

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

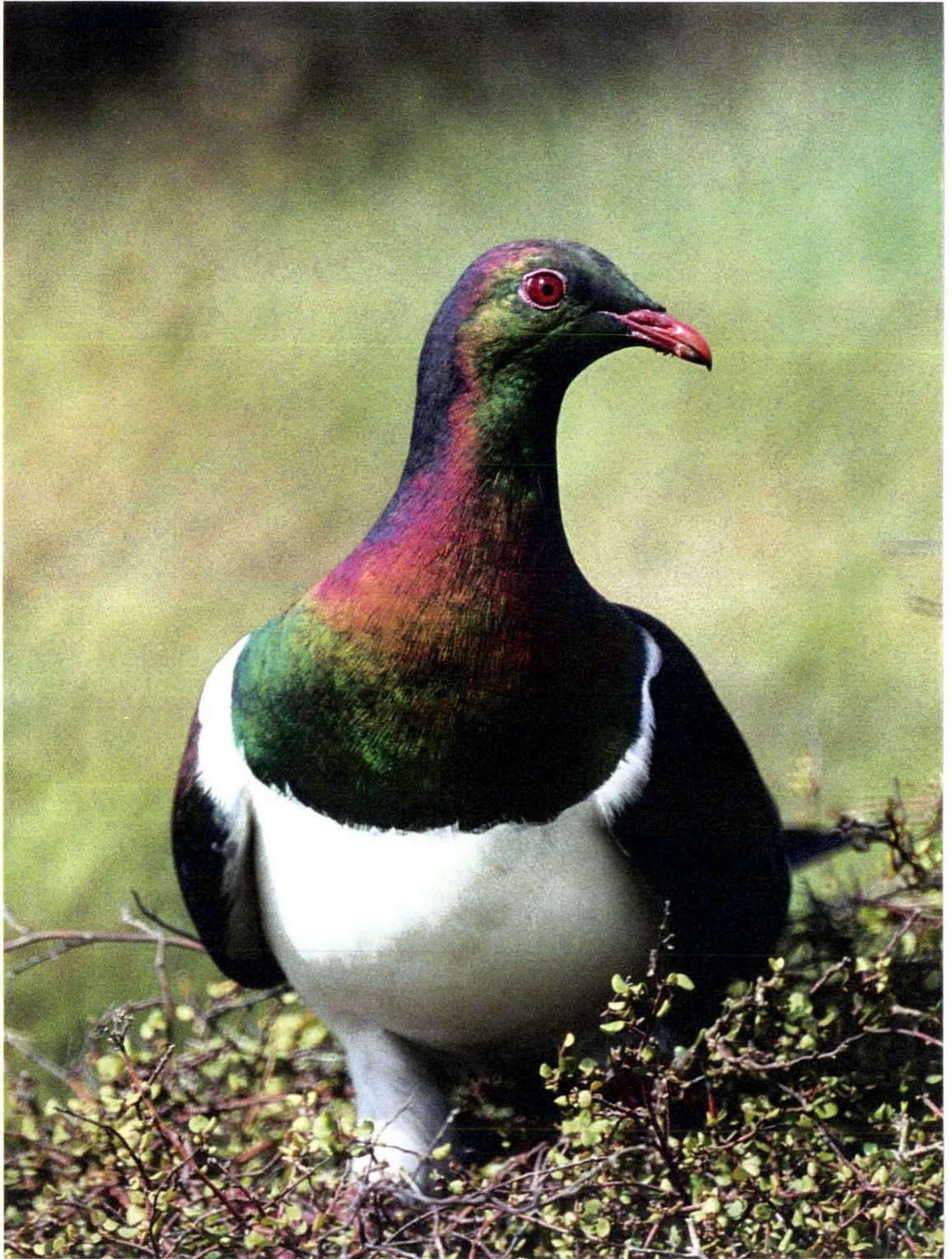
Diet, dispersal and distribution of kereru (*Hemiphaga
novaeseelandiae novaeseelandiae*) in a lowland podocarp-
hardwood forest

Myfanwy Teresa Hill

A thesis presented in partial fulfillment of the requirements for the degree of
Master of Science in Ecology at Massey University, Palmerston North, New
Zealand.

February 2003

Frontispiece



Kereru (photo courtesy Matt Wong)

Abstract

The complex relationship between food availability, nutrient content, diet and feeding behaviour, and how these factors relate to home range and movement of kereru, was examined at Whirinaki Forest between 1999 and 2001.

The phenology of 11 plant species was monitored and the availability of mature and immature fruit and vegetation was measured and considered in relation to climatic factors. Kereru were mist-netted and radio-tagged, then the birds were radio-tracked and observations on diet, feeding ecology and location were made. The spacing and movements of kereru within Whirinaki Forest were examined, and home ranges calculated for 18 radio-tagged individuals. Six species of fruit and two species of leaf consumed by kereru were analysed to determine their nutritional content and physical composition.

Phenology results showed two main fruiting groups, which fruited in summer and autumn. At different times of year, the most important species to kereru in Whirinaki appear to be miro, tawa, makomako and kowhai. Miro and tawa were clearly preferred fruit in autumn and summer respectively. Kereru specialised on these species, but behaved as generalist feeders when the ripe fruit of preferred species was not readily available. Diet was related to the habitat in which the kereru foraged and the accessibility of trees in the forest and food on the trees is likely the main force behind many aspects of feeding ecology. The results from nutrient analysis are consistent with a view that there has been some co-evolution of kereru and the nutritional value of their significant food species. The species that contain the necessary nutrients for differing seasonal requirements are species sought after by kereru. Diet, forest composition and habitat most likely had an influence on range size, which varied from 13.9 ha to 704.2 ha. Movements were related to changes in food availability and food types.

The preferred food species and the habitat that surrounds them need to be protected to ensure the future survival of kereru.

Acknowledgements

This project would not have been possible without the assistance and support of many people.

I am extremely grateful to my head supervisor, Robin Fordham, for remaining constantly enthusiastic, for supporting me when things went wrong and for his unending patience, guidance and understanding. I am thankful to my co-supervisor Ian Henderson for being so positive and constructive, for helping me through my statistical dilemmas and posing the questions that needed to be answered. The field trips up to Whirinaki Forest to see what I was talking about and the supplies they brought on their trips were hugely appreciated.

Thank you also to Matt Wong for participating in the great fruit hunt and for the use of his fabulous kereru photo.

Erica Reid and Barbara Just, along with the rest of the Massey University Ecology Group kindly offered me help and support as needed.

Mike Bretherton assisted me in finding the necessary weather data, Duncan Hedderley assisted with the complicated statistics and Fliss Jackson performed all the nutritional analyses.

Ralph Powlesland provided me with access to his incredible knowledge and the opportunity to perform this study; I am grateful for his accommodating and attentive nature and his passion for kereru. Dave Wills, Claude August and Andrew August provided me with somewhere to live, food, transport and a quad when necessary; they assisted with observations; answered my never-ending questions; scaled 30m trees to collect fruit and even put up with a dalmatian!

Staff at the Department of Conservation's Murupara field centre were very generous with their time and resources and a special thank you to Andy Blick for allowing me access to his files.

Astrid Dijkstraaf gave helpful advice on some of the nutritional aspects and kindly lent me a copy of her thesis.

Finally, thank you to Nick for de-seeding thousands of fruit, for computer advice and for simply putting up with having a thesis writer in the house.

This thesis was supported by the Department of Conservation, Massey University Research Fund, Julie Alley Bursary, Waikato Forest & Bird, Coombs Memorial Bursary and the New Zealand Federation of University Women.

Table of contents

Abstract	i
Acknowledgements	ii
Table of contents.....	iv
List of Figures.....	v
List of Tables	vi
List of Photos	vii
 Chapter 1	
Introduction	1
 Chapter 2	
Study areas.....	4
2.1 Location	4
2.2 History.....	4
2.3 Climate.....	5
2.4 Soil Type.....	5
2.5 Forest Type.....	6
2.6 Forest Fauna.....	8
 Chapter 3	
Phenology.....	12
3.1 Abstract.....	12
3.2 Introduction	12
3.3 Methods	14
3.3.1 Criteria for selecting plants.....	14
3.3.2 Data collection.....	15
3.4 Results	16
3.4.1 Phenology.....	16
3.4.2 Phenology in relation to abiotic factors.....	22
3.5 Discussion.....	27
3.6 Conclusions	31
 Chapter 4	
Diet of kereru	32
4.1 Abstract.....	32
4.2 Introduction	32
4.3 Methods	34
4.4 Results	36
4.5 Discussion.....	49
4.6 Conclusions	53
 Chapter 5	
Feeding ecology of kereru	54
5.1 Abstract.....	54
5.2 Introduction	54
5.3 Methods	55
5.4 Results	58
5.4.1 Feeding habitat	58
5.4.2 Foraging level	60
5.4.3 Foraging height and vertical range	63
5.4.4 Feeding station.....	66
5.4.5 Feeding rate and bout length.....	68
5.4.6 Other kereru in vicinity	71
5.5 Discussion.....	72
5.6 Conclusions	79

Chapter 6	Nutritional characteristics of food eaten by kereru	81
6.1	Abstract	81
6.2	Introduction	81
6.3	Methods	84
6.3.1	Criteria for selecting plants for analysis	84
6.3.2	Preparation of plant material	85
6.3.3	Nutrient analysis	85
6.3.4	Statistical analysis	86
6.4	Results	86
6.5	Discussion	93
6.6	Conclusions	98
Chapter 7	Home range and movements of kereru	100
7.1	Abstract	100
7.2	Introduction	100
7.3	Methods	102
7.3.1	Capturing and radio-tagging kereru	102
7.3.2	Home range and core area calculations	104
7.3.3	Movements and dispersal	105
7.4	Results	106
7.4.1	Home range and core area	106
7.4.2	Movements and dispersal	111
7.4.2.1	Repeated movements between home ranges	114
7.5	Discussion	115
7.5.1	Home range and core area	115
7.5.2	Movement and dispersal	119
7.6	Conclusions	121
Chapter 8	Synthesis of kereru feeding in Whirinaki forest	123
8.1	Feeding behaviour in relation to food availability	124
8.2	Food nutrient levels and kereru diet	128
8.3	Kereru feeding ecology, distribution and dispersal	130
8.4	Conclusions	134
Chapter 9	General discussion	135
9.1	Conservation implications	135
9.2	Future research	136
References	137

List of Figures

Figure 2.1:	Location of Whirinaki Forest and study areas Oriuwaka and Otupaka	11
Figure 3.1a:	Vegetation abundance over a 14 month period on two common kereru food species in the two study areas of Whirinaki Forest	16
Figure 3.1b:	Availability of fruit over a 14 month period on some common kereru food species in the two study areas of Whirinaki Forest	20
Figure 3.2a:	Fruit abundance in relation to radiance for karamu, miro, maire, mahoe and putaputaweta	23
Figure 3.2b:	Fruit abundance in relation to radiance for rimu, kahikatea, makomako, kotukutuku and tawa	23
Figure 3.3a:	Fruit abundance in relation to rainfall for karamu, miro, maire, mahoe and putaputaweta	25

Figure 3.3b:	Fruit abundance in relation to rainfall for rimu, kahikatea, makomako, kotukutuku and tawa.....	25
Figure 3.4a:	Vegetation in relation to radiance for mahoe and kowhai.....	26
Figure 3.4b:	Vegetation in relation to rainfall for mahoe and kowhai.....	27
Figure 4.1:	The proportion of foraging observations recorded from each group of kereru in each area during each month	35
Figure 4.2:	Monthly trends in the proportional composition of the three major food types in kereru diet in Oriuwaka, expressed as a percentage of feeding observations	38
Figure 4.3:	Monthly trends in the proportional composition of the three major food types in kereru diet in Otupaka, expressed as a percentage of feeding observations	38
Figure 4.4:	Monthly trends in the proportional composition of diet of kereru in Oriuwaka, expressed as a percentage of feeding observations.....	40
Figure 4.5:	Monthly trends in the proportional composition of diet of kereru in Otupaka, expressed as a percentage of feeding observations	40
Figure 4.6:	Principal component analysis for Oriuwaka based on months in which food types were eaten	42
Figure 4.7:	Principal component analysis for Otupaka based on months in which food types were eaten	42
Figure 4.8:	The variations in the number of species on which foraging observations were made each month in the two study areas	48
Figure 5.1:	Monthly percentage of feeding use of main forest types over a 14 month period	59
Figure 5.2a:	Change in the use of forest structure for feeding over a fourteen month period in Oriuwaka.....	61
Figure 5.2b:	Change in the use of forest structure for feeding over a fourteen month period in Otupaka	61
Figure 5.3:	Monthly average feeding heights over a 14 month period in Oriuwaka and Otupaka	64
Figure 5.4:	Relative proportions of feeding stations among eight common food species.....	67
Figure 5.5:	Relationships between feeding rate, the foraging bout length, and the amount of food per peck.....	70
Figure 6.1:	Cluster analyses for kereru food species using Ward's Minimum Variance method based on nutritional components	89
Figure 6.2:	Cluster analyses for fruits using Ward's Minimum Variance method based on nutritional components and physical characteristics	89
Figure 6.3:	Principal component analysis based on nutritional components	91
Figure 6.4:	Principal component analysis for fruits based on nutritional components and physical characteristics	93
Figure 7.1:	Utilisation plot for one kereru (Tx 80), with the point of inflection taken as 50% of fixes.....	105
Figure 7.2	Home range boundaries for 18 kereru caught in Whirinaki forest.....	107

List of Tables

Table 4.1:	Diet of the kereru in Whirinaki Forest, comprised of percentages of food species and types in both study areas.	37
Table 4.2:	Whirinaki food species ranked in order of importance for both study areas, expressed as a percentage of feeding observations	39
Table 4.3:	Component loadings for principal component analysis for both study areas based on months in which certain food types were eaten.....	41

Table 5.1:	Categories for forest type, foraging level and feeding station at Whirinaki forest	56
Table 5.2:	Approximate percentages of different forest types within study area of Whirinaki forest	60
Table 5.3:	Percentage kereru foraged in each level within each species for the two study site	62
Table 5.4:	Foraging heights and heights of food trees over 14 months in Whirinaki forest	63
Table 5.5:	Percentage of total tree height where kereru feeding sites are located for eight dominant food species	65
Table 5.6:	Total vertical distance ranged during feeding bouts	65
Table 5.7:	Average vertical distance ranged by kereru during a feeding bout, depending on food species and type	66
Table 5.8:	Average horizontal distance moved by kereru during a feeding bout	68
Table 5.9:	Average feeding rates and total food ingested per average feeding bout for main kereru food species	69
Table 6.1:	Nutritional composition for a range of species	88
Table 6.2:	Physical measurements of fruits for a range of species	88
Table 6.3a:	Component loadings for principal component analysis based on nutritional components	90
Table 6.3b:	Component loadings for principal component analysis based on nutritional components and physical characteristics	92
Table 7.1:	Cluster analysis ranges (as calculated by RANGESV) for 18 kereru at Whirinaki, obtained between November 1998 and May 2001	110
Table 7.2:	Monthly movements of kereru departing from, and returning to, areas within Whirinaki forest (all data from November 1998-May 2001 combined)	112
Table 7.3:	Month of departure and duration of absence from areas within Whirinaki forest	113
Table 7.4:	Keru usage of multiple home ranges over the tracking period (January 1999 to July 2001)	114

List of Photos

Photo 2.1:	Mixed podocarp-hardwood forest at Oriuwaka, showing scattered podocarps and abundant tawa	7
Photo 2.2	Large emergent rimu at Otupaka	8
Photo 6.1	Dave Wills (DoC) collecting ripe tawa fruit	84
Photo 7.1	Radio-tracking using the Telonics TR4 receiver and a hand-held yagi aerial	103

Chapter 1

Introduction

The endemic kereru (*Hemiphaga novaeseelandiae novaeseelandiae*), also known as the New Zealand pigeon, kuku and kukupa, is an inhabitant of the lowland forests of New Zealand. The kereru is a large fruit pigeon weighing 550-850g (Clout 1990), with similar morphology to other fruit pigeons: a large body, relatively small head and a soft-based bill allowing for a distensible gape which enables them to swallow large fruit up to 26mm in diameter (Gibb 1970). The sexes are monomorphic. It is a particularly attractive bird, with the head, neck and chest green, but often with an intense metallic iridescence (Frontispiece). The mantle and wings are maroon, with brown orange and green tones. The rump and upper tail are pastel blue-green, with faint iridescence. The upper surface of the tail is black. The breast, belly, shoulder straps and leg covers are white. The eyes, eye rings, beak and feet range from crimson to orange depending on age and season (Higgins & Davies 1996).

The closest living relative of the kereru is the parea (*Hemiphaga novaeseelandiae chathamensis*), also known as the Chatham Island pigeon (Millener & Powlesland 2001). The third described member of the genus *Hemiphaga* is the Norfolk Island pigeon (*Hemiphaga novaeseelandiae spadicea*), now extinct (Flux *et al* 2001). Another form which inhabited Raoul Island was also exterminated last century (Pierce 1993). *Hemiphaga* has probably been isolated in the New Zealand archipelago since the mid to late Tertiary (James 1995).

About 70% of New Zealand's trees and shrubs have fruits that are dispersed by vertebrates (Clout & Hay 1989), but although New Zealand has representatives from many avian orders and, therefore, a reasonably diverse avian fauna (Bell 1990) it currently supports a limited number of frugivorous native species, particularly those able to deal with larger fruits. Many of the species capable of eating larger fruit, for example those greater than 10mm in width, (with the inclusion of the seed to enable dispersal) are now either extinct, for example the moa (Burrows *et al.* 1981, Lee *et al.* 1991), or greatly restricted in distribution,

for example the kakapo (Clout & Hay 1989). The kereru remains the only widespread consumer of these larger fruits and a number of plant species are thought to depend on birds for seed dispersal (Clout and Hay 1989, Lee *et al.* 1991, Pierce 1993). Therefore extinction of the kereru would at least disrupt local or regional ecological processes and, in the long term, almost certainly alter forest composition.

The kereru was once common throughout New Zealand forests (Best 1977). It has been heavily harvested by both Maori and Europeans and much of its forest habitat has been destroyed by the clearing of lowland forest (Heather & Robertson 1996). The kereru became a fully protected species in 1921 (Dunn & Morris 1985), and although it remains widespread its numbers are probably declining (Clout *et al.* 1995). Now the kereru is threatened by introduced mammalian predators (of particular concern in Whirinaki are stoats *Mustela erminea* and cats *Felis catus*), along with human poaching (Pierce 1993), and mammalian competitors for food (sometimes indirectly, e.g. kotukutuku (*Fuchsia exorticata*) eliminated from many forests by possum browse on leaves also means the removal of that fruit source). Continuing habitat degradation is of concern because forest fragmentation may affect the dispersal patterns of the kereru. There is some evidence that kereru are adjusting to changes in forest availability and new food sources because birds can be found in areas far from native forest, feeding on exotic shrubs such as broom, holly, lucerne and elderberry (Dunn & Morris 1985, Clout *et al.* 1991, Clout *et al.* 1995). One kereru was found feeding in plum trees on agricultural land 25km away from its summer range in beech/podocarp forest (unpubl. data cited in Clout *et al.* 1991). Whether these changes will maintain production of kereru at levels previously associated with native forests remains to be seen.

Several studies have described general aspects of kereru ecology such as diet (McEwen 1978), movements (Clout *et al.* 1986, Clout *et al.* 1991) and breeding (Clout *et al.* 1995), but none have also looked at nutrition and linked these factors together in a comprehensive way. There is little published information on the link between availability of food, its nutrient content and the affect this may have on kereru diet and feeding behaviour, although a similar study has been performed on the parea (Powlesland *et al.* 1997).

This study was undertaken in the tall podocarp forest of Whirinaki, a habitat in which kereru ecology has not been examined in detail. Tall podocarp forest was possibly the main habitat of kereru in pre-human times but most studies have been based in disturbed semi-urban areas, small forest remnants or on islands. The research was initially undertaken to look at the breeding patterns of kereru in relation to diet and movement and to identify the differences between juvenile kereru and adult kereru in these areas. However, because the kereru did not breed in two successive seasons (1999-2000; 2000-2001) the focus of the research shifted to the complex relationship between food availability, nutrient content, diet and feeding behaviour, and how these factors relate to the movement of the kereru. Thus the work attempts to improve understanding of a broader ecological pattern influencing the general behaviour of the kereru. The principal questions addressed were:

1. What is the phenology of plants that are significant food sources for kereru?
2. What foods compose the main diet of kereru in Whirinaki forest and what is the feeding ecology of kereru while on these species?
3. How do significant plant foods vary in nutritional value?
4. What pattern of kereru home range and dispersion is characteristic of tall podocarp forest?
5. How is kereru movement and behaviour affected by the availability and nutritional value of food plants?

Chapter 2

Study areas

2.1 Location

Whirinaki Forest Park lies in the eastern central area of the North Island (Figure 2.1). The Park is about 100km south east of Rotorua and is south of Murupara on State Highway 38. Whirinaki forest forms a boundary between exotic Kaingaroa pine plantations to the west and Te Urewera National Park to the east, stretching over 55,000 ha. The two areas within Whirinaki Forest where the study took place are called Oriuwaka (1750 ha) and Otupaka (1830 ha) (Fig 2.1); these areas were part of a continuous tract of forest.

2.2 History

The original human inhabitants of Whirinaki Valley were believed to have been "te Tini o te Marangaranga", held to have arrived in the forest about 1150 AD (McGlone 1983). These people were conquered at around 1620 by Wharepakau and his nephew Tangiharuru, descendants of Toi, the great Maori chief. It is from Wharepakau that the tribe Ngati Whare originated (C. August pers. comm.). Ngati Whare regard themselves as the guardians of Whirinaki forest and maintain a keen interest in the management of the park, and administer Minginui Village (C. August pers. comm.). The first pakeha to visit the area was the Reverend William Colenso who came to Te Whaiti in 1842. By 1885 surveying of the proposed SH38 began but met with resistance (Morton *et al.* 1984).

The broad outlines of the forest are at present much as described by Europeans 100 to 130 years ago (McKelvey 1955, Nicholls 1966). Forest patterns suggest that some forest may have been destroyed by burning in the pre-European times, when large clearings were also created (McGlone 1983).

Timber milling first began at Whirinaki in 1928 and for several years was largely confined to the felling of totara in relatively small areas in Whirinaki Valley (C. August pers. comm.). This increased until by 1976 the annual cut of native trees was large - up to 30,000m³ (Morton *et al.* 1984). Ongoing demand

saw fast-growing exotic species planted where the much slower-growing native species had been taken (Beveridge & Herbert 1978). In 1978-79 a bitter public controversy raged over the future of the forest. Conservation groups actively campaigned to stop the native harvest and came into direct conflict with the local community, which saw this as a threat to lifestyle and employment (Morton *et al.* 1984). In 1985 a new government ended the logging of native trees and by 1987 all logging of native timber had stopped, apart from totara taken for carving. This wood was either fallen or dying at the time it was used (C. August pers. comm.).

2.3 Climate

Otupaka has an average elevation of about 1,200m above sea level, compared to Oriuwaka, which is 600-800 m above sea level (Nicholls 1966). Climatic recordings obtained from weather stations at the Rotorua aerodrome and Whaeo power station show mean annual rainfall (as recorded between 1990 and 2001) is 1449 mm. Past recordings have shown higher rainfall over the more hilly ground towards the head of the Whaeo River and towards the Whirinaki River (Nicholls 1966). This indicates that a higher rainfall can be expected at Otupaka than Oriuwaka. The variation in rainfall between years can differ by as much as 100%. The mean annual temperature in Whirinaki is 12°C, with a mean annual minimum temperature of 7°C and mean annual maximum temperature of 17°C. Due to the higher elevation of Otupaka it is generally 1 to 2 degrees Celsius colder than Oriuwaka (pers. obs.). The mean annual number of ground frosts is 130 (Nicholls 1966) and mean annual radiation is 5165 MJ/sq.m.; this translates to a daily mean of 14 MJ/sq.m.

2.4 Soil Type

The soils of the Whirinaki area have developed mainly from volcanic ash and lapilli erupted from sources east of Rotorua or Lake Taupo. Successive topsoils evolved during volcanically quiet periods (Grindley 1960). The mean thickness of weathered ash is about 6 m (Healy 1964), and only on the very steepest slopes is ash absent or very thin. Certain areas of both Oriuwaka and Otupaka have particularly thick deposits of rhyolitic ash erupted from the Taupo district about 1500 BC and 150 AD (Healy 1964). Generally brown to grey brown sands or silty sands overlie pale yellow to red-brown coarse loamy sands and

partially weathered pumiceous sands and gravels (Gibbs 1968). The underlying rock is Mesozoic greywacke or rhyolite of Pleistocene origin (Gibbs 1968). Although the topsoils under native plant cover are relatively fertile due to the input from vegetative matter, the subsoils of Oriuwaka and Otupaka are comparatively thin, poor and more due to the nature of the rock and ash from which they were derived (Field & Garratt 1979).

2.5 Forest Type

There are two main types of forest in the areas studied; mixed podocarp-hardwood forest and dense lowland podocarp forest (Nicholls 1966). Both forest types are present in Otupaka and Oriuwaka.

Mixed podocarp-hardwood forests are forests of diverse composition (Beaven *et al.* 2000). At Whirinkai, podocarps are large in size and plentiful but do not form a continuous high canopy; instead they occur as scattered emergents from a lower canopy of hardwoods. On the lower levels, rimu (*Dacrydium cupressinum*) and matai (*Prumnopitys taxifolia*) are the main emergent species, with occasional kahikatea (*Dacrycarpus dacrydiodes*) and low miro (*Prumnopitys ferruginea*) stands. Tawa (*Beilschmedia tawa*) forms the greater part of the canopy (Photo 2.1). The under-storey is chiefly tree fern (*Cyathea* spp) and ground fern (primarily *Blechnum* spp). At the higher altitudes, tawa is replaced by more cold-tolerant hardwood species, kamahi (*Weinmannia racemosa*) being the most dominant. Oriuwaka tends to have more tawa and Otupaka, being higher altitude, a greater abundance of kamahi. Kotukutuku (*Fuchsia exorticata*) is a common understorey species in Oriuwaka, but is not common in Otupaka. In Otupaka, makomako (*Aristotelia serrata*) and hinau (*Elaeocarpus dentatus*) are relatively more frequent.

Whirinaki is said to contain the best remaining example of dense lowland podocarp forest in the North Island (Morton *et al.* 1984). In some locations the most extensive type of dense podocarp forest contains rimu, matai, miro, kahikatea and totara (*Podocarpus totara*). Except where podocarps are at their densest, there is a high, thick subcanopy of tawa. This forest type is found on flatter country, apparently on a thick covering of volcanic ash (Katz 1980). In dense lowland podocarp forests, rimu is denser on the ridges and is generally large, with the other podocarps throughout the forest (Herbert 1978). There

are moderate numbers of miro and matai in this forest type, with most of the totara dying or standing dead. Shrubs are very abundant and ferns are locally abundant. The other common type of dense podocarp forest mainly consists of rimu and kahikatea (Photo 2.2). This forest type has large tall rimu and kahikatea with occasional totara, miro, matai, and tawa. Locally abundant sapling and pole tawa can be found along with shrubs and tree ferns. Dense lowland podocarp forest is more prolific at Otupaka, where there are larger numbers of miro.

Other forest types in the area of Oriuwaka and Otupaka include beech (*Nothofagus* spp) forests (and a mixture of beech and podocarps), hardwood ‘nursery’ scrub (areas of regeneration after logging) and the frost flats, but kereru were not commonly found in these patches.

Photo 2.1 Mixed podocarp-hardwood forest at Oriuwaka, showing scattered podocarps and abundant tawa.



Photo 2.2 Large emergent rimu at Otupaka.



2.6 Forest Fauna

The dense podocarps in Whirinaki forest support a total of 31 bird species, 24 native and 7 introduced (Morton *et al.* 1984). Apart from the kereru (*Hemiphaga novaeseelandiae novaeseelandiae*), the frugivorous birds include the tui (*Prosthemadera novaeseelandiae*) and bellbird (*Anthornis melanura*), which feed mainly on rimu, totara and kahikatea, as well as taking nectar. The kaka (*Nestor meridionalis*) is one of the dominant species in Whirinaki and can compete for food with kereru by decimating numbers of unripe fruit, particularly miro, to gain access to the seed (pers. obs.). Kiwi (*Apteryx*

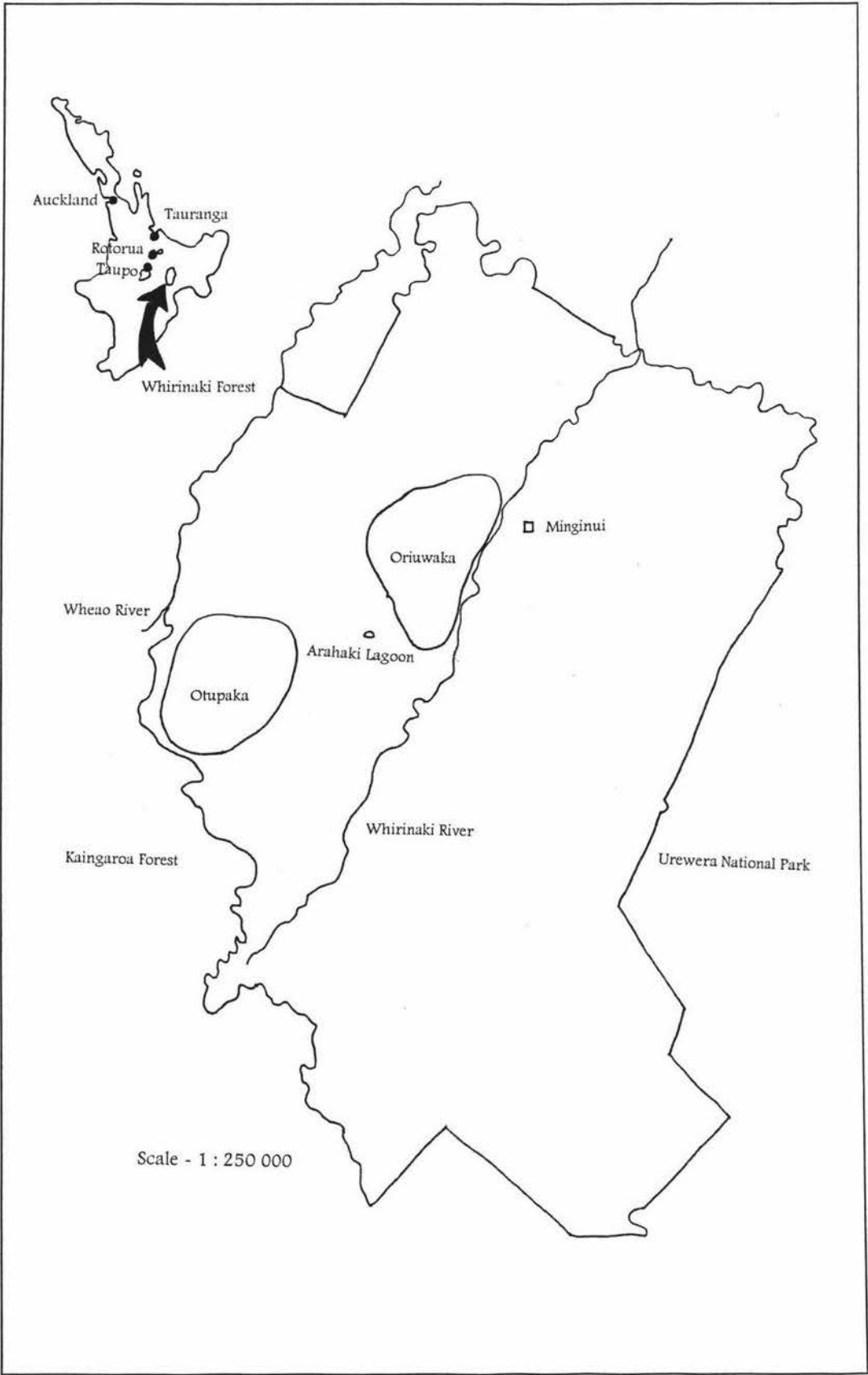
australis) are present but not found in either of the study areas (D. Wills pers. comm.). Kakariki (*Cyanoramphus novaeseelandiae*) can also be found in the forest but are not common (R. Powlesland pers. comm.). The shining cuckoo (*Chrysococcyx lucidas*) and the long-tailed cuckoo (*Eudynamus taitensis*) inhabit the canopy. The grey warbler (*Gerygone igata*), whitehead (*Mohoua novaeseelandiae*), rifleman (*Acanthisitta chloris*), fantail (*Rhipidura fuliginosa*), robin (*Petroica australis*) and tomtit (*Petroica macrocephala*) are the common insect-eating passerines. Raptors include the morepork (*Ninox novaeseelandiae*) and the New Zealand falcon (*Falco novaeseelandiae*). The New Zealand falcon is a frequent predator of the kereru (Clout 1990), unlike the Australasian harrier (*Circus approximans*), which is a bird of the open scrub and does take small birds as prey but primarily feeds on carrion. Kereru will swoop close to the ground in order to escape from the falcon, but exhibit the same behaviour when an Australasian harrier flies overhead (pers. obs.).

The non-avian indigenous vertebrates of Whirinaki include Hochstetter's frog (*Leiopelma hochstetteri*), two species of gecko (*Naultinus elegans* and *Hoplodactylus granulatus*) and both the long-tailed bat (*Chalinolobus tuberculatus*) and short-tailed native bat (*Mystacina tuberculata*) (Morton *et al.* 1984).

Introduced mammals of Whirinaki forest are numerous. Feral dogs (*Canis familiaris*) and cats (*Felis catus*) can be found close to the forest margins, along with ferrets (*Mustela furo*) and hedgehogs (*Erinaceus europaeus*). Deeper in the forest are deer (mostly red deer (*Cervus elaphus*)), pigs (*Sus scrofa*), possums (*Trichosurus vulpecula*), stoats (*Mustela erminea*), rats (*Rattus rattus*) and mice (*Mus musculus*). The effect of these mammals on the ecosystem of the forest is significant. Red deer and pigs affect the food supply of kereru (Herbert 1978) while cats, possums, stoats and rats are predators of kereru (Pierce 1993, Heather & Robertson 1996). Possums also compete with kereru for food (Williams 1982, A. Dijkgraaf pers. comm.). Commercial and recreational hunting of deer, introduced to Whirinaki in 1919 and 1921 (Nicholls 1966), and pigs, present for about 150 years (Nicholls 1966), is an important activity for local residents. Possum hunting for fur is also encouraged (pers. obs.). During the study period the Otupaka area was poisoned to reduce possum

numbers. This was achieved via a single aerial drop of carrots laced with 1080 poison.

Figure 2.1 Location of Whirinaki Forest and study areas Oriuwaka and Otupaka.



Chapter 3

Phenology

3.1 Abstract

The phenology of eleven plant species expected to compose a large part of the diet of the kereru in Whirinaki Forest (McEwen 1978, Dunn 1981, Clout 1990, Langham 1991) was monitored at two locations in Whirinaki Forest between February 2000 and March 2001. The availability of mature and immature fruit and vegetation was measured and considered in relation to climatic factors.

Results showed two main fruiting groups, one that fruited in summer and one that fruited in autumn. There were three months of the year (September – November) when no ripe fruit was available. New vegetative growth appeared as early as winter for mahoe and during spring and summer for kowhai. The amount of available radiation appeared to have the strongest influence on the fruiting patterns and the patterns of new vegetative growth. The majority of ripe fruit was available after the peak of radiance had occurred, during the period of warm temperatures and increased rainfall.

The availability of fruit and vegetation of different species is also strongly affected by the strategy of that species (e.g. deciduousness, consecutive fruiting, asynchronous fruiting), and there is considerable variation in the strategies shown in Whirinaki Forest, including consecutive fruiting, synchronous and asynchronous fruiting, alternate fruiting years and the level of deciduousness.

3.2 Introduction

The seasonal rhythms of fruiting, flowering and vegetative growth differ from plant to plant and from species to species. These rhythms, or phenological markers, have been linked to climate patterns through the year (Rathcke and Lacey 1985, Smith-Ramirez and Armesto 1994), but also to interactions with animal pollinators and seed dispersers (Herrera 1982, Berlin *et al.* 2000). Rainfall and solar irradiance are said to be the main seasonal, abiotic influence

on the phenology of tropical and sub-tropical plants (van Schaik *et al.* 1993, Wright *et al.* 1999) which produce flowers and new foliage during periods of high irradiance, and ripening fruits at the end of the dry season or during the rainy season (to reduce seedling mortality) (Janzen 1976). The peak in fruiting can also coincide with an abundance of migratory frugivores (Loiselle and Blake 1991, Kannan and James 1999). In the tropics, where climate is relatively aseasonal, and animal pollinators and seed dispersers are present the whole year, the fruiting and flowering peaks can be less pronounced and may occur repeatedly or continuously over the year (Putz 1979, Rathcke and Lacey 1985). In temperate forests fruiting and flowering tend to have more pronounced peaks and fruit is not continually available, so generally there is only one distinct peak per season (Adler & Kielipinski 2000).

Research on fruiting phenology in the tropics has introduced the concepts of pivotal plant species (Howe 1977) and keystone plant resources (Leighton and Leighton 1983, Lambert and Marshall 1991). These refer to species and resources considered vital for sustaining frugivore populations, particularly during periods of resource scarcity. Identifying such food species could have important conservation implications for an entire food web where a prominent frugivore acts as a keystone disperser. In New Zealand the kereru fills this role for many forest species and accordingly plays a crucial role in forest dynamics (Clout & Hay 1989, Lee *et al.* 1991).

The aim of this chapter is, therefore, to determine the patterns of fruiting and vegetative growth of principal foods consumed by kereru over a 14 month period to assess the year-round pattern of food availability, and to aid in later identifying plant species of consequence to the survival of the kereru in Whirinaki Forest.

3.3 Methods

3.3.1 Criteria for selecting plants

Eleven species were chosen for regular monitoring because they formed the principal diet of the kereru in other areas of New Zealand (McEwen 1978, Clout & Hay 1989, Clout *et al.* 1991, O'Donnell & Dilks 1994). These consisted of small-fruited hardwoods: mahoe (*Melicytus ramiflorus*), karamu (*Coprosma robusta*), makomako (*Aristotelia serrata*), putaputaweta (*Carpodetus serratus*); large-fruited hardwoods: white maire (*Nestegis lanceolata*), tawa (*Beilschmedia tawa*), kotukutuku (*Fuchsia exorticata*); small-fruited podocarps: rimu (*Dacrydium cupressinum*), kahikatea (*Dacrycarpus dacrydioides*); a large-fruited podocarp: miro (*Prumnopitys ferruginea*), and another hardwood: kowhai (*Sophora tetraptera*). Of these species, karamu, rimu, kahikatea, miro, white maire, tawa, kotukutuku, makomako and putaputaweta were monitored for fruiting; kowhai was monitored for vegetative growth; and mahoe was monitored for both.

Five 100 by 100m grids were randomly located in each study site where kereru were regularly observed. Within each of these grids, a representative from each of ten species was chosen. Five areas containing the eleventh species, kowhai, were randomly selected using a different grid due to the patchy distribution of this species. Kowhai was not present within the Otupaka study site. The plants within each grid were chosen based on three criteria: (1) They had to be mature, i.e. of fruit-bearing age and of a size that kereru would usually feed from. Dunn (1981) showed that kereru will sometimes disregard sapling trees, regardless of whether they produce fruit. (2) Because weak or injured trees can differ markedly from 'normal' phenological patterns (Janzen 1976) plants that were obviously unhealthy were not chosen. (3) To allow for accurate records, a good proportion of the canopy had to be visible. The selection process was independent of existing fruit scores or anticipated productivity as these plants were intended to represent the available range in fruit abundance.

3.3.2 Data collection

Each of the 105 trees in the study that met the selection criteria was marked and its location mapped. The trees were monitored monthly over two day periods from February 2000 until March 2001.

To avoid discrepancies between the amount of fruit/vegetative growth possible on each of the different species, a scale was developed that could be used across various species. The fruit or leaves seen on each species were given a score from zero to five: zero = absent; 1 = scarce; 2 = below average; 3 = average; 4 = above average; 5 = high (heavily laden - the maximum production). For the fruit bearing plants this scale was used to separately describe unripe and ripe fruit. For mahoe and kowhai foliage, values were obtained for both mature vegetative cover and the cover of new leaf growth.

