THE INFLUENCE OF BROWSING BY INTRODUCED MAMMALS ON THE DECLINE OF NORTH ISLAND KOKAKO

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SUMMARY: The diet of the North Island kokako *(Callaeas cinerea wilsoni)* was studied in three central North Island habitats, Pureora, Mapara, and Rotoehu, for three years. Possum *(Trichosurus vulpecula)* diet was less intensively studied for part of the same time in Pureora and Mapara. A literature review was made of the diet of possum, red deer *(Cervus elaphus),* and feral goat *(Capra hircus).* There is considerable overlap between the diets of kokako and the three mammalian browsers; leaves and/or fruit of some species are eaten by all four, e.g. mahoe *(Melicytus ramiflorus),* fivefinger *(Pseudopanax arboreus),* lawyer *(Rubus cissoides),* pigeonwood *(Hedycarya arborea),* and raurekau *(Coprosma australis).* Possums, red deer, and goats have reduced the abundance of preferred kokako food plants in much of the remaining kokako habitat. The present distribution of kokako suggests that their decline has been caused not only by forest clearance and introduced predators, but also by impoverishment of habitat resulting from the introduction of browsing mammals.

KEYWORDS: browsing; food preference; indigenous forest; kakako; Callaeas cinerea; Callaeatidae; red deer; Cervus elaphus; Cervidae; goat; Capra hircus; Bovidae; possum; Trichosurus vulpecula; Phalangeridae; interspecific competition; Pureora State Forest; Mapara State Forest; Rotoehu State Forest.

INTRODUCTION

The kokako is one of three species making up the endemic family of New Zealand wattlebirds (Callaeidae). It is listed in the New Zealand Red Data Book (Williams and Given, 1981) where the South Island subspecies *(Callaeas cinerea cinerea)* is classified as extinct, and the North Island subspecies *(C.c. wilsoni)* is classified as vulnerable. The other two species in this family are the extinct huia *(Heteralocha acutirostris),* and the saddleback *(Philesturnus carunculatus),* the two subspecies of which are now confined to small off-shore islands.

Controversy over the future of central North Island forests containing kokako, particularly at Pureora, resulted in the declaration of a three year moratorium on logging in that area. This period, between December 1978 and December 1981, was designated to allow study of the biology of kokako, and the likely effects of logging on its survival.

North, Island kokako have shown a marked reduction in both range and numbers since the arrival of Europeans (Lavers, 1978). They were once widespread and locally abundant throughout the North Island but populations are now mainly restricted to the central North Island' forests, including those from Urewera to King Country and north Taranaki. Birds have also been reported recently at Puketi in Northland (Anderson, 1979).

Several explanations for this decline have been advanced. St Paul and McKenzie (1974) attributed the decline in Hunua Range almost entirely to the effects of introduced predators, particularly the ship rat *(Rattus rattus).* In contrast, Williams (1976), discussing kokako decline in general, regarded destruction of habitat since European settlement as clearly being the main cause. However, neither forest modifi.-cation nor predator introduction fully explains the decline of kokako in unlogged forest, nor the existence of good populations of kokako where predators have been present for up to 80 years. These exceptions suggest the existence of one or more complicating factors. Though Crook (1971) suggested that the impoverishment of habitat caused by introduced browsing mammals could be responsible for the kokako's decline, the impact of possums *(Trichosurus vulpecula),* red deer *(Cervus elaphus),* or goats *(Capra hircus)* has been given only cursory treatment in the literature. Until this study was carried out there had been no comprehensive investigation to substantiate Crook's suggestion, nor to document the considerable evidence of dietary overlap among possums, deer, goats, and kokako.

STUDY AREAS

The forest cover of much of the northern central North Island consisted originally of podocarps up to 40 m in height emergent over a hardwood canopy. Much of this forest has been clear-felled, and over large areas of the remainder, most podocarps have been logged, leaving modified forests dominated by hardwoods. Three study areas were chosen encompassing a range of forest types and degrees of modification.

Pureora

The Pureora study area (38° 30'S, 175° 35'E) was 40 ha of gently undulating country (mean slope 5.2°), consisting of broad ridges separated by shallow gullies within the altitude range of 585-620 m a.s.l. Soils are formed on Taupo pumice and are classified as podsolised yellow-brown pumice soils belonging to the Tihoi series (Rijkse and Wilde, 1977). The climate recorded at Pureora State Forest Park headquarters is cool and moist with an average air temperature of 10.3°C; monthly averages range from 5.2°C in July to 15.6°C in February. Annual rainfall over the period 1940-1970 averaged 1829 mm with most falling between May and November. Ground frosts are common, and although concentrated in the winter months, may occur at any time of the year.

The forest within the Pureora study area, unlike much of that within the central North Island, has been only very lightly modified by logging. However, the adjacent forest on three sides has been clear-felled and exotic conifers planted; the remaining (western) side of the study area abuts the Pikiariki ecological area which consists of a further 450 ha of unlogged forest. Within the study area several narrow skid tracks were formed in 1978 and a very small number of podocarps removed. These tracks are now regenerating in. a dense cover of wineberry *(Aristotelia serrata)**, pate *(Schefflera digitata)* and toetoe *(Cortaderia fulvida).*

Pigs *(Sus scrofa),* red deer, possums, feral cats *(Felis catus),* ferrets *(Putorius putorius),* stoats *(Mustela erminea),* ship rats, mice *(Mus musculus),* and hedgehogs *(Erinaceus europaeus)* are all found locally. Weasels *(Mustela nivalis)* may also be present. Pigs probably colonised the area by 1840 (Woozicki, 1950). The population was high in the 1950s but declined following the commercialisation of game meats in the 1960s (D. Yanko, *pers. comm.)* and remains low, a result of constant recreational hunting. Red deer probably did not reach the area until the 1950s, and have never reached high densities. Possums arrived in the pureora study area in the late 1960s (D. Yanko, *pers. comm.)* and appear to have steadily increased. Browsing on species such as raukawa *(Pseudopanax edgerleyi),* fivefinger *(P. arboreus),* fuchsia *(Fuchsia excorticata),* and pate has been observed to increase both during and since the three year study period. Little is known about the populations of the other introduced mammals found in the study area.

Mapara

The Mapara study area (38° 34'S, 175° 17'E) was 85 ha of moderately steep country with a mean slope of 17° and whose altitude ranged from 300-500 m a.s.l. Soils belong to the Mahoenui series and are classified as steep land soils related to yellow-brown earths (Rijkse and Wilde, 1977).

The nearest climate station is at Taumarunui (171 m a.s.l.) approximately 15 km to the south. Here, annual rainfall averaged 1432 mm over the period 1947-1970, with the highest monthly precipitation occurring from May to July. The average air temperature was 12.7°C, with extreme monthly averages in February (18.2°C) and July (7.3°C).

