0.8
Libocedrus bidwillii	2.16	3.06	1.26	0.7
Coprosma rotundifolia	0.23	0.73	0.0	0.3
Dracophyllum traversii	0.23	1.01	0.0	0.2
Pennantia corymbosa	0.11	0.48	0.01	0.2
Pittosporum eugenioides	0.11	0.94	0.0	0.1
Podocarpus ferrugineus	0.11	1.12	0.01	0.1
Griselinia littoralis	0.23	6.09	0.11	0.0
Quintinia acutifolia	0.23	8.09	0.15	0.0

of these forest species was examined by comparing dietary intake, preference ratios, and the volume of dead stems present in the study area (Table 5). With some exceptions, the species most commonly eaten generally had preference ratios considerably higher than 1.0, and their populations contained many dead stems.

Southern rata, kamahi, cedar, and Hall's totara predominated among dead trees. The first two species were also common in the living forest and in the possum food intake. Cedar and Hall's totara were considerably less common in the living forest and much less prevalent in the diet. Hall's totara was a preferred food, whereas cedar was eaten in quantities proportional to its occurrence. Of the other species listed, mahoe and wineberry stood out as being resilient. Populations of both species contained low volumes of dead stems, yet were favoured and often seasonally defoliated by possums. Populations of all other species eaten (Table 5) contained few dead stems and were of lesser dietary importance.

Discussion

General patterns of possum diet

Patterns of possum browse in indigenous New Zealand forests were first detailed by Kean and Pracy (1953) who noted that possums fed on more than 70 species of trees, about 20 ferns, and a few vines and epiphytes. A more detailed study based on the contents of possum stomachs collected over 11 months in Orongorongo Valley, Wellington (Mason, 1958), identified over 32 indigenous species in the ingesta, and listed a further 21 species eaten. However, only eight of all these species occurred in 12 (9.2%) or more stomachs. The same dietary pattern emerged on Mt Bryan O'Lynn, where possums ate the leaves of at least 53 species of woody plants, 10 ferns, 14 forest herbs, and 24 pasture herbs and grasses. Of these, only 10 'species' contributed more than 1 % each to the total leafy intake, and of these, three provided 69% of the foliage ingested; southern rata, kamahi, and mahoe. These three species are major possum foods wherever both occur.

Fruits eaten by possums proved difficult to evaluate in this as in previous studies (Fitzgerald, 1976; Fitzgerald and Wardle, 1979). Our study showed that fruit from a wide range of forest species, and to a lesser degree pasture species, provided an important part of the possum's diet, especially in autumn and winter and at all altitudes. As for ingested foliage, the fruit fraction of the diet was dominated (80%) by just four species. Some fruits common on Mt Bryan O'Lynn and favoured by possums elsewhere in New Zealand were apparently not eaten, e.g. wineberry, *Podocarpus dacrydioides, Dacrydium cupressinum* (Kean and Pracy, 1953), and *Ripogonum scandens* (Mason, 1958). Such absences may be an artifact of sampling (e.g., indicate years of poor fruiting of some species), but may equally well represent local variations in preference.

Animal foods identified in possum faeces were confined to insects and arachnids, which were eaten at all seasons and altitudes, but as chiton (relative to foliage) is highly resistant to digestive processes, such species were probably over-represented in faeces.

The possum is clearly a generalist feeder which has strong preferences for a small number of key species. The reasons for such behaviour are unclear. Freeland and Winter (1975) argued thar the co-evolution of forest systems and marsupial browsers in Australia has led to plants evolving protective (toxic) chemical defences which ensure browsers ingest several different foods per day to meet their energy requirements. By inference, New Zealand's vegetation, having evolved largely in geographic isolation and relatively free from browsing vertebrates, should be more palatable and capable of supporting higher possum densities.

The well documented destruction of New Zealand's forests by introduced mammals seems consistent with this hypothesis (Howard, 1964; Gibb and Flux, 1973). However, in a recent review Green (1984) has discounted any central role for the 'toxic hypothesis' as a major determinant of possum densities in New Zealand forests, as the species diet spectrum is very wide. Several of the species eaten on Mt Bryan O'Lynn either contain, or are suspected of containing toxins, e.g., *Coriaria* spp., *Urtica ferox,* horopito, and mahoe, but most species are believed to be largely toxin-free (Connor, 1977). One genus, apparently toxin free, illustrates the consequences of being palatable to mammals through its disparate distribution between New Zealand and Australia. In New Zealand, *Metrosideros* is represented by 11 species (Allan, 1961) many of which are browsed by possums, while in Australia it only occurs in the fossil record, and as two extant species in the far north-east forests (Beadle, 1981).

Use of pasture

The dietary importance of pasture species to possums living on forest/pasture interfaces is well documented. Such species commonly comprise 20% or more of local diets (Gilmore, 1965b; Harvie, 1973; Warburton, 1978), with only one New Zealand study (Jolly, 1916) indicating little use of freely available pasture.

On Mt Bryan O'Lynn, clovers, grasses, and other pasture plants comprised 12% of the year-round diet of possums denning within 300 m of the forest/pasture margin; 90% of this consisted of clovers and grasses. Pasture foods were eaten most frequently in autumn and more commonly by males than females.