Fruit was categorised as either immature or ripe, the latter being any fruit that was full-sized and consisting of more than 80% of the normal ripe colour for the species, i.e. usually orange to purple. Anything which did not fit into the ripe category was classed as immature.

Vegetation was scored as either young/actively growing or mature, based on leaf colour, texture and size. Leaves classified as young were generally a pale shade of green and less than 80% of the size of the mature vegetation. Young leaves were also soft in texture compared with mature leaves.

These categories were assessed visually using binoculars and a telescope, fruit and vegetation was also picked to gain a better understanding of the categorisation.

Weather data were obtained from weather stations at the Rotorua Aerodrome and the Wheao Power Station.

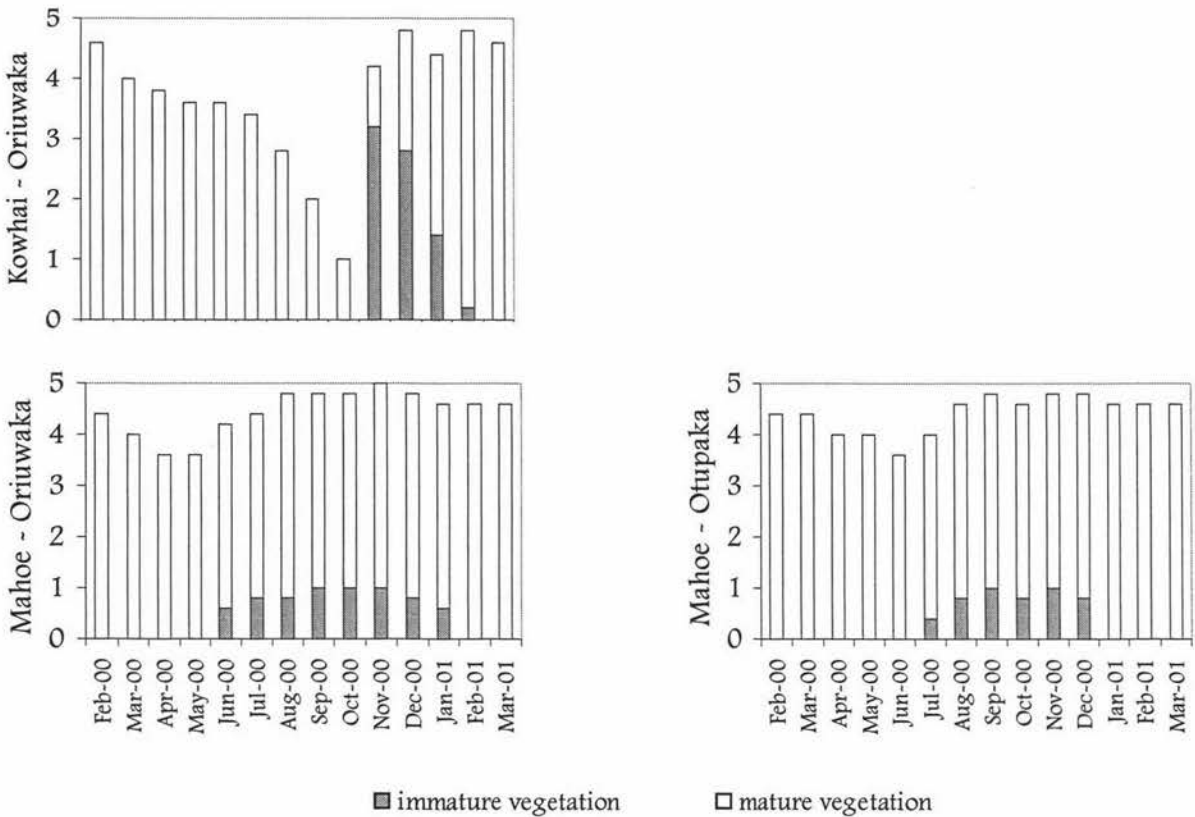
For the analysis, months were divided into seasons according to climactic changes. These seasons were: March – May (autumn), June – August (winter), September – November (spring) and December-February (summer).

3.4 Results

3.4.1 Phenology

Mature mahoe vegetation was available throughout out the study period, remaining plentiful with only minor fluctuations in abundance (Fig 3.1a). The amount of vegetative cover fell in late summer/early autumn before young leaves began to appear during winter. This growth continued until late summer, boosting the presence of mature vegetation. In Oriuwaka new growth began in June and was present until January. In Otupaka new vegetation appeared a month later, in July, and finished a month earlier, in December. Some individual trees began growing new leaves in June and others not until September. The new growth comprised a median score of 0.8 (interquartile range= 0.8-1.0) at Oriuwaka and 0.8 (interquartile range= 0.6-1.0) at Otupaka.

Figure 3.1a Vegetation abundance over a 14 month period on two common kereru food species in the two study areas of Whirinaki Forest, kowhai phenology was recorded only in Oriuwaka as it was virtually absent in Otupaka.



The vegetative cover of kowhai changed dramatically over the course of the study period (Fig 3.1a). Throughout autumn and winter kowhai vegetation declined steadily, then fell more dramatically from July until October, when some trees were virtually leafless while others retained a vegetative cover score of more than 4. In November there was a significant burst of new leaf growth which gradually subsided and had changed into mature vegetation by March.

Karamu fruit was present for all but two months of the year in Oriuwaka and three months in Otupaka, during spring (Fig 3.1b). Ripe fruit was available throughout autumn and winter. Immature fruit reached full size over summer and ripened over a long period, with a peak of ripe fruit in late summer/early autumn around February and March. After this peak fruit abundance declined quite rapidly to complete absence in September. Karamu not only fruited asynchronously, but individual trees carried fruit in different stages of ripeness. For the majority of the study, therefore there was both ripe and unripe fruit on individual trees, and this provided ripe fruit for most of the year, with an average score of 0.85 (interquartile range= 0.5-1.25).

Rimu and kahikatea produced very little ripe fruit over the study period (Fig 3.1b) and there was a total absence of fruit during the 1999/2000 season. Immature rimu fruit was visible in Oriuwaka from September and in Otupaka from December, developing slowly over a 6 month period with the first ripe fruit seen in late summer/early autumn. Kahikatea produced modest amounts of unripe fruit towards the end of the study season. Low numbers of immature fruit were present over the summer, with some ripening in Oriuwaka in March.

Miro and maire followed a similar fruiting pattern to each other (Fig 3.1b) with the main fruiting period during autumn. In Oriuwaka, miro fruit developed over the early summer and ripe fruit was present from March – July, peaking in April and in average amounts until May. Ripe maire fruit was available from February with the peak of fruiting in autumn; mature fruits were substantially absent by June. Maire fruit in Otupaka was never plentiful and ripe fruit was present for only two months during autumn. In contrast to the short period during which ripe fruit was available, immature fruit had a long development over summer and the beginning of autumn. In Otupaka, miro fruit was available until the end of winter, individual trees carrying fruits at varying

stages of ripeness and so producing a continuous supply of freshly ripened fruit over this period. Fruit persistence in miro was augmented by a second pulse of later-developing ripe fruit in April on a small proportion of trees. Immature fruit began to appear again in summer. Miro resumed fruiting in Oriuwaka in November and maire resumed fruiting in January. Overall fruiting for both species began a month later in Otupaka than it did in Oriuwaka.

The general pattern of mahoe fruiting was similar to that of miro and maire, the main difference being that fruits ripened rapidly on individual trees, once they reached full-size, and since the fruiting was relatively asynchronous between trees each appearance of ripe fruit was sequential and short-lived (Fig 3.1b). Also, like miro, a mixture of immature and full-sized green fruit seen on some mahoe trees indicated that two cohorts of fruit had been produced. In Otupaka, mahoe fruited over a long period. Ripe fruits were available in moderate amounts at the start of the study and fruiting did not stop until August. Over autumn the number of fruit recorded dropped but small amounts of ripe fruit were still available in June and July. At Oriuwaka ripe fruit was available in relatively larger amounts over a shorter period (March – May), then declined sharply. Fruiting began again in January, with ripe fruit being available in small to medium quantities in March.

Tawa, kotukutuku and makomako all fruited over the summer/early autumn (Fig 3.1b). Prior to this study, makomako had a very heavy fruiting season, which finished in February 2000. Immature fruit then began to develop the following spring (November) and ripen in early summer, but large numbers aborted and this fruiting was not as heavy as the previous year. Fruit was present over a long period and peak abundance of ripe fruit occurred in January/February. Kotukutuku had finished fruiting in Otupaka when the study began, and a small amount of ripe fruit was still available in Oriuwaka. Kotukutuku then fruited from late spring/early summer until the late summer/early autumn period. The final ripening process (from green full-sized fruit to mature) for makomako and kotukutuku appeared to be rapid, particularly among fruits exposed to direct sunlight. Immature kotukutuku fruit was on the trees in Oriuwaka in November and a month later in Otupaka. Ripe fruit peaked in January and February, a month after the first ripe fruit had become available. A small amount of unripe tawa fruit was present in

Oriuwaka in February 2000, but these trees aborted their entire fruit crops before they began to ripen. No tawa fruit was present at this time in Otupaka, but immature fruit was present from September and developed slowly, reaching full size in late spring. Ripe fruit occurred from December and reached a peak in February. Although in Oriuwaka in March ripe fruit was available in moderate amounts, much of this was desiccated. In Otupaka, although total fruit had declined slightly in numbers by the completion of the study, the amount of ripe fruit available had increased.

Putaputaweta fruited only in small amounts over the summer/early autumn period of both years (Fig 3.1b). Ripe fruit was first visible in March and had finished by June in Oriuwaka and May in Otupaka. Fruit was available in greater quantities in Oriuwaka. There was a definite peak in ripe fruit abundance in May, particularly in Otupaka, although this peak was still low compared to some of the other fruiting species such as karamu and miro.

Figure 3.1b Availability of fruit over a 14 month period on some common kereru food species in the two study areas of Whirinaki Forest.

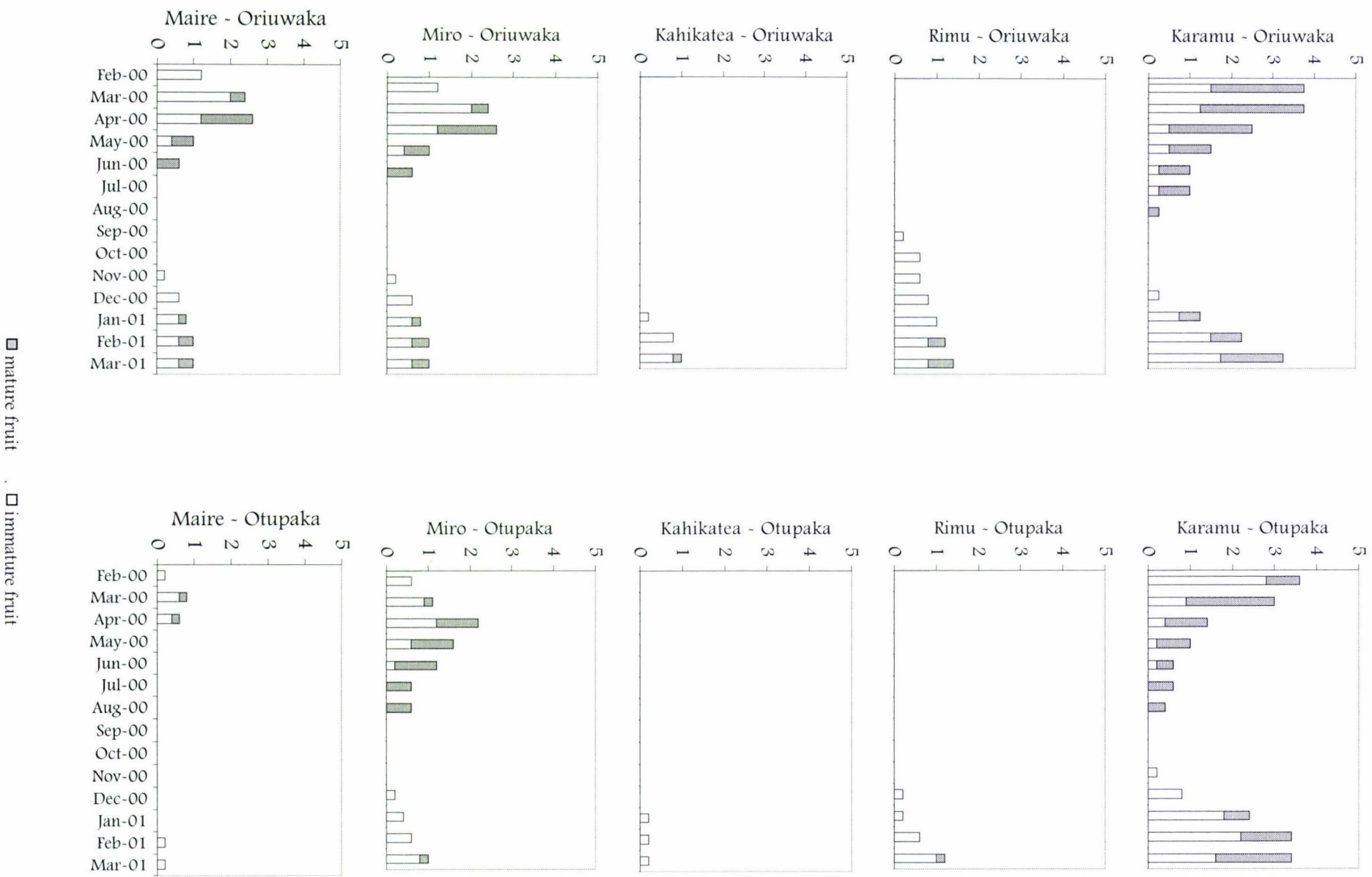
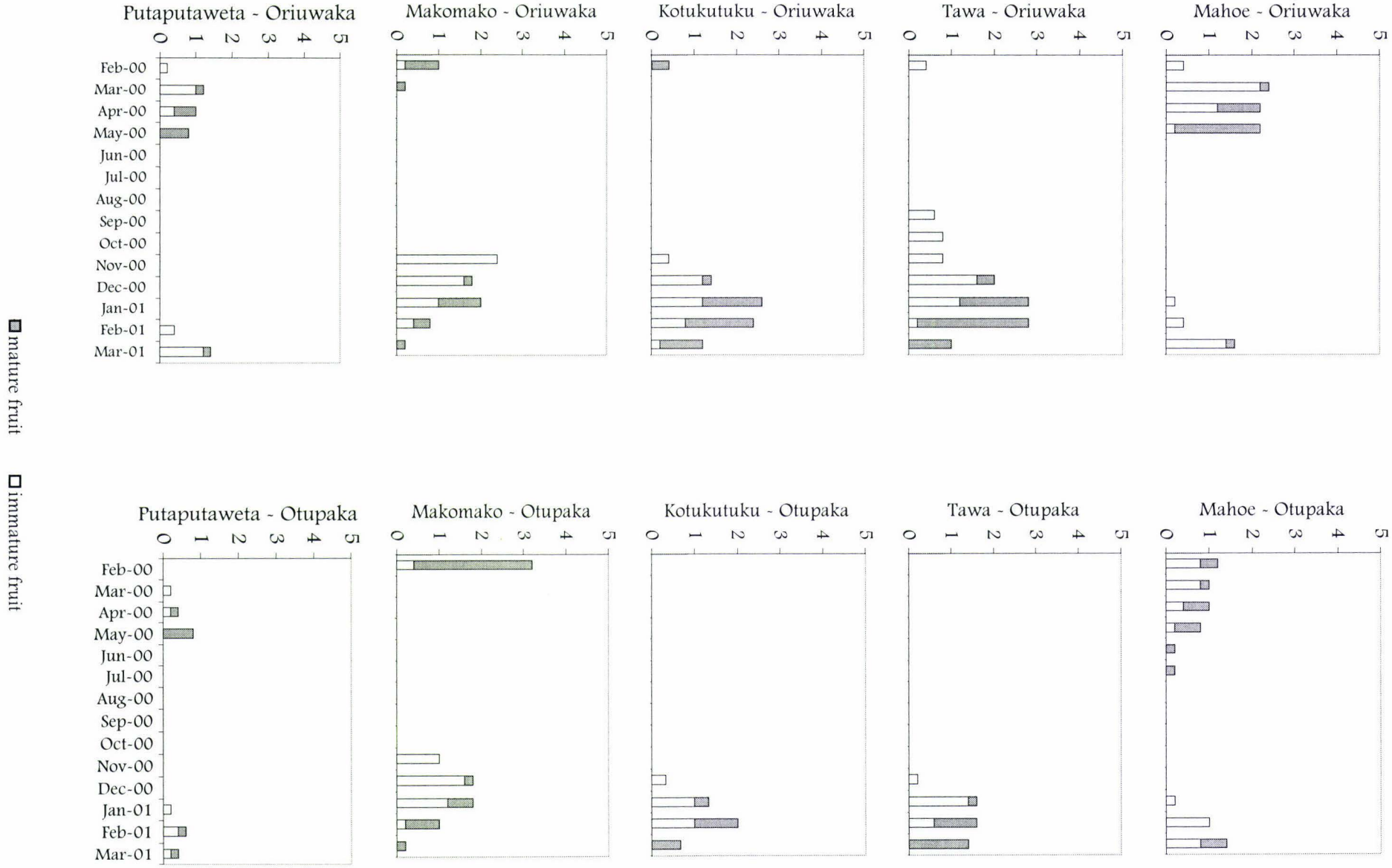


Figure 3.1b continued



3.4.2 Phenology in relation to abiotic factors

All the fruiting species appeared to have some stage of fruit development during the time leading up to the period of highest radiance (November – February). The changes in radiance almost directly reflect the changes in temperature, with the exception of the peak in temperature occurring in February, a month after the peak in radiance. Karamu, miro, maire, mahoe and putaputaweta (Fig 3.2a) all carried less fruit as the amount of radiance decreased. Many species were devoid of fruit over winter and none of them fruited during September and October. The radiance increased over spring and into summer, and by December, the month of peak radiance, all these species had some form of fruit present. Karamu appeared to most closely follow the amount of radiance present, with fruit availability falling with the radiance and increasing to a lesser degree as the amount of radiance increased. The fruit abundance of the other species began to increase towards February 2001. The majority of ripe fruit became available during autumn once the period of highest radiance was finished, but before temperature had dropped significantly.

Makomako, kotukutuku and tawa (Fig 3.2b) behaved a slightly different way in relation to radiance. These species had the bulk of their fruiting a few months before, with peak ripe fruit availability occurring directly after the period of maximum radiance. There was no fruit of any sort on the trees for five months during autumn and winter, which was also the period of lowest radiance and temperature.

As rimu and kahikatea never fully fruited during the study they cannot be accurately described in relation to radiance and temperature.

Figure 3.2a Fruit abundance in relation to radiance for karamu, miro, maire, mahoe and putaputaweta.

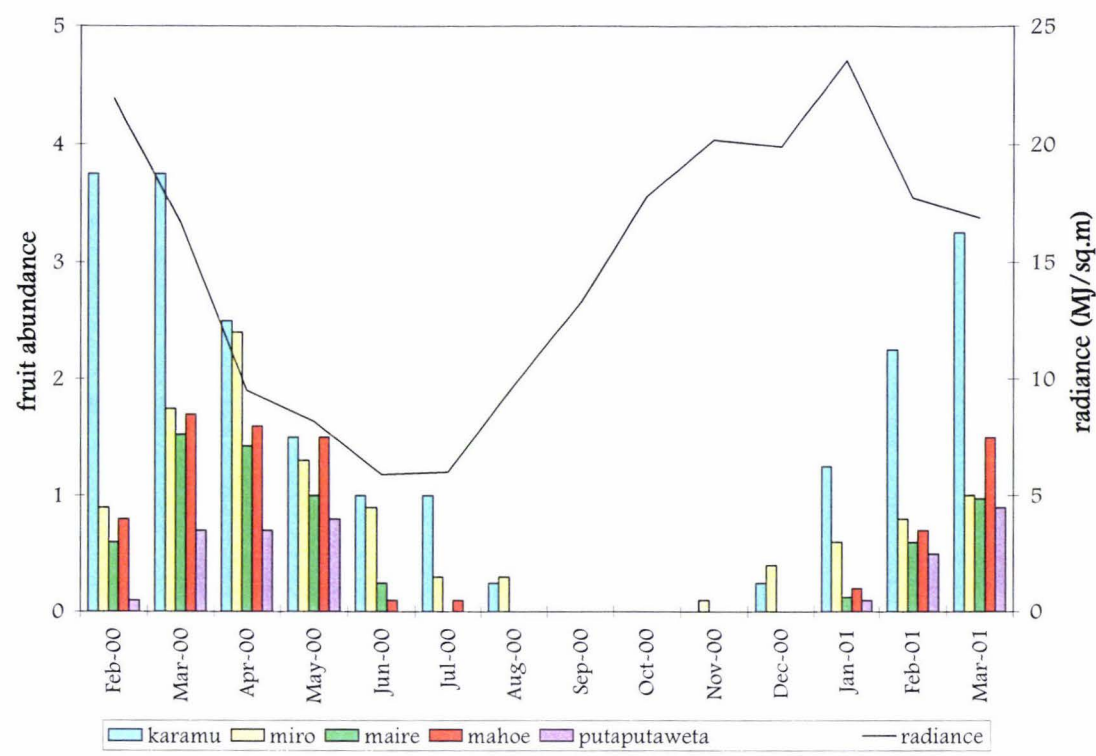
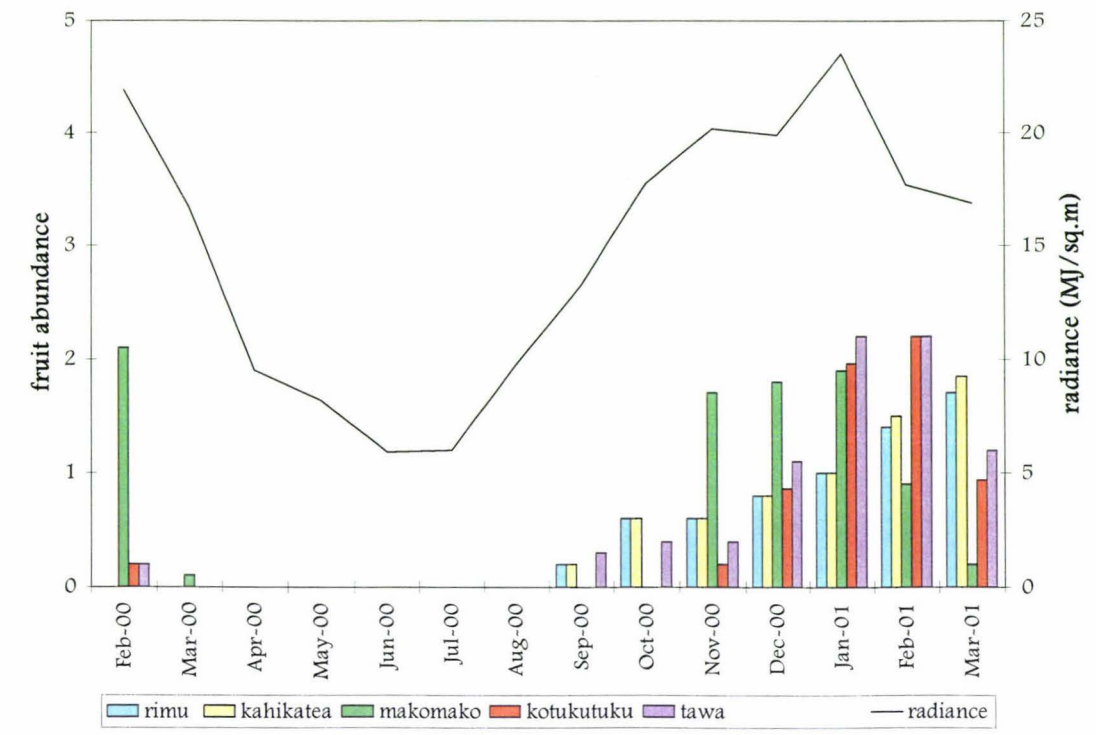


Fig 3.2b Fruit abundance in relation to radiance for rimu, kahikatea, makomako, kotukutuku and tawa.



Partly due to an exceptionally wet December in 2000, the relationship between fruit abundance and rainfall is not quite as clear as that for radiance. For karamu, miro, maire, mahoe and putaputaweta (Fig 3.3a) ripe fruit was available in reasonable quantities after February, coinciding with the increase in rainfall. The abundance of these species (with the exception of karamu) increased along with the increase in rainfall. The fruit abundance for all these species then dropped as the rainfall stayed relatively high. Immature fruit began appearing after a drop in the rainfall, particularly after the relatively dry month of January.

Rainfall could be a factor in the abscising of immature fruit on makomako (Fig 3.3b) during summer. Large numbers of immature fruit were aborted from makomako during December, coinciding with a high peak in rainfall. The period where no species were fruiting coincided with the period of high rainfall. The bulk of the ripe fruit for makomako as well as kotukutuku and tawa was available during and after January, when rainfall lessened. For all species concerned, there was a visible lack of fruit during the rainy season (April 2000 - August 2000).

Over the fourteen months, the rainfall fluctuated repeatedly. The spring/summer of 1998-1999 before the study began had some major fluctuations with a very dry October (0.55mm) leading to a very wet November (9mm) then back down to February (0.33mm). The previous year (1997) had not been so extreme.

Figure 3.3a Fruit abundance in relation to rainfall for karamu, miro, maire, mahoe and putaputaweta.

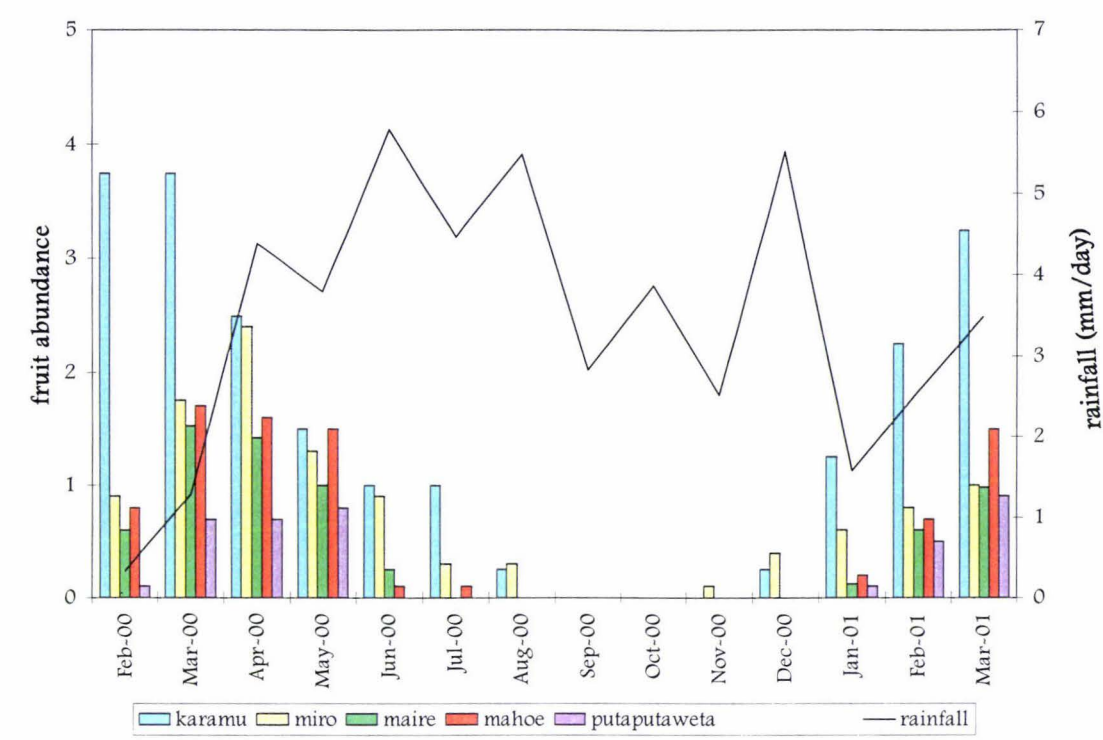
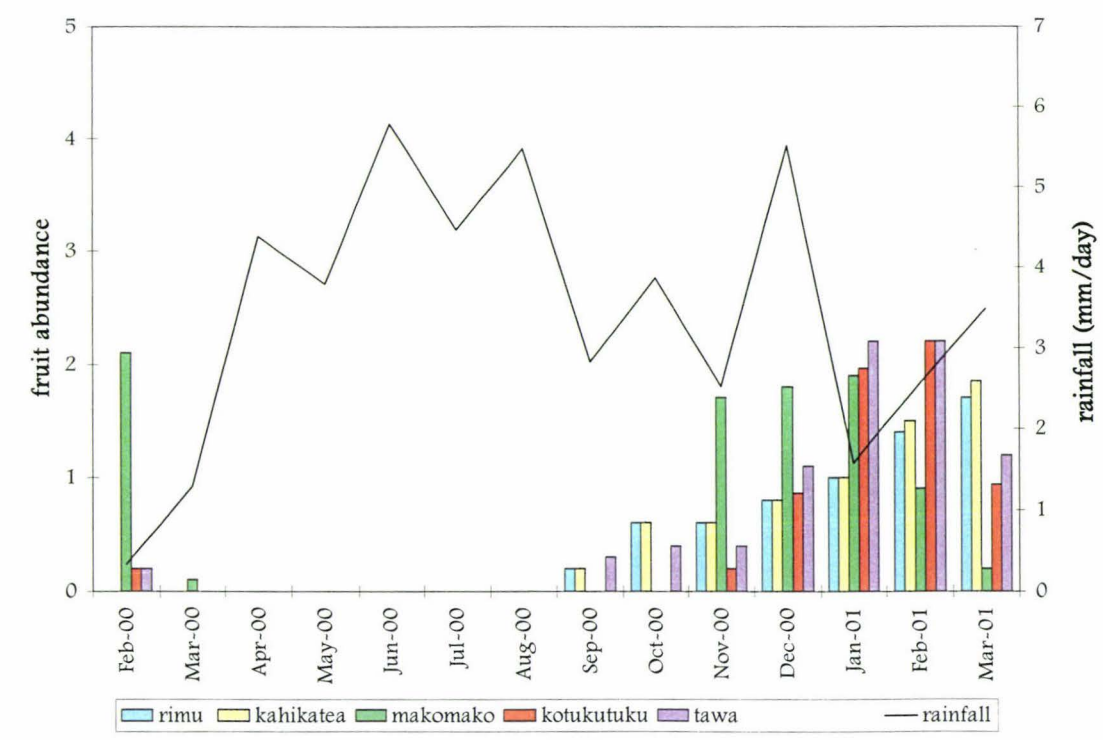


Fig 3.3b Fruit abundance in relation to rainfall for rimu, kahikatea, makomako, kotukutuku and tawa.



Mahoe vegetation was not significantly influenced by abiotic factors as it is not a deciduous species. There was some defoliation and a small amount of leaf fall on mahoe that coincided with a decrease in radiance (Fig 3.4a). The growth of new vegetation occurred on individual trees at some stage between the period of lowest radiance in June and the peak of radiance in January, i.e. during the time that radiance was increasing. Kowhai showed a strong relationship with radiance, with new foliage being produced during the period radiance was at its highest.

The relationship between leaf abundance and rainfall (Fig 3.4b) is less apparent. The slight reduction in vegetation abundance for mahoe coincided with an increase in rainfall. The beginning of kowhai leaf fall did coincide with the period of heaviest rainfall, and continued as rainfall lessened. The erratic nature of rainfall over the 2000/2001 summer meant that any annual pattern was less obvious.

Figure 3.4a Vegetation in relation to radiance for mahoe and kowhai

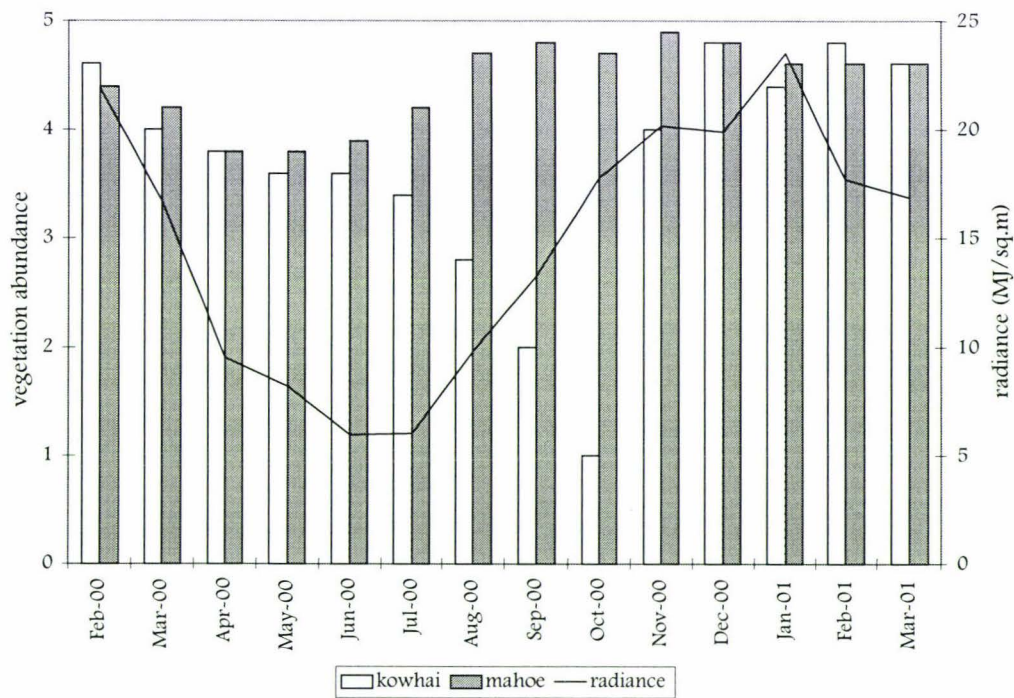
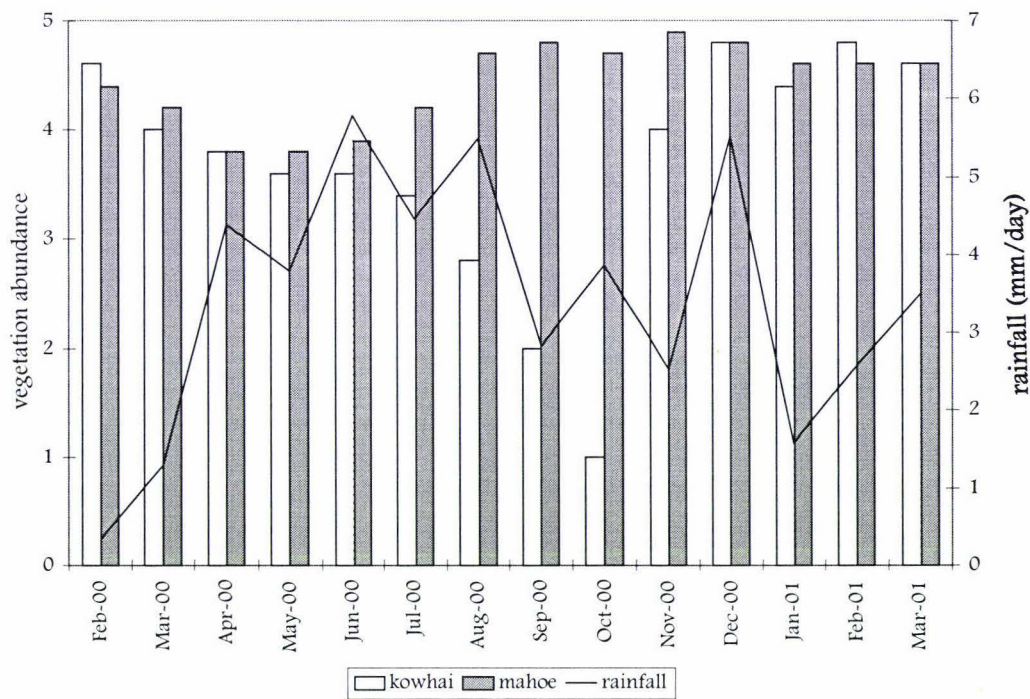


Figure 3.4b Vegetation in relation to rainfall for mahoe and kowhai



3.5 Discussion

Based on observations of the whole study area, the phenology of the eleven selected species appeared to be reasonably representative of fruit abundance in the areas where kereru were most frequently observed. Because of the prevalence of old logging trails, random phenology plots could be placed deep in the two study sites, as well as in more marginal areas. A high proportion of these plots happened to fall in areas of relatively open, less mature forest. This may have influenced the degree of total fruiting of the sub-canopy species because when these species had more access to direct sunlight they appeared to carry a higher fruit load than those in shadier areas (pers. obs.).

Another factor influencing foliage and fruit availability may have been the feeding pressure applied by birds (including kereru) and possums. Although the kereru is the only bird capable of swallowing certain fruit (tawa, miro, maire) whole, other birds and possums would still destroy the fruit by picking the flesh off the seed. Male kaka (females did not have the required beak strength) drastically reduced the numbers of miro fruit on certain trees by picking the fruit while it was green, cracking it open and eating the seed. This

behaviour was noted on four of the monitored trees, one in Oriuwaka and three in Otupaka.

Defoliation by browsing possums was obvious on a number of mahoe, which is one of their preferred browse species (Williams 1982). Severe defoliation was apparent on one of the mahoe in Otupaka and to a lesser degree on one other tree in Otupaka and one in Oriuwaka. Kereru fed on young mahoe leaves to a greater degree at Otupaka, perhaps explaining the lower percentage of new growth in that area. Kowhai are considered to be semi-deciduous, particularly in colder climates (Poole & Adams 1990). However, this could not explain the almost complete defoliation of some kowhai. Kowhai vegetation is eaten heavily during some periods of the year (winter and early summer), predominantly by kereru. This factor, coupled with the semi-deciduous nature of this species, would go further to explaining the absence of leaves.

Most species displayed highly seasonal and synchronous patterns in fruiting. According to when the majority of their ripe fruit was available, the fruiting species monitored at Oriuwaka and Otupaka fell into one of two fruiting groups: summer fruiterers or autumn fruiterers. Makomako, kotukutuku and tawa were all summer fruiterers, although if the trend for tawa was followed fruit would be available into the autumn. Miro, maire, mahoe and putaputaweta were autumn fruiterers. Karamu was predominantly an autumn fruiter, although it continued fruiting into the winter in lesser quantities and was fruiting heavily at the end of the summer when the study began. Kahikatea and rimu did not reach a point in fruiting where they could reliably be allocated to a group.

Most species exhibited annual peaks that collectively were spread across several months. Most of these peaks occurred over autumn, following the November through February period of increased temperatures and solar radiance. Five of eight annual peaks of ripening occurred during this period, compared to the remainder of the year.

Peak fruiting at the end of the hottest season in the study area was similar to patterns observed in tropical forests (Janzen 1976, Bullock & Solis-Magallanes 1990, van Schaik *et al.* 1993, Foster 1996). Fruiting at the end of the hottest, driest season may have evolved to reduce seedling mortality by dispersing seeds

when soil moisture conditions are favourable for seed germination and rapid seedling growth (van Schaik *et al.* 1993). Lack of fruit during the late rainy season has also been seen in other studies (Fredericksen *et al.* 1999, Justiniano & Fredericksen 2000), and may be an adaptation to avoid seedling mortality. The greater proportion of ripe fruit from the group which fruits in summer is available in the late summer, when the rainfall in Whirinaki is already starting to increase, but while the temperature remains relatively high. This could indicate a germination preference for warm damp conditions.

While solar radiance and temperature during the study followed the same basic pattern they had for the past 20 years (according to data obtained from weather stations at the Rotorua Aerodrome and the Wheao Power Station), there were some changes in the year leading up to the study period. Radiance remained consistent with the peaks and troughs being virtually the same. The main difference came from the temperature; the summer of 1999/2000 being, on average, slightly colder than the two summers preceding it. This may have influenced a number of phenological factors, including the setting of fruit for the 2000 year.