The forest of the Mapara study area has been considerably modified by logging. Old stumps on the ridges and upper faces indicate once abundant rimu *(Dacrydium cupressinum),* totara *(Podocarpus totara)* and miro *(P. ferrugineus);* matai *(P. spicatus)* and kahikatea *(P. dacrydioides)* were probably dominant in the basins and valley bottoms. Logging of the most profitably exploited timber occurred prior to the 1940s, while in the 1950s most of the remaining podocarps and small amounts of tawa *(Beilschmiedia tawa)* were extracted.

The forest also has been considerably modified by introduced mammals. Goats have been in the area at least since the 1930s (A. Leigh, *pers. comm.)* and their impact has been severe, especially adjacent to sunny slips and open grassy areas. Many palatable species have been almost eliminated, and seedlings, including those of tawa, matai, and totara, are often severely hedged. A New Zealand Forest Service goat control operation, which commenced in the study area and surrounding forest in January 1981, resulted in over 3500 animals being destroyed in nine months

*Nomenclature follows Moore and Edgar (1970) for monocotyledons, Philipson (1965) for the family Araliaceae, and Allan (1961) for all remaining species.

(R. Guest, *pers. comm.)*. A marked recovery of the lower understorey vegetation has since been observed.

Possums reached the study area approximately 10 years ago (R. Kerridge, *pers. comm.)* and appear to be still increasing. Damage to species such as north. ern rata *(Metrosideros robusta),* kamahi *(Weinmannia racemosa),* fuchsia, and titoki *(Alectroyon excelsus)* is common. All fuchsia tagged in August 1979 as part of plant phenology studies (J. Leathwick, *in prep.)* were killed by possum browsing in the following two years.

Pigs occur in low numbers throughout the area, and domestic cattle and sheep are also present, mainly during the winter. Stoats, ship rats, and mice are known to be present, and ferrets, weasels and hedgehogs are probably present also. Little is known of either the numbers or distribution of these animals.

Rotoehu

The Rotoehu study area (37° *58'S,* 176° 32'E) occupied 125 ha of native forest within Rotoehu State Forest. The southern part of the study area consists of a large plateau with shallow but steep-sided dry pumice gullies. Northwards the plateau divides into a series of more sharply defined ridges. The altitude ranges from 195-285 m a.s.l. The nearest climate station is located at Forest Headquarters, approximately 5 km to the north. Annual rainfall over the period 1941-1970 averaged 1680 mm, with the highest monthly totals occurring from May to August. The mean air temperature was 12.7°C with extreme monthly temperatures ranging from 7.7°C in July to 17.8°C in February.

The Rotoehu study area was logged for podocarps in the early 1940s and is now dominated by tawa. Podocarps were present at a low to moderate density before logging, with rimu dominant and perhaps some kahikatea also present (J. L. Nicholls, *pers. comm.)*. Only three or four individual podocarps now remain.

Populations of pigs, red deer, and possums were considered to be high throughout the study area in the late 1950s but fell following a local trial aerial poisoning with 1080 (sodium monofluoracetate) in May 1959. In 'subsequent years (especially 1961) large scale aerial poisoning operations covered extensive areas of native forest at Rotoehu and presumably included the forests of the study area (H. Vipond, *pers. comm.)*. At present populations of all three animals are low compared with those of the late 1950s (H. Vipond, *pers. comm.),* a result of present commercial trapping of possums for fur, and reoreational hunting of red deer and pigs. Ferrets, stoats, black rats, feral cats, and possibly weasels are found in the study area.

METHODS

Vegetation description

The species composition of the vegetation of each study area was described using the point height intercept sampling technique (Park, 1972; Hay and Leathwick, *in prep.)* Species were allocated to one of the following six groups:

i. Podocarps-rimu, matai, totara, kahikatea, miro.
ii. Dicotyledonous trees-species capable of forming high canopy forest 12-20 m in height, e.g. tawa, kohekohe *(Dysoxylum spectabile),* hinau *(Elaeocarpus dentatus),* pukatea *(Laurelia novaezelandiae),* mangeao *(Litsea calicaris), Olea* spp., tarata *(Pittosporum eugenioides),* kamahi, puriri *(Vitex Jucens)*.
iii. Dicotyledonous shrubs-species rarely attaining more than 12 m in height, and often present as understorey species, e.g. raukawa, fivefinger, kaikomako *(Pennantia corymbosa),* mahoe *(Melicytus ramiflorus),* fuchsia.
iv. Epiphytes.
v. Lianes.
vi. Tree ferns, ground ferns, and herbs.

Kokako diet

Kokako diet was studied using time sampling of behaviour. Study areas were visited for 3-5 days each month and observations were made of as many birds as possible. Individuals or pairs of birds were followed for up to three hours and their activity during five second periods recorded at one minute intervals using a tape recorder. Details of feeding were coded according to food species, type (e.g. leaf, insect), and source (e.g. tree, liane, epiphyte). Over 14 500 such observations were made between spring 1978 and autumn 1981.

Possum, deer, and goat diet

Possum diet was determined by analysis of leaf cuticle fragments remaining in faecal pellets with corrections made for differential digestion of major species (Fitzgerald, 1976). Pellet collections were made at Mapara in May, June, July, August, October, and November, 1980, and in February and March, 1981. At Pureora collections were made in May, June, August, and December, 1981. Three pellets were collected from each of 30 fresh defecations throughout the study areas at each collection.

Both published and unpublished possum diet studies and published descriptions of forest modification by possums were reviewed to supplement our study. Red deer and goat diets were not directly investigated. Only limited accounts of their diet in New Zealand exist in the literature, but we have reviewed descriptions of forest modification by both deer and goats, and records of plants eaten by them.