The use of pasture by possums (especially males) denning up to 1000 m into the forest helps explain the high numbers often seen foraging on pastures adjacent to forests containing relatively few (1-2/ha) possums, as well as the localised economic losses resulting from their grazing (Harvie, 1973; Spurr and Jolly, 1981), the frequent transmission of bovine tuberculosis between possums and farm stock, and the higher levels of infection seen in male than in female possums (JDC, unpubl.).

Sexual differences in diet

Possums on Mt Bryan O'Lynn showed considerable sexual biases in their diet. That males should eat proportionately greater amounts of pasture foods than females was not entirely unexpected. Males have greater home ranges and range lengths than females (Green, 1984) and may travel up to 1.0 km through continuous forest then over open fields to feed on pasture (Green and Coleman, unpubl.). However, even amongst possums dwelling on the forest / pasture margin, males ate relatively more pasture foods than females. On the other hand, females ate proportionately greater amounts of fern than males in most seasons and at most altitudes. Sexual differences in the use of woody species, herbaceous forest species, or 'other' foods were less pronounced.

Sexual differences in diet have been documented infrequently in vertebrates and have been generally attributed to differences either in body size or nutritional demands. Male and female possums in Westland are similar in size (Green and Coleman, 1984), and the additional nutritional demands of females arising from reproduction may be expressed though the diet selection evident in all seasons. Such demands have led female red kangaroos *(Megalela rufa)* to select forbs rich in nitrogen (Newsome, 1980) and female ship rats *(Rattus rattus)* to select protein-rich arthropods over vegetable foods (Gales, 1982). A consequence of such diet selection is a decrease in the diet overlap between males and females and, by inference, an increase in the carrying capacity of the habitat. On Mt Bryan O'Lynn, sexual differences in diet in possums were greatest on the forest I pasture margin, where food was most diverse, and possum densities 3 to 5 times those recorded in local mid- to high-altitude forests (Coleman et al., 1980).

Impact of possums on rata-kamahi forests

The role of possums in the accelerated mortality of the canopy in New Zealand's rata-kamahi forests has been debated extensively. Early botanists (Kirk, 1920; Perham, 1924 unpubl.) largely dismissed the possum as an agent of forest change. Observations during 1940-60, however, identified extensive canopy death in rata-kamahi forests (Kean and Pracy, 1953; Wodzicki, 1950; Howard, 1966), generally associated with high possum densities. Recent canopy death in Westland, argued to result from possum browsing, was estimated at 10-15% of stems in high volume southern rata/kamahi forest on Mt Bryan O'Lynn (Coleman et al., 1980), more than 40% in similar forests in the T aramakau catchment (Pekelharing, 1979), and still greater losses in the Kokatahi catchment (Allen and Rose, 1983). Many northern rata *(M. robusta)/kamahi* stands in the Ruahine Range have been similarly affected (Batcheler, 1983).

Other recent studies of possums have identified rata and kamahi as major species in the animal's diet (for references, see above). Heavy possum browse on such trees followed shortly by their death is common, as is the coincidence of increasing high possum densities with spectacular forest modification (Batcheler, 1983). Additional evidence has come from the experimental use of metal sheathing to exclude possums from heavily browsed northern rata in Orongorongo Valley, Wellington (Meads, 1976) and from southern rata on Stewart Island (Coleman and Pekelharing, unpubl.), which has preserved and even restored dying trees to full vigour. Experimental defoliation of southern rata in Westland led to depressed shoot growth and shoot death (Payton, 1983).

Such observations illustrate the damage arising from the presence of high numbers of possums in susceptible forests. However, a cautionary note has recently come from Veblen and Stewart (1982), who argued that "in central Westland rata-kamahi forest, it is not clear the degree to which the excessive tree mortality should be attributed to opossum browsing as opposed to natural stand dynamics", because such "dynamic processes may also contribute significantly to this mortality". Stewart and Veblen (1983) stated further, that "biotic agents responsible for immediate tree death may only be triggers to mortality. . ." with "the synchronous senescence of the trees. . . an essential contributory factor. . .".

The inferences implicit in such a caution are that the possum is blamed unjustly for a significant fraction of rata-kamahi death, and that some possum control carried out to protect indigenous forests is unwarranted. Our results, by contrast, confirmed earlier findings linking possum browse to tree mortality. Comparisons from Mt Bryan O'Lynn of possum diet, possum browse, and the frequency of dead stems provide strong evidence of extensive possum-induced mortality in southern rata and kamahi and also in some less common species (e.g., Hall's totara and cedar) not previously considered at risk.

Under a continued regime of possum browsing, the Mt Bryan O'Lynn forests are likely to change in composition, with a subsequent change in possum diet, as documented in Orongorongo Valley by Fitzgerald (1976). Species palatable to possums may become rare or locally extinct. Mature live specimens of Hall's totara and *Fuchsia excorticata* are now rare, and southern rata and cedar must also eventually become rare. Other species such as mahoe and pate, though heavily browsed, are remarkably resilient and seem likely to survive, even if at lowered densities. In contrast, kamahi, the single most important food, which frequently occurs as dead stems (Coleman *et al.,* 1980), is regenerating freely. As in similar forests existing under prolonged possum browsing pressure (e.g., at the Fox River in Westland National Park, Allen and Rose, 1983), kamahi appears likely to remain the dominant canopy species on Mt Bryan O'Lynn for the foreseeable future.

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