Extended fruiting of some species has been observed in other studies (Burrows 1996) and it has been suggested that these long fruiting periods are achieved by extended consecutive flowering followed by consecutive development and ripening of fruit on an individual plant, also differences in fruiting times between individuals within a population. Burrows (1996) notes that ripe fruit could be found on some individual plants for periods exceeding three months. This pattern of continuous fruiting was more apparent in the autumn fruiters.

It has been observed that sub-canopy species are less seasonal than canopy and emergent species in their fruiting and flowering (Justiniano & Fredericksen 2000), perhaps because of reduced variability in solar radiation, soil moisture and relative humidity in the forest understory (Opler *et al.* 1980, van Schaik *et al.* 1993). This could partly explain the fruiting pattern of karamu, although the other sub-canopy species follow patterns similar to that of some emergents.

Results for some species may have been affected by the fact that they are dioecious. Mahoe and karamu fall into this category. An unknown proportion

of non-fruiting trees may have been females. This would result in the score being lower than it may otherwise have been, but still reflects the total availability of fruit in the Whirinaki forest.

It is well known that deciduous trees lose their leaves over the cold, wet season. While mahoe is not a deciduous species, there was still fluctuation in the abundance of mature vegetation, most likely due to predation. New growth was staggered between individual trees by up to three months within each area and four months between the two areas. Studies show that tree species, and individuals within that species, vary in leaf fall and leaf regeneration (Bullock & Solis-Magallanes 1990, Justiniano & Fredericksen 2000). This creates temporal and spatial patchiness within the area that can be advantageous to species feeding on vegetation in one form or another. There was large variability in the leaf fall of kowhai, which can be related to the variability explained by Justiniano & Fredericksen (2000) and also the varying levels of mineral elements that can be found in the foliage of individuals of the same species (Lee & Johnson 1984). This latter factor can be related to leaf predation and palatability.

There were major contrasts in the phenology of rimu, kahikatea, makomako, kotukutuku and tawa between the 1999/2000 fruiting season and the 2000/2001 fruiting season. This variation in the phenology of the timing and abundance of fruit is consistent with what has been seen in other regional studies (e.g. Cowan 1990, James *et al.* 1991). Observations before the start of the study showed that makomako had an exceptional fruiting season in 1999/2000 and kotukutuku also fruited more heavily. Climatic changes could be partly responsible for the aborting of immature fruit on the makomako. The peak in radiance occurred a month later in January 2001 than the previous year when it peaked in December 1999. This could be partly responsible for the peak of fruiting of kotukutuku occurring a month later in the second season.

Tawa can have annual, biennial and masting patterns of fruit production (Knowles and Beveridge 1982, Wright 1984, West 1986, Burrows 1999). Knowles and Beveridge (1982) stated that tawa sets fruit annually but the amount of fruit produced can fluctuate from year to year. Tawa also has

alternate heavy and light fruiting years (Wright 1984, West 1986). Burrows (1999) noted that tawa production in the Marlborough area was low for two years, and then heavier in the third. Rimu and kahikatea are also known to have masting years and it is not unusual for them to produce no fruit in some seasons.

3.6 Conclusions

All fruiting plants had the peak of their ripe fruit availability during the summer/autumn period, after the period of highest radiance, but while temperature was still relatively high and the rainfall was increasing. There was no time of the year in which no fruit was present; however, there was no ripe fruit available from September until December.

Factors influencing availability of fruit and vegetation include climatic changes, location of the plant in its micro- and macro-habitat, predation, and natural fruiting/vegetation strategies such as deciduousness, asynchronous or synchronous fruiting, consecutive fruiting, masting or alternate fruiting years.

The climatic factor that appears to have had the most influence on fruiting in Whirinaki Forest was radiation, which directly affects temperature. The pattern for rainfall was more erratic but high availability of ripe fruit did occur just prior to, and during, the period of increasing rainfall.

Chapter 4

Diet of kereru

4.1 Abstract

The diet of kereru in two study areas in Whirinaki forest was studied using a combination of radio-tagged and untagged birds to investigate food preferences in this area, and the relative importance of different species to Whirinaki kereru. Diet observations were obtained over a fourteen month period in conjunction with phenology observations to enable availability to be measured.

The most important species differed between the two areas, primarily as a result of differing species abundance within the forest. Overall, at different times of year, the most important species to kereru in Whirinaki appear to be miro, tawa, makomako and kowhai. Kereru specialised on these species, but behaved as generalist feeders when the ripe fruit of preferred species was not readily available.

4.2 Introduction

The kereru typically has a more varied diet than that of its tropical and subtropical relatives overseas (Crome 1975a, Innis 1989). Most fruit pigeons are tropical and are able to feed solely on fruit (Poulin *et al.* 1992). When the ancestors of the kereru arrived in New Zealand in the late Tertiary, under climate conditions warmer than now, they would have found forests dominated by angiosperms (Fleming 1962). Eventually the climate cooled to become more temperate and the forests developed distinct seasons and fruit was no longer produced year round. This resulted in the kereru broadening its diet to include leafy material, buds, flowers and shoots as well as fruit when it was available (McEwen 1978).

At the top of the North Island where fruit is available year round, the kereru is a “true” frugivore (Pierce 1993). Studies on the diet of the kereru indicate that fruit remains the preferred food (McEwen 1978, Dunn 1981, Clout 1990,

Langham 1991), but vegetation now composes an important part of the diet of the kereru during winter and spring in most areas of New Zealand. Some literature claims that kereru are “forced to subsist” (Tisdall 1992, Pierce and Graham 1995) on foliage. The diet of the kereru is highly seasonal as it follows the seasonality of the fruit produced (McEwen 1978).

Dudley & Vermeij (1992) proposed that the lack of folivory in most birds was due to the energy constraints imposed by flight (Hill & Smith 1984). They postulated that folivory would impose these constraints by the need to consume a large volume of energy-poor food and also to have a specialised gut to digest the leaves. Kunz & Ingalls (1994) found that in frugivorous bats that also engaged in folivory there would not be high energy constraints imposed and that due to the manner of digestion, folivory would be highly compatible with flight. Several important questions were raised in regards to diet, namely do frugivores feed selectively on the leaves from only a few preferred tree species and do they engage in folivory around the year?

It is widely known that the kereru performs a vital ecological role in New Zealand forests and its role is crucial to maintaining community diversity and forest composition through seed dispersal (Clout & Hay 1989, Lee *et al.* 1991). Many of our native large-fruited tree and shrub species are virtually dependent on the kereru for seed dispersal. To some degree the kereru is thought to specialise on these large-fruited species that may have facilitated co-evolution. By selecting species with larger fruits more calories may be ingested per feeding movement.

There have been numerous studies involving aspects of the foraging and diet of the kereru (McEwen 1978, Clout & Hay 1989, Clout 1990, Clout & Tilley 1992, Pierce 1993, O'Donnell & Dilks 1994, Pierce and Graham 1995). These studies have been primarily conducted in the South Island or in Northland. The present study fills a gap in the knowledge of the kereru feeding ecology in the central North Island.

In this chapter the diet of the kereru is investigated to determine whether the food selected by the birds directly reflects availability, or whether certain food

species are preferred over others. The importance of particular food species to kereru is also discussed.

4.3 Methods

Between February 2000 and March 2001 feeding observations were made on 34 radio-tagged kereru and numerous other kereru, which were untagged and could not be distinguished.

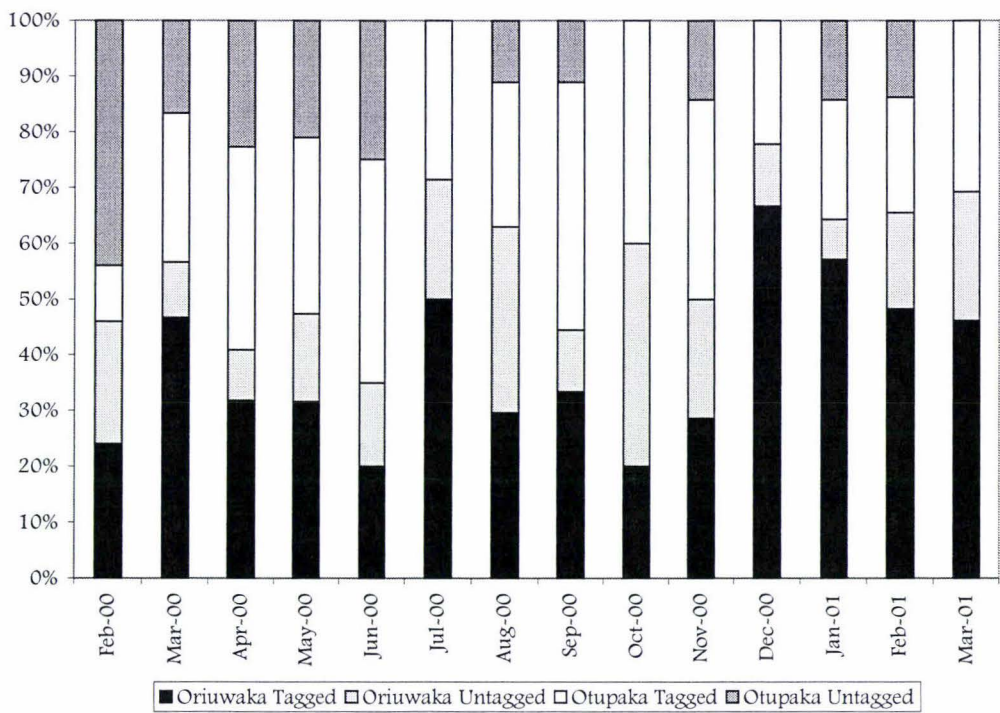
Radio-tagged kereru were caught in 10 cm mesh mist nets erected in the two study sites of Oriuwaka and Otupaka (see Chapter 2). Kereru were brought into the nets by either placing them in known flight paths, or playing a recording of kereru wingbeats that the birds investigated.

Each kereru was weighed, banded (with a numbered metal ring) and marked with pvc-coated nylon leg jesses using unique colour combinations for individual identification. They were then fitted with a Sirtrack transmitter which weighed between 20 and 30 gms and had a battery life of about 20 months. The transmitters were attached to the kereru as 'backpacks' using a weak-link harness (Karl & Clout 1987). Released kereru were subsequently located on foot using a Telonics TR4 receiver and a hand held yagi aerial. If kereru did not release well and remained on the ground (in danger of being preyed on) they were taken to Rainbow Springs in Rotorua for recuperation and later re-released at the capture site.

Radio-tagged kereru were located at least once every 10 days and tracked until a feeding observation was taken. On occasion the kereru would not feed within the 2 hour limit set to follow each individual.

Independent observations were made whenever an untagged kereru was located. If not feeding they were followed as far as possible in attempts to gain a feeding observation. If more than one kereru was using the same food source, an observation from only the first kereru observed was recorded (to maintain independence of observations). The relative proportions of observations obtained from tagged and untagged kereru are seen in Figure 4.1.

Figure 4.1 The proportion of foraging observations recorded from each group of kereru in each area during each month.



Each feeding observation was considered to be continuous unless the kereru spent at least 10 minutes engaged in a non-feeding activity (e.g. roosting or preening). The species and food type recorded was the first food item to be swallowed by the kereru. It was recorded if the kereru moved to feed on a different plant or a different food type on the same plant. Food items were separated into three major categories; fruit, flowers and vegetation. The food types within these categories were: unripe fruit, ripe fruit, leaf bud/young leaf, mature leaf, flower bud, flower. The stage of fruit and vegetation development was determined the same way as described in Chapter 3 (Phenology). Other related details recorded for each observation were: identity of kereru (if radio-tagged) food species, time, date, location.

Differences in diet between months and differences in food type use were tested statistically using contingency tables (χ^2 test) and using the PROC GENMOD command in SAS Version 8.e.

4.4 Results

Diet was examined separately for Oriuwaka and Otupaka due to the difference in food availability and forest composition between these two areas. The diet for the kereru was composed of 22 different plant species. Within these species, the kereru fed on 35 food type/species combinations (Table 4.1). Seven of the species provided only fruit, two provided vegetation and one provided flowers. Six of the species provided both flowers and vegetation or flowers and fruit, five provided vegetation and fruit, and only one (kotukutuku) provided all three food types.

The use of fruit, flowers and vegetation as a food source varied significantly throughout the fourteen months of the study ($\chi^2=1022$, $df=26$, $p<0.001$) in both areas. The proportional composition of the three major food types over the study period was also different between the two areas ($\chi^2=7$, $df=2$, $p<0.05$).

Over the study period the diet of the kereru consisted predominantly of fruit. Of the total feeding observations of kereru at Oriuwaka, 65.4% were of fruit, 26.5% were of vegetation and 8.1% were of flowers. At Otupaka the comparative figures were 86.5%, 7.9% and 5.6% respectively.

In Oriuwaka fruit was consumed in every month of the year (Fig 4.2). The fruit component of the diet did vary markedly throughout the 14 months, from 100% in March, April and May 2000 and February and March 2001 to less than 13% in June and July. Fruit consumption was relatively low throughout winter and spring, from June until December. The central part of the diet in June and July was formed by vegetation and in September by flowers. For the rest of the months in which flowers occurred in the diet, they composed 14 to 43% of the food types eaten.

A greater proportion of the feeding observations of kereru in Otupaka were of fruit. In ten of the fourteen months studied, fruit formed over 70% of the monthly diet (Fig 4.3). Fruit formed 100% of the diet for eight months, mainly over summer and autumn, although fruit consumption was prevalent through winter. With the availability of the various food types changing markedly through the seasons, diet changed accordingly, with flowers and vegetation forming the greater part of the diet in late spring/early summer.

Table 4.1 Diet of the kereru in Whirinaki Forest, comprised of percentages of food species and types in both study areas.

	Oriuwaka				Otupaka				Overall			
	Flower	Fruit	Vegetation	Total	Flower	Fruit	Vegetation	Total	Flower	Fruit	Vegetation	Total
Broom	0.6		0.6	1.2				0.0	0.3		0.3	0.6
Five-finger		0.6		0.6				0.0		0.3		0.3
Kotukutuku	0.6	1.9	1.2	3.7				0.0	0.3	1	0.7	2.0
Hinau				0.0		3.2		3.2		1.4		1.4
Horopito				0.0	2.4			2.4	1			1.0
Houndstongue			0.6	0.6			0.8	0.8			0.7	0.7
Kamahi	0.6	1.2		1.8		0.8		0.8	0.3	1		1.3
Karamu		3.1		3.1	0.8	3.2		4.0	0.3	3.1		3.4
Kowhai	4.3		18.5	22.8			0.8	0.8	2.4		10.8	13.2
Mahoe		0.6	1.9	2.5		4	4.8	8.8		2.1	3.1	5.2
Maire		8	0.6	8.6		3.2		3.2		5.9	0.3	6.2
Matai		1.9		1.9				0.0		1		1.0
Makomako		7.4		7.4		28.6	1.6	30.2		16.7	0.7	17.4
Miro		14.8		14.8		34.9		34.9		23.6		23.6
Mahoe wao	1.2			1.2	2.4	0.8		3.2	1.7	0.3		2.0
NZ Jasmine	0.6		1.2	1.8				0.0	0.3		0.7	1.0
Nikau		0.6		0.6				0.0		0.3		0.3
Putaputaweta		1.2		1.2				0.0		0.7		0.7
Ribbonwood			1.2	1.2				0.0			0.7	0.7
Rimu		0.6		0.6				0.0		0.3		0.3
Supplejack				0.0		0.8		0.8		0.3		0.3
Tawa		23.5	0.6	24.1		7.1		7.1		16.3		16.3
Total	7.9	65.4	26.4	100.0	5.6	86.6	8.0	100.0	6.6	74.3	18.0	100.0

* See appendix for list of common and scientific plant names

Figure 4.2 Monthly trends in the proportional composition of the three major food types in kereru diet in Oriuwaka, expressed as a percentage of feeding observations.

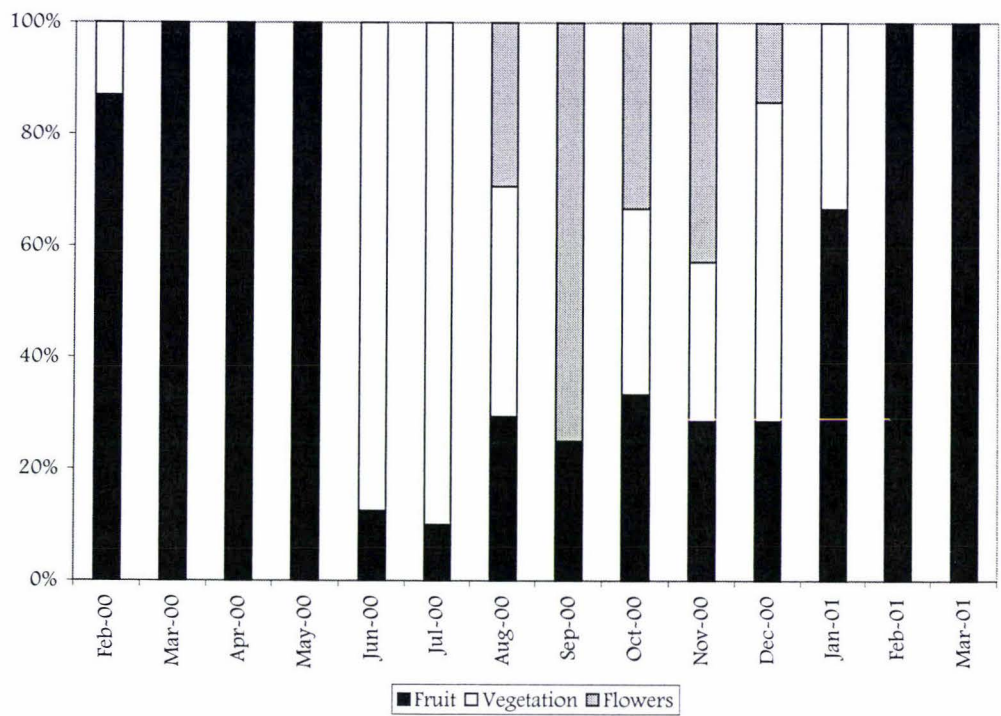
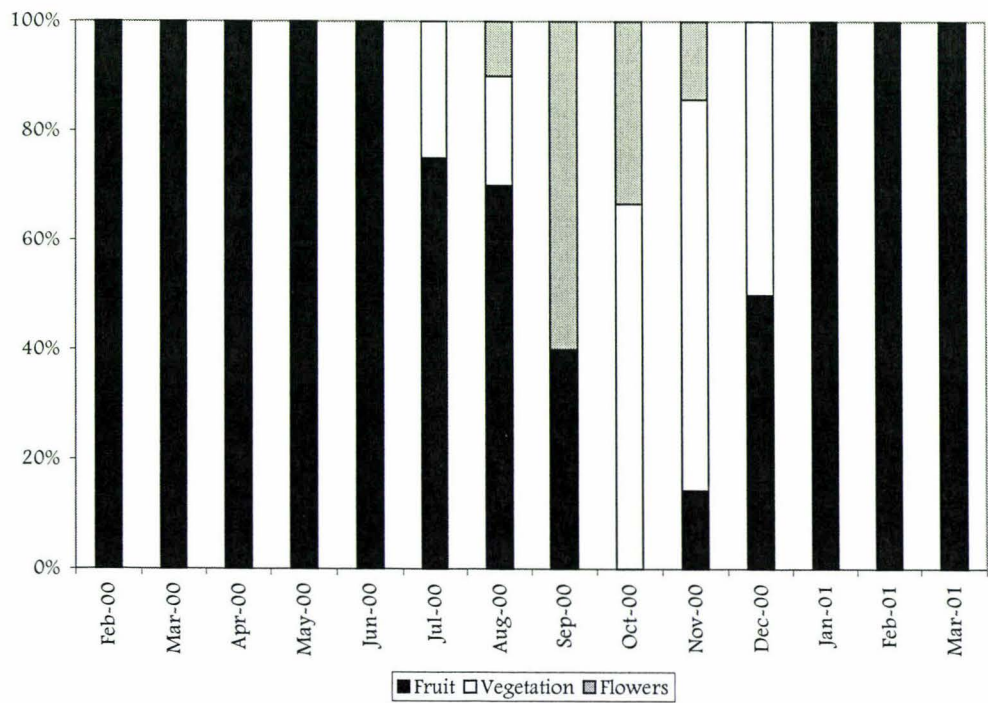


Figure 4.3 Monthly trends in the proportional composition of the three major food types in kereru diet in Otupaka, expressed as a percentage of feeding observations.



The food species in Table 4.2 are listed in order of importance. In Otupaka only two species make up 65.1% of the kereru diet and seven species make up over 90% of the diet. The diet for the kereru in Oriuwaka appears to be a little more varied, with the first two species making up 46.9% of the diet and twelve species composing over 90%. There is quite a difference in ranking between the two study sites, most noticeably due to the virtual absence of kowhai in Otupaka. Miro forms over twice the percentage of feeding observations in Otupaka than it does in Oriuwaka and tawa is over three times more likely to form part of the diet at Oriuwaka than it is in Otupaka. Makomako was over four times more important to the diet at Otupaka.

Table 4.2 Whirinaki food species ranked in order of importance for both study areas, expressed as a percentage of feeding observations.

Oriuwaka		Otupaka		Overall	
Tawa	24.1	Miro	34.9	Miro	23.6
Kowhai	22.8	Makomako	30.2	Makomako	17.4
Miro	14.8	Mahoe	8.8	Tawa	16.3
Maire	8.6	Tawa	7.1	Kowhai	13.2
Makomako	7.4	Karamu	4.0	Maire	6.2
Kotukutuku	3.7	Hinau	3.2	Mahoe	5.2
Karamu	3.1	Maire	3.2	Karamu	3.4
Mahoe	2.5	Mahoe wao	3.2	Kotukutuku	2.0
Matai	1.9	Horopito	2.4	Mahoe wao	2.0
Kamahahi	1.8	Houndstongue	0.8	Hinau	1.4
NZ Jasmine	1.8	Kamahahi	0.8	Kamahahi	1.3
Broom	1.2	Kowhai	0.8	Horopito	1.0
Mahoe wao	1.2	Supplejack	0.8	Matai	1.0
Putaputaweta	1.2	Broom	0.0	NZ Jasmine	1.0
Ribbonwood	1.2	Five-finger	0.0	Houndstongue	0.7
Five-finger	0.6	Kotukutuku	0.0	Putaputaweta	0.7
Houndstongue	0.6	Matai	0.0	Ribbonwood	0.7
Nikau	0.6	NZ Jasmine	0.0	Broom	0.6
Rimu	0.6	Nikau	0.0	Five-finger	0.3
Hinau	0.0	Putaputaweta	0.0	Nikau	0.3
Horopito	0.0	Ribbonwood	0.0	Rimu	0.3
Supplejack	0.0	Rimu	0.0	Supplejack	0.3

The monthly composition of the diet will next be considered on an individual species scale. The generally important food species are graphed individually,

In Oriuwaka (Table 4.3, Fig 4.6), the general diet trend over the fourteen month period starting February 2000 was a combination of fruits with some vegetation; followed by predominantly miro fruit; then kowhai vegetation as a large part of the diet succeeded by kowhai flowers until tawa increased; and finally kowhai foliage once again over December and January 2001.

Table 4.3 Component loadings for principal component analysis for both study areas based on months in which certain food types were eaten.

	Eigenvalue	Difference	Proportion	Cumulative
Oriuwaka Prin1	5.21779017	2.29585895	0.3727	0.3727
Prin2	2.92193122	0.56538944	0.2087	0.5814
Otupaka Prin1	5.66492589	2.36553161	0.4046	0.4046
Prin2	3.29939428	0.71545952	0.2357	0.6403

	Oriuwaka		Otupaka	
	Prin1	Prin2	Prin1	Prin2
Feb-00	-0.18365	0.130265	-0.101678	0.286076
Mar-00	-0.26041	-0.092059	0.401059	0.135337
Apr-00	-0.21734	-0.070415	0.382637	0.086868
May-00	-0.25363	-0.073151	0.403918	0.111234
Jun-00	0.12976	0.493413	0.404425	0.109305
Jul-00	0.1634	0.514718	0.345335	-0.062623
Aug-00	0.26285	0.294563	0.395826	0.001191
Sep-00	0.25441	-0.184119	0.121893	-0.178204
Oct-00	0.3144	-0.246611	-0.048841	-0.343278
Nov-00	0.36652	-0.106366	-0.059165	-0.381598
Dec-00	0.36073	0.232922	-0.048924	-0.336544
Jan-01	0.32279	-0.025399	-0.139676	0.390799
Feb-01	0.26764	-0.318317	-0.135849	0.403554
Mar-01	0.26536	-0.326855	-0.136588	0.374134

In Otupaka (Table 4.3, Fig 4.7) the general dietary pattern starting in February 2000 was for a large component of makomako fruit, rapidly changing to miro fruit (which remained a prominent part of the diet for five to six months). Other fruit and vegetation was eaten around August, and then vegetation (particularly mahoe) and flowers became important components, followed by a karamu fruit and assorted vegetation in December 2000, before the diet became predominantly a mixture of tawa and makomako fruit in January and February 2001.

Figure 4.6 Principal component analysis for Oriuwaka based on months in which food types were eaten, FRT = fruit flesh, VEG = leaf tissue including midrib.

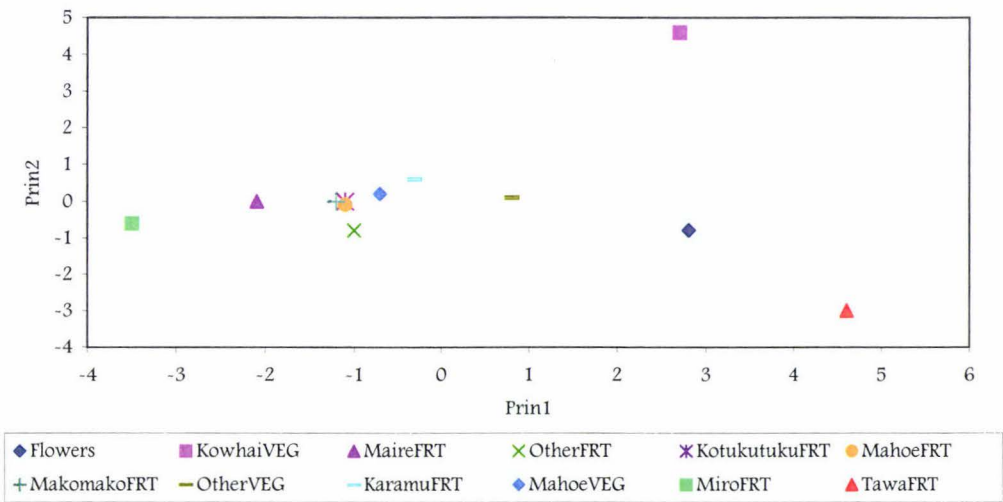
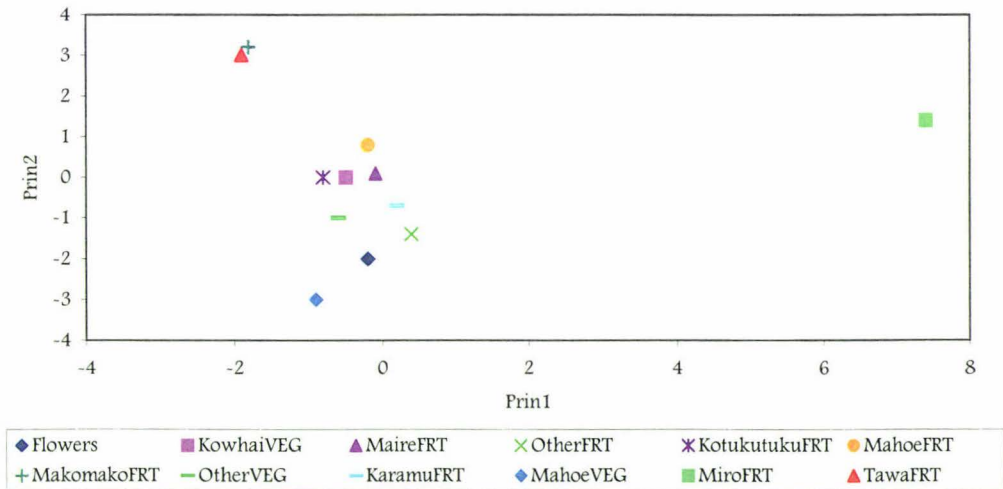


Figure 4.7 Principal component analysis for Otupaka based on months in which food types were eaten, FRT = fruit flesh, VEG = leaf tissue including midrib.



The following changes in diet composition were significant (according to the Proc Genmod procedure in SAS). In Oriuwaka the significant changes in diet ($F=3.01$, $df=2$, $p<0.05$) were from miro fruit to mature kowhai leaves to tawa fruit and flowers/young vegetation to tawa fruit. Miro could be seen to be re-

entering this cycle in March 2001, but the change was not yet significant. In Otupaka the changes in diet were more abrupt and therefore were more significant when tested. These changes ($F=7.32$, $df=2$, $p<0.01$) occurred between makomako and miro, then from miro to foliage and flowers (including mahoe leaves) and finally back to makomako and tawa. Some of the changes remained significant after availability of the food species was taken into account (i.e. were related more to kereru preference than availability). The changes that remained significant in Oriuwaka were (1) the change between February and March 2000 from a mixed diet to one consisting predominantly of miro and; (2) the change between August and October from flowers and foliage to tawa fruit. Excluding tawa, the change from flowers and foliage to kowhai foliage between October and December was also significant. In Otupaka, the two switch-overs that remained significant were from makomako to miro between February and March 2000 and from a mixed diet in December to one of predominantly tawa and makomako in January.

Miro (*Prumnopitys ferruginea*) was the single most important food source during the course of this study (Table 4.2). It was particularly important over the autumn and winter months, from March until June in Oriuwaka and from March until September in Otupaka. During many of these months it formed well over half the diet of the kereru, and it featured again in the diet in Oriuwaka in March 2001. The highest level of miro feeding occurred in Otupaka in June (92.3% of the diet) and in Oriuwaka in April (88.9% of the diet). No miro was eaten in Oriuwaka from July until March in Oriuwaka and in Otupaka miro feeding finished in October and did not begin again by the completion of the study. This coincides with the presence of ripe fruit in the two areas, kereru were very rarely seen feeding on unripe miro fruit. At times there was no miro fruit on the phenology trees but it remained a part of the diet. Kereru actively sought out trees with remaining fruit (pers. obs.). In the early stages of fruiting during 2000, kereru found the ripe miro fruit which was present. In 2001 miro was not such a prominent component of the diet although the quantity of ripe fruit available was similar. The probable reason for this difference was the presence of tawa fruit over the 2000/2001 season. A notable feature of miro was the supply of ripe fruit in both areas for a six month period. This gradual ripening of miro on individual and separate trees appeared to be of great value to kereru because it constituted a long term food supply over the colder autumn and winter months.

Makomako (*Aristotelia serrata*) was a commonly eaten fruit when available. It was available in large amounts in Otupaka in February 2000 and correspondingly formed 88.9% of the diet in this area. In Oriuwaka the berries had begun to decrease in abundance and formed only 21.7% of the diet. It appears that in March 2000 in Otupaka, and April 2000 in Oriuwaka the kereru searched for any remaining berries that did not feature in the phenology plots (therefore were not commonly available) yet appeared in the diet. The percentage of fruit found in the diet approximately followed availability over the ensuing summer, more prominently in Otupaka, peaking at 60% of the total diet. This difference in proportion of makomako in the diet of the kereru inhabiting the two areas could be explained by the greater presence of tawa and its resulting fruit availability in Oriuwaka.

Tawa (*Beilschmiedia tawa*) fruit was eaten in Oriuwaka from August, despite there being no ripe fruit available on the phenology trees. Kereru took ripe tawa fruit, but no unripe fruit was taken during the feeding observations. Tawa formed a dominant part of the diet in Oriuwaka, peaking at 89.5% of the total diet in February 2001. Tawa was a common food species while remaining uncommon in the forest, which indicates that kereru sought out any available ripe tawa fruit, such as that on trees that fruited earlier than others. Tawa consumption in Otupaka tended to follow the general availability of ripe fruit, although there was a decrease in the amount of tawa fruit eaten in February 2001, which coincided with a peak in makomako availability and consequent feeding on makomako in this area. At Otupaka makomako was a far more common species than tawa, so was more readily available. At Oriuwaka, however, tawa was the more prevalent species.

Kowhai (*Sophora tetraptera*) vegetation was fed on in Oriuwaka but was virtually absent in Otupaka where it featured in August as 10% of the total diet. This recording was because of a radio-tagged kereru found feeding along the Whaeo River, 3 km west of the study site. In Oriuwaka the diet comprised 13 - 87.5% kowhai vegetation during two main periods, one from June until August 2000 and one from November 2000 until January 2001. Kowhai vegetation was also a part of the diet (13%) in February 2000. During June, July and August kowhai formed a large part of kereru diet, which may have resulted from the lack of fruit in Oriuwaka during this time, and lead to a noticeable decline in the abundance of kowhai vegetation after this period. In July the diet

was 80% all vegetation (60% of which was kowhai) and in August it was composed of 64.7% vegetation and flowers (29.4% of which was kowhai vegetation). When the new vegetative growth appeared in November 2000, kowhai again became an important food species. In December 42.9% of feeding observations in Oriuwaka were on kowhai. The kereru could be seen selectively plucking the young, immature vegetation throughout the period this new growth was available.

Maire (*Nestegis lanceolata*) fruit did not form a large part of the diet in Otupaka - 7.7% in March 2000 and 23.1% in April 2000. However, these were the only two months that maire was available in Otupaka. They were also the months that ripe miro fruit was readily available. Miro is also a more locally common species than maire in Otupaka. In Oriuwaka maire is more widespread and accessible, and formed the greatest part of the diet (34.8%) in February 2000 when maire availability was low. This difference indicates that maire was actively selected and not just eaten because it was easily attainable or the values for availability and consumption would match each other more closely. In April, when ripe miro fruit availability peaked, along with the percentage of kereru feeding on the ripe miro fruit, maire did not form part of the diet. It was, however, eaten again in May, when the abundance of ripe miro fruit had decreased. Although ripe maire fruit was available in Oriuwaka in February and March 2001, there were no feeding observations made on it, and as already mentioned with other species this could have been due to the availability of tawa fruit over this period.

Mahoe (*Melicytus ramiflorus*) fruit formed only 11.1% of the diet in Oriuwaka in the month of May. This coincided with the peak in availability for this area. As this was the only time kereru in Oriuwaka fed on ripe mahoe fruit it may have been an issue of convenience rather than mahoe fruit being a particularly desirable food source. The period of availability for mahoe fruit overlapped that of miro, which was a preferred part of the kereru diet. In Otupaka the pattern of feeding on ripe mahoe fruit was rather erratic, with it forming small parts (10% or less) of the diet in March, May, June and August 2000. This period was also the same as the presence of miro fruit in Otupaka. Over this time kereru may have fed on mahoe if it was readily available but did not seek it out as they did other species. In Otupaka over January and February 2001 ripe mahoe fruit formed 20 and 10% of the diet respectively. During this time

kereru were also feeding on tawa and makomako fruit. Mahoe was relatively common in Otupaka and it also fruited in cohorts, so that ripe fruit were available over an extended period. Mahoe appeared to be an important fruit for kereru to fall back on when a more preferred species was presently unobtainable.

Mahoe vegetation provided a far greater proportion of the diet in Otupaka than it did in Oriuwaka. In Oriuwaka, where kowhai vegetation was also readily available, mahoe leaves formed only 10 and 5.9% of the total diet in July and August respectively. In Otupaka, however, mahoe vegetation formed up to 57.1% of the diet in November. With the exception of one observation of a kereru feeding on pieces of mature leaf (February 2000), the period of mahoe vegetation forming part of the diet in Otupaka corresponded with the period of availability of young vegetation. This was also a period of general low fruit abundance. 86% of the feeding observations on mahoe vegetation in Otupaka were of the kereru selectively plucking young leaves and leaf buds. Occasionally part of a mature leaf was plucked, and was swallowed if small enough, but more commonly they were dropped and not consumed. In Oriuwaka, the kereru fed exclusively on young vegetation during the period when the new growth had only just begun, and directly before ripe tawa fruit became readily available. Other vegetation and mature kowhai leaf was also eaten at this time.

Ripe karamu (*Coprosma robusta*) was available for most of the year in both study sites. It was eaten during three months in Oriuwaka and Otupaka and the month it formed part of the diet in both areas was August. During August in Oriuwaka it was the only fruit available and consequently the only fruit eaten. Karamu fruit was mainly eaten when other fruit species were not readily available. As karamu fruits asynchronously, has fruit in different stages of ripeness within each individual tree, and is a common species, it produces the most commonly available fruit in the forest. Despite this karamu did not feature strongly in the diet of the kereru, especially when compared to the more seasonal availability of tawa and miro fruit.

Kotukutuku (*Fuchsia excorticata*) was only eaten in Oriuwaka in February 2000 when it formed 13% of the diet. It had already ceased fruiting in Otupaka at the start of the study. Although ripe fruit was present from December until the

completion of the study, no more kereru were observed feeding on the fruit. During the time of fruit availability for Kotukutuku, kereru predominantly fed on tawa in Oriuwaka, and on tawa and makomako in Otupaka.

Other fruits each formed 3.2% or less of the total diet over the fourteen months. This group consists of hinau (*Eleocarpus dentatus*), kamahi (*Weinmannia racemosa*), five-finger (*Pseudopanax arboreus*), matai (*Prumnopitys taxifolia*), nikau (*Rhopalostylis sapida*), putaputaweta (*Carpodetus serratus*), rimu (*Dacrydium cupressinum*) and mahoe wao (*Melicactus lanceolatus*). Of these species, kamahi was the only one eaten in both study areas. Hinau was the most commonly eaten of the group and along with mahoe wao were the only other species eaten at Otupaka. The remaining species were recorded in feeding observations at Oriuwaka. These fruits were eaten during January 2001 and March of both years. In Otupaka they were evenly spread throughout the year.

The other vegetation eaten comprised of the leaves of already mentioned kotukutuku, maire, tawa and makomako; as well as broom (*Carmichaelia aligera*), houndstongue fern (*Phymatosorus pustulatus*), New Zealand jasmine (*Parsonsia heterophylla*) and ribbonwood (*Plagianthus regius*). Houndstongue was the only species consumed in both areas. The only other species from this group consumed in Otupaka was makomako. All of these species individually contributed between 0.6 and 1.4% to the diet of the two areas.

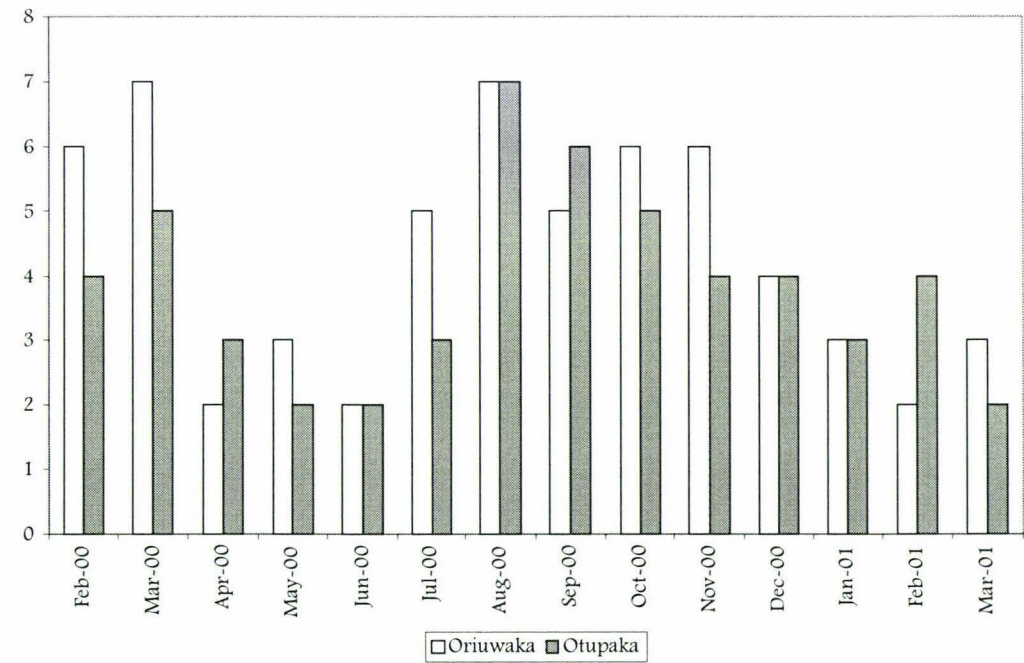
The flowers of eight plants - broom, kotukutuku, karamu, kowhai, kamahi, New Zealand jasmine, mahoe wao and horopito (*Pseudowintera colorata*) formed part of the diet of the kereru. Of these kowhai flowers were the most common item in the diet in Oriuwaka, and horopito and mahoe wao flowers in Otupaka. The other species whose flowers were eaten in Otupaka was karamu. Mahoe wao flowers were consumed in both areas. The other species were recorded in feeding observations in Oriuwaka. Flowers were a prominent part of the diet from August until November in Otupaka and December in Oriuwaka, basically over the entire period of availability. Flowers were more commonly eaten in Oriuwaka.