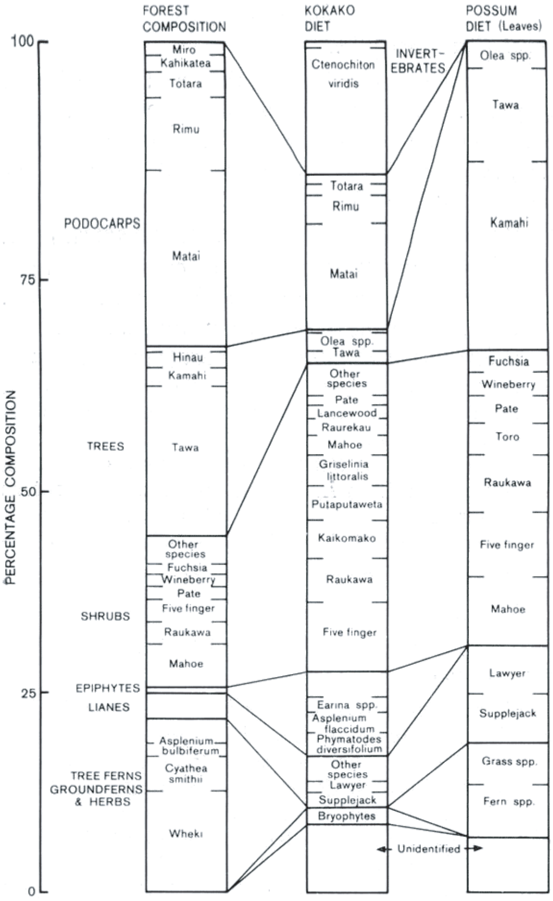

FIGURE 1. *The diets of kokako and possum in relation to forest composition at Pureora. Individual species are shown only if they comprised greater than 1 % of the total quantity. The kokako diet was recorded from December 1978 to May 1981 and includes leaves, buds, flowers, fruit and insects; possum diet was recorded during May, July, August and December, 1980 and refers to leaf diet alone.*

Kokako distribution and habitat modification

Distribution records for kokako, and descriptions of habitat modification by introduced browsers, were used to examine the degree to which the bird's disappearance is related to past habitat modification.

Vegetation

The forest vegetation at Pureora consists of tall podocarps emergent through a canopy of hardwoods and tree ferns (Fig. 1). Matai is the dominant podocarp, though rimu is common on well-drained ridges. Large totara occur throughout and miro and kahikatea are also present. The hardwood canopy is diverse, with mahoe, raukawa, fivefinger, pate, wineberry, fuchsia, kamahi, and hinau all common. Tawa, present throughout as scattered seedlings, saplings, and poles, is locally dominant on some ridges and knolls. Wheki *(Dicksonia squarrosa)* and *Cyathea smithii* are the two most abundant tree ferns. Lianes and

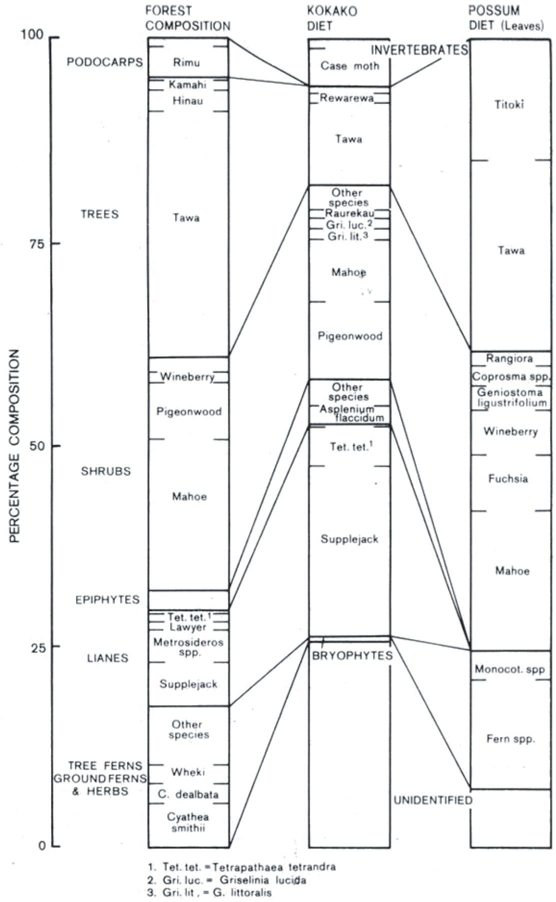

FIGURE 2. *The diets of kokako and possum in relation to forest composition at Mapara. Individual species are shown only if they comprised greater than 1 % of the total quantity. The kokako diet was recorded from September 1978 to May 1979 and September 1979 to May 1981 and includes leaves, buds, flowers, fruit and insects; possum diet was recorded during June, July, August, October, November, 1980, and February and March, 1981 and refers to leaf diet alone.*

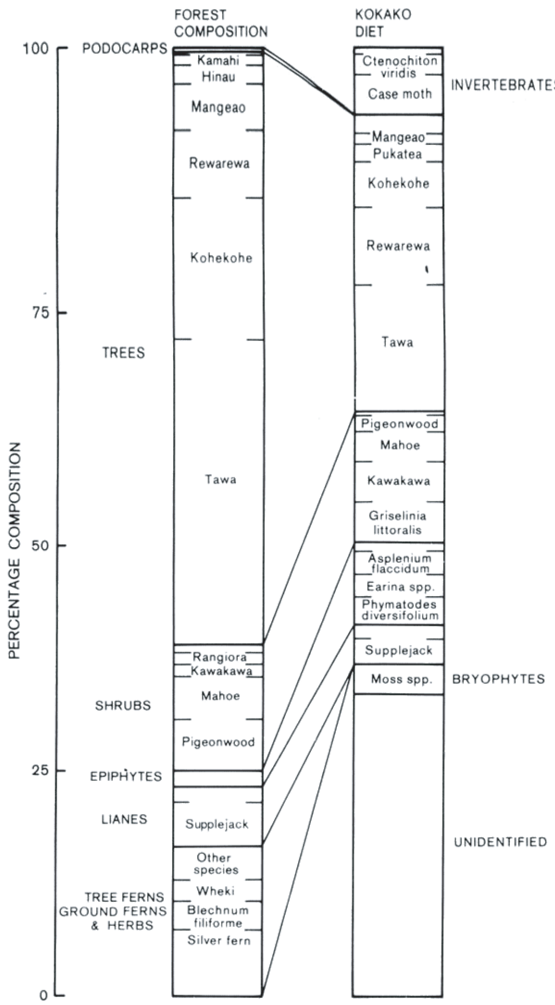

FIGURE 3. *The diet of kokako in relation to forest composition at Rotoehu. Individual species are shown only if they comprised greater than 1 % of the total quantity. The kokako diet was recorded from December 1978 to May 1979, September 1979 to February 1980 and June 1980 to May* 1981 *and includes leaves, buds, flowers, fruit and insects.*

epiphytes form a small but diverse component of the forest.

At Mapara (Fig. 2), the forest cover consists of an interspersion of two major types. Ridges and knolls are dominated by tawa associated with such species as pigeonwood *(Hedycarya arborea),* hinau, kamahi, and silver fern *(Cyathea dealbata).* In the gullies and stream basins mahoe is dominant with pigeonwood, wheki and *Cyathea smithii* abundant. Only a few podocarps remain, principally rimu and totara, on inaccessible knolls and in some gullies. Lianes are abundant throughout, with many trees draped with supplejack *(Ripogonum scan dens),* rata vines *(Metrosideros diffusa, M. colensoi),* lawyer *(Rubus cisso ides),* and native passionfruit *(Tetrapathaea tetrandra).* Old logging tracks have been colonised principally by wineberry, but introduced grasses and ring fern *(Paesia scaberula)* are dominant on old slips.

The forest at Rotoehu (Fig. 3) contains several lowland species not found at Mapara and Pureora, e.g. kohekohe, mangeao, pukatea, puriri, and kawakawa *(Macropiper excelsum).* Tawa and kohekohe dominate the dense canopy on ridges and plateaux in the south and east in association with occasional rewarewa *(Knightia excelsa),* mangeao, hinau, pigeonwood, mahoe, kawakawa, and silver fern. In the dry pumice gullies pigeonwood, mahoe, kawakawa, rangiora *(Brachyglottis repanda),* and rewarewa, are common, with pukatea and titoki scattered throughout. Old Jogging tracks have been colonised principally by wineberry and pate. In the north and west tawa and large-crowned mangeao dominate, but small discrete patches of kamahi and rewarewa suggest previous modifiction by fire. Lianes and epiphytes are common throughout, except in areas dominated by kamahi and rewarewa.

Kokako diet

Kokako were seen to eat over 100 different foods during the study (Appendix I), 44 of which contributed more than 5% to the observed diet in anyone season (Table 1). The composition of the diet varied between study areas, broadly reflecting the forest species composition in each. At Pureora (Fig. 1), the largest contribution to the diet (38.4%) was made by the abundant and diverse dicotyledonous shrub group; in particular fruit of fivefinger, raukawa, kaikomako, and putaputaweta *(Carpodetus serratus)* and the leaves of mahoe were commonly eaten. Major food items from other plant groups included the fruit and leaves of matai, supplejack fruit, and fronds of the two epiphytic ferns *Phymatodes diversifolium* and *Asplenium flaccidum.* Large numbers of the sixpenny scale insect *(Ctenochiton viridis)* were also eaten. At Mapara (Fig. 2), shrubs (24.3 %) and lianes (26.5%) provided much of the food; important individual foods included both leaves and fruit of supplejack, native passionfruit, pigeonwood, mahoe, and tawa, the fruit of *Griselinia littoralis,* and *Asplenium flaccidum* fronds. At Rotoehu (Fig. 3), the largest proportion of the diet was contributed by the dicotyledonous tree group (28.9 %), followed by the shrub group (14.5 %). Important individual foods included leaves of supplejack, fronds of *Phymatodes*

TABLE 1: *Foods contributing more than 5 % of the observed kokako diet in any one season at Pureora, Mapara or Rotoehu, and those which have been recorded as being eaten by possum, deer, and goats. Food categories are leaf (L), bud (B), flower (F), fruit (D) and invertebrate (I). For sources of information on possum and deer diets see appendices I and II respectively.*

Food species eaten by	Kokako	Possums	Deer	Goats
Asplenium falcatum	L			
A. flaccidum	L			
Beilschmiedia tawa	L,D	L,D,		L
Clematis sp.	L	L		L
Carpodetus serratus	D	D	L	L
Coprosma australis	L,D	L	L	L
Ctenochiton viridis	I	L*	L*	L*
Dacrydium cupressinum	L			L
Dysoxylum spectabile	B,D	L,D		L
Earina autumnalis	L			
Elaeocarpus dentatus	D	L,D		L
Griselinia littoralis	L,B,D	L,D	L	L
Hedycarya arborea	L,D	F,D	L	L
Hymenophyllum spp.	L			
Knightia excelsa	F,D	B,F,D		L
Laurelia novae-zealandiae	L	L		L
Liothula omnivorus (Case moth)	I			
Macropiper excelsum	D	D		L
Melicytus ramiflorus	L,F,D	L,F,D	L	L
Mosses	L			
Muehlenbeckia australis	L	L	L	L
Olea cunninghamii	D	L,D		L
Pennantia corymbosa	L,D	L,D		L
Phymatodes diversifolium	L			
Podocarpus spicatus	L,D	D		L
Pseudopanax arboreus	D	L,F,D	L	L
P. crassifolius	D	D	L	L
P. edgerleyi	D	L	L	L
Ripogonum scandens	L,D	L,D		L
Rubus cissoides	D	L,D	L	L
Tetrapathaea tetrandra	L,D	D		

* Browse on principal host plants *(Schefflera digitata, Griselinia littoralis)*.

diversifolium and *Asplenium flaccidum*. and the fruits of *Griselinia littoralis,* kawakawa, mahoe, tawa, rewarewa, and kohekohe; rewa rewa flowers were also important. (Because it was sometimes difficult to identify positively food items as the birds ate them, the unidentified proportions of the diet are considerable, especially at Mapara and Rotoehu).

Fruit contributed the greatest percentage of identified foods (about 50%), closely followed by leaves (36%) (Fig. 4). Insects contributed a small part of the diet (10 %), with smaler amounts contributed by flowers (4%), buds (1 %), and gymnosperm cones. There was, however, considerable variation from season to season; some items (e.g. sixpenny scale) comprised a large proportion of the diet in one season, but were eaten in very small amounts in other seasons.

Possum diet and impact on vegetation

At Pureora, kamahi (19.8%), tawa (10%), mahoe (8.5%), fivefinger (7.8%), and raukawa (7.8%) comprised just over 50% of the leaf diet of possums (Fig. 1). Supplejack, lawyer, fern species, toro *(Myrsine salicina)*. pate, wineberry, and *Olea* spp. all contributed lesser amounts (3-6% each). At Mapara, tawa (23.8%), mahoe (17.5%), and titoki (14.2%) together contributed over 50 % of the leaf diet (Fig. 2). Fern species (13.5%), fuchsia (6.8%), and wineberry (5.6%) were the other main foods eaten, though, as at Pureora, smaller amounts of other species were identified in the pellets. No estimate was made of either the quantities or species of fruit ingested.

The diet of forest-dwelling possums has been investigated in several studies, either by direct analysis

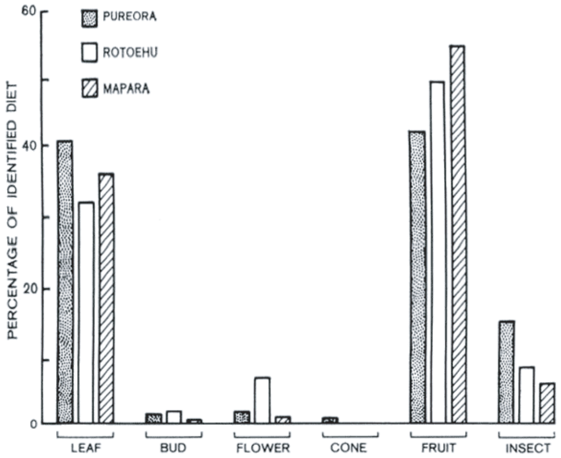

FIGURE 4. *The types of foods eaten by kokako at Pureora, Mapara, and Rotoehu and their percentage contribution to the diet.*

of stomach contents (Mason, 1958; Gilmore, 1967; Purchas, 1975) or by analysis of leaf cuticle fragments in faeces (Gilmore, 1967; Fitzgerald, 1976; Fitzgerald and Wardle, 1979). Information from these studies and from unpublished studies on Kapiti Island (A. E. Fitzgerald) and at Haupiri, Westland (J. Coleman), have been combined with our data to identify plant species commonly eaten by possums (Appendix II). Those species which are also important kokako foods are identified in Table 1.