The fruit composition of the diet varied markedly from month to month. The difference in the fruit composition of the diet between the study sites, between

seasons and throughout the study period was significant (χ^2 test, in all cases $p<0.001$). The composition of the vegetative and flower sections of the diet were also significantly different (χ^2 test, in all cases $p<0.01$) between the above mentioned variables.

Overall the number of different species used as food sources by the kereru differed significantly over the fourteen months ($\chi^2=1.9$, $df=13$, $p<0.001$) (Fig 4.8). During times when the kereru were concentrating on a food source, such as miro (April-July 2000) or tawa (January-March 2001), there was less variation in their diet. The broadest range of diet species was found in the months before miro started fruiting (i.e. during the season that tawa did not fruit) and during the period when miro fruit was declining in abundance and tawa fruit had not yet become frequent. During this period the diet comprised more vegetation and flowers.

Figure 4.8 The variations in the number of species on which foraging observations were made each month in the two study areas.



4.5 Discussion

The results show that kereru specialise on fruit although they are more generalist feeders when compared to their close relatives overseas (Crome 1975a, Innis 1989). In the present study kereru exhibited a general preference for fruit, and would feed on certain species almost exclusively when available. Food preferences were indicated by the exploitation of specific species when the fruit abundance of that species was low, to the exclusion of other species which had high fruit abundance. Kereru had quite frequent opportunity to select amongst the ripe fruit of different species, for example during some months (especially in late summer/early autumn) there were between six and ten species producing ripe fruit. Despite this, in most months when fruit was consumed, between one and three species were eaten. The maximum number of different fruit species consumed was five in March 2000 in Oriuwaka. In March 2001 at Oriuwaka, ten of the species whose phenology was recorded (Chapter 4) were producing ripe fruit, yet the kereru were feeding on only two of those species. In the same month at Otupaka, eight of the phenology species could provide the kereru with a fruit supply, yet the kereru were seen feeding only on tawa and makomako fruit. This certainly indicates a preference for these fruits.

Karamu fruit was not eaten in quantities that reflected its widespread and heavily laden nature. This agrees with what was found in previous studies, where karamu fruit was not a highly sought after food source (Dunn 1981, Tisdall 1992, Baker 1999), but karamu foliage was an important food source. Dunn (1981) found that the foliage of *Coprosma* species made up almost 70% of the diet in October when all fruit supplies were exhausted. In Whirinaki, kowhai and mahoe foliage is the preferred browse for kereru and no feeding observations were made on any *Coprosma* vegetation. Karamu fruit was mainly eaten during periods of low availability, or complete absence of, other fruit species. In Oriuwaka it was predominantly eaten along with leaves and flowers, and still remained a smaller component of the diet. Karamu was the only species of *Coprosma* eaten by kereru in Whirinaki and there the birds never ate foliage, only fruit.

Tawa is certainly a preferred food for kereru. The difference in diet composition between the season where there was no tawa fruit and the season where tawa fruit is plentiful is significant ($F=3.02$, $df=2$, $p<0.001$). In Oriuwaka the difference is the most dramatic, most likely due to the greater abundance of tawa in the forest and the more plentiful amounts of ripe fruit. Comparing the overlapping months of February and March, when tawa fruit was available; karamu, maire, Kotukutuku and leaves were not part of the diet in 2001, and far less miro and makomako was consumed. The number of species eaten went from six and seven in February and March 2000 to two and three during the same months in 2001 (Fig 4.8). In Otupaka, two other favoured species, makomako and miro were available in 2000, so although fewer species were eaten when tawa was available, the numbers are not so influential. Four species were eaten during both Februaries while five were eaten in March 2000 and only two in March 2001. Less makomako was eaten in 2001, although this could reflect the fall in availability between years. Miro was eaten in smaller quantities while abundance had remained the same between the years. Even when no fruit was present on the monitored tawa trees, feeding observations on ripe fruit were recorded, indicating that kereru were seeking out the few trees which were fruiting in order to access the available fruit. These factors show a definite preference for tawa fruit.

Miro was eaten in large amounts while it was available, more so in Otupaka where it was more abundant. Transient kereru flew into Otupaka while the miro was fruiting to utilise the abundant supply (pers. obs.). Plants with fruiting seasons that occur during annual periods of scarcity are particularly important in sustaining populations (Anderson 1997). When these seasons also coincide with the harshest physical period for the frugivore these resources would become even more important. Miro fruit provided the main food supply for kereru over winter, making it a valuable resource.

Other fruiting species did not appear to have the same importance to kereru. Some species, such as mahoe, maire and kotukutuku, were eaten when easily obtainable but were not as sought after as tawa and mahoe. Anderson (1997) found that during periods when there were few high reward resources available or these were restricted in area, birds utilised lower value resources. Fruit not commonly eaten in great amounts, even when readily available, could fall into

this category, and were essential in terms of helping to create a continual, if varied, food supply.

Vegetation formed an important part of the diet of kereru, more so in Oriuwaka, where it formed 26.5% of the diet, than in Otupaka, where only 7.9% of the diet comprised leaves. Kereru fed selectively on the leaves from only a few preferred species, kowhai and mahoe being the dominant two. Kowhai appears to have two functions in the kereru diet. Over the winter months it appears to be a subsistence food, filling in the gaps while no fruit is available. It forms a larger component of the diet than any other species during this time. The other time kowhai appears in the diet, kereru appear to have a slight preference for folivory. Although tawa fruit is available, as are other species such as kotukutuku and makomako that are known to be eaten by kereru, many feed on the young kowhai vegetation, some to the complete exclusion of fruit. Young kowhai foliage was eaten during all the months it was readily available. Foliage contains high protein levels (Williams 1982, Nelson *et al.* 2000) and protein is important for all forms of growth (Fisher 1972, Payne 1972), including the development of eggs, the growth of young birds and the growth of new feathers during moult (Poulin *et al.* 1992). The period in which kereru feed on young kowhai vegetation coincides with the kereru breeding season and the period of greatest moult (Higgins & Davies 1996). This indicates that during some periods of the year, certain foliage may be more than a forced diet and may be carefully selected to meet the nutritional needs of kereru. In Otupaka, young mahoe leaves fulfil this function, as they are also eaten during the early breeding season. Vegetation does not form such a large part of kereru diet in Otupaka, probably due to the longer fruiting season of miro in this area. Therefore, if certain fruits are available, they will be taken in preference to foliage at certain times of year, but during other periods of the kereru lifecycle, leaves could be considered a favoured food source.

Apart from the instances already mentioned regarding the young vegetation, fruit tended to dominate the diet whenever it was available. There were distinct changes in the composition of the diet as the availability of the different food species changed. The changes which were statistically significant implied that these switches in food species were not simply related to availability, but to a definite feeding preference of kereru. This indicates once again that miro, tawa and young kowhai are important food species. Clearly resource utilisation is

influenced by the relative availability of resources. The key periods of change in the diet of kereru differed between the two study areas. This is because these changes were based on the availability of the different resources and the phenology of the two areas was staggered due to the higher elevation and therefore colder temperatures of Otupaka. The forest composition also affected diet as in some areas species were profuse and in others they were rare. Hinau was an important kereru food species in Otupaka, yet was not prevalent in Oriuwaka and did not feature in the diet of the kereru residing in that area. Tawa and kowhai are more common in Oriuwaka and miro and makomako are more common in Otupaka and the importance of these species in the diet of the kereru illustrates this difference. So to some extent the diet is reflecting the availability of the food trees in different parts of the forest.

Due to the unpredictability of food resources in a temperate climate (Banack 1998) frugivorous animals in this environment would be expected to be able to diversify their diet as required. Kereru behave as both fruit specialists and generalists throughout the year. While a main fruit source is readily available they will feed only on that source, individual kereru were seen feeding solely on miro for a period of three months. They also specialise on tawa fruit. Kereru appear to adopt a more generalist attitude towards the smaller fruited species, makomako being the only species which was eaten repeatedly over an extended period of time. Other small seeded fruits were only eaten in conjunction with other species. This may be a result of the availability of one species coinciding with availability of numerous other fruiting species. However ripe tawa fruit was available at the same time as nine other monitored species yet was still preferentially selected. During the periods of high miro and tawa fruit availability, the number of different species consumed was reduced (Fig 4.8), but when a preferred food species was not readily available kereru became generalist feeders, taking a greater number of different species in a combination of fruit, vegetation and flowers; although within these food types there remained species which were eaten preferentially. Among frugivores, this sort of differential use of food sources has been shown in fruit pigeons (Crome 1975a), some species of tanagers and honeycreepers (Snow & Snow 1971) and in three species of saltators (Jenkins 1969).

4.6 Conclusions

In the Whirinaki Forest tawa and miro form a large part of kereru diet, as does makomako and kowhai vegetation. These species are eaten in amounts outweighing their availability, indicating certain positive selection. Kowhai features strongly in the diet during two distinct periods of the year as foliage and flowers, indicating a separate function in the diet for each of the periods. Some species, e.g. karamu, are not eaten in amounts relative to their availability, suggesting negative preference to these species. Other small-seeded fruits are eaten when available but do not seem to have the same attraction to kereru as the large-fruited species.

The change in kereru diet over the year is clearly related to fruit availability, including not only fruit production of individual trees, but the abundance of tree species in the forest. These factors influence the relative importance of the main diet species in the two study areas. Diet is also strongly influenced by kereru preference for certain species.

Kereru specialise on certain fruit when they are available, sometimes feeding solely on a single species. Although kereru feed on the foliage of some species to a large extent, this vegetation is always eaten in conjunction with other food types and species. Kereru feed on a greater range on species and food types when these preferred foods are not present.

Chapter 5

Feeding ecology of kereru

5.1 Abstract

Between February 2000 and March 2001 aspects of kereru feeding ecology were observed in different forest types within Whirinaki Forest. Observations were made on habitat and microhabitat use by foraging kereru, and on their feeding rates. Diet was related to the habitat in which the kereru foraged. The growth form of the trees, and of fruit and foliage on the trees affected microhabitat use, as well as the bird's range during a feeding bout. Kereru foraged mostly in the canopy, where the fruit was mainly available. Feeding rate was inversely related to fruit size and the kereru gained more food per feeding bout from larger fruit. The total food gained per bout differed between plant species, but the foraging bout length remained similar between plant species. Kereru spent substantially longer foraging on foliage than on fruit. It is likely that some of the foraging by kereru is shaped by the risk of predation by raptors. Ripe fruit was taken over both unripe fruit and vegetation, and young foliage was taken preferentially before mature leaves. Kereru generally feed alone but will feed near other kereru when the resource in question is highly sought after. Accessibility of trees in the forest and food on the trees is likely the main force behind many aspects of feeding ecology.

5.2 Introduction

Physical constraints such as tree structure (accessibility of fruit) and seed load, imposed upon frugivores by the plant species can result in diet selectivity in frugivore/plant relationships (Moermond & Denslow 1983). Seed load per fruit is argued to be influenced by the method of dispersal of the species (Ridley 1930, Uma Shaanker *et al.* 1988). Frugivores are said to generally prefer few-seeded fruits that have a high pulp to seed ratio (Howe & Vande Kerckhove 1981, Herrera 1981). However the selection criteria can differ among species (Herrera 1981, Jordano 1984, Martin 1985). Other studies have shown that the seed load is not a significant factor in fruit selection, but accessibility and

ease of harvesting is (Pough & Andrews 1985, Foster 1990, Hedge *et al.* 1991). Size of fruit may be an issue in kereru fruit choice. Gibb (1970) observed kereru feeding in a plum tree and noted that only a small proportion of the fruit was of a suitable size and accessible to the bird, so food that appears plentiful may not be available as a resource for frugivores.

Many studies have shown that frugivores exhibit a general preference for ripe over unripe fruit (Foster 1977, Beehler 1983, Moermond & Denslow 1983, Poulin *et al.* 1992). Foster (1977) showed that long-tailed manakins will only feed on unripe fruit during times of food shortage and they gain only 15% of the nutritional value that they would from ripe fruit, their preferred choice. Kunz & Ingalls (1994) reported that ripe and unripe fruit and foliage all have similar nutritional characteristics so there must be other reasons for avoidance of these so called 'famine' foods. A further question on folivory raised by Kunz & Ingalls (1994) is whether frugivores choose leaves with certain characteristics on a particular tree species (e.g. young or mature).

Numerous studies have investigated aspects of the foraging and diet of the kereru (McEwen 1978, Clout & Hay 1989, Clout 1990, Clout & Tilley 1992, Pierce 1993, O'Donnell & Dilks 1994). However none performed a thorough investigation of the feeding ecology of kereru in an area offering the variety of forest types found in Whirinaki. The feeding behaviour of kereru in tall podocarp forest at Whirinaki is examined to better understand of the diet, and whether the feeding of kereru is influenced by factors such as tree structure and seed load.

5.3 Methods

Observations on the feeding ecology of 34 radio-tagged kereru and an unknown number of untagged kereru within Whirinaki Forest were made between February 2000 and March 2001. Observations were made from the ground using focal animal sampling (Martin & Bateson 1995) with the aid of 10x50 binoculars. Further details of basic methods are provided in Chapter 4.

During each feeding observation, the following details were recorded: time, location, identity of the kereru (if radio tagged), forest type, canopy height, food

species and food type, height of food tree, dominant plant species, foraging level, foraging height, feeding station, feeding rate, number of other kereru in vicinity.

Each of these feeding microhabitat measurements was taken using instantaneous sampling every minute of the feeding bout.

Canopy height and the height of the food tree were estimated in metres. Food species and food types were classified as in Chapter 4. The dominant plant species was recorded if one species composed more than 25% of the vegetation within a 15 metre radius. Foraging height was estimated as the height from ground level in metres to the kereru within the food tree. When recording foraging height, the effect of the kereru depressing branch height was corrected as this resulted from a horizontal movement towards the outer branch, not a vertical movement. Standardisation for tree height used the known average height for that species (Salmon 1986). The percentage of food trees in each height class was obtained from the estimates of the height of each food tree.

The categories used for forest type, foraging level and feeding station are listed below (Table 5.1).

Table 5.1 Categories for forest type, foraging level and feeding station at Whirinaki forest (see text for details).

Forest type	Foraging level	Feeding station
dense lowland podocarp (DLP)	emergent	trunk
mixed podocarp-hardwood with tawa (MPH-T)	unshaded canopy	inner branch
mixed podocarp-hardwood with kamahi (MPH-K)	shaded canopy	centre branch
podocarp beech (B)	upper understorey	outer branch
hardwood 'nursery' scrub within native forest (HNS-N)	lower understorey	
hardwood 'nursery' scrub within exotic pine forest (HNS-E)		

Classifications for forest type were adapted from Nicholls (1966) and Morton *et al* (1984). The approximate quantity of each forest type was estimated from these forest maps, and personal observation.

The foraging level was the level at which the kereru was situated. For example, a bird may have been foraging low in an emergent tree, so was actually at the level of the canopy. The foraging level was classed as unshaded if the overhead cover of that location was estimated to be less than 20%. The lower understorey consisted of the vegetation that was less than 50% of the height of the canopy. The upper understorey consisted of all vegetation between the lower understorey and the canopy.

The feeding station was defined as the position on the branch that the kereru was situated. The classification 'trunk' is when the kereru was positioned within 20cm of the trunk (to allow for one average body width). The next three categories were determined by dividing the tree from the trunk to the outer branches into three parts. The first third from the trunk was the 'inner branch', the middle section was the 'centre branch' and the outer third was the 'outer branch'.

The total number of movements between the different feeding stations combined with measurements of branch length allowed approximate horizontal range to be estimated. Measurements of branch length were obtained from direct measurements on smaller trees, and from cut branches of larger trees (tawa and miro) were obtained from (branches were cut in order to create space for mist net sites). Standardisation by branch length used the averaged value of branch length obtained for each species. This was an approximate estimate only to allow for a general estimate of total horizontal distance moved by kereru during a feeding bout.

Feeding rate was recorded over five successive one minute periods and then averaged to give a value per minute. Feeding rate on fruit was measured as fruit swallowed per minute and vegetation was measured in pecks swallowed per minute. If the kereru could not be clearly seen, the feeding rate was not recorded. Food size was measured as a whole fruit or leaf. The amount of flesh per peck was the weight in grams of the fruit flesh minus the seeds and the weight of a typical beakful of vegetation (as determined through close observation).

Kereru in the immediate vicinity were either in the same tree as the kereru being observed, in an adjacent tree or within visual range. The number of kereru was recorded as 0= none, 1= one, 2 = between two and five, 3 = more than five.

Differences in feeding ecology variables were tested statistically using contingency tables (χ^2 test), single-factor ANOVA (analysis of variance), two-factor ANOVA and multivariate ANOVA.

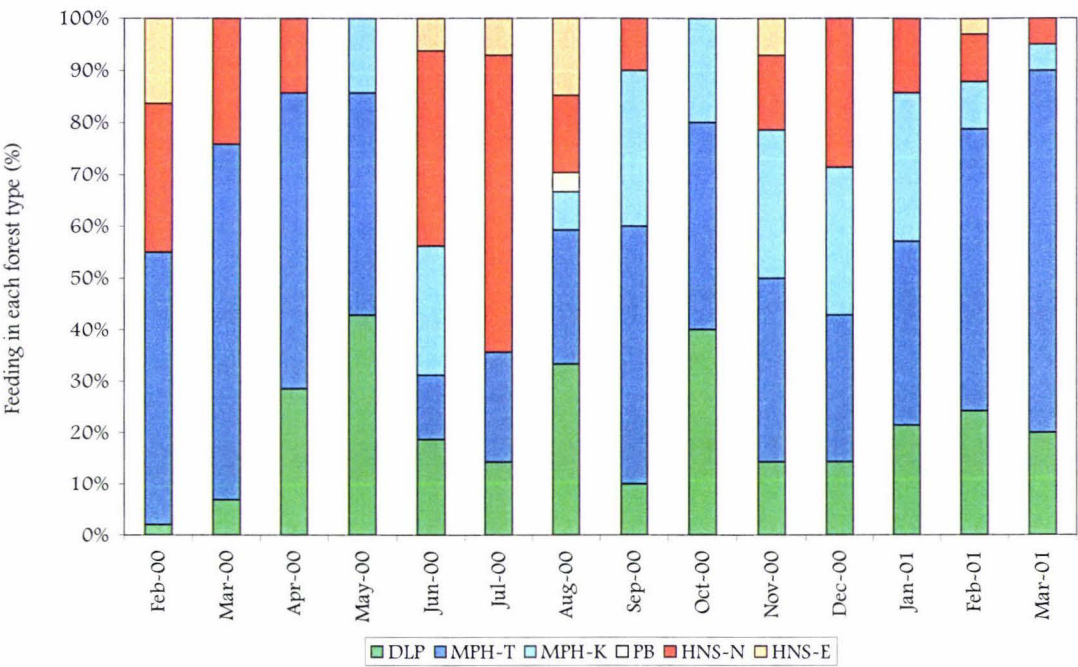
5.4 Results

A total of 281 foraging observations were made, 69% of these observations were on the 34 radio-tagged kereru and 31% on untagged kereru. They were observed for a total of just under 4000 minutes.

5.4.1 Feeding habitat

Kereru did not forage equally in all vegetation types (Fig 5.1). There was a significant difference ($\chi^2=167.28$, $df=5$, $p<0.001$) in the number of foraging observations in the various habitat types over the study period, after rough quantities of the various forest types were taken into account (Table 5.2). The most common forest type, mixed-podocarp hardwood formed the bulk of the foraging observations. Hardwood-scrub nursery was locally common, found in guts within exotic forest and native forest and also in clearings and along trails (formed by old logging activities) in native forest. As a result the amount of localised hardwood-scrub nursery was hard to quantify, and there were large patches where there was major logging. The original dense lowland podocarp forest was less abundant due to logging. There was little podocarp-beech forest, except in the higher areas, on the exterior of the official study areas.

Figure 5.1 Monthly percentage of feeding use of main forest types over a 14 month period.



There were more observations of kereru feeding in mixed-podocarp with tawa than with kamahi, although this could reflect the fact that the kamahi type was predominantly found in the higher altitudes not as common in the study areas. The food species kereru made use of in hardwood scrub were mainly makomako and kowhai, also kotukutuku, putaputaweta, broom and young mahoe and maire. Although the study areas were surrounded on one side by exotic forest, kereru appeared to prefer feeding on hardwood scrub within native forest. The main feeding difference between the dense lowland podocarp forest and the mixed-podocarp hardwood forest resulted from a higher abundance of miro in the former type, and tawa in the latter. Other than these species, feeding observations on species such as mahoe and maire were evenly distributed between the forest types. The feeding observations within the podocarp-beech forest consisted of kereru in the Otupaka region feeding on miro fruit. Kereru utilised the hardwood scrub nursery areas more when fruit was not readily available. Makomako was mainly found in these areas, which explains the higher usage in February, when it still formed a large component of the diet, particularly in Otupaka.

Table 5.2 Approximate percentages of different forest types within study area of Whirinaki forest.

Forest Type	Amount (%)
Dense lowland podocarp	30
Mixed podocarp hardwood with tawa	35
Mixed podocarp hardwood with tawa	15
Podocarp beech	2
Hardwood nursery scrub within native	10
Hardwood nursery scrub within exotic	8

5.4.2 Foraging level

Over the fourteen months:

0.7% of the total feeding occurred in the lower understorey,
6.1% occurred in the upper understorey,
24.5% in the shaded canopy,
47.1% in the unshaded canopy and
21.6% in the emergent layer.

The use of the various forest layers changed over the study ($\chi^2=423.1$, $df=9$, $p=0.001$), as seen in Figure 5.2. There was also a significant difference in the use of the various foraging levels between the two study sites ($F=6.24$, $df=2$, $p=0.01$).

Kereru changed their foraging level less than 5% of the time during a feeding bout. In all these cases, it was a change from unshaded canopy to shaded canopy or vice versa, usually as a result of moving along a branch or a slight height change.

Figure 5.2a Change in the use of forest structure for feeding over a fourteen month period in Oriuwaka.

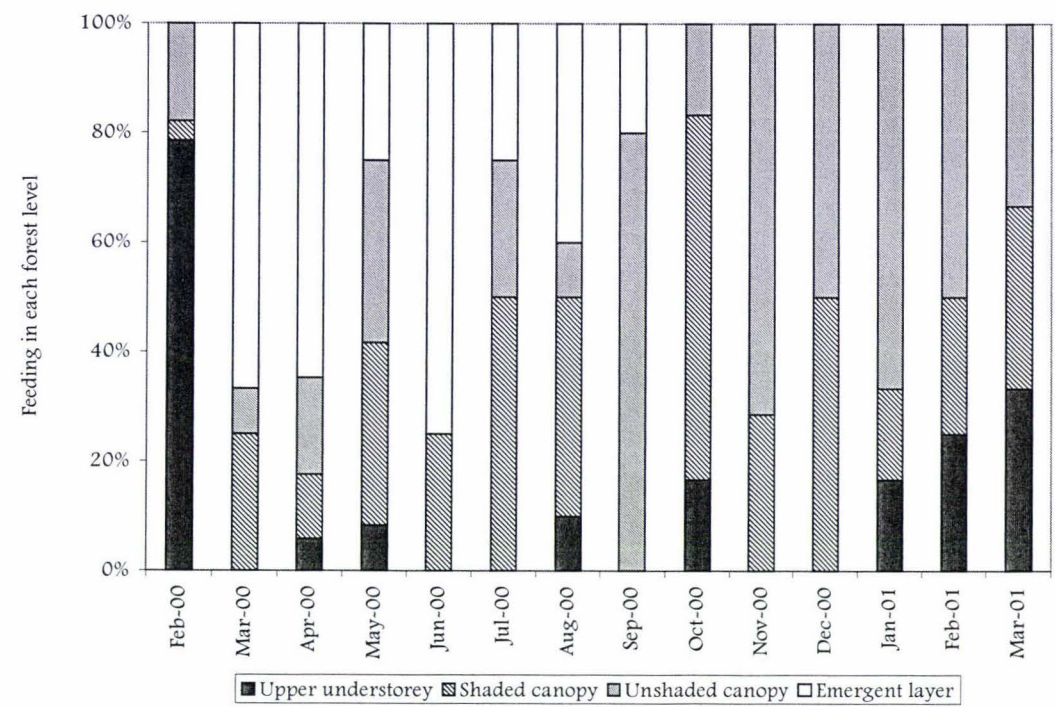
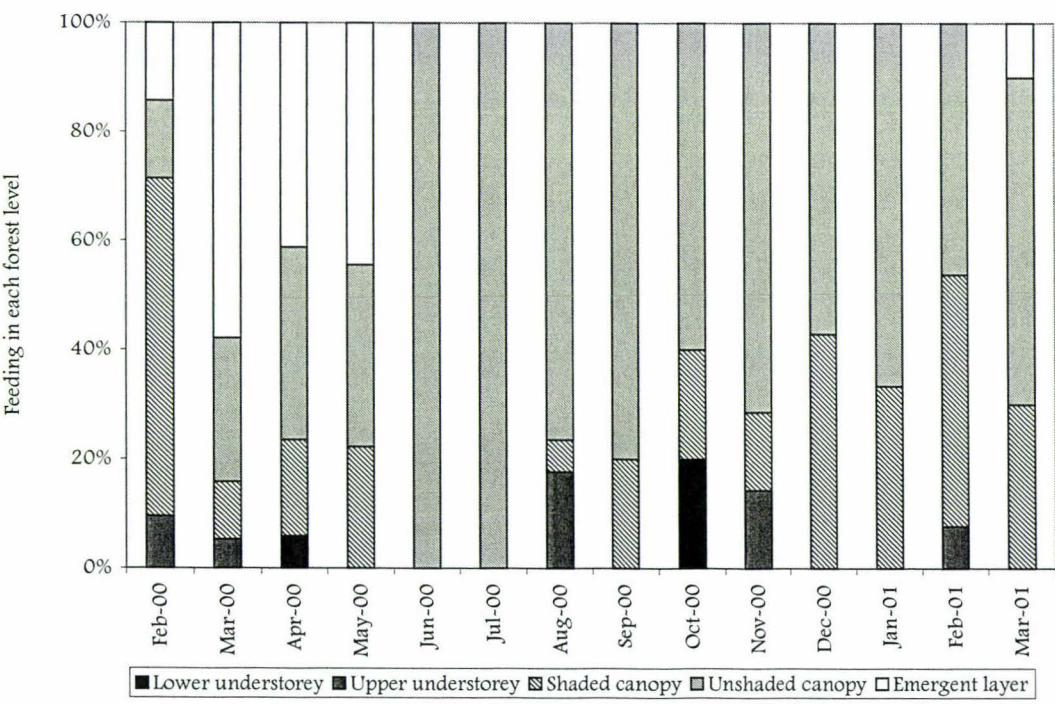


Figure 5.2b Change in the use of forest structure for feeding over a fourteen month period in Otupaka.



While kereru were feeding in the canopy they were more likely to be in an unshaded area. Most of the feeding (71.6%) was done in the canopy, although kereru did use almost all forest levels, with the exception of the ground. The position of the kereru within the forest seemed to mainly be based on the food species of the kereru (Table 5.3). They were found in the emergent level while feeding on miro, in the canopy layer while feeding on canopy species such as tawa and found in the understorey layers when feeding on makomako and karamu. Occasionally they were recorded in the canopy level while feeding on miro but fruit was not often available in this level.

Table 5.3 Percentage kereru foraged in each level within each species for the two study sites. EME=emergent, USC=unshaded canopy, UUN=upper understorey, LUN=lower understorey.

		EME	USC	SHC	UUN	LUN
Oriuwaka	MiroFRT	74	13	13	-	-
	TawaFRT	5	46	49	-	-
	MakomakoFRT	-	-	20	75	5
	MahoeFRT	-	-	-	-	-
	KotukutukuFRT	-	25	-	75	-
	MaireFRT	12	56	25	7	-
	KaramuFRT	-	-	15	71	14
	MahoeVEG	-	34	66	-	-
	KowhaiVEG	-	100	-	-	-
Otupaka	MiroFRT	76	11	13	-	-
	TawaFRT	-	44	66	-	-
	MakomakoFRT	-	72	8	14	6
	MahoeFRT	-	-	100	-	-
	KotukutukuFRT	-	-	-	-	-
	MaireFRT	-	100	-	-	-
	KaramuFRT	-	25	25	50	-
	MahoeVEG	-	25	75	-	-
	KowhaiVEG	-	-	-	-	-

The differences between the foraging levels of the two study sites can be directly linked to the difference in phenology between the two areas. This is particularly noticeable when the fruiting period of miro is examined in relation to the percentage of foraging in the emergent layer. Foraging in this layer in Oriuwaka begins earlier than in Otupaka and finishes earlier, over the same

time span as ripe miro fruit is available. Emergent foraging in Otupaka starts a month later and continues through until September, when the last of the miro fruit is no longer available. The proportion of foraging in unshaded canopy was higher in Otupaka (Table 5.2), perhaps reflecting the different forest composition of the two areas. When kereru foraged on kowhai (in Oriuwaka) they were generally in an unshaded position, mainly due to the sunny locations in which kowhai grew. When kereru foraged on mahoe foliage (predominantly in Otupaka) they were often in the shaded part of the canopy within the forest.

5.4.3 Foraging height and vertical range

Foraging height is related to foraging level but the level of feeding is determined by absolute units of height rather than forest structure.

Table 5.4 Foraging heights and heights of food trees over 14 months in Whirinaki forest.

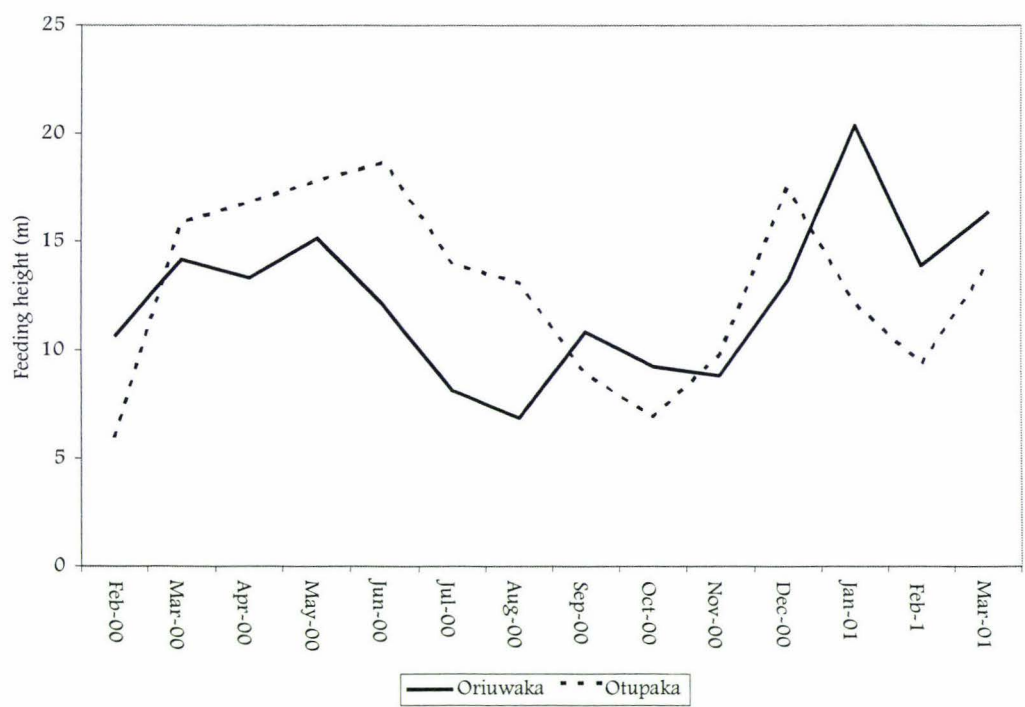
	% of kereru feeding in height class	% of food trees in height class
0-5m	17	13
6-10m	27	27
11-15m	28	23
16-20m	22	19
>20m	6	18

There was no significant difference ($\chi^2=7.24$, $df=4$, $p=0.2$), between the percentage of kereru feeding in a particular height class and the percentage of food trees in that height class (Table 5.4). This supports the null hypothesis that the height at which kereru forage is directly related to the height of the food tree.

The species in which the kereru fed had an affect on feeding height because of the size difference between trees. This is reflected in the changing feeding heights over the year (Figure 5.3), because the pronounced changes can be related to changes in significant food species in the diet (Chapter 4). There was a difference in seasonal changes of feeding height between the two areas

($F=3.01$, $df=2$, $p<0.05$). In February 2000 when kereru were feeding on makomako the feeding height was low, it increased as the birds moved to miro, especially in Otupaka where miro was more prolific. There was a marked difference in feeding height between the two study areas in July and August 2000, probably due to kereru feeding on miro in Otupaka, but kowhai in Oriuwaka. There was also a difference between the two study areas in early 2001, when more kereru in Oriuwaka were feeding on tawa.

Figure 5.3 Monthly average feeding heights over a 14 month period in Oriuwaka and Otupaka.



The relative height of the feeding site in the tree did not significantly differ between species. All feeding observations were taken with kereru at 62% to 100% of the total height of the tree. The average values for eight of the dominant food species are shown in Table 5.5.

Table 5.5 Percentage of total tree height where kereru feeding sites are located for eight dominant food species.

	% of total food tree height
Makomako	89.46 (se=1.32)
Karamu	89.44 (se=3.14)
Maire	88.46 (se=1.80)
Mahoe	88.11 (se=1.71)
Kowhai	87.89 (se=1.96)
Fuchsia	85.11 (se=2.62)
Tawa	81.86 (se=1.43)
Miro	75.11 (se=2.19)

Miro, an emergent tree, was the only species with an average feeding site height below 80% of the height of the tree.

During most feeding bouts kereru moved little, ranging 0.5 m or fewer (Table 5.6).

Table 5.6 Total vertical distance ranged during feeding bouts.

range of vertical movement (metres)	percentage of feeding bouts
0-0.5	65.4
0.6-1	18.3
1.1-1.5	8.7
1.6-2	5.8
>2	1.8

The vertical distance moved was influenced by the size of the tree and the abundance of fruit. All distances over 1.5m were observed in podocarps over 20m in height and during periods of diminished fruit abundance. The largest distance ranged by a kereru was 6 m on a miro while searching for fruit in August.

The vertical ranges of kereru during a feeding bout differed significantly between tree species ($\chi^2=33.39$, $df=16$, $p<0.01$) (Table 5.7).

Table 5.7 Average vertical distance ranged by kereru during a feeding bout, depending on food species and type.

	tree height (metres)	range (metres)	range (% tree height)
MiroFRT	23.74 (se=1.52)	0.48 (se=0.09)	2.01 (se=0.38)
TawaFRT	16.94 (se=0.53)	0.54 (se=0.16)	3.18 (se=0.94)
MaireFRT	12.94 (se=0.45)	0.39 (se=0.06)	3.04 (se=0.46)
KowhaiVEG	12.12 (se=0.73)	0.32 (se=0.10)	2.63 (se=0.83)
MahoeFRT	10.33 (se=0.91)	0.22 (se=0.08)	2.15 (se=0.77)
MahoeVEG	10.33 (se=0.91)	0.13 (se=0.07)	1.26 (se=0.67)
KotukutukuFRT	9.80 (se=0.64)	0.38 (se=0.11)	3.83 (se=1.12)
MakomakoFRT	7.32 (se=0.38)	0.53 (se=0.08)	7.26 (se=1.09)
KaramuFRT	4.20 (se=0.32)	0.16 (se=0.06)	3.81 (se=1.42)

The range of vertical movement was not significantly related to tree size. However, when the data were standardised, the vertical distance ranged by kereru during a feeding bout appeared to be inversely proportional to the height of the tree. For example, kereru moved the second smallest relative vertical distance in the largest tree (miro) and the largest relative vertical distance in one of the smallest trees (makomako).

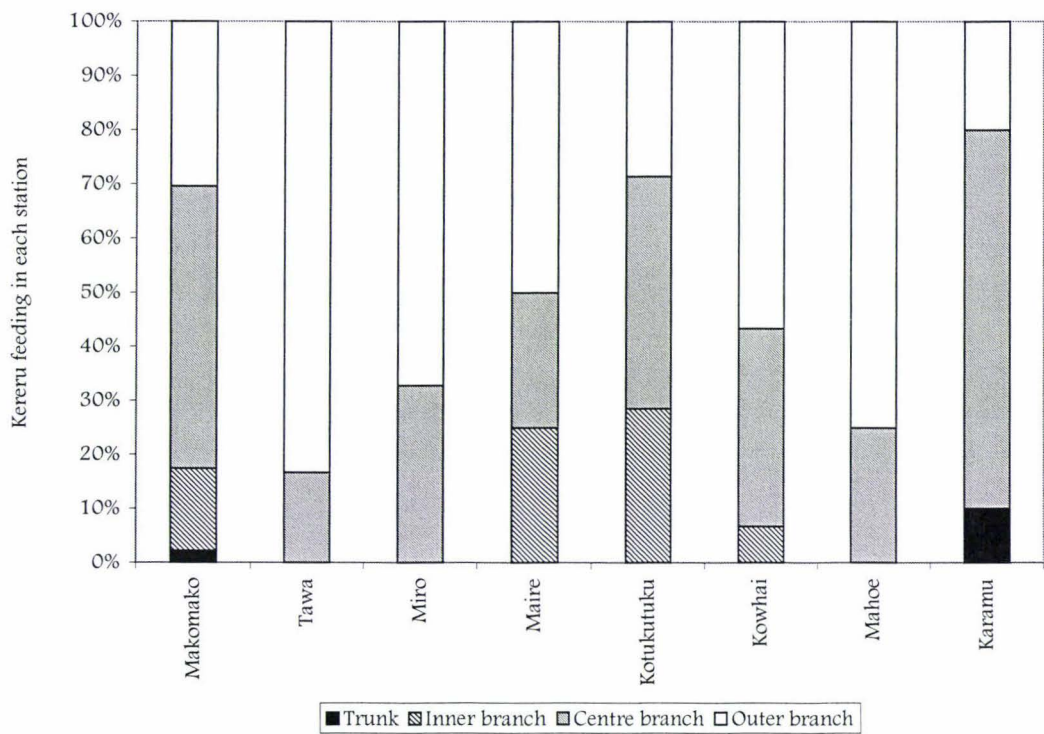
The height at which the kereru fed within mahoe did not differ significantly when the birds were taking fruit or foliage ($F=0.25$, $df=2$, $p=0.62$), however the average vertical distance moved while foraging was markedly different between these two food types ($F=3.94$, $df=2$, $p<0.05$). When feeding on fruit kereru would range vertically almost twice as far compared to when they were feeding on vegetation.

5.4.4 Feeding station

Kereru foraged predominantly in the outer branches of the trees. 56% spent their time foraging in the outer branches and 38% in the centre branches. Only 1% and 5% of individual foraging observations were taken while kereru were in the trunk or inner branch region. This probably reflects the relative availability of fruit and foliage within the tree with most species carrying a higher abundance of fruit amongst the outer branches (pers. obs.). New leaf growth (the more commonly eaten form of foliage) was also more prolific towards the ends of the branches. In the smaller tree species, kereru were able to perch in

one of the inner stations of the branch yet feed on fruit from the outer stations. The station in which the kereru fed was significantly different between the tree species ($\chi^2=292.28$, $df=21$, $p<0.001$) (Fig 5.4).