Much has been published on the effects of possums on vegetation in New Zealand. Initially the impact was thought to be slight (Kirk, 1920; Cockayne, 1928); however Thomson (1922), and later Zotov (1949), recorded browse-induced mortality of some plant species on Kapiti Island and in the Tararua Range. Many accounts of the impact of possums on vegetation followed. Kean and Pracy (1953) categorised a wide range of plant species according to possum preference for them; Holloway (1959) described forest modification as a result of mortality of southern rata *(Metrosideros umbellata)* in the Hokitika catchment and PekeIharing (1979), describing the Taramakau catchment, attributed 41 % canopy mortality primarily to possums. In a detailed study in central Westland, Coleman, Gillman, and Green (1980) concluded that possums, in conjunction with red deer were favouring an increase in the abundance of less palatable and more browse-resistant species, in place of highly pal~table species such as southern rata, fuchsia, and *Pseudopanax* spp. In Orongorongo Valley, southern North Island, Mason (1958), Fitzgerald (1976), and Meads (1976) also showed that possums could induce changes in plant species composition.

Deer diet and impact on vegetation

Red deer have considerable overlap in range with kokako. Unfortunately, study of deer diet in New Zealand has been only cursory, most published information relating specifically to forest modification. Information from a number of authors has been combined to indicate those plant species most com. monly eaten by deer (Appendix III). Those plant species which are also important kokako foods include lancewood *(Pseudopanax crassifolius),* five-finger, raukawa, mahoe, pigeonwood, *Griselinia littoralis,* raurekau *(Coprosma australis),* and putaputaweta (Table 1).

As early as 1893 the potentially serious effects of deer in indigenous forests were recognised, when Walsh (1893) pointed out that the New Zealand flora had evolved in the absence of browsing mammals. The consequences of the introduction of red deer into forests, and the subsequent removal of understorey species, is described by Cockayne (1928) and Poppelwell (1929). Later, general accounts of damage by browsing mammals (McKelvy, 1959; Holloway, 1959), as well as more specific descriptions were published (e.g. Druce and Atkinson (1959), Holloway et aI. (1963), Wardle and Guest (1977), and Veblen and Stewart (1980)). For a more complete early review see Howard (1966). AU authors agreed that deer selectively browse certain species and reduce their abundance, often profoundly altering the species composition of forests. More recently, however, Veblen and Stewart (1982) have pointed out that natural forest dynamics may also contribute to these changes in forest species composition.

Goat diet and impact on vegetation

Because of the unselective nature of their feeding (Atkinson, 1964), goats may be regarded as eating all those kokako food species accessible to them (Table 1). Goats are numerous in many of the forests in which kokako still occur, and were one of the earliest colonising mammals over large areas of North Island lowland forest. There are few accounts of their impact on vegetation, though Atkinson (1964) described the severe impact that goats can have on vegetation, and listed only 12 species *not* eaten by them. Damage by goats is frequently localised, a reflection of their relatively sedentary habits and wide food preferences (Atkinson, 1964; Riney and Caughley, 1959; Dale and James, 1977).

Kokako distribution and habitat modification

The present distribution of North Island kokako appears to reflect to a great degree the history of browsing mammal invasion and forest modification.

In Wellington and Wairarapa, birds were widespread and abundant in the late 1800s but are now absent (Lavers, 1978). Much of the early decline can probably, be attributed to forest clearance, although shooting by collectors may have played a part. However, in Tararua Range, one of the few extensive areas of southern North Island forest not cleared, birds were sighted as late as 1961 (Lavers, 1978), many years after the spread of predators to the area in the late 1800s (Atkinson, 1973). From the early 1900s to 1950 the forests of Tararua Range were considerably modified by browsing mammals (Davidson and Kean, 1960; Holloway et al., 1963; Zotov, 1949), with a marked reduction in the abundance of palatable species such as raurekau, fuchsia, putaputaweta, pate, and *Pseudopanax* species (Holloway et. al., 1963). Many of these species are also eaten by kokako.

Further north, in the forests stretching from Ruahine Range to Kaimanawa and Kaweka Ranges, few kokako have been seen. Most of this forest has been extensively modified by browsing mammals (Cunningham, 1979; Elder, 1959, 1962). Sightings of kokako at Waitawhero Saddle in 1979 (P. Mayhill *pers. comm.)* may be attributable to regeneration of food species after the rapid decline of deer population in the mid 1940s.

In Urewera forests, present kokako distribution relates well to the intensity of local forest modification. Birds, although not everywhere abundant, were once widespread, both in the northern podocarp / tawa/mixed hardwood forests, and in the beech *(Nothofagus spp.)* dominated forests in the south (Lavers, 1978). Red deer were liberated at Lake Waikaremoana, Galatea, and Te Whaiti from 1899-1923 (Logan and Harris, 1967), and reached a peak in the southern forests in the early 1940s to 1950s. Since then they have gradually moved northwards, although densities are reported to have remained low in the eastern corner of the tract (J. Knowlton, *pers. comm.).* Possums were liberated between 1898 and 1945 and their spread followed a similar pattern to that of red deer (J. Knowlton, *pers. comm.).* Two factors influenced the impact of these animals on the forest. Firstly, the floristically simple, beech-dominated forests were more susceptible to browsing modification; the understorey, dominated by a few highly palatable species, was drastically reduced leaving a depleted forest apparently unsuitable for kokako. The northern forests, in contrast, had a diversity of species in both canopy and the understorey and were less modified (McKelvey, 1973). Secondly, animal populations built up in the southern forests before the commencement of large-scale deer culling operations in the early 1960s. These operations were concentrated on the northern, forests and reduced animal numbers considerably (H. Vipond, *pers. comm.).* The majority of records of kokako since 1960 have been from the more diverse, less modified, northern podocarp/tawa/hardwood forests; birds were last reported from the beech forests of Huiarau Range in 1924, and in podocarp forest at Te Whaiti in 1942 (Lavers, 1978).

Less is known of forest change or kokako populations in Raukumara Range. Kokako numbers appear to have declined in the forest south of Opotiki around Toatoa (Lavers, 1978) where a "heavy to dense" possum population existed in the late 1940s (unpubl. New Zealand Forest Service reports). A recent sighting of birds in the Waingakia catchment, in unmodified beech forest (P. Alley, *pers. comm.),* confirms that beech forest can provide suitable kokako habitat where shrub hardwoods have not been lost through browsing.

In Taranaki, kokako are thought to have been widespread throughout the lowland forests west of Wanganui River (Lavers, 1978), but the majority of recent sightings have been north of Whangamomona, mainly in Waitaanga State Forest (O'Donnell, 1982). Goats were probably established in much of the forest after World War I or earlier, and they had caused severe damage virtually throughout the region by 1948-50 (unpubl. New Zealand Forest Service reports). There is no apparent difference between the degree of forest modification caused by browsing animals in the northern and southern forests which could explain the disappearance of the southern kokako population.

In King Country, kokako are still widespread, al~though forest clearance has severely reduced the area of suitable habitat. Goats have been present for some time (at least since the 1930s (A. Leigh, *pers. comm.*)), but possums are a recent arrival (unpubl. Agricultural Pest Destruction Council report). Kokako distribution may have been localised even prior to European settlement, as there are no records of birds from the southern Hauhungaroa forests. Further north the population of kokako at Pureora occupies habitat which has had, until recently, only low numbers of possum and deer, and consequently is little modified. In the west, kokako are reported to be declining in several areas, including parts of Mount Pirongia, around Mount Kokako, Oparau, and Herangi Range (O'Donnell, 1982); all these forests have at various times contained large numbers of goats.

In Bay of Plenty forests, kokako are still widespread and locally plentiful. These forests are less modified by browsing mammals than those in many other parts of North Island. Easy access for hunters has generally kept deer numbers lower than in the less accessible forests of the main axial ranges. In

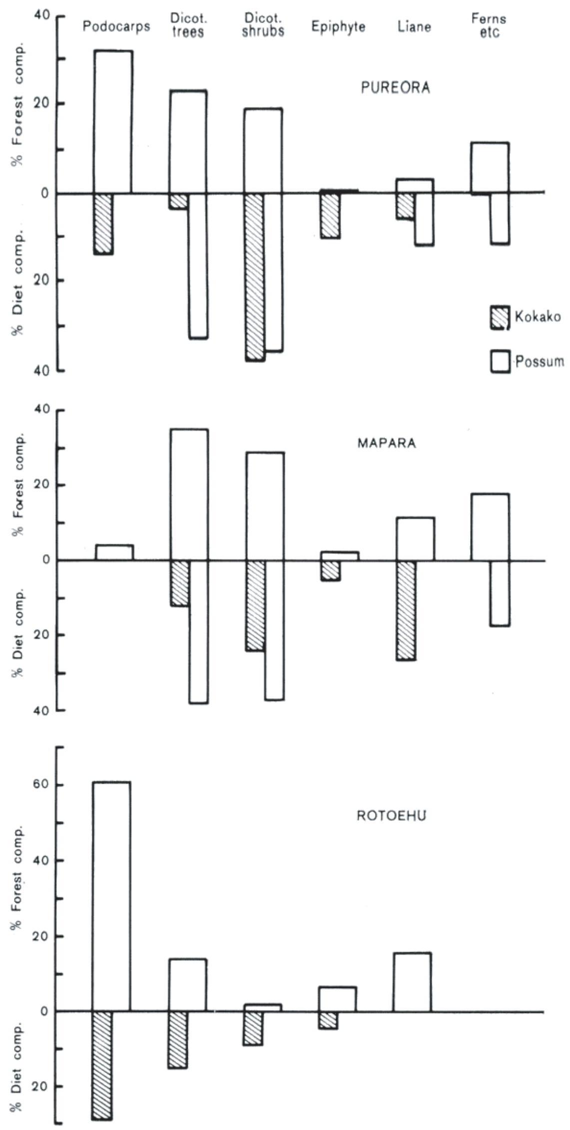

FIGURE 5. *Percentage composition of the major vegetation categories at Pureora, Mapara and Rotoehu, and the composition of these three categories in the diet of possums and kokako.*

addition, although deer were sighted on the edges of the Mamaku plateau from early times, densities have only recently built up in the central areas of forest (H. Vipond, *pers. comm.).* Possums have also only recently colonised large areas of the region, with the exception of those associated with liberations at Okataina in 1906 and Rotoiti in 1905 (Pracy, 1974). Finally, the impact of introduced browsers may reflect the local species composition; in the north of this region particularly, a number of species are found which are not abundant at higher altitudes or further south, e.g. pukatea, kohekohe, puriri, mangeao, and titoki. The resultant high species diversity, combined with the warm coastal climate, may encourage a more rapid rehabilitation of browsed forest.

Severe browsing, principally by goats, has occurred in the forests of Kaimai and Coromandel Ranges (Moore and Cranwell, 1934; Dale and James, 1977) Effects of possum (and goat) browsing have been locally severe in the Kaimai forests but possums have only recently colonised northern Coromandel. Kokako are now sparse throughout.

In the Auckland region, kokako were once reasonably widespread (Lavers, 1978) but are now localised because of extensive forest destruction. Recent records have all been from Hunua Range, but the numbers of birds appear to be dwindling and their breeding success much reduced (St Paul and McKenzie, 1974). The Hunuas have been extremely modified by browsing mammals with goats and cattle present from 1860 (Silvester, 1964). Cattle were shot out by 1914, but goats remain, although subject to control programmes (Barton, 1972).

The forests of Northland have fewer browsing mammals and consequently are less modified than those elsewhere in North Island. Red deer are absent, and possums are still not established in parts of the north and west. Although kokako have never been widespread in Northland, Buller (1888) did regard them as locally "comparatively plentiful". Recently, at least 70 birds have been located in Puketi State Forest (Anderson, 1979) and some birds have also been seen in Raetea and East Waipoua State Forests (Moynihan, 1980), areas only recently colonised by possums and not yet much affected by them.

The only naturally occurring offshore island kokako population is on Great Barrier Island. Though records of them are few and isolated (Ogle, 1981), forest in the north of the island is now known to support a small number of birds (Hay, *pers. obs.).* Possums are absent from this forest, but goats and pigs have caused severe modification.

DISCUSSION

Kokako diet preference

When considering the diet preferences of kokako, not only must the observed diet be noted, but also the relationship of that choice to forest composition. Comparison of overall time spent feeding on a particular vegetation category with its abundance in the forest (Fig. 5) reveals that epiphytes and lianes provided the most preferred foods, closely followed by dicotyledonous shrubs: Dicotyledonous trees and podocarps, despite providing large proportions of the diet where they were common, were less sought after. However, these latter two categories were often important as feeding sites where they supported large numbers of epiphytes and lianes.