Figure 5.4 Relative proportions of feeding stations among eight common food species.



Kereru foraged in the same feeding stations when feeding on mahoe fruit and mahoe foliage, but the distance moved along the branches differed, although not as dramatically as the vertical range (Table 5.8). Kereru moved between stations less frequently on the larger trees, probably because of the greater distance they would have been required to travel. If distance moved is expressed as percentage of branch length the greatest bird movements while feeding were obtained from observations on the smallest trees (with the exception of karamu). Conversely, the smallest ranges were obtained from the largest trees (miro and tawa). Kereru feeding on kowhai foliage were the exception to this and hardly moved in search of leaves within a feeding bout.

Table 5.8 Average horizontal distance moved by kereru during a feeding bout.

	single branch length (metres)	range (metres)	range (% branch length)
MiroFRT	7.94 (se=0.44)	1.44 (se=0.30)	18.12 (se=3.78)
TawaFRT	4.24 (se=0.31)	1.18 (se=0.29)	27.78 (se=6.83)
KowhaiVEG	3.03 (se=0.26)	0.26 (se=0.11)	8.64 (se=3.63)
MahoeFRT	2.58 (se=0.51)	0.98 (se=0.25)	38.10 (se=9.69)
MahoeVEG	2.58 (se=0.51)	0.77 (se=0.13)	29.63 (se=5.03)
MaireFRT	2.16 (se=0.21)	1.11 (se=0.31)	51.52 (se=14.35)
KotukutukuFRT	1.73 (se=0.35)	1.25 (se=0.21)	72.22 (se=12.14)
KaramuFRT	1.05 (se=0.13)	0.30 (se=0.08)	28.57 (se=7.61)
MakomakoFRT	0.92 (se=0.16)	0.82 (se=0.08)	89.68 (se=8.69)

Kereru were systematic feeders and would generally walk along a branch only when all appropriate (i.e. ripe) and accessible fruit had been eaten. In nearly 45% (n=281) of observations kereru did not change stations during the feeding bout. Horizontal movements rarely incorporated flight, even vertical movements would be described more as a brief flutter as kereru moved between branches. The most common movement during a feeding bout was a careful walk along a branch.

5.4.5 Feeding rate and bout length

As expected, the feeding rate (food ingested per minute) was inversely related to fruit weight (Table 5.9). The species with smaller fruit had a higher abundance of individual fruit than the species with larger fruit (pers. obs.), which also aided in a higher feeding rate since the fruit were closer to each other. Kereru spent longer searching for the larger fruit, due to their lower density, and that is reflected in the lower feeding rate.

Table 5.9 Average feeding rates and total food ingested per average feeding bout for main kereru food species, feeding rates on young vegetation only were included as that was the most commonly eaten food type.

Species	Total unit weight (g)	Flesh per peck (g)	Feeding rate per minute	Food per minute (g)	Foraging bout length (mins)	Total food per bout (g)
TawaFRT	5.230	2.340	4.05	9.48	8.90	84.35
MiroFRT	1.350	0.780	6.77	5.28	10.10	53.35
KotukutukuFRT	1.060	0.610	9.00	5.49	11.20	61.49
MakomakoFRT	0.110	0.070	23.82	1.67	13.60	22.68
KaramuFRT	0.080	0.060	13.20	0.79	12.20	9.66
MahoeFRT	0.040	0.030	20.40	0.61	14.60	8.94
MahoeVEG	0.032	0.024	28.60	0.57	18.70	10.70
KowhaiVEG	0.026	0.016	42.10	0.34	24.60	8.36

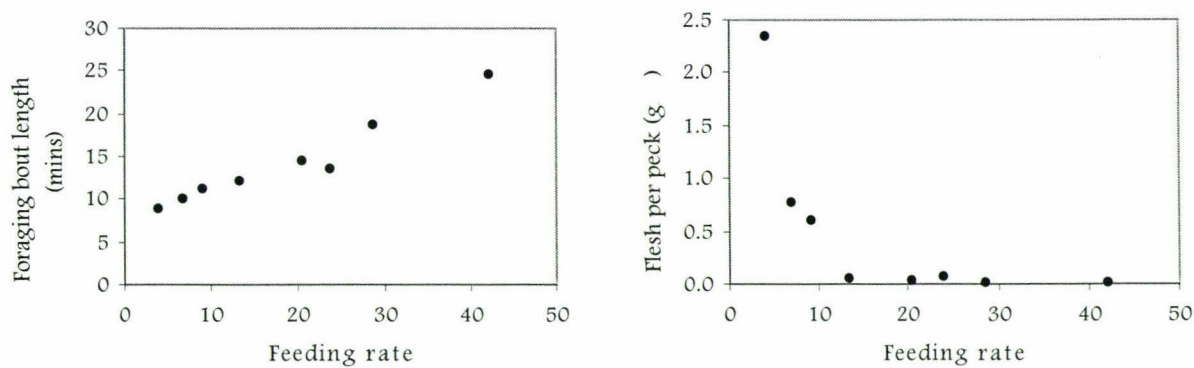
Kereru foraged for a shorter amount of time overall on tawa yet gained the greatest amount of food per bout from this fruit due to its large size. The foraging bout length was more uniform across the different fruit species than the amount of food gained per bout. Kereru devoted slightly less time to the larger fruits with a single large seed such as tawa and miro. Small-seeded fruits gave the least amount of flesh per foraging bout. The extended bout length while feeding on these fruits was not long enough to compensate for the reduced flesh intake per minute, particularly for mahoe and karamu.

During times when fruit was not prolific, such as at the beginning and end of each species' fruiting cycle, the total feeding bout length did not increase significantly as might have been expected when fruit becomes harder to find, but the feeding rate did decrease. So kereru spent the same amount of time in the tree for less reward. This was particularly noticeable at the beginning of miro fruiting as the kereru spent the same amount of foraging time in each tree but were only ingesting ripe or semi-ripe fruit and discarded many unripe fruit once they had been manipulated in their bill. Kereru were very selective about picking ripe fruit over unripe fruit, irrespective of fruit species. There was a longer period of time between each intake of fruit when the amount of ripe fruit on a tree was low. The average feeding rate on miro in March 2000 (when a high percentage of fruit on the tree was unripe) was 3.8 compared to 6.6 in May 2000.

In only one instance did a kereru feed on two different species within one feeding bout. This occurred when maire and kowhai branches overlapped, and while remaining in the maire the kereru ate one kowhai leaflet. On another occasion a kereru did pick kotukutuku leaves while feeding on kotukutuku fruit, but dropped them and did not swallow any foliage during this feeding bout. In all other instances only one species and one food type within that species was ingested during a feeding bout.

Figure 5.5 shows the relationships between some independent variables from Table 5.9. There was a strong positive correlation between the feeding rate and the foraging bout length ($r=0.97$, $p<0.0001$). Feeding rate was strongly influenced by the amount of food kereru gained per peck ($r=0.66$, $p=0.07$), with lower feeding rates on larger fruits. Although the larger fruits had a lower feeding rate and a shorter foraging bout length, a lower feeding rate was indicative of a higher value for total food consumed per feeding bout. Kereru with shorter bout lengths (indicating a lower feeding rate and a larger amount of food per peck) ended up with more food per total feeding bout.

Figure 5.5 Relationships between feeding rate, the foraging bout length, and the amount of food per peck.



The general pattern was that kereru foraged for a shorter amount of time on larger fruits, and although they consumed fewer fruits per minute, the amount of flesh gained was higher. When feeding on smaller fruits and foliage kereru consumed less flesh per minute and foraging bout length was longer, but not by so much that the amount of food consumed per total feeding bout was similar regardless of size.

There is a difference in the feeding rate between the two types of foliage eaten (mahoe and kowhai), most likely a result of mahoe leaves being larger than kowhai leaves. When compared to young kowhai foliage, young mahoe leaves were less prolific and more widespread on individual trees. Although the average foraging time on mahoe foliage was shorter than kowhai foliage, more mahoe leaves were eaten per minute and kereru feeding on mahoe foliage ate about 2.4 gms more during the total food bout.

The range of foliage ingested per minute differed significantly within a feeding bout. For kowhai this value varied from 0 to 52 beakfuls, although this was complicated by the fact that the type of kowhai leaf eaten also differed. When feeding on younger foliage the whole compound leaf was eaten approximately 68% of the time. Young foliage was consumed in far greater quantities than the older foliage, and the same applied to mahoe leaves (Chapter 4). When feeding on mature foliage kereru usually ate individual leaflets but occasionally would pull off and ingest an entire compound leaf, which bears from 40 to 80 leaflets. Approximately 3.8% of single feeding observations on mature kowhai foliage were of compound leaves.

5.4.6 Other kereru in vicinity

Over the fourteen month period most of the kereru observed were solitary. Of the 281 feeding observations, 66% involved no other kereru in the vicinity. There was one other kereru nearby during 23% of the feeding observations, between two and five kereru nearby during 8% of the feeding observations and more than five only 3% of the time. During the study period, only 4.8% of feeding observations involved more than one kereru feeding in the same tree. When there were two kereru in a single tree, there was a roughly 60% chance that they were a bonded pair (established from observation of radio-tagged kereru known to be single and paired, pers. obs.). In smaller trees, kereru were not often found in the same tree. However in very large trees such as miro, up to 8 kereru were seen feeding in one tree, particularly trees that fruited early or late, providing an especially valuable food source. Makomako, miro and kowhai provided 74.4% of the observations of other kereru in the vicinity while one was feeding. While feeding on tawa kereru were solitary in 84.4% of cases, and the figure was very similar for mahoe (at 83.3%). Kereru did not generally congregate around the more widespread species that were

evenly distributed, such as tawa and mahoe. If multiple kereru were in the same vicinity while feeding on the more evenly distributed trees, e.g. tawa, they were not in the adjacent trees and most did not stay for long. Kereru were more territorial when feeding on tawa (as opposed to other tree species) and would occasionally interrupt a feeding bout to chase off another kereru, or to be chased off.

5.5 Discussion

Many factors affect the choice of food by a bird. Previous studies (Crome 1975a, Howe & Vande Kerckhove 1980, Herrera 1981, Sorensen 1981, Wheelwright 1988) have shown various degrees of food choice among frugivores, but attempts to find the reasons behind differences in diet have had limited success. Factors that have been shown to influence diet selection include the relative amounts of seed and fruit pulp (Howe & Vande Kerckhove 1980, Herrera 1981); plant form, fruit size, colour, ripeness and nutrient content (Crome 1975a, Wheelwright 1988). Sorensen (1981) did not find any significant association between food preference in thrushes and the fruit characteristics she studied. However, in a study on the fruit preferences of blackbirds (1984) Sorenson found that blackbird preference was related to energy intake, digestibility and seed passage rates. Fruit intake rates did not appear to constrain energy intake in the blackbirds and it was shown that plant growth form may play an important role in determining frugivore preference. Moermond & Denslow (1983) found that accessibility and tree structure had an important influence on fruit choice among manakins, tanagers and salators (small tropical passerine frugivores).

Occasionally kereru fed on unripe fruit, particularly in Oriuwaka at the start of miro fruiting. Mainly, however, kereru have been shown to prefer ripe fruit (Dunn 1981, Lee *et al.* 1988, Tisdall 1992, James 1995). Unripe fruit are considered a famine food, as is vegetation (Foster 1977, McEwen 1978). Nelson *et al.* (2000) found that both unripe fruit and leaves contained amounts of nutrients comparable to those found in ripe fruits, which suggests the birds avoid them for other reasons. According to Snow (1971) unripe fruits are less accessible as they are more firmly attached to the tree, therefore more energy must be expended in order to pluck the fruit and a slightly longer

period of time would exist between fruits. Bats are said to avoid unripe fruit because they contain high levels of secondary compounds and tannins (Dasilva 1994). Kinzey & Norconk (1993) found that frugivorous primates would eat fruit which contained moderate amounts of secondary compounds (i.e. semi-ripe fruit), and would leave fruits (i.e. unripe fruits) that contained excessive amounts of these compounds. Secondary compounds are known to act as feeding deterrents or inhibit protein digestion in some species (Freeland & Janzen 1974, Choo *et al.* 1981, Kunz & Ingalls 1994). Cain *et al.* (1961) found that the more developed a vegetative structure became, the more secondary compounds it would contain. This implies that young leaves would have fewer secondary compounds than mature leaves, and therefore may be more palatable to folivores. Another possible reason for the preference of young leaves, also found in other *Hemiphaga* studies (Dunn 1981, Tisdall 1992), is that the midrib in mahoe leaves has a very high fat content compared with surrounding tissues (Williams 1982). When feeding on mature mahoe leaves, kereru could only pick pieces off the leaf that were of a size that could be swallowed. A mature leaf including the midrib was too large to swallow. Mature whole compound kowhai leaves were only eaten 3.8% of the time, although kereru often attempted to pull off a whole compound leaf. Usually the small leaflets were eaten one by one. When the young foliage was eaten, the size limitation had been removed and the whole compound leaf was ingested. Unripe fruit and mature leaves may also be passed over due to the hard pericarp of the fruit and the higher fibrous content of the leaf, both these aspects reduce digestibility (Kunz & Ingalls 1994, Nelson *et al.* 2000), which has been shown to affect fruit choice among other frugivores (Sorenson 1984). Kereru feeding on unripe miro fruit were seen to pass the fruit virtually undigested (pers. obs.), suggesting the outer tissues of the fruit were never broken by digestion.

It has been suggested (Foster 1977) that when other food sources are not readily available, frugivores will switch to eating unripe fruits that are abundant, because no increased time has to be spent searching for them. Kereru could spend more time searching for trees with ripe fruit however they often appear to know the location of key food sources in their area so searching for ripe fruit probably would not lead to a major new food source unless extensive travelling was undertaken. Kereru have also been known in other areas to travel from food source to food source (Clout *et al.* 1991) on a

regular basis. The energy expended to try to find a totally new food source may not be worth the risk of no other major concentration of profitable food sources being available. For a frugivore this may result in a strategy of feeding on a less desirable form of food, i.e. unripe fruit or mature vegetation. When fruits become low in availability some kereru make the switch to feeding on foliage because even though leaves are not as high in nutritional value they are considerably less energetically expensive to obtain. There was no significant difference in weight between kereru caught during periods of food abundance and periods of food scarcity, indicating that they were able to compensate for possible deficiencies faced when confined to an apparently sub-optimal diet. Foster (1977) obtained a similar result when studying the effects of a tropical food shortage on long-tail manakins.

The changing diet of the kereru had a strong influence on the habitat and microhabitat in which they foraged. The location of preferred food trees determined the forest type in which kereru foraged. Plant form imposed strict limitations on foraging level and height. Dunn (1981) found that kereru are physically incapable of feeding for very long at steep perch angles, which is the probably the factor which prevents the complete removal of flowers, leaves and fruit from some heavily browsed species, for example the defoliation of kowhai. While trees gain from having fruit consumed by a disperser (Snow 1971), defoliation can substantially reduce the photosynthetic capabilities of a plant and have serious consequences. Kereru usually feed for less than two hours a day when on a leaf diet (Clout & Hay 1989). Using the known feeding rates and the assumption that a kereru would spend 100 minutes a day feeding (Clout & Hay 1989), a single kereru would feed on over 30gms of foliage per day, which equates to over 3 m². If the kereru fed on the same diet for a fortnight, it would consume over 42 m² of foliage. Kereru also tend to feed in the same tree (Dunn 1981, James 1995, pers. obs.), intensifying the effects. The tree species in which the kereru was feeding also affected the station in which they fed. As the majority of the fruit and young foliage was found towards the outer branches a kereru could not physically be in the trunk or inner branch regions of the larger trees, such as miro and tawa, and feed on their preferred food type. However this was quite possible in the more shrubby species like makomako and karamu. These species essentially forced the kereru to sit towards the inner branches as the outer branches could not hold their weight. Moermond and Denslow (1983) found with tanagers and

manakins that both fruit type and accessibility influence preference. If a fruit is difficult to reach the bird may switch to a less-preferred fruit. Similarly, a bird would reach farther for a more-preferred fruit than for a less-preferred fruit. Kereru would feed on all of the accessible food before endeavouring to reach the food at the tips of the branches. When food was plentiful they had a higher tendency to remain within a limited range and not exert a great amount of effort in reaching certain fruits. Previous field experiments have shown that accessible fruits are removed from trees more rapidly than the less accessible fruits of the same species (Denslow & Moermond 1982, Moermond & Denslow 1983). As the food abundance decreased kereru would not spend longer foraging but had a lower overall feeding rate and went to greater efforts to reach fruit that they may have ignored earlier in the season. Therefore the period between swallowing was greater as more time was spent obtaining the fruit. If food was not obtained after a brief search the kereru would move on to another tree indicating that they only search when there are proven rewards to be gained.

The range while foraging was influenced by plant growth form. In relation to tree size, kereru moved around the most in the smaller trees. In standard metres they travelled a greater distance in the larger trees. This could enable kereru to be more selective of the food gathered from smaller trees as travelling a similar distance allows them to cover far more of the tree's area. In terms of feeding rate, the kereru feed on a higher amount of smaller food as they forage over a larger area of the tree. While foraging in karamu, kowhai and mahoe (on both fruit and foliage), kereru moved over a relatively small area of the tree. The foraging bout length while feeding on foliage is almost twice as long as when feeding on fruit and the range is far less. Vegetation is considered to offer lesser rewards (Foster 1977, McKey 1975) so perhaps less energy is expended while foraging on these foods to compensate for less energy gained. Kereru fed in one place for a longer period of time with little movement on these food types. The nature of the grouping of some fruit and leaves enabled kereru to eat large numbers with minimal movement. Mahoe (a ramiflorous species) fruit grows in fascicles of 2-10 all along the branches or on branchlets below the leaves (Allan 1961). Karamu fruit is also concentrated in one place so would require fewer movements, particularly when the systematic feeding method of the kereru is taken into account.

Therefore range moved by kereru during a feeding bout also appears to be affected by accessibility.

The accessibility of food, along with food size, played a part in the feeding rate of the kereru. Species that produced more easily accessible food, i.e. more closely grouped/clustered, had a higher feeding rate than the species that produced their fruit in a more even widespread distribution. The species that produced fruit in clusters also tended to produce smaller fruit, which have a shorter handling and swallowing time (Levey 1987), thus can be eaten in rapid succession. The more widely distributed fruits tended to be the larger ones that offered more flesh per fruit consumed. Kereru had a shorter foraging bout length while feeding on these larger fruits, presumably as their crop filled sooner (Kenward & Sibly 1978). This was reflected in the lower feeding rate associated with shorter foraging bout lengths and a higher total of food consumed per bout. Other studies (Kenward & Sibly 1977, Dunn 1981) have indicated that wood pigeons will commence feeding rapidly, slowing as their crops fill. No such pattern was found in the present kereru study. The only difference in feeding rate within a food species was a result of differing availability of the food. While kereru would move on if not instantly rewarded in some species (mahoe, maire) they allowed longer to search for food before moving off in other species, most notably miro. This could again be a result of the availability of miro trees within the forest. While it is quite possible to move to another mahoe tree in the near vicinity, miro trees were not generally so readily accessible. There may also be a difference in nutritional rewards that make miro fruit worth expending more energy to find. There appeared to be a limit to the time a kereru spent feeding which was not related to food consumption. The foraging bout length was far more consistent between species and food types than the total food per bout. Frugivores are often at greater risk of predation while feeding (Beehler 1983), so a limited feeding bout may be a method of predator avoidance.

Kereru rarely rested or preened in the area in which they were feeding. Usually to perform such activities they would fly to adjacent vegetation and sit closer to the inner regions of the tree where they had ample cover above. When feeding on smaller species they would invariably fly to a larger tree that provided more cover, in trees such as tawa and miro they sometimes walked towards the inner region of the tree before exhibiting resting or preening

behaviours. While feeding they were often in emergent trees or in unshaded canopy where they were relatively exposed. When feeding in exposed areas the tendency appeared to be for the kereru to sit as close to the inner regions as possible while retaining uncomplicated access to the food source. Paired kereru would take turns at feeding and were not often seen feeding simultaneously (pers. obs.). Kereru showed a very strong adverse reaction to raptor species. When an Australasian harrier (*Circus approximans*) or a New Zealand falcon (*Falco novaeseelandiae*) flew overhead, particularly while kereru were feeding, the kereru would drop almost vertically toward the ground then level off and fly low through the vegetation. Previous studies have reported the same type of pattern (Howe 1977, Beehler 1983). Wheelwright (1988) found that hawks threatened fruit-eating birds at a high rate that undoubtedly affects their foraging behaviour. The falcon is a common predator of kereru in Whirinaki, although an Australasian harrier has never been seen to kill one. Powlesland (pers. comm.) has reported that the one consistent tendency for kereru nest sites is to have dense overhead cover, perhaps to avoid nestling predation by raptors. It appears likely, therefore, that fear of predation may be one of the forces modifying foraging behaviour of kereru.

Courtney and Sallabanks (1992) reported that in the presence of predation, animals may be forced into periods of vigilance and as digestion can occur at the same time as scanning for predators there may be no net disadvantage to gut passage of seeds. After a feeding bout kereru rest for an extended period of time while the food is digested. This form of vigilance also favours seed dispersal as the fruits are ingested and then removed from the fruiting parent plant before being digested. The resting period is usually ended with defecation unless the bird is disturbed. Frugivorous birds tend to have shorter gut passage times (Karasov & Levey 1990). The average passage time for all foods eaten is not known, but as an example, for miro it ranges from 55 to 140 minutes (Clout & Tilley 1992). It has been suggested (Courtney and Sallabanks 1992) that the act of swallowing fruit whole is a method of predator avoidance, because if predation risk is higher in one situation than another (e.g. in an exposed area), then frugivores will tend to ingest fruits whole and digest them in a lower risk situation. "Gulpers" (to use a term coined by Moermond and Denslow (1983) to describe a bird that swallows fruit whole with minimal handling before swallowing) could digest fruit that

perhaps would not be eaten by a bird using another method of feeding. A large seed, tough or adherent pericarp and fruit pulp containing bitter compounds are all mechanisms that would reduce the probability of any bird other than a gulper taking the fruit (Levey 1987).

Seeds pass rapidly through the gut in relation to pulp (Karasov & Levey 1990) functioning to minimize the time that indigestible seeds are retained in the absorptive area of the digestive system, while allowing the retention of pulp for the further absorption of nutrients (Witmer 1998). The frugivore gut may be able to distend to accommodate indigestible matter, and may process fruit foods discretely rather than continuously (Witmer 1998). Witmer (1998) suggests that the seeds of bird-dispersed fruits often do not impose bulk-processing limitations on frugivores. This was particularly found to apply to sugar-rich fruits, as lipid-rich fruits require longer retention times for absorption and digestion (Afik & Karasov 1996). Hegde *et al.* (1991) found that the preference of the red-vented bulbul did not appear to depend on the seediness of the fruit but on the cost to benefit ratio of harvesting them. Travest *et al.* (2001) found that seed size affects the response to passage through the bird gut and that large seeds are more rapidly ejected. Some older studies have shown a negative relationship between amount of seed content in the fruit and preference by frugivores (Snow 1971, Howe and Vande Kerckhove 1980, Sorenson 1984). The number and size of seeds within a fruit did not appear to limit the intake of fruit for kereru for although the kereru did not forage for as long on the larger seeded species, more flesh was gained per feeding bout. The larger seeded species are also the preferred food species of the kereru (Chapter 4).

Fruit pigeons in other areas of the world often feed and roost in flocks (Dunn 1981). Crome (1975a) found several different species of fruit pigeon feeding in a single tree. In contrast, kereru are normally solitary feeders. Social feeding seemed based on localised abundance of a patchy food source. Kereru would flock around makomako patches or miro when they were fruiting heavily, similarly with kowhai during the spring flush of foliage. When feeding on more widely distributed species kereru tended to feed with no other kereru nearby. Kereru would feed on tawa during the breeding season, and most territoriality was shown when they were on this species. It appears, therefore, that kereru will overcome their solitary tendencies when a valuable

and limited food supply is available. After feeding, however, they flew away from other kereru and perched in another area, generally within 100m of the food source.

5.6 Conclusions

The species on which the kereru was feeding predominantly determined the habitat and microhabitat in which it foraged. Plant habits and form imposed strict limitations on kereru, which had to feed where the plants grew and at the height where the tree produced the fruit and foliage. Feeding ranges moved while the birds were foraging, in both a vertical and horizontal direction, was strongly influenced by the plant growth form and the pattern in which the fruit and foliage grew on the tree. Predator avoidance also could have an impact on foraging behaviour through kereru feeding closer to the inner regions of the branches if food could be reached in this position, and perhaps even their method of feeding and digestion could be influenced by fear of predation.

Accessibility of food types played a major part in the feeding ecology of kereru. The range moved during a feeding bout, and feeding station and feeding rate were particularly affected by the accessibility of the food supply. Social feeding also seems to result from temporal accessibility of certain food supplies within the forest. Usually kereru are solitary feeders, unlike most tropical fruit pigeons.

Kereru obtained more food per feeding bout while feeding on the larger fruits, and the foraging time was shorter, thus it seems likely that less energy is expended while foraging. Foraging in the larger trees that typically produce single seeded fruits also makes predation less of a concern, because overhead cover is more available. Seed load did not appear to have an impact on the preference of the kereru as the fruit with the larger seed loads offered more fruit per seed and when kereru were feeding on these species they obtained more food per feeding bout. Large seeds can be digested during periods of vigilance and the gut of the frugivore may be able to distend to accommodate them.

Unripe fruit and mature vegetation appear not to be preferred forms of food, although studies have shown nutrition levels to be similar between all food types (Nelson *et al.* 2000). Suggestions for this lack of appeal include secondary compounds in the food making it unappetising and/or inhibiting protein digestion. Further, they may be undigestible due to the hard pericarp and high fibrous content. The preference for young leaves may reflect the bird's ability to include the midrib in the diet, which contains most of the fat in the leaf structure.

The kereru is a versatile species that shows adaptation to a wide variety of forest types while utilising a variety of different food sources.

Chapter 6

Nutritional characteristics of food eaten by kereru

6.1 Abstract

Six species of fruit and two species of leaf consumed by kereru were analysed to determine their nutritional content and physical composition. Five nutritional characteristics were assayed for: gross energy, protein, lipids, carbohydrates and glucose. The physical features measured were: number of seeds per fruit, fruit weight, seed weight and the percentage of fruit flesh.

Lipids were high in species that fruited over the kereru breeding season. Protein was high in species that fruited over the moulting/growth period (January – June) and was also high in young vegetation which, in kowhai foliage, was available during the period of greatest moult. Carbohydrates were higher in species which ripened in the colder seasons. The moisture content of the summer fruiting species was higher than that of the species which fruited during autumn.

The differences and similarities of nutritional components between the species were more marked than for the physical components.

Overall the results are consistent with a view that there has been some co-evolution of kereru and the nutritional value of their significant food species.

6.2 Introduction

The relationship between fruit-eating birds and fleshy-fruited plants is one that has been evolving for over 200 million years (Willson 1991). Early theories on the relationship between fruit eating birds and fleshy-fruited plants proposed tight, species-specific mutualisms (McKey 1975, Howe & Estabrook 1977). More recently it has been suggested that frugivorous birds and bird-dispersed plants are involved in 'diffuse coevolution', in which

evolutionary changes in traits result from interaction between groups of species rather than between individual species (Janzen 1980). They are involved in a coevolutionary race in which each tends to obtain the most reward in return for the least expenditure (Snow 1971, Herrera 1982). The dispersal performed by the birds is assumed to be related to the nutritional reward offered by the flesh from the fruit.

One aspect that is not often studied is the importance of non-fruit material to the nutrition of generally frugivorous birds. Vegetative matter can play a large part in the survival of birds, especially during times of food shortage. Periods of food scarcity may be regular and predictable, occurring seasonally for example. Organisms experiencing a period of food scarcity respond both physiologically and behaviourally, and behavioural modifications commonly are manifest as changes in feeding ecology (Foster 1977). It has been suggested (Foster 1977) that these alternate food resources are nutritionally inferior to the ones preferred.

There are still gaps in the knowledge about the nutritional relevance of food species to the bird. For instance it is not well known what nutritional features of the fruit are important to bird survival, and how both plant species and birds adjust for the changing nutritional demands that come with seasonal habits and habitats.

There is evidence that birds select among food types available. Howe & Vande Kerckhove (1980) and Herrera (1981) have shown discrimination among fruits with different seed volumes, and Hartley (1954), Sorensen (1981) and Moermond & Denslow (1983) described apparent preferences among different food types, for ripe over unripe fruit, fruit over foliage and preference for certain species. Some species also choose a wider selection of food types than others. Studies have reported striking differences in the quantities of different species of food consumed by birds (Jordano & Herrera, 1981, Sorenson 1984). The reasons for these different patterns of food consumption are often unknown. In many cases, preference has been linked to the nutritional value of food types (Sorenson 1984, Powlesland *et al.* 1997). It has been hypothesised (Whelan *et al.* 1998) that this mixing of food species

could produce a 'resource complementary' diet, where the nutrient combination of food consumed is more beneficial than one species alone.

Snow (1971) and Herrera (1982) suggest that there is competition between different plant species to attract a disperser. The observation that many fruits are left to rot on the plants in seasons of fruit abundance (Snow 1965, Leck 1972, Foster 1977) suggests that plants may compete for dispersers at some times of the year. Several ways in which plants could compete with each other have been postulated: species could produce fruits with a high nutritional value (McKey 1975); species could provide nutritional characteristics that are important for specific parts of the disperser's life cycle (Whelan *et al.* 1998); species could provide nutritional characteristics that complement the disperser's changing needs during the seasonal cycle; species could produce high quality fruits for short periods or low quality fruits for a longer period (Herrera 1982).

Nutritional elements in plant material which may be relevant to birds include carbohydrates, minerals, lipids, and protein (Herrera 1982). The last mentioned two have been the components most dealt with in the literature (Snow 1971, Foster 1977, James *et al.* 1991, Powlesland *et al.* 1997) and are likely to be among the most valuable components to frugivores. In hot seasons when water is limited, moisture content of the pulp may increase in importance. During the breeding season of the Chatham Island parea, Powlesland *et al.* (1997) proposed that a particular fruit (hoho), relatively rich in lipids and carbohydrates, was of importance to the successful breeding of this species.

This chapter investigates the different nutritional qualities of the kereru's main food species in Whirinaki Forest. Fruit and vegetation have both been analysed as they have important roles in the nutrition of the kereru. The availability of the fruit, and fruit quantities is also analysed to determine whether any of the plants may have adapted to suit the needs of their predominant disperser.

6.3 Methods

6.3.1 Criteria for selecting plants for analysis

Certain individual plants within a species may carry higher levels of toxins than others and therefore be more unpalatable to animals (Lee & Johnson 1984, Martinez Del Rio & Karasov 1990, Schmidt 2000), therefore plants were selected only if kereru had been seen feeding on them. Because of the amount of plant material required, in some circumstances samples from several trees (growing in the same general area) had to be combined. Fruit was picked from the trees when it was ripe and at a stage that kereru were feeding on it (Photo 6.1). Only new mahoe and kowhai foliage was picked for analysis as it was mainly at this stage that kereru fed on it. Leaf buds were also included among the new leaves.

Photo 6.1 Dave Wills (DoC) collecting ripe tawa fruit.



6.3.2 Preparation of plant material

Vegetation and fruit samples were frozen for transportation as soon as possible after being picked. The fruit samples (with the exception of kotukutuku) were then de-seeded using sterile equipment to avoid contamination. Kotukutuku was left entire as there are hundreds of minute seeds within each fruit so de-seeding was not a realistic option. All samples were freeze-dried to wait for testing.

Additional fruit samples were gathered to obtain physical measurements of number of seeds per fruit, fruit weight and seed weight.

6.3.3 Nutrient analysis

The Nutrition Laboratory at Massey University, Palmerston North was contracted to analyse the nutritional components. The following methods were used:

Total Dietary Fibre	AOAC Method 991.43
	AOAC Method 985.29
Gross Energy	BS1016 Method (Part 5)
	BS3804 Method
	BS4379 Method
	IP 12, ASTM D240, DIN 5108, DIN 51785 (Gallenkamp Autobomb)
Dry matter/ ash	AOAC Method 950.46 (B)
	AOAC Method 950.02
	(105°C 16hrs/500°C 16hrs)
Fat	AOAC 1995, 16 th Edition, 39.2.05 (Soxtec Analyser)

Protein	Leco Analyser Leco Corporation 1994: FP-2000 Protein/Nitrogen Analyser Instruction Manual
Soluble sugars	Boehringer Mannheim enzymatic test kits. Cobas Fara autoanalyser
Hot water soluble CHO	Nelson's determination of reducing sugars

The dry weight percentages and amount per weight were used for analysis.

6.3.4 Statistical analysis

The nutrition data were analysed using SAS version 8.e. PROC CLUSTER was used to elucidate similarities and differences between species. For this, Ward's minimum variance method (Sas Insititute Inc. 1990) was used, an approach based on within-group sums of squares rather than the distances. PROC TREE was then used to produce dendrograms. Principle component analysis (PROC PRINCOMP) was used to ordinate the species according to their nutritional composition. Analysis of variance (ANOVA) was used to analyse differences between groups.

6.4 Results

The most noticeable difference between the fruit and the vegetation was that the vegetation was very high in protein and very low in carbohydrates (Table 6.1). The food species were broadly divided into two main clusters (Fig 6.1) for, respectively, the vegetation and the fruit. Between the two vegetation types mahoe was higher in protein and kowhai was higher in sugars.

The fruit cluster was subdivided into two further clusters, a sugar-rich cluster and a sugar-poor cluster. The fruit in the sugar-rich cluster also had high levels of protein. The main factor separating the two fruits in this cluster was

the high levels of carbohydrates and glucose in the mahoe and the high levels of lipids in the tawa.

The two most closely linked fruits of the sugar-poor cluster were remarkably similar in all nutrients tested with the exception of carbohydrate, for which miro had a considerably higher percentage than kotukutuku. Miro had a low percentage of moisture, as did kotukutuku, however all these factors may have been influenced by the inclusion of seeds in the analysis of kotukutuku. Makomako is included in the sugar-poor cluster, also being relatively deficient in lipid levels, makomako did not have high levels of any of the nutrients tested for. Karamu was more distant from the other fruits in the sugar-poor cluster, mainly due to the high lipid levels it contained.

When the physical characteristics (Table 6.2) were included with the nutritional characteristics for the fruits, the clustering pattern showed some changes (Fig 6.2). Miro and makomako were the most closely grouped, in a cluster with karamu and kotukutuku. Mahoe and tawa were again separated from this cluster but were also separated from each other.

Species	Moisture %	Organic Matter%	Protein %	G.E. kJ/g	HWSC %	Lipid %	Glucose %
Tawa FRT	81.3	94.78	10.13	22.5	42.14	10.86	23.86
Mahoe FRT	77.54	88.84	14.7	23.68	71.47	2.1	35.2
Miro FRT	64.01	94.35	6.59	19.13	52.36	4.45	14.75
Kotukutuku FRT *	68.46	95.04	8.48	20.46	33.04	3.08	15.18
Makomako FRT	73.93	93.93	4.52	17.24	35.81	1.21	14.59
Karamu FRT	80.93	93.35	4.49	22.56	44.06	8.1	17.95
Mahoe VEG	88.82	92.86	43.85	19.6	8.23	2.3	4.57
Kowhai VEG	75.44	95.88	27.89	20.72	9.55	3.01	11.02

* Because kotukutuku seeds were extremely difficult to separate from the fruit flesh the seeds were included in the analysis.

Table 6.2 Physical measurements of fruits for a range of species

Species	Sample size	Number of seeds / fruit		Fruit weight (g)		Seed weight (g) (single / total)		Percentage fruit flesh	
		mean	range	mean	s.d.	mean	s.d.	mean	s.d.
Tawa	40	1	1	5.23	0.81	2.89	0.38	44.74	3.64
Mahoe	40	8.6	6-12	0.04	0.02	0.001 / 0.01	0.01	69.29	6.84
Miro	40	1	1	1.35	0.3	0.57	0.1	57.78	5.42
Kotukutuku	40	450*	400-500*	1.06	0.2	0.0001 / 0.45	0.0005	57.55	7.29
Makomako	40	7.8	5-9	0.11	0.03	0.005 / 0.04	0.01	63.64	7.63
Karamu	40	2	2	0.08	0.02	0.01 / 0.02	0.01	75.31	8.05

* Figures obtained from L.A.Sessions 2000, Forest & Bird website (www.forest-bird.org.nz)

Figure 6.1 Cluster analyses for kereru food species using Ward’s Minimum Variance method based on nutritional components.

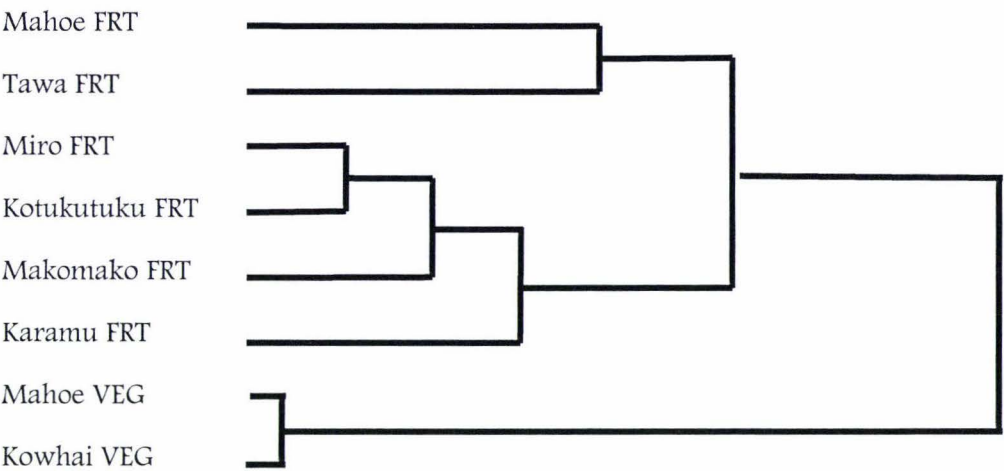
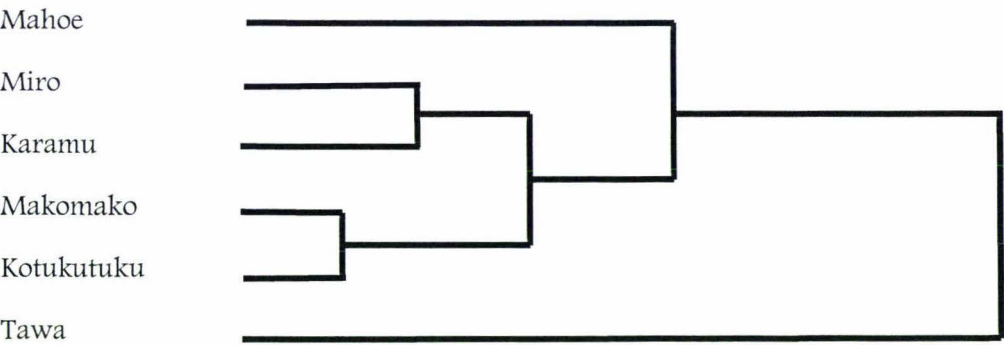


Figure 6.2 Cluster analyses for fruits using Ward’s Minimum Variance method based on nutritional components and physical characteristics.



The cluster analysis (Figs 6.1 & 6.2) indicated five main types within the foods studied:

- Type 1: Foliage high in protein and low in sugars (mahoe and kowhai).
- Type 2: Small sugar-poor fruits with one or two seeds with reasonable levels of carbohydrates (miro and karamu).
- Type 3: Small sugar-poor fruits with multiple seeds with relatively low levels of all nutrients (makomako and kotukutuku).
- Type 4: Small sugar-rich fruits with low lipid levels and high levels of carbohydrate and protein (mahoe).

Type 5: Large sugar-rich fruits with very high lipid levels and high levels of protein (tawa).

Overall the levels of gross energy did not fluctuate much between species, regardless of food type.

A principal component analysis was performed on the nutritional components of all food types and on the nutritional components and physical characteristics of the fruits (Figs 6.3 and 6.4).