Many of the species on which kokako were observed feeding produce fruit in abundance only sporadically. For example, matai was the only podocarp to produce large amounts of fruit during the study when it contributed 40 % of kokako diet in autumn 1981. Other species showing marked fluctuations in fruiting included raukawa, kaikomako, supplejack, putaputaweta, wine berry, lawyer, and tawa. In general terms, therefore, food preferences shown by kokako (Table 1) refer only to diet over the three year study period, and may be a conservative record of fruits eaten by them.

Dietary overlap

Many of the plant species eaten by kokako are also eaten by possums, deer, and goats (Table 1). For example, leaves of raurekau, *Griselinia littoralis,* pigeonwood, mahoe, kaikomako, and supplejack are all eaten by kokako and two or more introduced mammals. Fruit of a large number of species are also eaten by both kokako and possums, including tawa, putaputaweta, kohekohe, hinau, pigeon wood, rewarewa, mahoe, kaikomako, and supplejack. At both Pureora and Mapara, possums appeared to eat about equal quantities of food from the dicotyledonous tree and dicotyledonous shrub categories (Fig. 5), potentially competing more with kokako for the latter. Deer and goats probably intensify this by eating a large number of kokako food species also from this category. Possums probably exert a more immediate effect on kokako both by their habit of feeding in the canopy and by their consumption of fruit. By comparison, deer and goats eat understorey species and seedlings or saplings of canopy species, thus taking longer to influence species composition in the canopy and (by inference) kokako feeding. Though the spectacular damage resulting from uncontrolled populations of browsing mammals is not as common today as in the early and mid-1900s, and though there are some plant species favoured by browsing mammals that do not appear to be highly preferred by kokako (e.g. kamahi, kanuka *(Leptospermum ericoides),* and rangiora), possums, deer, and goats are still affecting forest species composition in a manner which reduces the abundance of kokako food.

Reduction in abundance of foods by mammals does not automatically imply that kokako will be adversely affected, as the birds could respond by eating other foods. However, this presumes that alternative foods are as nutritious as those reduced by possums, deer, or goats. Most herbivores select food plants in markedly different proportions to those in which they occur; New Zealand examples include the native pigeon *(Hemiphaga novaeseelandiae)* (McEwan, 1978), and the takahe *(Notornis mantelli)* (Mills and Mark, 1977). Attempts have been made to rationalise such selection through the theory of opti. mal foraging (Schoener, 1971), reviewed by pyke, Pullam and Charnov (1977) or the theory of nutritional wisdom (Arnold and Hill, 1972). Results from several studies, and typified by Mills and Mark (1977), have shown high correlations between the degree of selection for a food plant and its concentrations of elements such as calcium, phosphorus, and nitrogen, as well as proteins or soluble sugars. Mills and Mark, for instance, showed that takahe and red deer both selected plant species with the highest nutrient levels, as well as individual plants containing higher than average nutrients.

Kokako were able to obtain the nutritional requirements necessary for survival and reproduction before the arrival of Europeans in New Zealand. However, we suggest that the survival of kokako is now jeopardised by the major reduction in abundance of its food, resulting from disruption or downgrading of its habitat. Their present reduced range probably reflects predator introduction, major change in land use and also the continuing decline in the diversity of plant species in the remaining native forests brought about by the feeding habits of possums, deer, and goats.

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APPENDIX I

The observed diet of kokako at Pureora, Mapara, and Rotoehu between September 1978 *and May* 1981. *Food categories are leaf (L), bud (B), flower (F), cone (C), fruit (D) and invertebrate (I).*

Species	Category	Percent use		
		Pureora	Mapara	Rotoehu
Alectryon excelsus	L		0.24	
	D			0.34
Amphisalta zealandica	I		0.10	
Aristotelia serrata	L		0.45	
Asplenium falcatum	L	0.15	0.68	
A. flaccidum	L	2.63	2.36	2.33
Astelia solandri	L	0.13	0.05	
Beilschmiedia tawa	L	0.53	1.71	0.54
	F		0.19	0.51
	D	0.51	8.52	11.50
		(1.04)	(10.42)	(12.55)
Blechnum sp.	L	0.03		
Bulbophyllum pygmaeum	L			0.36
Carpodetus serratus	L	1.49		
	F	0.04		
	D	3.18		
		(4.71)		
Clematis spp.	L	0.88	0.05	
Coprosma australis	L	1.24		
	F	0.21	0.11	
	D	0.66	0.90	
		(2.10)	(1.01)	
C. robusta	L		0.32	
Ctenochiton viridis	I	13.73	0.55	2.13
Cyathea dealbata	L	0.03		
C. smithii	L	0.13		
Dacrydium cupressinum	L	2.94		
Dysoxylum spectabile	L			0.96
	B			1.43
	D			1.90
				(4.29)
Earina autumnalis	L	0.96	0.15	1.48
	D	0.54		
		(1.50)		
E. mucronata	L	0.36	0.35	1.08
	F	0.20	0.16	
		(0.56)	(0.51)	
E aeocarpus dentatus	L	0.14	0.05	
	D	0.68	0.04	1.24
		(0.82)	(0.09)	
Fuchsia excorticata	L	0.33	0.35	
	B	0.02		
	F	0.16		
	D	0.14		
		(0.65)		
Geniostoma ligustrifolium	D		0.11	
Grammitis heterophylla	L	0.09		
Griselinia littoralis	L	1.37	0.19	1.79
	B	0.70		
	D	1.91	1.22	3.79
		(3.98)	(1.41)	(5.58)
G. lucida	L		0.49	
	F			0.26
	D		0.66	
			(1.15)	
Hedycarya arborea	L	0.08	2.06	0.36
	D		7.68	1.51
			(9.75)	(1.87)
Hymenophyllum spp.	L	0.56	0.77	
Knightia excelsa	L		0.26	
	F			4.43
	D		1.13	2.80
			(1.59)	(7.23)
Laurelia novae-zealandiae	L			1.60
Leaf roller	I		0.23	0.08
Lichen spp.	L	0.11		
Liothula omnivorus (Case moth)	I	0.51	4.14	3.75
Litsea calicaris	L			0.50
	D		0.04	0.50
				(1.00)
Macropiper excelsum	D			4.51
Mantis	I		0.04	

APPENDIX I (*continued*)