For all food types, the first principal component explained about 57% of the variation in the data but did not reveal clear groupings consistent with the results of the cluster analysis (Table 6.3a). The first principal component could be labelled ‘a weighted average of all food types’ or, as they have relatively stronger loadings compared to the other nutrients, ‘sugars and lipids’. The second principal component explains about 22% of the variation. This principal component can be labelled ‘protein’ and has a moderate negative loading for fat.

Table 6.3a Component loadings for principal component analysis based on nutritional components.

Eigenvalues of the Correlation Matrix

	Eigenvalue	Difference	Proportion	Cumulative
Prin1	2.86030838	1.75438035	0.5721	0.5721
Prin2	1.10592803	0.25447213	0.2212	0.7932

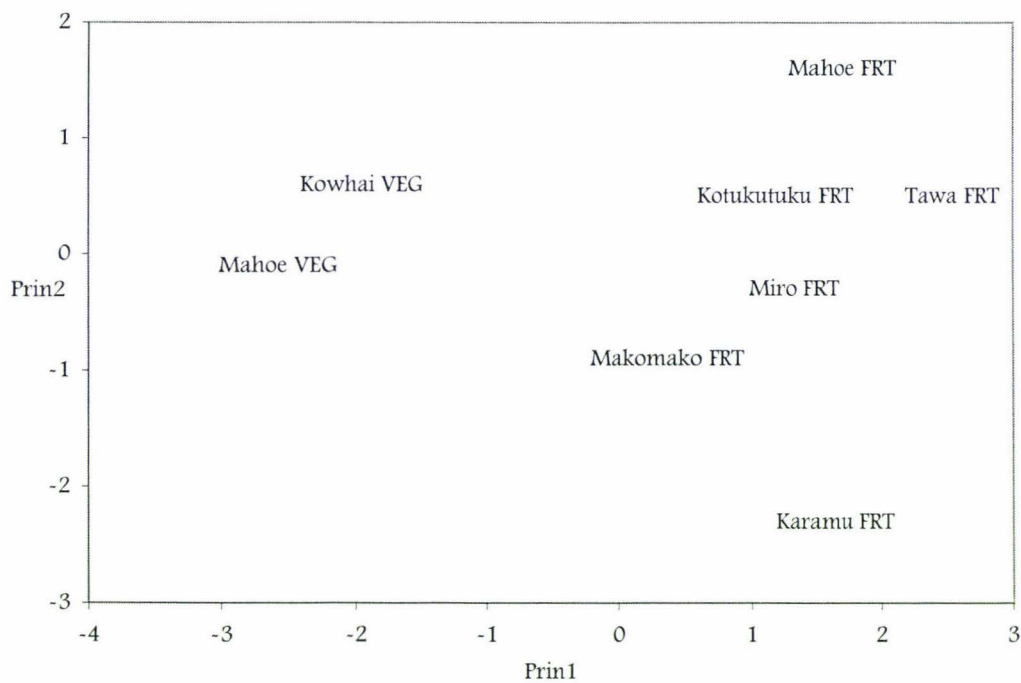
Eigenvectors

	Prin1	Prin2
Protein	0.234682	0.912583
Energy	0.520481	-0.240682
Carbohydrates	0.502364	-0.103952
Lipids	0.409823	-0.309421
Glucose	0.523015	0.159604

The first two principal components (Fig 6.3) show distinct separation of vegetation and fruit. Although vegetation was comparable with fruit along the second principal component, due to high protein levels, it was not as nutritious

as fruit when sugars and lipids were taken into account. Kowhai was slightly more nutritious than mahoe because it had higher loadings for proteins and sugars and fats. Among the fruits, karamu had moderate amounts of sugars and fats but was low in protein. Mahoe fruit was high in protein but not quite as nutritious in terms of all other nutrients. Makomako fruit had moderate amounts of all nutrients, but kotukutuku was slightly more nutritious overall than makomako. Miro had high loadings for sugars and lipids and a moderate loading for protein. Mahoe was very high in sugars and protein but not fat. Tawa appeared to be the most nutritious fruit overall with high levels of sugars, fats and protein.

Figure 6.3 Principal component analysis based on nutritional components, FRT = fruit flesh, VEG = leaf tissue including midrib.



When the nutritional components for the fruit types were combined with the physical characteristics of the fruit a similar pattern to that just described was seen. The first principal component explained about 44% of the variation and can be called ‘physical characteristics and lipids’ (Table 6.3b). The second principal component (which explained a further 28% of the variation) can be called ‘protein and sugars’. The number of seeds in a fruit did not impact on either of the first two principal components.

Table 6.3b Component loadings for principal component analysis based on nutritional components and physical characteristics.

Eigenvalues of the Correlation Matrix

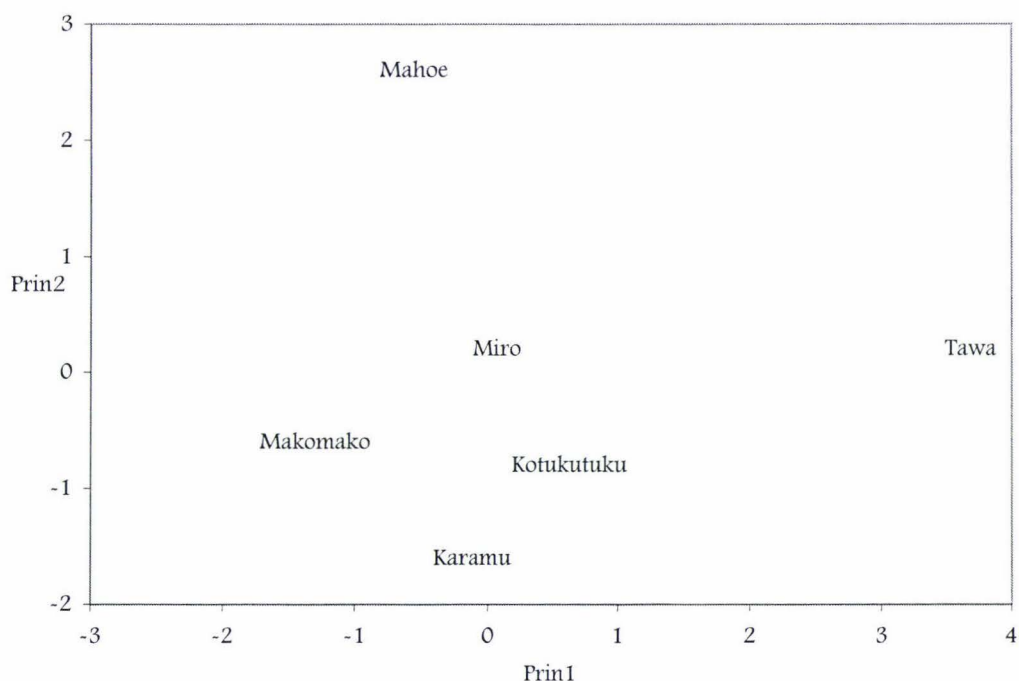
	Eigenvalue	Difference	Proportion	Cumulative
Prin1	3.07869208	1.12170467	0.4398	0.4398
Prin2	1.95698741	0.82234524	0.2796	0.7194

Eigenvectors

	Prin1	Prin2
Protein	0.302154	0.533005
Energy	0.347838	-0.455601
Carbohydrates	-0.042698	0.400441
Lipids	0.462727	-0.247596
Glucose	0.248393	0.535327
Fruit weight	0.550788	-0.009603
Fruit flesh	-0.454651	-0.003103
Seeds	-0.050086	-0.044653

Karamu and miro had similar values for physical characteristics and size but were separated when the levels of protein and sugars were taken into account (Fig 6.4). Miro was higher in protein and sugars than karamu. In the same way, makomako and kotukutuku were similar in terms of protein and sugars but differed in physical characteristics and lipids. Kotukutuku was larger with more flesh and had higher lipid levels than makomako. Mahoe and tawa were at different extremes: mahoe had small fruit with very high levels of protein and sugars but low lipid levels, whereas tawa fruit was very large with higher levels of protein and sugar than most other fruits and also much higher lipid levels.

Figure 6.4 Principal component analysis for fruits based on nutritional components and physical characteristics, FRT = fruit flesh, VEG = leaf tissue including midrib.



6.5 Discussion

The amounts of gross energy in each food type were very similar and the differences between the species may be biologically insignificant for kereru. The other nutritional components, however, varied much more between the food types.

Of the nutrients tested, lipids and proteins are frequently dealt with in the literature (White 1975, Foster 1977) and are probably among the most valuable ones for frugivores (Herrara 1982). Lipid-rich or protein-rich fruit require intensive digestion and are not absorbed as readily as sugars (Afik & Karasov 1996, Witmer 1998). Thus fruits with high levels of simple sugars (e.g. glucose) would have an advantage because frugivores are not energy-limited when eating sugary fruits. None of the fruits tested contained extremely low levels of sugar - even young kowhai foliage contained a significant level of glucose.

Contrary to previous studies (Snow 1971, Howe & Vande Kerckhove 1980, Karasov & Levey 1990), Witmer (1998) found that the seeds of bird-dispersed fruits often do not impose bulk-processing limitations on frugivores. So the physical composition of the diet can become far less important than the nutrient content. At Whirinaki the species grouping did change, but not dramatically, when the physical characteristics were included in the analysis. The physical factor that created the most division was fruit size and, consequently, percentage of flesh. But this factor separated only the largest fruit from the remainder.

According to Herrera (1981) the physical characteristics of a fruit can affect its nutrient composition. Large-seeded species, whose seeds are close to the maximum gape widths of attendant frugivorous birds, should tend to keep the thickness of the flesh to a minimum. Such an adaptation would not increase total fruit size to a point where the fruits would no longer attract appropriate dispersers of sufficient size but would, instead, facilitate fruit-eating species which attack the whole fruit and leave the seed attached. In such situations dispersal of the tree's propagules is impeded. In the case of tawa, the seeds have a low percentage of fruit flesh but it is more nutritious than the flesh/vegetative matter of the other species. However, the evolutionary question of whether this is an adaptation of tawa fruit to attract dispersers to a large seeded fruit (as thought by Snow 1970, Snow 1971, McKey 1975, Howe & Estabrook 1977) or simply a scaling effect resulting in a higher concentration of nutrients in a smaller percentage of fruit (as suggested by Herrera 1981) remains unanswered. As mentioned by Snow (1973) for some frugivores, the distensible gape of some bird species probably constitutes an adaptation to feeding on large-seeded fruits. Kereru provide an example.

Past studies have suggested that the sugar composition of fruit has been influenced by the birds that consume and disperse the fruit (Levey 1987, Levey & Grajal 1991). The preferences of fruit-eating birds for different sugars may have important coevolutionary consequences. Martinez Del Rio *et al.* (1988) and Martinez Del Rio and Karasov (1990) found that frugivorous birds are often sucrose intolerant and that the pulp of most bird-dispersed fruits is rich in glucose and fructose but contains only small amounts of sucrose. They found that the inclusion or exclusion by birds of many fruits was associated with their

sugar composition. This finding has been confirmed in New Zealand by A. Dijkstraaf (unpublished data) and M. Clout (unpublished data). Only one simple sugar was tested for in this study so preferences related to sugar composition cannot be accurately determined. However glucose does not appear to have an over-riding influence on fruit preference as the two most important fruit species, tawa and miro, (Chapter 4) had significantly different glucose compositions of 23.86% and 14.75% respectively.

The importance of lipid-rich fruits as a source of energy and nutrition is well documented for many vertebrate frugivores (McKey 1975, Snow 1981, Leighton 1982, Powlesland *et al.* 1997, Kannan & James 1999). The nutritious quality of the pulp of lipid-rich fruits means that even small amounts can offer a significant contribution to a bird's daily energy needs. This is particularly important around the breeding season because of the heavy metabolic demands for energy on parents and young birds. The fruiting of tawa normally extends over the typical breeding season of the kereru. Karamu fruiting also peaks during this period, although it is available over the greater part of the year, and is high in lipids. Many studies have shown a positive correlation between breeding activity of frugivores and fruiting peaks (Berthold 1976, Leighton & Leighton 1983, Powlesland *et al.* 1997, Kannan & James 1999).

Protein is an important nutrient for growth and that the protein requirements of dispersers are probably highest during the period of moult and when young are fledging due to the increased need for protein that these activities imply (Fisher 1972, Payne 1972, Roudybush & Grau 1986). The fruits that have the highest levels of protein in Whirinaki Forest are tawa and mahoe. These two species fruit sequentially, and encompass the breeding and fledging period of kereru. This may represent diffuse coevolution as both plants provide a needed resource for the disperser at slightly different times of the year. The other food types that have high protein levels are mahoe and kowhai foliage. New growth kowhai leaves are available over the period in which 75% of kereru have shown some signs of moulting (Higgins & Davies 1996) and partly during the period of the growth and fledging of the chicks. Kereru also undergo a slow continuous moult year round (Higgins & Davies 1996). New mahoe leaves are also available during the period when the young are growing and still gaining their adult plumage (Heather & Robertson 1996). Since the protein content of new

foliage is, on average, 4.4 times that of the fruit (Table 6.1) it may play a more important role in kereru nutrition than originally thought.

According to Herrera (1984) if plant species were competing with each other for the attention of seed dispersers, two strategies they might use would be to produce poor-quality fruits for a long period of time or high-quality fruits for a short period of time. In Whirinaki forest the highest quality fruit, tawa, appeared for a short time, even having occasional biennial and mast seeding patterns, therefore being available only every second or third year. However, another highly nutritious fruit, mahoe, had ripe fruit available for seven months of the year, peaking in autumn. This extended fruiting was primarily achieved by having two cohorts of fruit on the same tree. The other autumn fruiters, miro and karamu, also had staggered fruiting within the population and produced ripe fruit for seven and ten months of the year respectively. Although miro and karamu fruits are sugar-poor they have high levels of carbohydrates, and karamu has high lipid levels. Of the six species tested, makomako and kotukutuku produced the poorest-quality fruits for a period of five and six months respectively. It appears, therefore, that with the possible exception of tawa, these species seem to follow a seasonal trend for fruiting longevity rather than a nutritional trend because the groups of summer fruiters and autumn fruiters fruited for a significantly different period of time ($F=4.75$, $df=2$, $p=0.09$) whereas the division between nutrient-rich and nutrient-poor fruits was not significant in regards to fruiting period (Table 6.1). Kannan & James (1999), in a study on the relationship between fruiting phenology and the great pied hornbill in southern India, found that lipid-rich fruits were highly seasonal in availability while sugar-rich fruits were available throughout the year. There was no evidence in the Whirinaki kereru study of such a pattern among the small number of species analysed.

The levels of carbohydrates are significantly higher ($F=4.92$, $df=2$, $p=0.09$) among the species (e.g. miro, mahoe) that produce ripe fruit in the colder season. Studies have shown that many birds will select foods with high levels of carbohydrates during cold temperatures (Mills *et al.* 1980, Herrera 1982). Carbohydrates can be very important during this stage because a high energy source is needed in order to meet the metabolic requirements of thermoregulation and lipids are not always readily available during this time

(Foster 1977, Mills *et al.* 1980, Herrera 1981). A literature search did not reveal a reason for the seasonal availability differences between lipids and carbohydrates.

Lipids and soluble carbohydrates are probably the primary suppliers of energy. If enough energy is available their relative amounts within a food source may be of minor importance unless the food source is also a significant source of moisture. Once the basic energy demands of kereru are met excess energy is of less importance than sufficient moisture. The general moisture content of the fruit did not vary significantly between the dry season and the wet season, as reported in previous studies (Foster 1977, Herrera 1981, Herrera 1982, Kannan & James 1999). However, miro is one of the predominant fruiters of the wet season and has low moisture content. After feeding on miro fruit kereru have been observed to fly directly to water sources to drink (R. Powlesland, pers. comm.). Kotukutuku also appears to have low moisture content but this may result from the inclusion of the many minute seeds in the chemical analysis. The rainfall at Whirinaki forest is relatively consistent, so standing water is generally available, although amounts can differ depending on season and location. In a location with readily available water, therefore, any lack of moisture in fruit may be no disadvantage in attracting mobile seed dispersing birds as they can always fly to a water source. Williams (1982) came to the same conclusion while studying possum nutrition in Orongorongo Valley. However, predation must also be considered as kereru drinking ground water are far more vulnerable to predation (R. Powlesland, pers. comm.).

With the different plant forms examined in this study it is difficult to generalize about possible environmental conditions resulting in the fruits nutritional qualities. The summer season represents a relatively harsh time for plant species because of generally lower water tables. One theory offered for the coevolution of plants and their dispersers and the competition between plant species for dispersers is the production of watery fruit over the driest months when water is scarcest to the plant (Herrera 1982). That did not occur to a very significant degree within the limited group of plants studied at Whirinaki ($F=1.38$, $df=2$, $p=0.3$). However, (excluding kotukutuku) fruit collected over the summer did have an average of 77.6% moisture compared to 74.2% moisture for the plants with ripe fruit production peaking in autumn (and

collected at this time). The production of high levels of carbohydrates over the coldest months also indicates a loss of energy that could be otherwise used for growth or maintenance. It has been shown (Snow 1971, White 1975) that higher fat levels in fruit during cold periods can make fruit more vulnerable to frosts, so it could be of selective advantage to plants to have very low fat levels in winter. It appears that the nutritional aspects of fruiting phenology are not simply adaptations to environmental conditions and should not be considered as coincidental to the needs of frugivorous birds.

6.6 Conclusions

Of the nutrients studied, lipids, carbohydrates and protein could be the most important for kereru (examined further in Chapter 7). These nutrients are needed to enable the different stages of the life cycle of kereru (i.e. breeding, growth, moulting) and to complement the differing nutritional needs brought about by seasonal changes. Providing the sugar levels meet a minimum requirement the relative amounts may be of little importance.

Lipids are of particular importance during the breeding season (November to March) considering the heavy metabolic demands for energy placed on parents and young birds during this period. Tawa and karamu are both high in lipids and produce ripe fruit over this period. Miro and mahoe fruit into the winter (June to August) and are high in carbohydrates, which are a necessary energy source for frugivores due to the metabolic requirements of thermoregulation. Protein is a vital component of growth and is provided over the moulting period and the period of the growth of the young by tawa and mahoe (which fruit sequentially) and also by young vegetative growth.

The high protein content of new foliage (mahoe and kowhai) suggests it is of greater importance to kereru than previously thought, because of the relatively long growth period of the young and because adult kereru undergo a slow continuous moult. Both of these activities require a constant supply of protein.

There is slight variation between the moisture content of summer and autumn fruiters, providing support for the theory that plants produce moisture for their

seed dispersers during water-limited periods. Other indicators of a coevolutionary strategy are high levels of carbohydrates during the winter, when that energy could be well used by the plant for other purposes and increased fat levels during winter, placing the fruit at greater risk from frosts.

Some species, such as tawa and miro, have high nutritional value, and also exhibit nutritional characteristics that are important for parts of the kereru life cycle and changing seasonal needs (such as high lipid levels in tawa over the breeding season and high carbohydrates levels in miro over the winter). The species do not show a pattern of fruit with similar nutritional qualities being available over the same temporal period.

The physical composition of fruit can be of less relevance to the disperser than the nutritional content; in some cases the size and structure of the fruit may directly affect its nutrient status, for example the large size of a tawa seed could affect the maximum amount of flesh on the fruit and consequently affect the concentration of nutrients in the flesh.

Chapter 7

Home range and movements of kereru

7.1 Abstract

The spacing and movements of kereru within Whirinaki Forest were examined, and home ranges calculated for 18 radio-tagged individuals. Home ranges were estimated using a cluster method to detect disjoint areas within a home range and to give the area of the total home range, which varied from 13.9 ha to 704.2 ha for different birds. Core areas, defined as the area covered by an animal's main feeding and resting sites, showed less individual variation, ranging from 2.3 to 12.2 ha. Some kereru were transient and never settled in the study area; some had a single home range; and some had multiple home ranges. Reasons for these differences are unclear because the ages and sexes of the kereru were unknown, but habitat, forest composition and diet most likely had an influence on range size. Movements were analysed using these birds and data from 35 additional radio-tagged birds. Thirty-one of 53 kereru made short-term movements greater than 1.5 km. The mobile kereru tracked to a different location travelled between 2 and 24 km. Some of these kereru moved to an alternative range, while others made short term movements out of their range and later returned. Indirect evidence suggests that some kereru which were not located after dispersal travelled more than 40 km. Kereru with multiple home ranges were typically in a different location for less than six months but tended to remain in one area for longer over the summer period than the winter period. Movements were related to changes in food availability and food types.

7.2 Introduction

Knowing how animals react to changing patterns of resources in relation to their use of space and time is very important in understanding behavioural, ecological and evolutionary processes. Tracking variation in home range use and movements is essential when studying these responses (Harris *et al.* 1990).

Home range can be defined as the total area an animal traverses regularly while conducting all its principal activities, such as food gathering, preening and roosting. This can include breeding activities such as mating, nesting and caring for young (Burt 1943). The important feature of a home range is that it contains everything the individual needs; food and other life-sustaining factors such as water, protection from predators and the physical environment. An animal's home range can contract, expand or shift seasonally during the year. During the breeding season important features of the home range include nest sites and other requirements for caring for offspring. Another important feature of a home range is its familiarity (Smith 1996). A nomadic animal could find important resources somewhere, but a critical advantage of a regular home range is that the individual may know the location of key resources.

Kereru show complex patterns of seasonal movement (Dawson *et al.* 1978, Clout & Gaze 1984, Wilson *et al.* 1988, Clout *et al.* 1991). Such movements have been associated with their dependence on certain food sources and the breeding season (Clout *et al.* 1986, Clout *et al.* 1991, Ryan & Jamieson 1998). Fruit dependence is seasonal and movements outside the breeding season occur when kereru follow fruiting of certain tree species (Clout *et al.* 1991) which have irregular fruiting and crop sizes that vary from year to year (Lee *et al.* 1991). This may result in different range patterns in consecutive years.

The patchy and uneven distribution of some food species (Stewart & Craig 1985) suggests that individual kereru must make movements relative to available food sources. Differing availability of suitable habitat (e.g. containing food trees, water sources and nest sites) in an area will also affect the spatial and temporal patterns of animals (Carroll *et al.* 1995).

Kereru are highly mobile, as shown by seasonal changes in abundance (Dawson *et al.* 1978, Clout & Gaze 1984, Clout *et al.* 1986, Wilson *et al.* 1988). Using radio telemetry, Clout *et al.* (1991) recorded kereru travelling to areas of native forest 2 - 18 km away from the principal study site and remaining absent from the study site for up to nine months. This study will provide more detail on kereru home ranges, and will add a data set for kereru ranges within a North Island forest. This work is important for conservation, to determine the patch size necessary for forest restoration and to define management units.

In this chapter, the sizes of home ranges and the movement patterns of kereru in Whirinaki Forest are determined, along with variation among individuals and possible reasons for observed differences. Relationships between home range size, movement patterns, food availability and breeding are explored in Chapter 8.

7.3 Methods

7.3.1 Capturing and radio-tagging kereru

Kereru were caught in 10 cm mesh mist nets hung from emergent trees in the two study sites of Oriuwaka and Otupaka, Whirinaki Forest (see Chapter 1 for further details of site). Kereru were attracted to the nets either by placing them in known flight paths, or playing a recording of kereru wing beats.

Each captured kereru was weighed, banded (with a numbered metal band) and marked with pvc-coated nylon leg jesses using unique colour combinations for individual identification. Birds were then fitted with a Sirtrack transmitter, weighing between 20 and 30 g with a battery life of about 20 months. The transmitters were attached to the kereru as 'backpacks' using a weak-link harness (Karl & Clout 1987). Kereru were released at the site of capture, generally within 20 minutes. If a newly caught and processed kereru showed signs of stress or injury and remained on the ground (in danger of being preyed on), it was taken to Rainbow Springs (a wildlife park) in Rotorua for recuperation and later re-released at the original capture site. Kereru were then re-located at regular 10-day intervals on foot, using a Telonics TR4 receiver and a hand-held yagi aerial (Photo 7.1). Some kereru that dispersed out of the study area were first located from a helicopter (four flights over the study period) then located on foot if accessible. Each radio-tagged kereru was searched for at least once every fortnight, and was usually located two to four times during this period.

Photo 7.1 Radio-tracking using the Telonics TR4 receiver and a hand-held yagi aerial.



The marked kereru were tracked over a 32 month period between December 1998 and July 2001. The study birds experienced high rates of real and apparent mortality, consequently, individuals were tracked for an average of only 11.3 months before dispersing or being preyed on. The shortest period of tracking was less than a month after capture and release, and the longest 32 months.

Banding and radio-telemetry of juveniles had also been intended but there was no breeding during the 1999/2000 and 2000/2001 seasons.

7.3.2 Home range and core area calculations

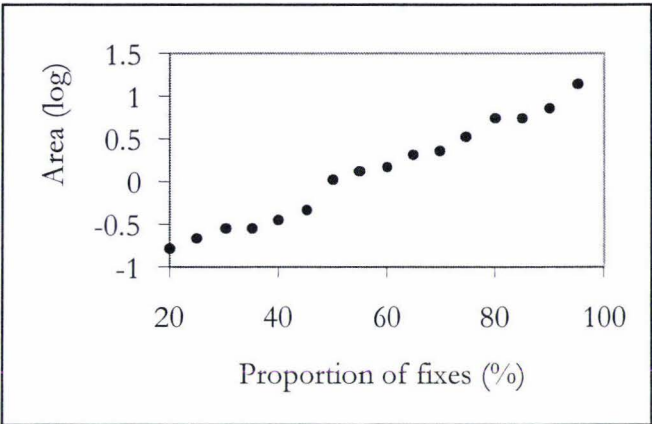
The RANGES V computer package (Kenward 1996) was used to analyse the home ranges of 18 kereru caught at Whirinaki. This package was the most suitable for analysing larger data sets (Gallerani Lawson & Rodgers 1997). Cluster analysis was used to avoid gross over-estimation of the home range. Although minimum convex polygons are commonly used to estimate home ranges, they are drawn around the outermost locations and often reflect the presence of a few isolated fixes, rather than the area in which the animal spends most of its time (Kenward 1996). Peeled polygons (based on excluding the fixes furthest from a single range centre) are also frequently used, however it is less appropriate for studying habitat use when there are several separate foraging areas, because cores can be excluded, or include large areas that are not visited (Kenward 1996). Cluster analysis is useful for such cases as the algorithm draws separate polygon around several centres of activity and creates division between foraging areas. According to Kenward (1996) a core area from cluster analysis is often the best index of the area covered by an animal's main feeding and resting sites.

By plotting the cumulative percentage of home range against the number of fixes and the number of months, the data were visually checked to determine the minimum number of fixes needed over a suitably long period to obtain accurate values (Voigt & Tinline 1980). Of the 53 kereru for which regular fixes were obtained, only 18 met the criteria (followed for a minimum of 12 months with a minimum of 25 fixes – obtained from a visual inspection following Voigt & Tinline's method) for accurate home ranges and were used for home range analysis.

Core area was established by determining the point of inflection on a utilisation graph (Fig 7.1). The graphs were constructed on a log scale and the point of inflection was taken as a step or change of slope. This value differed between kereru but core area remained between 50 and 70% of observations and approximately 6% of total home range. In the case of kereru with multiple ranges, the core area value is the cumulative value of both clusters.

Figure 7.1 Utilisation plot for one kereru (Tx 80), with the point of inflection taken as 50% of fixes. The core area for this bird = 1.07 ha.

% of fixes	ha.	% of fixes	ha.
95	13.71	55	1.31
90	7.28	50	1.07
85	5.52	45	0.47
80	5.52	40	0.36
75	3.4	35	0.28
70	2.24	30	0.28
65	2.01	25	0.21
60	1.44	20	0.16



Home ranges were also computed separately for each season; summer = December-February, autumn = March-May, winter = June-August, spring = September-November.

As the range data and residuals were highly skewed, a log transformation was used when comparing home ranges statistically.

7.3.3 Movements and dispersal

Kereru movements have been analysed following the methods of Clout *et al.* (1991) to allow for comparison. Any kereru travelling at least 1.5 km from its last known location or unlocated for more than 1 week was recorded as having moved. The date of departure by the bird was taken to be the median date between when the kereru was last found in its previous location and the date on which it was first known to be absent. Missing kereru were located by searching in places away from their regular area; searching from high points to allow for an uninterrupted signal; occasional radio-tracking from a helicopter; and regular monitoring of their last known location. The date of return by the bird was taken as the median date between when the kereru was last known to be absent from its previous location and the date it was first known to have returned.

The kereru movements studied were not daily shifts within a range, but longer distance excursions between areas, thus movements were defined in terms of

distance travelled and length of absence. All kereru captured and tracked were included in the analysis for general movements. Kereru tracked over a longer term were examined in greater depth than transient birds by looking at return movements, dates of departures and returns and the habitats they moved between.

7.4 Results

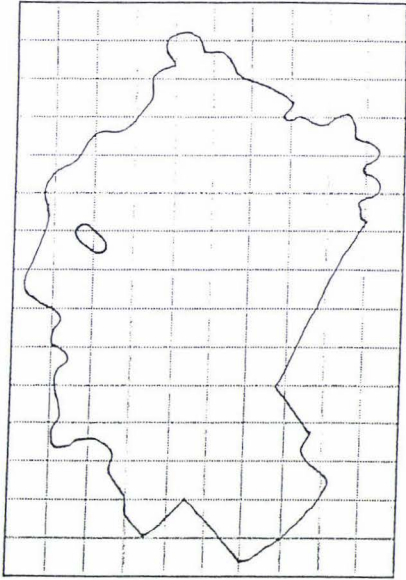
7.4.1 Home range and core area

There was considerable variation in the home ranges of kereru studied at Whirinaki (Fig 7.2, Table 7.1). The mean home range was 163.2 ha ($se=43.4$) with a minimum of 13.9 ha and a maximum of 704.2 ha.

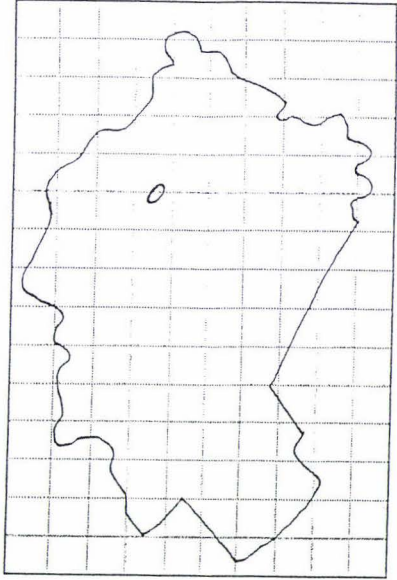
Twelve kereru had a continuous home range and six had a home range consisting of two clusters. One kereru (which did not qualify for further examination due to the short time period over which it was tracked) appeared to have three clusters. Some kereru with one home range showed repeated movements out of this range, but did not spend a significant amount of time in the new location and returned to their home range frequently. Cluster analysis prevented these sporadic movements from being included in the analysis, thus avoiding over-estimation of the range. The kereru with the smallest range was never recorded making movements out of its home range, while the kereru with the largest home range roamed extensively and regularly over the 704.2 ha.

Figure 7.2 Home range boundaries for 18 kereru caught in Whirinaki forest. The boundary of Whirinaki forest is shown on each plot. 1: 1 000 000.

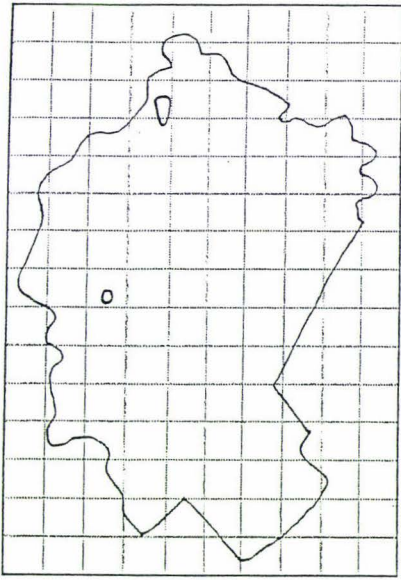
Tx 05



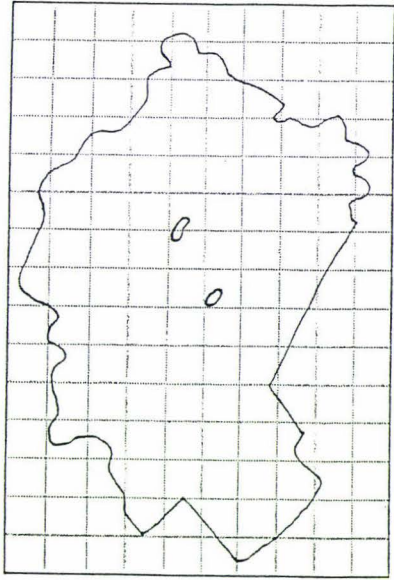
Tx 13



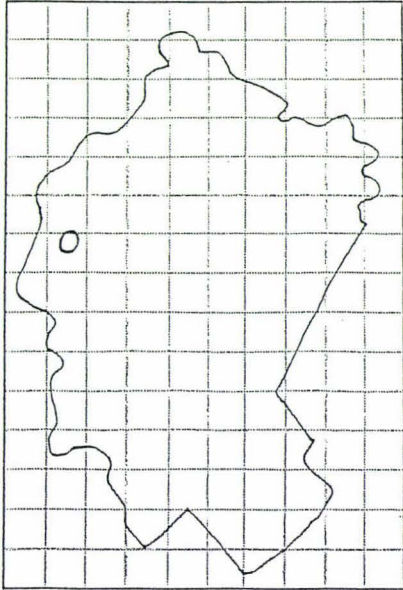
Tx 15



Tx 20



Tx 33



Tx 63

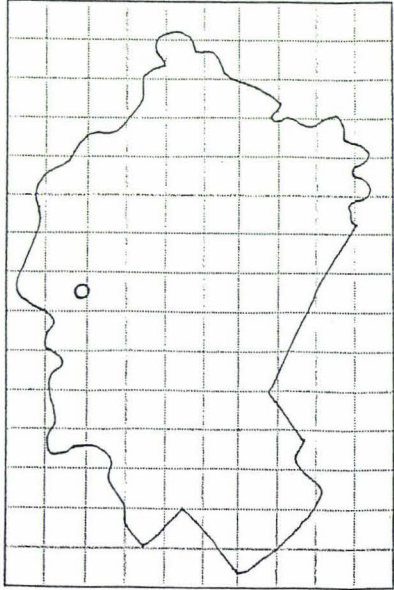
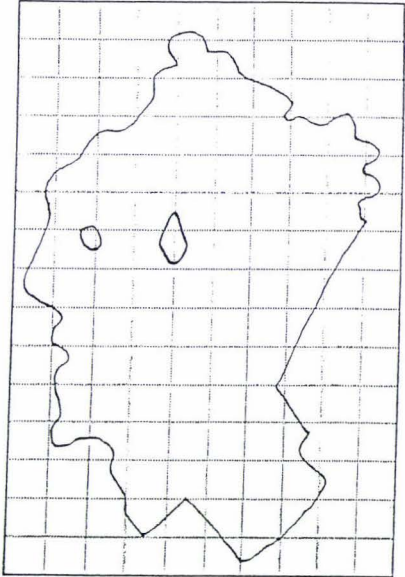
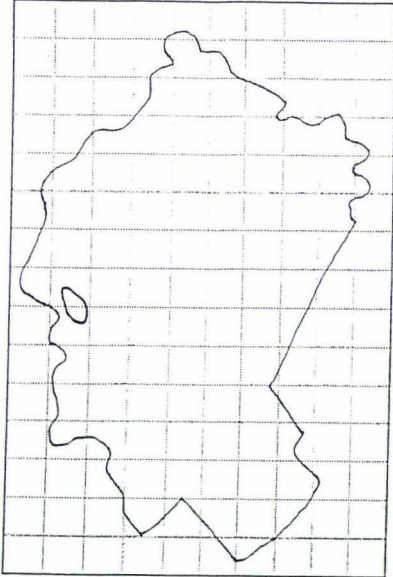


Figure 7.2 continued

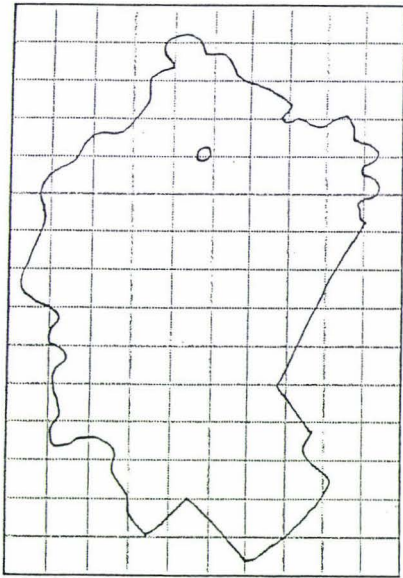
Tx 67



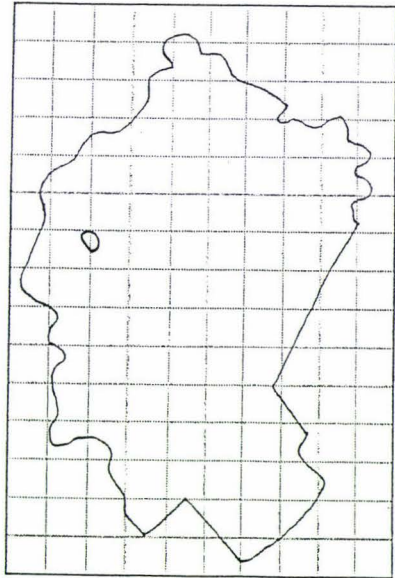
Tx 71



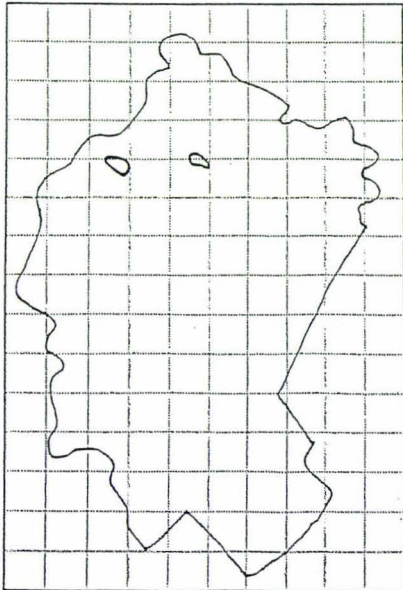
Tx 74



Tx 75



Tx 76



Tx 77

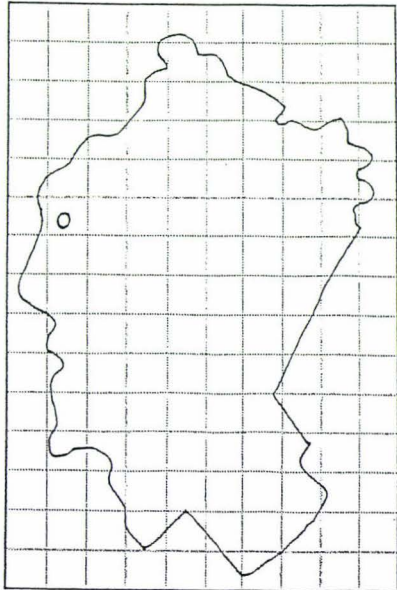
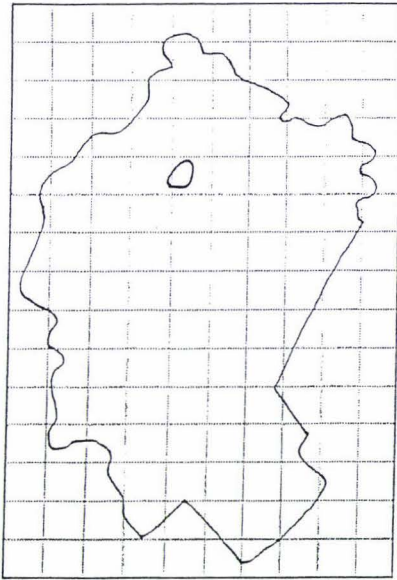
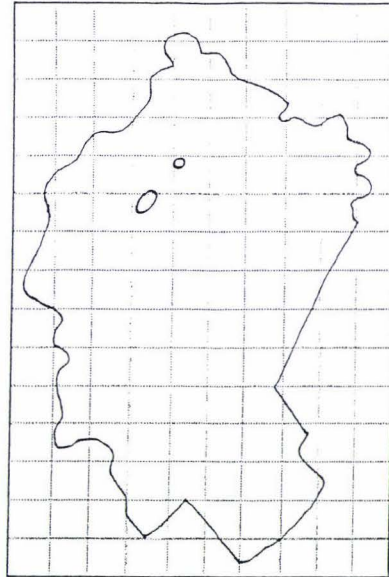


Figure 7.2 continued

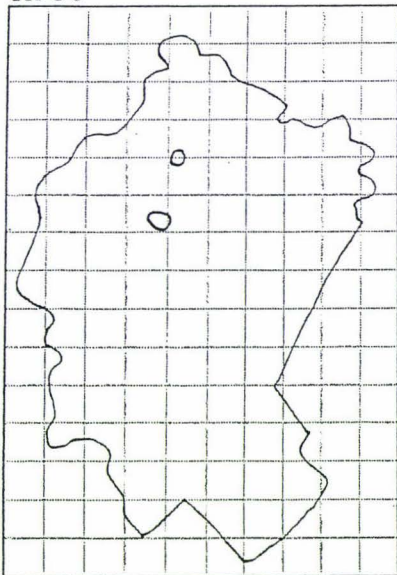
Tx 78



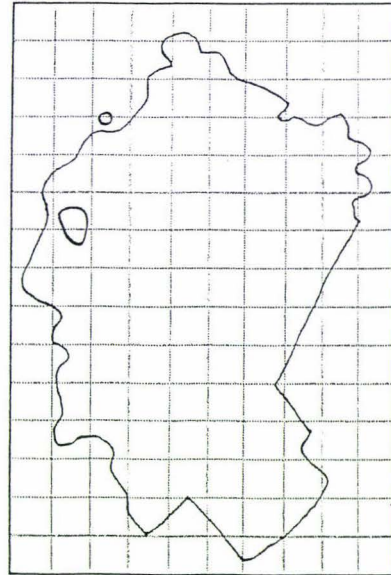
Tx 80



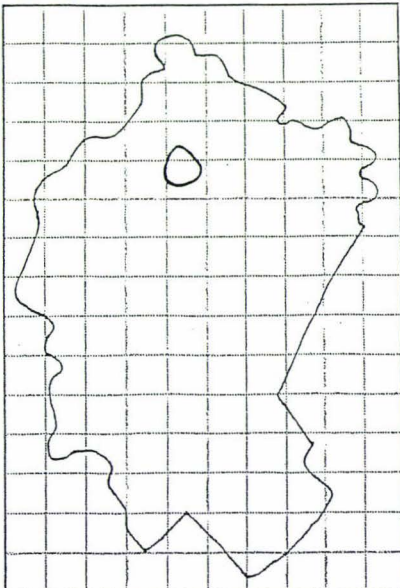
Tx 86



Tx 87



Tx 88



Tx 89

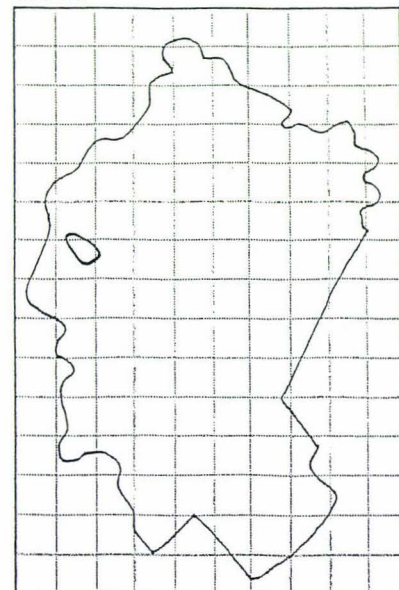


Table 7.1 Cluster analysis ranges (as calculated by RANGESV) for 18 kereru at Whirinaki, obtained between November 1998 and May 2001. Forest type for kereru with multiple clusters is listed as 1=largest range, 2=smallest range. DLP=dense lowland podocarp, MPH=mixed podocarp hardwood, HNS=hardwood ‘nursery’ scrub.

Kereru id number	Range (ha)	Core (ha)	Clusters	Main forest type	Months	Obs
5	117.8	6.0	1	DLP	32	91
13	13.9	1.0	1	MPH	18	43
15	286.4	7.4	2	1. MPH 2. DLP	28	36
20	59.5	4.2	1	MPH	12	41
33	69.7	4.2	1	DLP	13	25
63	16.4	2.0	1	DLP	13	48
67	515.8	11.7	2	1. MPH 2. DLP	25	75
71	372.9	15.9	1	MPH	23	72
74	22.7	1.6	1	HNS	15	34
75	54.8	4.7	1	DLP	15	41
76	181.0	7.9	2	1. DLP 2. HNS	26	43
77	41.0	2.3	1	MPH	17	65
78	83.0	6.7	1	HNS	20	60
80	18.7	1.1	2	1. MPH 2. HNS	16	47
86	61.6	4.4	2	1. MPH 2. HNS	11	25
87	202.1	9.4	2	1. MPH 2. HNS	23	25
88	704.2	26.7	1	MPH	33	53
89	115.5	6.3	1	DLP	18	42

The kereru with two home range clusters spent periods of 2 to 12 months in each cluster. When switching between the two clusters the birds may have flown directly from one to the other, because they were never located between the two disjoint ranges. The distance between these areas ranged from 2 to 16 km. There were no significant differences in size between the home ranges ($T=-1.12$, $df=16$, $p=0.28$) and core area ($T=-0.62$, $df=16$, $p=0.55$) of kereru with one or two range clusters.

The core area size was highly correlated with the home range size ($r=0.95$, $p<0.001$) (Table 7.1). Core area size varied between 1.0 ha and 26.7 ha and average core area was 6.06% (S.E.=0.56) of the entire home range. The kereru with two home ranges had a core area in each range.

There was no significant difference in home range size ($F=0.44$, $df=3$, 68, $p=0.72$) or core area size ($F=0.52$, $df=3$, 68, $p=0.89$) between the four seasons. Kereru with multiple ranges did, however, show obvious differences in range size between the different areas. The smaller of the two ranges was, on average, 30% of the size of the larger range, and neither range was consistently associated with seasonal use.

There was a marginally significant difference in range size between kereru living in different forest types ($F=2$, $df=51$, $p=0.053$) (Tukey-Kramer test). The largest ranges tended to be held by kereru living in mixed podocarp-hardwood forest and the smallest were found among kereru living in regenerating forest (hardwood 'nursery' scrub). Kereru with multiple home ranges consistently had their larger range within mixed podocarp forest and their smaller range within dense lowland podocarp or regenerating forest.

7.4.2 Movements and dispersal

Long distance movements (greater than 1.5km) were made by 31 of the total 53 radio-tagged kereru. Of these 31 birds, 25 were tracked for more than 12 months and were used for more detailed study. During 21 of the movements, the kereru were tracked to their new location, but for another eight the kereru moved to new unidentified locations, their whereabouts unknown until they returned to the original range. These kereru were not even located during extensive helicopter searches, indicating that they may have been over 40km away from their original location. Kereru that were successfully tracked to new locations were between 2 and 24 km away from their previous location.

Eleven kereru whose signals disappeared from the area did not return by the end of the study. Possibly some of their transmitters failed, or the birds died in a location where the transmitted signal could not be detected. On one occasion a located transmitter had undergone human interference and poachers were suspected. It is also possible that some of the 11 birds were transients passing through the study area when they were captured and radio-tagged.

During the study period 45 departures were recorded from areas within Whirinaki Forest (Table 7.2).

Table 7.2 Monthly movements of kereru departing from, and returning to, areas within Whirinaki forest (all data from November 1998-May 2001 combined).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Departures	3	6	7	7	1	2	4	6	5	2	0	2
Returns	3	5	6	2	3	4	2	0	2	0	1	1

Departures from the area had two peaks, the higher one during late summer - autumn (February and April) and the other in late winter – early spring (August and September). Although there were 45 departures, there were only 29 returns. Most of the difference was accounted for by the 11 kereru that did not reappear, while the five others were kereru that settled in another area and did not return to their original location. Nine of those 11 kereru left between the months of July and October and accounted for the majority of the late winter/early spring peak in departures. The other two kereru departed in April. There was a general downward trend in the number of kereru returning as the year progressed, with most returning around the same time as the majority were departing in late summer and early autumn. After a drop in April there was a smaller peak again at the beginning of winter (June). The total number of movements showed a decline over the year when months were grouped into seasons ($\chi^2=8.71$, $df=3$, $p<0.001$).

Twenty-nine return movements were made by 20 kereru (Table 7.3).

Table 7.3 Month of departure and duration of absence from areas within Whirinaki forest (all data from November 1998-May 2001 combined). DR=did not return to original location, M=missing (did not return to study area).

Departure	Duration of absence (months)										DR	M
	<1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	>9		
January	~	1	1	~	~	~	~	~	~	~	1	~
February	1	1	1	1	1	1	~	~	~	~	~	~
March	2	~	1	2	~	~	~	~	~	1	1	~
April	~	1	~	1	~	~	1	~	1	~	1	2
May	~	~	~	~	1	~	~	~	~	~	~	~
June	1	~	~	~	~	~	~	~	~	1	~	~
July	~	~	~	~	1	~	~	~	~	1	~	3
August	~	~	~	~	~	~	2	~	~	~	2	2
September	~	~	~	~	1	1	~	~	~	~	~	3
October	~	~	~	~	~	~	~	~	1	~	~	1
November	~	~	~	~	~	~	~	~	~	~	~	~
December	~	~	~	~	~	~	~	~	1	~	1	~

Fourteen of these birds made one return trip to another area during the time they were tracked; four made two return trips; and one each made three and four return trips. Both these latter birds had two home ranges. Some long distance movements were between home ranges; others were between the home range and another distinct locality, in which the kereru did not spend enough time for it to be considered a home range. Other long distance movements were to unknown locations. The kereru which made multiple return trips would sometimes make a short trip for less than a month, before returning to the area from which they came, and often make a second trip approximately a month later. Of the 29 long-distance movements that included a return to the area of departure, 18 (62%) involved periods of less than six months. Almost all kereru which left during the peak departure times in February and March were absent for less than six months, and only two returned after an absence of more than nine months. The longest absence was that of a bird which returned after 11 months away from the area, and was not located outside the study area. In general, kereru leaving later in the year tended to stay away longer, and all those kereru which departed after June were absent for at least four months. Kereru that left earlier in the year tended to have shorter absences (Table 7.3).

Of the 25 kereru for which movements were monitored for more than twelve months, 14 (56%) made a move out of their home range (nine were of birds with multiple home ranges) and 11 (44%) remained within the boundaries of their home range. The size of the home range of kereru with single main home ranges but which left their home range, and the size of the home ranges of those which remained within them, were not significantly different ($T=1.28$, $df=23$, $p=0.22$) and neither were the core areas ($T=1.19$, $df=23$, $p=0.26$).

7.4.2.1 Repeated movements between home ranges

The six kereru with multiple home ranges made repeated movements between them over the successive years (Table 7.4).

Table 7.4 Kereru usage of multiple home ranges over the tracking period (January 1999 to July 2001). 1=present in larger range, 2=present in smaller range, u=kereru location unknown.

							Keru id number													
15 67 76 80 86 87							15 67 76 80 86 87							15 67 76 80 86 87						
Jan-99	-	-	-	2	1	-	Jan-00	1	1	2	2	-	u	Jan-01	2	1	1	-	-	2
Feb-99	-	-	-	1	1	-	Feb-00	1	2	2	2	-	u	Feb-01	1	1	1	-	-	2
Mar-99	-	-	-	1	1	-	Mar-00	1	2	u	1	-	2	Mar-01	2	1	1	-	-	2
Apr-99	1	-	-	1	2	-	Apr-00	1	2	u	2	-	2	Apr-01	2	1	-	-	-	-
May-99	2	-	-	1	2	-	May-00	2	2	u	2	-	u	May-01	-	2	-	-	-	-
Jun-99	1	-	-	1	2	-	Jun-00	2	2	2	-	-	1	Jun-01	-	2	-	-	-	-
Jul-99	1	-	1	1	1	-	Jul-00	2	1	2	-	-	1	Jul-01	-	2	-	-	-	-
Aug-99	1	-	1	1	1	-	Aug-00	1	1	2	-	-	1							
Sep-99	1	2	1	2	1	-	Sep-00	1	1	2	-	-	1							
Oct-99	1	1	2	2	1	2	Oct-00	1	1	2	-	-	1							
Nov-99	1	1	2	2	1	u	Nov-00	2	1	2	-	-	1							
Dec-99	1	1	2	2	1	u	Dec-00	1	1	2	-	-	1							

Three kereru made repeated movements between the ranges, id"15", id"67" and id"80". These kereru each had two well-defined home ranges, 15km, 8km and 2km apart respectively. They visited these same ranges in successive years, although the timing differed. These ranges were within different mature forest types.

Id “76” and id “87” both performed more circular movements, and were each found in 4 different locations during the study period. Each bird only stayed in two of these locations long enough (between 3 and 7 months) for them to be considered part of the home range.

“67” and “80” had the most year-to-year consistency in their seasonal movements. However, there was variation in the date of their movements between the two areas. “15” followed a similar seasonal pattern, but showed less consistency between the years.

Of the five kereru with a single home range, but which made movements to another location, all were absent for less than two months, three were absent for less than one month. With one exception, all the kereru were missing at some stage over the months of January, February and March. This exceptional bird (id “74”) could have been associated with the disturbance created by the logging of a large area of pine trees less than 50 m away from the centre of its home range. Only one of the five kereru, id “63”, was found in the new location, 7 km away in hardwood scrub forest (its home range was within podocarp hardwood forest).

7.5 Discussion

7.5.1 Home range and core area

Comparisons between studies of spacing in animals cannot always be accurately made because of different methods used to determine home range. Even comparing home ranges for the same species derived from different research can be misleading, unless all choices for software and variables are reported (Lawson & Radgers 1997). The number of observations is also important.

Using the minimum convex polygon method Bell (1996) found at Wenderholm Regional Park that adult kereru had an average range of only 14.83 ha, but immature birds had a much larger average range size at 76.02 ha. In this study the average range size was 163.2 ha, and would have been larger if the minimum convex polygon method had been used. Pierce and Graham (cited in Bell 1996) found that kereru in Northland had average home ranges of 242 ha,

with the population ranging from 80 to 402 ha. The method of analysis used for that study was not reported. Powlesland *et al.* (1992) found that parea (*Hemiphaga chathamensis*) on the Chatham Islands generally had a home range of 20ha (this area was calculated roughly by joining the furthest points where the birds were seen during radio-tracking), but the birds also moved long distances out of their core area to utilise food sources. The results from the Whirinaki work fit within this very broad range of previous studies.

Habitat can influence range size among some avian species, for instance in wood thrushes (Anders *et al.* 1998), grey-headed woodpecker (Rolstad & Rolstad 1995), gray partridge (Carroll *et al.* 1995) and capercaillie (Storch 1995) the ranges differed among different types of habitats and among the differing quality of these habitats. This is a result of availability of habitat, and plant composition of habitat (Anders *et al.* 1998). For frugivores this would be particularly relevant due to the seasonal nature of their food source. If there is no readily available food in their range they could expand their range, make short trips to a food source, or travel to another area. Fruit availability clearly has an influence on the movements of fruit pigeons both in New Zealand (Clout *et al.* 1991, Powlesland *et al.* 1992, O'Donnell & Dilks 1994) and in Australia (Crome 1975, Innis 1989), as the pigeons disperse according to the available food sources. Thus habitat composition has a direct effect on food availability.

The Chatham Islands have 3000 ha of indigenous forest and wetland communities protected in 13 reserves (Coleman 1991). Whirinaki Forest is a 60,000 ha native rainforest (Morton *et al.* 1984). This large continuous tract of forest allows the kereru in Whirinaki to move relatively freely from one forest type to another, and the limited range size of the parea on the Chatham Islands may be a result of lack of available space and the habitat fragmentation of the area. Wenderholm Regional Park is also limited in terms of space when compared to Whirinaki Forest, primarily because of habitat loss and fragmentation; the entire park is 154 ha with 50 ha of coastal broadleaved forest.

Storch (1995) found that capercaillie home range size was inversely related to the amount of late successional forest within the home range. Kereru range size was also affected by forest type. When kereru home range included large

amounts of podocarp scrub forest (e.g. “74”; and the smaller of the two ranges of “86” and “80”) the range size was smaller overall than when it included more mixed podocarp hardwood or dense podocarp forest. These three kereru lived in areas (less than 25 ha) of limited natural forest as they were bordered by exotic pine forest. Although “86” and “80” each had another range within podocarp hardwood forest, “74” made only one short-term movement out of the area, presumably as a response to nearby logging, rather than because of a need to search for food. Kereru surrounded by podocarp hardwood forest had larger ranges, and most kereru with two ranges located them both in mature native forest. When this occurred forest composition within these ranges differed. “67” spent the majority of the fruiting season for wineberry (*Aristotelia serrata*) and miro (*Prumnopitys ferruginea*) in one area where these species were more prolific, and the fruiting season for tawa (*Beilschmiedia tawa*) in the other, where tawa was abundant (Chapter 4).

Total ranges varied between individual kereru in Whirinaki Forest. As bird age was unknown, other than the kereru were adult, it is unclear whether age influenced range size and movements. The sex of the bird may also have influenced range size and movement, but because few kereru were recovered dead and later sexed through dissection, no conclusions can be drawn. Breeding status of the birds was unknown, another factor possibly responsible for the variation. At Wenderholm Regional Park, Bell (1996) found that age and breeding status both had significant influences on the range of the kereru, with adult birds much more sedentary than immature or unpaired kereru. At least four of the kereru in Whirinaki with small, single ranges provided no evidence of a mate. Moreover, one kereru with a small single range was accompanied by another kereru throughout the normal breeding season (November to March) but showed no signs of breeding. Bell (1996) also discovered that the size of the core area did not differ between immature and adult kereru. Although there were no significant range size differences between Whirinaki kereru with one home range and those with multiple home ranges, it is possible that as well as differences in the kereru, there may be some other quality of the home range, such as habitat, that influences this pattern.

Frugivores use their home range with varying degrees of intensity but the bulk of the activity is centered around resting sites and key feeding areas (Wray *et al.*

1992). This is particularly important for kereru because food trees are scattered, therefore the areas within their home range where they can locate food are limited. These core areas are strongly related to the total home range size, but vary less between individuals than the total home range size. The strong correlation between range size and core area indicates that the disparity between kereru in range and core area size could be a result of habitat quality, so that when the habitat is poor a larger range, and core area, is needed to satisfy nutritional requirements. Some studies suggest that home range size is directly related to diet (Carroll *et al.* 1995, Kelt & Van Vuren 2001) however, at Whirinaki, no significant difference was found between range size during the different seasons, e.g. summer while kereru were predominantly frugivorous and winter while they were herbivorous. Some studies suggest that when feeding on foliage, birds do not need to travel far since leaves are a readily available resource (Carroll *et al.* 1995, Kelt & Van Vuren 2001). However, kereru feeding on foliage clearly preferred young leaves of certain tree species (Chapter 4), and moved freely to acquire this limited resource.

Frequently kereru with multiple ranges had a smaller range over the colder period of the year and a larger range over the warmer period, although this could not be statistically linked to season or diet. Kereru with single ranges showed no statistically significant difference in range size between seasons. Kereru leaving after summer and during autumn are gone for a shorter period over winter, and kereru leaving over winter and spring are gone for a longer period over summer. Mobile kereru tend to stay for a longer period in their summer range than they do their winter range.

It was expected that the Whirinaki birds would forage further during winter in order to find food. Rolstad & Rolstad (1995) found in the grey-headed woodpecker, that the winter shift in diet and feeding behaviour was accompanied by an approximately 100 times enlargement in home range size. Possibly kereru with a single range have an appropriate food source within that range and therefore do not need to search more widely. Kereru with multiple home ranges may disperse to an appropriate food source during certain months, then stay by that source while it lasts. The variability within kereru diet may influence home range size because if more species are eaten, then further travel within the area may be required. Another factor that may affect range size

during the colder months is energy conservation. Reducing activity conserves energy (Thomas 1984). Flight imposes large energetic costs (Morton 1978) and since vegetation comprises a large portion of the diet over winter (Clout *et al.* 1991, James 1995) and is not as nutritionally valuable as fruit (Chapter 6), less movement made by kereru implies more energy can be conserved throughout winter. So although folivory alone did not significantly influence home range, it may have been a contributing factor in reduced secondary range size over winter.

7.5.2 Movements and dispersal

The kereru that departed soon after capture and did not return were probably transient birds. At Whirinaki the majority of these birds departed around September and October, and probably represent part of a seasonal movement between winter feeding sites (generally areas consisting of various podocarps) and spring/summer feeding sites. Ripe fruit of tawa, makomako and kotukutuku became available in late spring/early summer and during this stage kereru switch their food preferences from foliage to these fruits (Chapter 4). The birds may also have been passing through the study area in Whirinaki while moving to traditional summer breeding areas, a pattern noted by Clout *et al.* (1991) at Pelorus Bridge. James (1995) found that the main breeding season for kereru at Wenderholm Regional Park began in October/November. Even though no successful breeding was detected at Whirinaki during the study period, display flights were observed on numerous occasions. Display flights are a simple method for detecting breeding activity in kereru (James 1995), so it is likely that breeding attempts were made.

The frequent long-distance movements, both departures and returns, between February and April most likely involved kereru leaving after unsuccessful breeding attempts (nest building was observed during this period), as well as kereru moving to other food sources. Kereru typically depart from an area at the conclusion of the breeding season, which is during early autumn (James 1995) and it is known that kereru at Whirinaki Forest made unsuccessful breeding attempts (pers. obs). Many of these kereru left for a relatively short period and some made brief return trips before leaving for several months. The brief return trips may have been scouting trips to evaluate food availability.

About ten birds left once the miro in their area had ceased fruiting, but were tracked to another area at a higher elevation where miro trees were more frequent, and the fruit remained abundant. These kereru lingered to feed on the miro fruit, then some returned to their original location, while others kept moving. The kereru returned to the study site during winter when they had switched to feeding predominantly or exclusively on foliage. Clout *et al.* (1991) also found at Pelorus Bridge that kereru leaving between February and June were visiting seasonal miro feeding sites. If the breeding site of the kereru contains ample numbers of miro trees, the birds tend to remain in these areas after the breeding season, to continue feeding on the miro fruit which becomes available (Clout *et al.* 1991).

The lack of short-term departures in the later months of the year (July to December) is similar to what Clout *et al.* (1991) found. No kereru departed from Clout's Pelorus Bridge study site between the months of July and October, possibly because the predominant food source at the time was foliage, which was widely distributed and the kereru did not have to travel to another area to feed. In both the present study and Clout's, kereru which did depart at this time of year were absent for relatively long periods, and most did not return until the end of summer, so it is likely that although they left early, they travelled to summer feeding and breeding sites. For tui, Stewart & Craig (1985), found that early seasonal movements enable birds to establish early breeding areas and subsequently obtain the first available food. The first tui to obtain nectar were also the first to breed, which allowed the first brood to favourably compete with other juveniles, and offered the possibility of a second brood. Kereru are strongly territorial while breeding (R. Powlesland, pers. comm.) so kereru arriving early in their breeding area may have similar advantages to those described for tui by Stewart & Craig (1985).

No differences in home range size were found between kereru that performed long-distance movements and those that did not. Rolstad *et al.* (1995) and Anders *et al.* (1998) suggested that birds less able to compete, such as juveniles, are more transient. Bell (1996) found, from a study of six immature and six adult kereru, that immature kereru made more frequent, and longer distance movements. When food is limiting in an area it might be expected that subordinate individuals would move away to a poorer area (Stewart & Craig

1985). However, when new and better food sources such as miro, become available elsewhere, only dominant individuals are expected to move because such birds can ensure access to these improved resources upon arrival (Berquist 1985, Stewart & Craig 1985). Variations in movement may, therefore, be partly explained by differences in status, and differing individual abilities (e.g. ability to compete) may indicate which birds are more likely to move.

7.6 Conclusions

Lack of information about sex, age and relationship status of individual kereru left unclear factors influencing range size and movements.

There is high variability among individuals in terms of home range size and type of movements. This is partly influenced by the different habitat and forest composition of an area. Twice as many kereru had a continuous home range as had a home range consisting of two clusters. A range can be small because it includes all necessary food species, therefore the kereru does not have to travel far to feed. Among kereru with multiple ranges, maintenance of a small secondary range over winter can be a method of energy conservation, or the result of travelling to feed on very specific food sources that do not call for extensive movements. Possibly subordinate individuals dispersed when food was limiting, but when new and more important foods became available only dominant individuals should disperse because they can ensure food upon arrival in a new area.

The number of movements of kereru at Whirinaki declined over the year. Movements, both departures and returns, predominantly occurred between February and April. These movements were influenced by changing food sources or, in some situations, by a shift to a breeding area. It is difficult to distinguish between these two factors because new food sources become available over the breeding season. The majority of transient kereru departed in spring. These were probably travelling to summer breeding or feeding areas, as were some kereru who made long-term trips during the later months of the year. However, some of these kereru left earlier in the year, possibly in an attempt to gain access to the best areas at their destination. Kereru making trips

early in the year often made a few brief return trips before leaving for a longer period. This mainly happened during the early fruiting season for miro. Lack of short-term departures in the later months of the year (June to December) may have been as a result of diet at that stage consisting of relatively accessible (and lower nutritional quality) foliage so there was no reason to expend energy on dispersal.

Chapter 8

Synthesis of kereru feeding in Whirinaki forest

The feeding of kereru, which have a wide diet of fruit and foliage, is influenced by individual and environmental variation. Social constraints on feeding are not addressed in this study, but there are complex interactions between components of feeding under direct environmental influence. These include the overall abundance of food sources in the forest, the density, duration and geographical location of food sources in an edible form, the physical characteristics of the food, the accessibility of the food on the plant, the nutritional content and composition of the food, and the rate of intake by the bird.

The change in kereru diet over the year is clearly related to fruit availability, including not only fruit production of individual trees, but the abundance of tree species in the forest. Accessibility also plays a major role in fruit choice. Diet is strongly influenced by kereru preference for certain species, however a preference index is needed to determine the strength of kereru preference for individual foods.

Of the nutrients studied, lipids, carbohydrates and protein could be the most important for kereru. These nutrients are needed for the different stages of the life cycle of kereru (i.e. breeding, growth, moulting) and to complement the differing nutritional needs brought about by seasonal changes. It needs to be determined whether kereru select foods according to their nutritional needs and the general nutrient content of each food, or if the selection is independent of nutrition *per se*.

There is high variability among individuals in terms of home range size and type of movements. It is likely that this is partly influenced by the different habitat and forest composition of an area. It will be useful to clarify the relationship between food species (i.e. forest composition and availability of certain species) and home range area and movements.

8.1 Feeding behaviour in relation to food availability

The frequency with which some foods are eaten by kereru does not necessarily reflect preference by the bird. Instead, high use may reflect the relative availability of various food items. An index of preference for separate food items can be derived from a Manly-Chesson preference index (Manly *et al.* 1993, Banack 1998). This index was calculated for each month using the data for plant phenology (Chapter 3) and kereru diet (Chapter 4). A yearly mean preference (P_i) was also calculated by pooling all values obtained for the year. The proportion of food in the diet (d_i) was divided by the proportion of food on the trees (N_i) (compared to the maximum possible amount of that food type). This ratio was then normalised so that the sum of all ratios equalled one. The formula applied was:

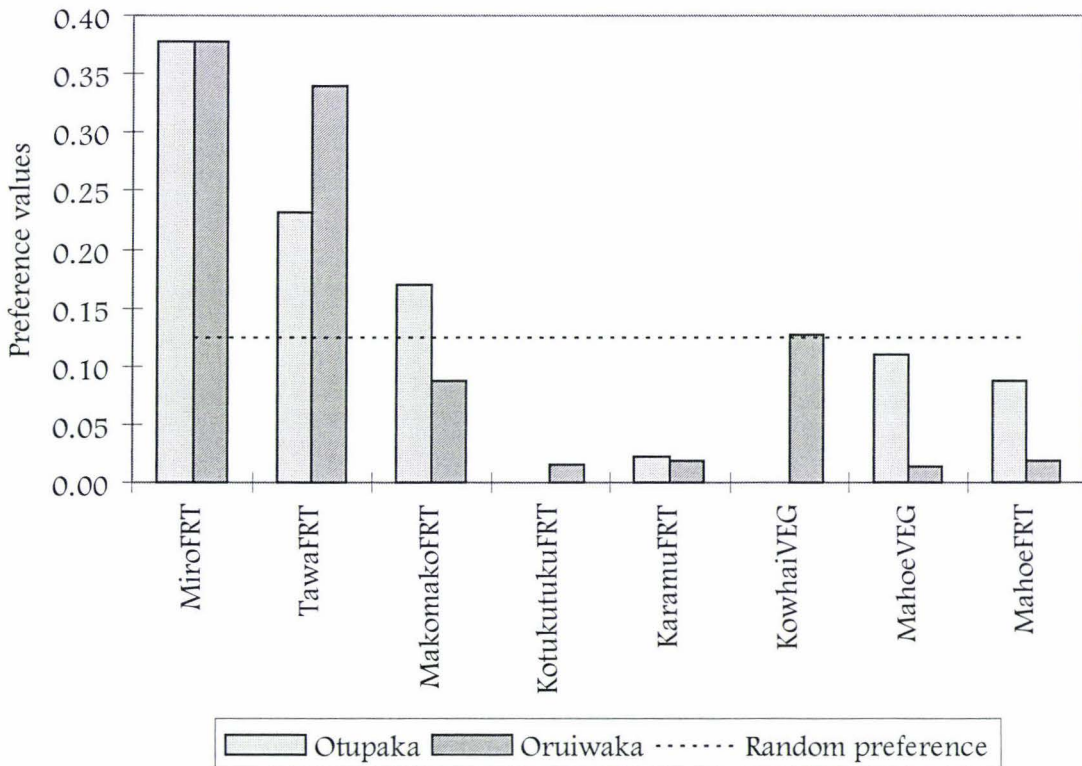
$$P_i = \frac{d_i / N_i}{\sum_{j=1}^k (d_j / N_j)}$$

where $i = 1, 2, 3, \dots, k$, for k food types; P_i = kereru preference values for food type i when foraging in an environment with these k food types available; d_i = the proportion of food of type i in the diet; N_i = the proportion of food of type i in the environment.

The results of this analysis show preferences in relation to the species assemblage chosen. A preference value above $1/k$ indicates a preferred food, values below $1/k$ show aversion to the food (Manly *et al.* 1993), and values close to $1/k$ indicate a food resource used in proportion to its occurrence in the environment (Banack 1998).

Fruits of two plant species, miro (*Prumnopitys ferruginea*) and tawa (*Beilschmiedia tawa*), were highly preferred by kereru (Fig 8.1).

Figure 8.1 Preference values of 8 food types sampled from February 2000 to March 2001. Data represent a mean yearly preference for the kereru population in two regions of Whirinaki Forest. The dashed line represents random preference (1/8). Values above this line reflect a positive preference while those below this line reflect use less than what would be predicted based on a random encounter rate.



Miro was favoured equally in both areas, but tawa was more favoured by kereru in Oriuwaka. Makomako (*Aristotelia serrata*) was preferred in Otupaka but not in Oriuwaka. Kowhai (*Sophora tetraptera*) was essentially taken as it occurred in Oriuwaka. In Otupaka, mahoe (*Melicytus ramiflorus*) foliage showed a preference slightly below random use on the preference index, indicating that it was eaten in a lower proportion than its occurrence in the forest. Mahoe fruit was avoided in both areas, particularly in Oriuwaka. Karamu (*Coprosma robusta*) was available almost year round and was identified as an avoided species (used in quantities far less than those present in the forest) in the analysis of overall yearly preference. Kotukutuku (*Fuchsia exorticata*) was also an avoided species. Kotukutuku in Otupaka and kowhai in Oriuwaka were present in marginal amounts.

Of all the species miro fruit had the highest preference in the yearly index, but when analysed on a monthly basis (Figs 8.2 a and b) it was not preferred in Oriuwaka in January 2001. It was, however, preferred in all other months in which it was available. The preference of kereru for miro fruit in Otupaka declined slightly between when ripe fruit first became available and when fruiting ceased.

Young kowhai foliage also decreased in preference over time, from being one of the most preferred foods in November 2000 to a slightly preferred food in January 2001.

Tawa fruit, the other highly preferred food type, was preferred during all months in Otupaka and three of the four months it was available in Oriuwaka (the exception being January 2001).

Makomako was always a preferred food when available in Otupaka, but only favoured in February both years in Oriuwaka.

When examined on a monthly basis, karamu was actually a preferred food in April and August 2001 in Otupaka. In Oriuwaka, karamu fruit was not used when it was ripening (January – March), but became a highly preferred food for two consecutive months (July and August 2000). Similarly, mahoe fruit was favoured in Otupaka in May and June 2000, although it was constantly avoided in Oriuwaka.

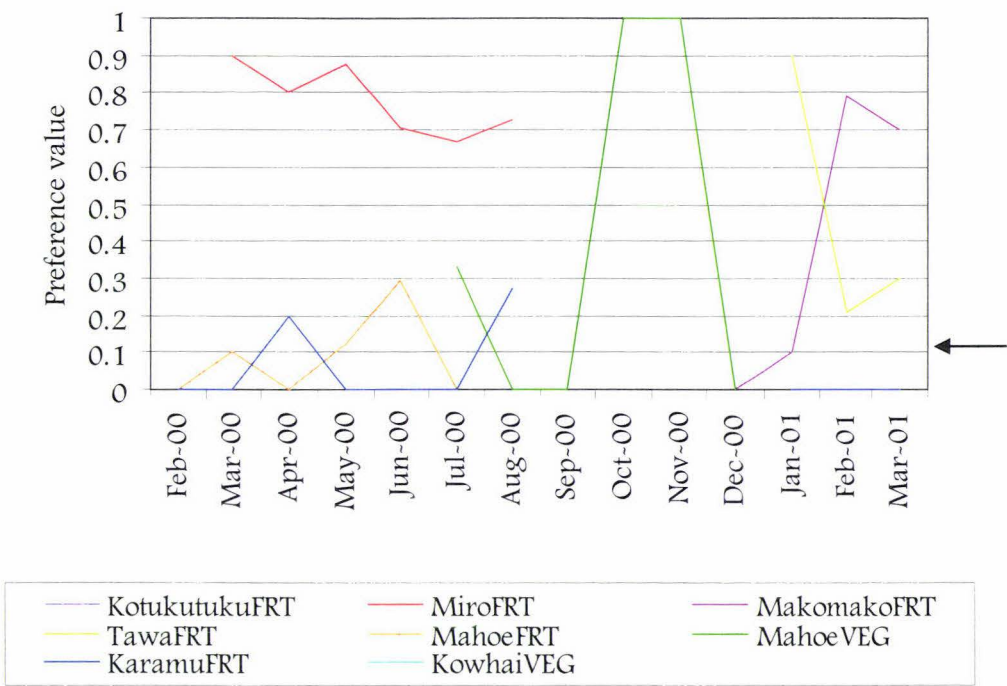
Young mahoe foliage was a preferred food in July 2000, and a highly preferred food in October and November 2000 in Otupaka, before becoming unavailable. In Oriuwaka, however, it was not highly preferred when first becoming available in June 2000, but was strongly preferred one month later, in July. After July, it was actively avoided once more.

Kotukutuku fruit, as indicated by the yearly preference index, was never a preferred food in either area.

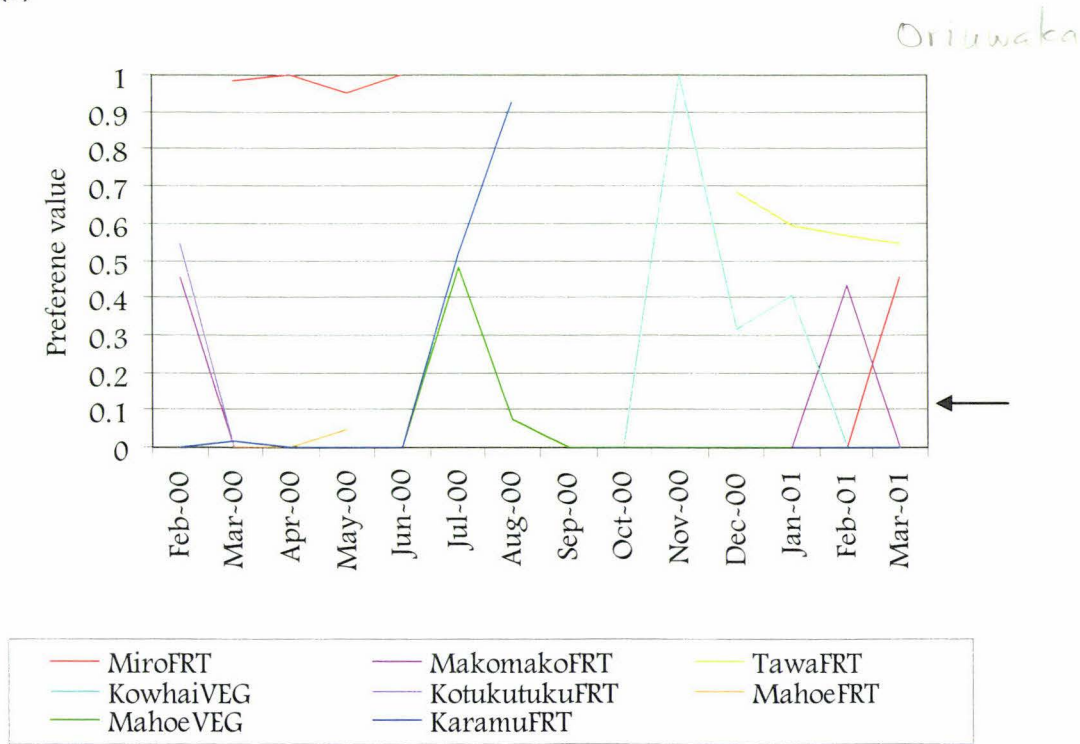
It must be remembered that there are other potential foods that are even more 'avoided' because never featured in the diet of the kereru.

Figure 8.2 Monthly preference index for eight food types in Otupaka (a) and Oriuwaka (b). The arrow indicates random preference of $1/k$. Values above the arrow indicate food types preferred by kereru; values below the arrow indicate a level of use less than what would be randomly expected. Breaks in the line indicate months where that food type was not available. Vegetation values are for young foliage only.

(a)



(b)



8.2 Food nutrient levels and kereru diet

Kereru appear to show preferences for large fruits high in lipids with moderate amounts of protein and carbohydrates. Foods that were avoided in both areas (kotukutuku, karamu and mahoe fruit) were nutritionally quite dissimilar. Mahoe fruit was very high in protein, carbohydrates and sugar while being low in lipids, karamu fruit was high in lipids but low in protein. Kotukutuku fruit was low in lipids, sugar and carbohydrates but relatively high in protein. The nutrition results of kotukutuku fruit may be affected by the inclusion of seeds. Karamu was avoided even though, in the nutritional analysis, it was found to be very similar to miro, the most preferred food. Although these foods are considered to be 'avoided', there are other food species in the forest that may be more actively avoided, i.e. only rarely recorded in a feeding observation (Chapter 4).

Two other fruit pigeons, the Torres Strait pigeon (*Ducula bicolor*) and the White-headed pigeon (*Columba leucomela*) are known to favour lipid-rich fruit (Crome 1975a, Crome 1975b). The kereru appears to have biogeographic, morphological and behavioural links with both these species (James 1995), although it belongs to a different genus (Higgins & Davies 1996). The kereru in northern New Zealand have also shown a preference for lipid-rich fruit (A. Dijkstraaf, unpubl. PhD thesis).

Food selection by frugivores is not, however, solely affected by the nutritional attributes of the food type (Freeland and Janzen 1974, Herrera 1982). Food selection also depends on local abundance and availability (Banack 1998), physical characteristics (Levey 1987), concentration and identification of secondary compounds (Oates *et al.* 1980), digestibility (Schwartz *et al.* 1980) and accessibility (Moermond & Denslow 1983).