Species	Category	Percent use: Pureora	Percent use: Mapara	Percent use: Rotoehu
Melicytus ramiflorus	L	1.47	3.52	0.09
	B		0.37	
	F		1.25	
	D	0.97	2.40	3.19
		(2.44)	(7.54)	(3.28)
Metrosideros diffusa	L			0.36
Moss spp.	L	1.84	0.43	3.14
Moth sp.	I			0.36
Muehlenbeckia australis	L	1.38	0.13	
Myrsine australis	D		0.67	
Olea cunninghamii	L	0.92		
	D	1.27		0.26
		(2.19)		
Parsonsia heterophylla	L	0.06	0.04	0.36
	F	0.16		
		(0.22)		
Pennantia corymbosa	L	1.90		
	D	2.91		
		(4.81)		
Phymatodes diversifolium	L	2.93	0.74	3.25
Pittosporum colensoi	L	0.63		
	D	0.07		
		(0.70)		
P. eugenioides	L	0.35		
	D	0.11		
		(0.46)		
Podocarpus dacrydioides	L	0.30		
	D	0.63		
		(0.93)		
P. ferrugineus	D	0.12		
P. spicatus	L	4.08		
	C	0.06		
	B	0.22		
	D	6.54		
		(10.90)		
P. totara	L	1.00		
	D	0.13		
		(1.13)		
Pseudopanax arboreus	L	0.53		
	F	0.03		
	D	8.10		
		(8.66)		
P. crassifolius	D	1.50	0.51	
P. edgerleyi	L	0.73		
	F	0.18		
	D	4.63	0.19	
		(5.54)		
Pseudowintera colorata	D	0.73	0.19	
Pyrrosia serpens	L	0.30	0.29	0.53
Ripogonum scandens	L	0.53	6.42	1.78
	F			0.09
	D	1.56	14.61	1.03
		(2.09)	(20.03)	(2.90)
Rubus cissoides	L	0.68	0.26	
	D	1.11		0.43
		(1.79)		
Schefflera digitata	L	0.56	0.62	
	D	0.65		
		(1.21)		
Slug	I	0.05		
Tetrapathaea tetrandra	L		3.43	
	D		1.58	
			(5.01)	
Vitex lucens	F			0.08
	D			0.31
				(0.39)
Weinmannia racemosa	L	0.17	0.30	
	D	0.22		
		(0.39)		
Total identified		89.68%	74.30%	66.94%
Unidentified		10.32%	25.70%	33.06%

APPENDIX II

*Plant species recorded as providing leaf, {lower or fruit material in the diet of possums at Rotoehu. Pureora and Mapara, and in other studies. Use of leaves is included where the plant species provided greater than 1 % of the leaf diet. Fruit diet was not quantified in the majority of studies. (*refers to flower and/or fruit, and leaf use; **refers to flower and/or fruit use alone).*

Species	Study
Alectryon excelsus	2, 3*,4,7
Aristotelia serrata	1, 2, 3, 8
Beilschmiedia tawa	1, 2, 3**, 4, 5, 9, 10**
Brachyglottis repanda	1, 2, 3
Carpodetus serratus	10**
Coprosma spp. (Large leaf)	7
Clematis spp.	2,3,6,7
Dysoxylum spectabile	5, 9, 10**
Elaeocarpus dentatus	3*, 4*, 5, 9, 10**
Fern spp.	1, 2, 3, 6, 9
Fuchsia excorticata	1, 2, 3*, 4, 6, 7*
Geniostoma ligustrifolium	2, 4
Griselinia littoralis	7*
Fledycarya arborea	3**, 4**, 10**
Hoheria spp.	3*, 6, 7
Knightia excelsa	3**, 4**, 10**
Laurelia novae-zelandiae	4
Leptospermum ericoides	3*, 5, 7
Macropiper excelsum	3**, 10**
Melicytus ramiflorus	1, 2, 4, 5, 6, 7, 8, 10**
Metrosideros spp.	3*, 4*, 5, 6, 8
Monocotyledon spp.	1, 2, 3*, 6
Muehlenbeckia australis	3, 7,9
Myrsine salicina	1, 4, 5
Olea cunninghamii	1, 3**, 10**
Pennantia corymbosa	3**, 7*, 8, 10**
Podocarpus spicatus	10**
Pseudopanax arboreus	1, 3*, 4, 5, 7, 9, 10**
P. crassifolius	3**, 7, 10**
P. edgerieyi	1, 3
Ripogonum scan dens	1, 3**. 4*, 6
Rubus spp.	1, 3**, 7, 8, 9
Schefflera digitata	1, 3**, 6*, 8
Tetrapathaea tetrandra	3**, 10**
Weinmannia racemosa	1, 3*, 4, 5, 6, 8

Study and region	
1. This study	Pureora study area
2. This study	Mapara study area
3. Mason (1958)	Orongorongo Valley, Wellington
4. Fitzgerald (1976)	Orongorongo Valley, Wellington
5. Fitzgerald (unpubl. data)	Kapiti Island
6. Fitzgerald and Wardle (1979)	Westland National Park
7. Gilmore (1967)	Banks Peninsula
8. Coleman (unpubl. data) and Coleman et al. (1980)	Flaupiri, Westland
9. Purchas (1975)	Otari, Wellington
10. P. Cowan (pers. comm.)	Orongorongo Valley, Wellington

APPENDIX III

Plant species recorded as *being heavily browsed by ungulates (mainly red deer).*

Species	Study
Carpodetus serratus	2, 3, 11, 12, 13, 14, 15, 16
Coprosma spp. (predominantly large leaf)	1-12, 16
Fuchsia excorticata	2, 3, 10, 11, 12, 14, 15, 16
Griselinia littoralis	1-3, 5-16
Hedycarya arborea	3, 16
Melicytus ramiflorus	5, 6, 7, 11, 12, 16
Muehlenbeckia australis	9
Myrsine spp.	2, 3, II, 16
Pseudopanax spp.	1-16
Rubus spp.	2
Scheffiera digitata	2, 5, 7, 8, 9, 10, 12, IS, 16
Weinmannia racemosa	2, 5, 6, 7, 9, 12, 14, 16

Study and region	
1. Clarke (1972)	Nelson
2. Holloway (1950)	Western Southland
3. Holloway et al. (1963)	Tararua Range
4. James and Wallis (1969)	Urewera
5. McKelvey (1959)	North Island
6. McKelvey (1963)	West Taupo (cattle also present)
7. McKelvey (1973)	Urewera
8. Mark and Bayliss (1975)	Secretary Island
9. Poole (1951)	Fioardland (wapiti also present)
10. Wardle (1967)	Aorangi Range (goats also present)
11. Wardle (1971)	Seaward Kaikoura (chamois also present)
12. Wardle (1974)	Grey River (chamois also present)
13. Wardle and Guest (1977)	Waitaki (chamois and thar also present)
14. Wardle and Hayward (1970)	Taramakau (chamois also present)
I5. Wardle et al. (1971)	Northern Fiordland (wapiti also present)
16. Wardle et al. (1973)	Southern Westland (chamois also present)