Feeding rate may influence food preference. Karamu and mahoe fruit, along with kowhai and mahoe vegetation, yielded relatively small amounts of food during each feeding bout. For example, when feeding on karamu for an average of 12 minutes (typical feeding bout length for this species – Chapter 5) kereru ingested just under 10 g of flesh. In contrast, when feeding on miro, during a

typical feeding bout (lasting an average of 10 minutes) kereru consumed just over 53 g of flesh. Miro also provides more cover against predation than karamu. When feeding on karamu (and other understorey species), ground dwelling predators such as cats (*Felis catus*) and stoats (*Mustela erminea*) are known to prey on kereru in high numbers (pers. obs.). Kereru are also more exposed to attack from raptors such as the New Zealand Falcon (*Falco novaeseelandiae*) when feeding on karamu because they are unable to sit within the safety of the small branches.

Kotukutuku offered a relatively large amount of flesh for each feeding bout, but preference may have been affected by the time it was available, i.e. over the same period as tawa in 2001, which offered higher quality fruit and even more flesh per feeding bout. Seed size may also have affected kereru preference for kotukutuku, where each single seed weighed only 0.0001 g. Relative to small seeds, large seeds are separated from pulp and passed more quickly through the gut (Levey & Grajal 1991). Small seeds may be less enticing for kereru because they impose a longer period of digestion before the birds are able to resume foraging (Courtney & Sallabanks 1992).

The definite preference by kereru for young mahoe and kowhai foliage in Otupaka and Oriuwaka respectively, regardless of fruit availability, supports previous suggestions (Chapter 6) that kereru may be seeking a high protein source during this pre-breeding period, because protein does not appear to be a sought-after nutrient during other periods of the year. Lipid rich fruits probably maintain the condition of the adult birds for breeding, but fruit pulp is considered nutritionally inadequate for frugivorous birds because of its low protein content (Bosque & Pacheco 2000). Protein is an important nutritive element in reproductive activities such as egg production and chick rearing (Ward 1969, Berthold 1976). A. Dijkstra⁹ (unpubl. PhD thesis) also suggested for Northland kereru that some switches by the birds to foliage feeding involved nutrient complementarity, during periods of egg development and nesting, rather than lack of food *per se*. Parea, on the Chatham Islands, also acquired supplementary protein during the nesting season by browsing on herb foliage and flower buds (Powlesland *et al.* 1997). However, excessive protein during the fledgling growth phase can cause chicks to grow more slowly (Roudybush &

Grau 1986), a further reason for foliage (typically high in protein) to be avoided during the autumn.

The high lipid fruit diet postulated for kereru could be associated with increases in body mass that are related to rates of nitrogen intake rather than sugar assimilation (Witmer & Van Soest 1998, A. Dijkstra unpubl. PhD thesis). Fruits (e.g. tawa) favoured over the usual breeding and fledgling periods were high in both lipids and protein/nitrogen. Sugary fruits are high in energy but tend to be low in nitrogen.

Miro fruit stands out as a highly favoured food over the autumn and winter period, and provides the high levels of energy (in the form of carbohydrates) needed to sustain life during the colder months (Herrera 1981). Miro also provides a large amount of food during a relatively short feeding bout.

Many factors affect the value of food types for kereru. The timing and duration of availability of the food type; the abundance of the species in the forest; the density of the food type on the tree; the accessibility of the food type on the tree; the habit and structure of the food tree; the amount of food gained per feeding bout; the food characteristics; the nutritional value of the food; whether the food contains any nutrients of particular importance; and whether the food may contain toxic secondary compounds. Crome (1975a) also found for Torres Strait and White-headed fruit pigeons, that plant form and fruit size, colour, ripeness and nutrient content were associated to some degree with apparent food preferences.

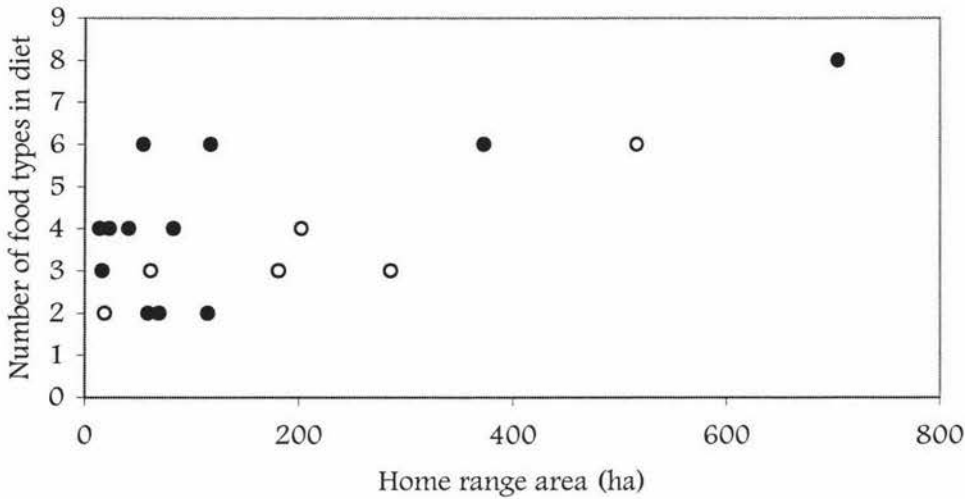
For kereru in Whirinaki Forest, the most important factors in food choice seem to be availability and accessibility of the food type, nutritional content and how much food can be gained from a feeding bout.

8.3 Kereru feeding ecology, distribution and dispersal

There was a positive relationship between number of different food types in a kereru's diet and the size of its home range ($r=0.68$, $p=0.002$) (Fig 8.3). The

relationship was stronger for kereru with multiple home ranges ($r=0.89$, $p=0.01$) than for kereru with a single home range ($r=0.70$, $p=0.01$).

Fig 8.3 Relationship between the number of food species in an individual kereru's diet and that individual's corresponding home range. Solid circle = one home range, open circle = multiple home ranges.



This suggests that in patchy forest there could be advantages to birds exploiting large, rather than small, home ranges. Benefits could include health of the individual through the year and it's likelihood of breeding successfully.

Working with honeyeaters Craig *et al.* (1981) considered that the more sedentary a species is, the more its diet will reflect the availability of preferred foods. Some kereru may have a patch that supplies all of their nutritional requirements; therefore there is no need to expend energy in searching for further food sources. Craig *et al.* (1981) found for the tui, bellbird, and hihi that subordinate individuals may be completely or partially excluded from highly preferred (and often concentrated) food sources, and are more likely to feed on more dispersed and less rewarding items. Kereru feeding on a highly preferred food (such as miro fruit) eat little else; but when feeding on less desirable or a range of equally desirable food items their diet is more variable (Chapter 4).

If food is not readily available, kereru may have to range further to find sufficient sustenance. However kereru with multiple ranges tended to occupy the smaller range over the colder months when preferred foods were scarce. During this period kereru predominantly fed on abundant and easily accessible foods such as mature foliage, which were not as nutritionally rewarding as fruit. They did not travel far to feed on mature vegetation during this period, possibly because this food was already accessible, and possibly because it was not energy-rich. Miro was also a major food during this period and when the kereru were focusing on single foods such as miro, there was clearly less variation in the diet (Chapter 4), as well as less need to travel to find different food sources. Because miro trees were scattered, and each individual tree produced large fruit crops, once kereru reached a miro tree they would stay in the general locality as long as fruit remained, rather than travel between different trees. Kereru with multiple ranges predominantly fed on miro while they were in the smaller range, where they stayed for the three to five months miro was fruiting.

In the colder months of autumn and winter, fewer species were consumed overall. During the warmer seasons (spring, summer) some higher energy foods (such as tawa) were available and were more evenly spaced through the forest. Kereru tended to travel over a greater area while feeding on tawa. The greater variation in the diet during the warmer months (spring and summer) was largely due to the kereru being less specialised during this time, i.e. there was a greater availability of preferred species, including immature foliage and different fruit species, and flowers were also readily available during spring. The shift in diet to encompass more species was accompanied by a corresponding shift in range size, which probably reflected the availability and spacing of the different food species. Kereru did not tend to be exclusive during this period; immature foliage formed a large part of their diet as did fruit. Therefore they tended to move about freely, feeding on all food sources. The same pattern of less diet specialisation leading to an enlarged range size has also been seen in the grey-headed woodpecker (Rolstad & Rolstad 1995) and gray partridge (Carroll *et al.* 1995).

It is tempting to explain the increase in home range size as simply a consequence of changing food availability, however, during the spring/summer

period some kereru were also involved in travelling to and from historic breeding sites (as determined by DoC workers prior to the commencement of this study (D. Wills, pers. comm.)), which increased the distance they travelled. Possibly these flights were made to evaluate food supplies in the area of the nesting site, and to determine the presence of mates. Increased home range size may also have been a function of territoriality over the breeding season, for although kereru did not successfully breed over these years, failed attempts at breeding were seen.

While range size increased as diet specialisation fell; the length and number of bird movements rose with increasing diet specialisation, particularly as kereru focused on miro. This increased specialisation meant that kereru had to move further to find the trees, even though they then remained in one localised area while feeding. Such behaviour has also been noted in tui (Craig *et al.* 1981). Thus the diet was less specialised and kereru travelled around their range, but did not leave the area to find new food sources.

Kereru left the Whirinaki study area in highest numbers when miro fruiting had finished and the birds were feeding predominantly on immature foliage and flowers. Although kereru did not travel far while feeding on mature vegetation, they did move extensively to feed on preferred sources of immature leaves. As the supply of this immature foliage became exhausted, short movements were made to feed on available fruit, growing in nearby forest margins. Most kereru then moved into neighbouring forest areas and began feeding on tawa fruit. The range of kereru while feeding on tawa included excursions back towards the forest margins to continue feeding on alternate food sources.

Other long-range movements were made at the end of the tawa fruiting season. Kereru tracked to their new location were found to be feeding predominantly on miro fruit, as well as some of the autumn fruiters such as hinau, maire and mahoe. Kereru that remained in one range throughout the year also fed on miro which could be found within their range. One exceptional bird fed on vegetation for a large part of the time. Some kereru made a number of short-range movements because miro in one area finished fruiting as miro at a higher altitude began.

Some kereru may find all required food sources in their range and therefore have no need to disperse. Others may be forced to move to obtain an adequate diet. When feeding on a food such as tawa, a widespread resource which kereru defend, observations of territorial disputes suggest that the less effective competitors would be excluded from some areas and would move elsewhere to a possibly poorer area. However, this role could be reversed when birds are moving away, rather than staying in one area. As larger more dominant individuals will have access to food sources while they move around, and lower ranking individuals will have access only in the absence of competition, it is more likely that only the large dominant individuals will travel when new and better food sources become available elsewhere. During autumn, while the majority of kereru travelled to find miro, a relatively limited resource compared with tawa, some birds stayed in a localised area and fed on the more easily accessible food that was not as nutritionally rewarding. When feeding on miro, the kereru which dispersed continued feeding on miro for a longer period, but the kereru which remained in their range resorted to feeding on vegetation after miro in their area finished fruiting.

8.4 Conclusions

Overall, the pattern of kereru use of home ranges indicates that the phenology of fruiting and foliage regrowth has a significant impact on the timing of movements in consecutive years. Keru movements reflect the changing availability of food sources, and food availability and distribution has a strong influence on range size. Factors such as the rate of food intake, and the structure of food trees, may also influence utilisation of different foods and kereru ranges.

Chapter 9

General discussion

9.1 Conservation implications

Kereru rely very heavily on certain plant species in Whirinaki - a lowland podocarp-hardwood forest. Of particular importance are tawa and miro. Any further habitat degradation resulting in the loss of these species in particular may result in a higher frequency of non-breeding years and increase adult mortality.

The movements of kereru are strongly influenced by changing food resources, which often have a patchy distribution. The high mobility of kereru and their ability to travel long distances indicates that when considering the local conservation of kereru, the surrounding area must also be taken into consideration. Kereru can rely on areas of habitat outside the boundaries of parks and reserves, and changes in these areas could impact heavily.

If the habitat is rich in the preferred food species of kereru, range size can be minimised and higher numbers of kereru could coexist. Conversely, if forest fragmented and its quality poor, each kereru needs to exploit a large range to find sufficient nutrition. However, patches of habitat can still be valuable, especially if they contain a preferred food. These patches could be used as 'stepping stones' between more continuous tracts of forest. Patches of native plant species within more extensive exotic forests (e.g. along stream banks and in areas too steep for logging) provide a proven food source for kereru, although such small stands are not valuable as examples of native forest.

Tawa and miro feature in the diet of possums (Cowan 1992). Kereru productivity and survival may decline if supplies are reduced by such introduced mammals. Natural competition comes from the kaka which deplete miro fruit supplies while the fruit are still inedible to kereru. Predation of fruits by possums also reduces seedling dispersal and future seedling recruitment into the population because they usually eat only the skin and flesh

of the large (>10mm) fruits, and discard the seeds (Cowan 1992). These possum damaged fruits were non-viable and no longer available for dispersal (A. Dijkgraaf, unpublished PhD thesis). Control of introduced competitors could be significant in ensuring sufficient, if not plentiful, food supply for kereru, and consequently the continuation of seed dispersal and propagation of these species.

9.2 Future research

More in-depth nutritional analysis of kereru food species is required, particularly in relation to the foliage consumed. Analysing the nutritional value of food, combined with diet observations over an active breeding season, would assist in augmenting understanding of kereru nutrition, for example, the existence of a link in kereru between protein consumption and growth. This may also assist in confirming species (such as tawa) thought to be important for bringing kereru into breeding condition.

Further studies on the climatic and environmental conditions that precede fruiting in the species important to kereru would be useful in determining the size of the fruiting crop, and aid in the management of kereru populations. This information could be used to guide predator control in areas/years when fruiting was expected to be minimal and kereru were particularly vulnerable. It would also refine ecological damage thresholds for pest control programmes. In addition, better knowledge of stimuli to fruiting would be valuable for replanting programmes with a focus on kereru habitat restoration/enhancement.

Further study of the home ranges and movements of kereru of known sex and age would be valuable in determining if any of the observed patterns can be related to either of these variables.

Finally, as this study originally intended, research on the behaviour, diet, dispersal and dispersion of post-fledging kereru is of utmost importance because these birds are the potential recruits for the future population. This area represents a significant gap in knowledge.

References

- Adler, G.H. and Kielpinski, K.A. 2000. Reproductive phenology of a tropical canopy tree, *Spondias mombin*. *Biotropica* 32(4a): 686-692.
- Afik, D. and Karasov, W.H. 1996. The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* 76: 2247-2257.
- Allan. 1961. Flora of New Zealand. Volume I. Indigenous Tracheophyta: Psilopsida, Lycopsida, Filicopsida, Gymnospermae, Dicotyledones. Wellington, New Zealand, R.E. Owen, Government Printer.
- Anders, A.D., Faaborg, J. and Thompson III, F.R. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile wood thrushes. *Auk* 115(2): 349-358.
- Anderson, S. 1997. Changes in native ecosystem processes. The dynamics of pollination and dispersal in New Zealand forests. *School of Biological Sciences*. Auckland, University of Auckland.
- Baker, A. 1999. Food plants of bellbird (*Anthornis melanura*), tui (*Prosthemadera novaeseelandiae*) and New Zealand pigeon (*Hemiphaga novaeseelandiae*) in Dunedin. *Notornis* 46(2): 270-272.
- Banack, S.A. 1998. Diet selection and resource use by flying foxes (genus *Pteropus*). *Ecology* 79: 1949-1967.
- Beaven, B.M., Burns, R., Harrison, A. and Shaw, P. 2000. Northern Te Urewera Ecosystem Restoration Project. East Coast/ Hawke's Bay Conservancy, Department of Conservation, Gisborne.
- Beehler, B. 1983. Frugivory and polygamy in birds of paradise. *Auk* 100(1): 1-12.
- Bell, B.D. 1990. Recent avifaunal changes and the history of ornithology in New Zealand. *Acta XX Congressus Internationalis Ornithologica*: 195-230. New Zealand Ornithological Congress Trust Board.
- Bell, R. 1996. Seed dispersal by kereru (*Hemiphaga novaeseelandiae*) at Wenderholm Regional Park. Unpublished MSc thesis. University of Auckland, Auckland.

- Bergquist, C.A.L. 1985. Differences in the diet of the male and female tui (*Prosthemadera novaeseelandiae* : Meliphagidae). *New Zealand Journal of Zoology* 12: 573-576.
- Berlin, K.E., Pratt, T.K., Simon, J.C., Kowalsky, J.R. and Hatfield, J.S. 2000. Plant phenology in a cloud forest on the island of Maui, Hawaii. *Biotropica* 32(1): 90-99.
- Berthold, P. 1976. The control and significance of animal and vegetable nutrition in omnivorous songbirds. *Ardea* 64: 140-154.
- Best, E. 1977. Forest lore of the Maori. Wellington, New Zealand, E.C. Keating Government Printer.
- Beveridge, A.E. and Herbert, J. 1978. Selection logging trials and their implications for management of the west Taupo forests. New Zealand Forest Service. Forest Research Institute. *Unpublished* Indigenous Siviculture Report No. 20.
- Bosque, C. and Pacheco, A. 2000. Dietary nitrogen as a limiting nutrient in frugivorous birds. *Revista Chilena De Historia Natural* 73(3): 441-450.
- Bullock, S.H. and Solis-Magallanes, J.A. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 25: 183-190.
- Burrows, C.J. 1996. Germination behaviour of seeds of the New Zealand woody species *Alectryon excelsus*, *Corynocarpus laevigatus*, and *Kunzea ericoides*. *New Zealand Journal of Botany* 34(4): 489-498.
- Burrows, C.J. 1999. Germination behaviour of seeds of the New Zealand woody species *Beilschmedia tawa*, *Dysoxylum spectabile*, *Griselinia lucida*, and *Weinmannia racemosa*. *New Zealand Journal of Botany* 37(1): 95-105.
- Burrows, C.J., McCulloch, B. and Trotter, M.M. 1981. The diet of moas based on gizzard content samples from Pyramid Valley, North Canterbury, and Scaifies Lagoon, Lake Wanake, Otago. *Records of the Canterbury Museum* 9(6): 309-336.
- Burt, W.H 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammology* 24: 346-352.
- Cain, B.F., Scannell, S. and Cambie, R.C. 1961. A New Zealand phytochemical survey – part 1. the gymnosperms. *New Zealand Journal of Science* 1(4): 3-12.
- Carroll, J.P., Crawford, R.D. and Schulz, J.W. 1995. Gray partridge winter home range and use of habitat in North Dakota. *Journal of Wildlife Management* 59(1): 98-103.

- Choo, G.M., Waterman, P.G., Mickey, D.B. and Gartman, J.S. 1981. A simple enzyme assay for dry matter digestibility and its value in studying food selection by generalist herbivores. *Oecologia* 49:170-178.
- Clout, M.N. 1990. The kereru and its forests. *Birds International* 2 (4): 10-19.
- Clout, M.N. and Gaze, P.D. 1984. Effects of plantation forestry on birds in New Zealand. *Journal of Applied Ecology* 21: 795-815.
- Clout, M.N., Gaze, P.D., Hay, J.R. and Karl, B.J. 1986. Habitat use and spring movements of New Zealand pigeons at Lake Rotoroa, Nelson Lakes National Park. *Notornis* 33:37-44.
- Clout, M.N. and Hay, J.R. 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. *New Zealand Journal of Ecology* 12(supplement): 27-33.
- Clout, M.N., Karl, B.J. and Gaze, P.D. 1991. Seasonal movements of New Zealand pigeons from a lowland forest reserve. *Notornis* 38: 37-47.
- Clout, M.N., Karl, B.J., Pierce, R.J. and Robertson, H.A. 1995. Breeding and survival of New Zealand pigeons (*Hemiphaga novaeseelandiae*). *Ibis* 137: 264-271.
- Clout, M.N. and Tilley, J.A.V. 1992. Germination of miro (*Prumnopitys ferruginea*) seeds after consumption by New Zealand pigeons (*Hemiphaga novaeseelandiae*). *New Zealand Journal of Ecology* 30: 25-28.
- Courtney, S.P. and Sallabanks, R. 1992. It takes guts to handle fruits. *Oikos* 65(1): 163-166.
- Cowan, P.E. 1990. Fruits, seeds and flowers in the diet of the brushtail possums *Trichosurus vulpecula* in lowland podocarp/mixed hardwood forest, Orongorongo Valley, New Zealand. *New Zealand Journal of Zoology* 17(4): 549-566.
- Cowan, P.E. 1992. Analysis of the characteristics of fruit eaten by possums, *Trichosurus vulpecula*, in New Zealand. *New Zealand Journal of Zoology* 19: 45-52.
- Coleman, J.D. 1991. The case for possum management on Chatham Island. Forest Research Institute Contract Report: FWE 91/34. Prepared for Department of Conservation, Christchurch.
- Craig, J.L., Stewart, A.M. and Douglas, M.E. 1981. The foraging of New Zealand honeyeaters. *New Zealand Journal of Zoology* 8: 87-91.

- Crome, F.H.J. 1975a. The ecology of fruit pigeons in tropical Northern Queensland. *Australian Journal of Wildlife Research* 2: 155-185.
- Crome, F.H.J. 1975b. Breeding, feeding and status of the Torres Strait pigeon at Low Isles, North-Eastern Queensland. *Emu* 75: 189-198.
- Dasilva, G.L. 1994. Diet of *Colobus polykomos* on Tiwai Island: Selection of food in relation to its seasonal abundance and nutritional quality. *International Journal of Primatology* 15: 655-678.
- Dawson, D.G., Dilks, P.J., Gaze, P.D., McBurney, J.G.R. and Wilson, P.R. 1978. Seasonal differences in bird counts in forests near Reefton, South Island, New Zealand. *Notornis* 25: 257-278.
- Denslow, J.S. and Moermond, T.C. 1982. The effect of accessibility on rates of fruit removal from tropical shrubs: an experimental study. *Oecologia* 54: 170-176.
- Dudley, R. and Vermeij, G.L. 1992. Do the power requirements of flapping flight constrain folivory in flying animals? *Functional Ecology* 6:101-104.
- Dunn, P.L. 1981. The feeding ecology of the New Zealand pigeon (*Hemiphaga novaeseelandiae*). Unpublished MSc thesis. University of Otago, Dunedin.
- Dunn, P. and Morris, R.B.M. 1985. New Zealand pigeon. Pages 238-239 in Reader's Digest Complete Book of New Zealand Birds. Reader's Digest Services Pty Ltd, Sydney.
- Field, D.A. and Garratt, K.J. 1979. Whirinaki State Forest – a study for the National Parks Authority. Unpublished report.
- Fisher, H. 1972. The nutrition of birds. Pages 431-469 in Farner, D.S. and King, J.R., editors. Avian Biology. Volume II. Academic Press, New York, New York, USA.
- Foster, M.S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its food source. *Ecology* 58: 73-85.
- Foster, M.S. 1990. Factors influencing bird foraging preferences among conspecific fruit trees. *Condor* 92: 844-854.
- Foster, R.B. 1996. The seasonal rhythm of fruitfall on Barro Colorado Island in Leigh, E.G., Rand, A.S. and Windsor, D.M., editors. The ecology of a tropical forest: seasonal rhythms and long term-changes. Pages 151-172. Smithsonian Institution Press, Washington, DC.

- Fleming, C.A. 1962. History of the New Zealand land bird fauna. *Notornis* 9(8): 270-274.
- Flux, I.A., Powlesland, R.G., Dilks, P.J. and Grant, A.D. 2001. Breeding, survival, and recruitment of Chatham Island pigeon (*Hemiphaga chathamensis*). *Notornis* 48: 177-206.
- Fredericksen, T.S., Justiniano, M.J., Rumiz, D. and Aguape, R. 1999. Harvesting free-standing fig trees for timber in Bolivia: potential implications for sustainability. *Forest Ecological Management* 116: 151-161.
- Freeland, W.J. and Janzen, D.H. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist* 108: 269-289.
- Gallerani Lawson, E.J. and Rodgers, A.R. 1997. Differences in home-range size computed in commonly used software programs. *Wildlife Society Bulletin* 25(3): 721-729.
- Gibb, J.A. 1970. A pigeon's choice of plums. *Notornis* 17: 239.
- Gibbs, H.S. 1968. Soils of the North Island in Soils of New Zealand Part 1. *Soil Bureau Bulletin* 26(1): 48-63.
- Grindley, G.W. 1960. Geological Map of New Zealand. 1:250,000. Map Sheet 8: Taupo. New Zealand Geological Survey Map. DSIR, Wellington.
- Harris, S., Cresswell, W.J., Forde, P.G., Trehwella, W.J., Woollard, T. and Wray, S. 1990. Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* 229(2/3): 97-123.
- Hartley, P.H.T. 1954. Wild fruits in the diet of British thrushes. A study in the ecology of closely allied species. *British Birds* 47: 97-107.
- Healy, J. 1964. Stratigraphy and chronology of late Quaternary volcanic ash in Taupo, Rotorua and Gisborne districts. *New Zealand Geological Survey Bulletin* 73.
- Heather, B.D. and Robertson, H.A. 1996. New Zealand pigeon (kereru, kukupa, parea). Pages 134-135, 348-350 in *The Field Guide to the Birds of New Zealand*. Penguin Books (NZ) Ltd, Auckland.
- Hedge, S.G., Ganeshaiah, K.N. and Uma Shaanker, R. 1991. Fruit preference criteria by avian frugivores: their implications for the evolution of clutch size in *Solanum pubescens*. *Oikos* 60: 20-26.
- Herbert, J. 1978. Forest patterns and regeneration ecology of the Rangitoto-Hauhungaroa forests. New Zealand Forest Service. Forest Research Institute. *Unpublished Indigenous Siviculture Report No. 19*.

- Herrara, C.M. 1981. Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos* 36: 51-58.
- Herrara, C.M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* 63: 773-785.
- Herrara, C.M. 1984. A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Management* 54(1): 1-23.
- Higgins, P.J. and Davies, S.J.J.F. 1996. New Zealand pigeon. Pages 1016-1025 in Handbook of Australian, New Zealand and Antarctic Birds. Volume 3, Snipe to Pigeons. Oxford University Press, Melbourne.
- Hill, J.E. and Smith, J.D. 1984. Bats – A Natural History. British Museum (Natural History), London.
- Howe, H.F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* 58: 539-550.
- Howe, H.F. and Estabrook, G.F. 1977. On intraspecific competition for avian dispersers in tropical trees. *American Naturalist* 111: 817-832.
- Howe, H.F. and Vande Kerckhove, G. 1980. Nutmeg dispersal by tropical birds. *Science* 210: 925-927.
- Howe, H.F. and Vande Kerckhove, G. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. *Ecology* 62: 1093-1106.
- Innis, G.J. 1989. Feeding ecology of fruit pigeons in subtropical rainforests of South-eastern Queensland. *Australian Wildlife Research* 16: 365-394.
- James, R.E. 1995. Breeding ecology of the New Zealand pigeon at Wenderholm Regional Park. Unpublished MSc thesis. University of Auckland, Auckland.
- James, K.A.C., Waghorn, G.C., Powlesland, R.G. and Lloyd, B.D. 1991. Supplementary feeding of kakapo on Little Barrier Island. *Proceedings of the Nutrition Society of New Zealand* 16: 93-102.
- Janzen, D.H. 1976. Seeding patterns of tropical trees. Tropical trees as living systems. Petersham, Massachusetts, Cambridge University Press.
- Janzen, D.H. 1980. When is it coevolution? *Evolution* 34: 611-612.
- Jenkins, R. 1969. Ecology of three species of saltators in Costa Rica with special references to their frugivorous diet. Unpublished PhD thesis. Harvard University, Massachusetts.
- Jordano, P. 1984. Seed weight variation and differential avian dispersal in blackberries *Rubus ulmifolius*. *Oikos* 43: 149-153.

- Jordano, P. and Herrera, C.M. 1981. The frugivorous diet of blackcap populations *Sylvia atricapilla* wintering in southern Spain. *Ibis* 123:502-507.
- Justiniano, M.J. and Fredericksen, T.S. 2000. Phenology of tree species in Bolivian dry forests. *Biotropica* 32(2): 276-281.
- Kannan, R. and James, D.A. 1999. Fruiting phenology and the conservation of the great pied hornbill (*Buceros bicornis*) in the Western Ghats of Southern India. *Biotropica* 31(1): 161-177.
- Karasov, W.H. and Levey, D.J. 1990. Digestive system trade-offs and adaptations of frugivorous passerine birds. *Physiological Zoology* 63: 1248-1270.
- Karl, J. and Clout, M.N. 1987. An improved radio transmitter with a weak link to prevent snagging. *Journal of Field Ornithology* 58: 73-77.
- Katz, A. 1980. Growth of podocarp pole stands in former Maori cleared sites in the Whirinaki River Valley. New Zealand Forest Service. Forest Research Institute. *Unpublished Indigenous Forest Management Report No. 24*.
- Kelt, D.A. and Van Vuren, D.H. 2001. The ecology and macroecology of mammalian home range area. *American Naturalist* 157(6): 637-645.
- Kenward, R. 1996. Ranges V - Software for analysing animal location data. Institute of Terrestrial Ecology, WAREHAM, United Kingdom.
- Kenward, R.E. and Sibly, R.M. 1977. A woodpigeon (*Columba palumbus*) feeding preference explained by a digestive bottleneck. *Journal of Applied Ecology* 14: 815-826.
- Kenward, R.E. and Sibly, R.M. 1978. Woodpigeon feeding behavior at brassica sites, a field laboratory investigation of woodpigeon feeding behavior during adoption and maintenance of a brassica diet. *Animal Behavior* 26: 778-790.
- Kinzey, W.G. and Norconk, M.A. 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *International Journal of Primatology* 14: 207-226.
- Knowles, B. and Beveridge, A.E. 1982. Biological flora of New Zealand 9. *Beilschmedia tawa* (A. Cunn) Benth. et Hook. f. ex Kirk (Lauraceae) tawa. *New Zealand Journal of Botany* 20: 37-54.
- Kunz, T.H. and Ingalls, K.A. 1994. Folivory in bats: an adaptation derived from frugivory. *Functional Ecology* 8: 665-668.

- Lambert, F.R. and Marshall, A.G. 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *Journal of Ecology* 79: 793-809.
- Langham, N.D. 1991. The ecology of the kereru or New Zealand pigeon (*Hemiphaga novaeseelandiae*). DSIR Land Resources Contract Report No. 91/45. DSIR Land Resources, Havelock North.
- Leck, C.F. 1972. Seasonal changes in feeding pressures of fruit and nectar-eating birds in Panama. *Condor* 74: 54-60.
- Lee, W.G., Clout, M.N., Robertson, H.A. and Wilson, J.B. 1991. Avian dispersers and fleshy fruits in New Zealand. *Acta XX Congressus Internationalis Ornithologica*: 1624-1629. New Zealand Ornithological Congress Trust Board.
- Lee, W.G. and Johnson, P.N. 1984. Mineral element concentrations in foliage of divaricate and non-divaricate *Coprosma* species. *New Zealand Journal of Ecology* 7: 169-173.
- Lee, W.G., Wilson, J.B. and Johnson, P.N. 1988. Fruit colour in relation to the ecology and habit of *Coprosma* (Rubiaceae) species in New Zealand. *Oikos* 53: 325-331.
- Leighton, M. 1982. Fruit resources and patterns of feeding, spacing and grouping among sympatric Bornean hornbills (Bucerotidae). Ph.D. Thesis. University of California, California.
- Leighton, M. and Leighton, D.R. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest in Sutton, L., Whitmore, T.C. and Chadwick, A.C., editors. Tropical rain forests: ecology and management. Pages 181-196. Blackwell Scientific Publications, Oxford, England.
- Levey, D.J. 1987. Seed size and fruit-handling techniques of avian frugivores. *American Naturalist* 129(4): 471-485.
- Levey, D.J. and Grajal, A. 1991. Evolutionary implications of fruit processing limitations in cedar waxwings. *American Naturalist* 138: 171-189.
- Loiselle, B.A. and Blake, J.G. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72(1): 180-193.
- Manly, B.E.J., McDonald, L.L. and Thomas, D.L. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall, New York, New York.

- Martin, P. and Bateson, P. 1995. Measuring behaviour: an introductory guide. Pages 84-85. Cambridge University Press, Cambridge, Great Britain.
- Martin, T.E. 1985. Resource selection by tropical frugivorous birds: integrating multiple interactions. *Oecologia* 66: 563-573.
- Martinez Del Rio, C., Stevens, B.R., Daneke, D.E. and Andreadis, P.T. 1988. Physiological correlates of preference and aversion for sugars in three species of birds. *Physiological Zoology* 61: 222-229.
- Martinez Del Rio, C. and Karasov, W.H. 1990. Digestion strategies in nectar- and fruit-eating birds and the sugar composition of plant rewards. *American Naturalist* 136(5): 618-634.
- McEwen, W.M. 1978. The food of the New Zealand pigeon (*Hemiphaga novaeseelandiae novaeseelandiae*). *New Zealand Journal of Ecology* 1:99-108.
- McGlone, M.S. 1983. Polynesian deforestation of New Zealand: A preliminary synthesis. *Archaeologia Oceania* 18: 11-25.
- McKey, D. 1975. The ecology of coevolved seed dispersal systems in Gilbert, L.E. and Raven, P.H., editors. Coevolution of animals and plants. Pages 159-191. University of Texas, Austin, Texas.
- McKelvey, P.J. 1955. A note on the forest edge at Te Whaiti. *New Zealand Journal of Forestry* 7(2): 77-80.
- Millener, P.R. and Powlesland, R.G. 2001. The Chatham Island pigeon (*Parea*) deserves full species status; *Hemiphaga chathamensis* (Rothschild 1891); Aves: Columbidae. *Journal of the Royal Society of New Zealand* 31(2): 365-383.
- Mills, J.A., Lee, W.G., Mark, A.F and Lavers, R.B. 1980. Winter use by takahe (*Notornis mantelli*) of the summer-green fern (*Hyolepis millefolium*) in relation to its annual cycle of carbohydrates and minerals. *New Zealand Journal of Ecology* 3: 131-137.
- Moermond, T. and Denslow, J. 1983. Fruit choice in neotropical birds. *Journal of Animal Ecology* 52: 407-419.
- Morton, E.S. 1978. Avian aboreal foliovores: why not? in The Ecology of Arboreal Foliovores. Montgomery, G.G., editor. Smithsonian Institution Press, Washington, DC.
- Morton, J., Ogden, J. and Hughes, T. 1984. To save a forest – Whirinaki. Auckland, New Zealand, David Bateman Ltd.

- Nelson, S.L., Miller, M.A., Heske, E.J. and Fahey Jr, G.C. 2000. Nutritional quality of leaves and unripe fruit consumed as famine foods by the flying foxes of Samoa. *Pacific Science* 54(4): 301-311.
- Nicholls, J.L. 1966. Forest Map of New Zealand. 1:63,360. Map Sheet N95: *Te Whaiti*. New Zealand Forest Research Institute, Rotorua.
- O'Donnell, C.F.J. and Dilks, P.J. 1994. Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. *New Zealand Journal of Ecology* 18: 87-107.
- Oates, J.F., Waterman, P.G. and Choo, G.M. 1980. Food selection by the south Indian leaf-monkey, *Presbytis johnii*, in relation to leaf chemistry. *Oecologia* 45: 45-56.
- Opler, P.A., Frankie, G.W. and Baker, H.G. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 68: 167-188.
- Payne, R.B. 1972. Mechanisms and control of moult. Pages 104-155 in Farner, D.S. and King, J.R., editors. *Avian Biology*. Volume II. Academic Press, New York, New York, USA.
- Pierce, R. 1993. Ecology of the kukupa in Taitokerau: problems and solutions. *Ecological Management* 1:44-48.
- Pierce, R.J. and Graham, P.J. 1995. Ecology and breeding biology of kukupa (*Hemiphaga novaeseelandiae*) in Northland. *Science and Research Series No. 91*. Department of Conservation, Wellington.
- Poole, A.L. and Adams, N.M. 1990. *Trees and shrubs of New Zealand*. Wellington, DSIR Publishing.
- Pough, F.H. and Andrews, R.M. 1985. Energy costs of subduing and swallowing prey for a lizard. *Ecology* 66: 1525-1533.
- Poulin, B., Lefebvre, G. and McNeil, R. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* 73(6): 2295-2309.
- Powlesland, R.G., Dilks, P.J., Flux, I.A., Grant, A.D. and Tisdall, C.J. 1997. Impact of food abundance, diet and food quality on the breeding of the fruit pigeon, Parea (*Hemiphaga novaeseelandiae chathamensis*), on Chatham Island, New Zealand. *Ibis* 139: 353-365.

- Powlesland, R.G., Grant, A.D., Tisdall, C.J., Dilks, P.J. and Flux, I.A. 1992. Ecology and breeding biology of *parea* (Chatham Island pigeon) on southern Chatham Island, July 1991-April 1992. Science and Research Internal Report No. 134. Department of Conservation, Wellington.
- Putz, F.E. 1979. Aseasonality in Malaysia tree phenology. *Malaysian Forestry* 42: 1-24.
- Rathcke B. and Lacey, E.P. 1985. Phenological patterns of terrestrial plants. *Annual Reviews in Ecology and Systematics* 16:179-214.
- Ridley, H.N. 1930. The dispersal of plants throughout the world. L.Reeve, Ashford, Kent, England.
- Rolstad, J. and Rolstad, E. 1995. Seasonal patterns in home range and habitat use of the Grey-headed woodpecker *Picus canus* as influenced by the availability of food. *Ornis Fennica* 72: 1-13.
- Rolstad, J., Rolstad, E. and Stokke, P.K. 1995. Feeding habitat and nest-site selection of breeding Great Spotted Woodpeckers *Dendrocopos major*. *Ornis Fennica* 72: 62-71.
- Roudybush, T.E. and Grau, C.R. 1986. Food and water interrelations and the protein requirement for growth of an altricial bird, the cockatiel (*Nymphicus hollandicus*). *Journal of Nutrition* 116: 552-559.
- Salmon, J.T. 1986. The Reed Field Guide to New Zealand native trees. A.H. and A.W. Reed, Wellington, New Zealand.
- Schmidt, K.A. 2000. Interactions between food chemistry and predation risk in fox squirrels. *Ecology* 81(8): 2077-2085.
- Schwartz, C.C., Regelin, W.L. and Nagy, J.G. 1980. Deer preference for juniper forage and volatile oil treated foods. *Journal of Wildlife Management* 44: 114-120.
- Smith, R.L. 1996. Ecology and field biology – 5th edition. Harper Collins College Publishers, New York.
- Smith-Ramirez, C. and Armestro, J.J. 1994. Flowering and fruiting patterns in the temperate rainforest of Chiloe, Chile – Ecologies and climatic constraints. *Journal of Ecology* 82(2): 353-365.
- Snow, B.K. 1970. A field study of the Bearded Bellbird in Trinidad. *Ibis* 112: 299-329.
- Snow, B.K. 1973. Notes on the behaviour of the White Bellbird. *Auk* 94: 623-645.

- Snow, B.K. and Snow, D.W. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. *Auk* 88: 291-322.
- Snow, D.W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. *Oikos* 15: 274-281.
- Snow, D.W. 1971. Evolutionary aspects of fruit-eating in birds. *Ibis* 113: 194-202.
- Snow, D.W. 1981. Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13: 1-14.
- Sorensen, A.E. 1981. Interactions between birds and fruits in a temperate woodland. *Oecologia* 50: 442-450.
- Sorensen, A.E. 1984. Nutrition, energy and passage time: experiments with fruit preference in European blackbirds (*Turdus merula*). *Journal of Animal Ecology* 53: 545-557.
- Stewart, A.M. and Craig, J.L. 1985. Movements, status, access to nectar, and spatial organisation of the tui. *New Zealand Journal of Zoology* 12: 649-666.
- Storch, I. 1995. Annual home ranges and spacing patterns of capercaillie in central Europe. *Journal of Wildlife Management* 59(2): 392-400.
- Thomas, D.W. 1982. Fruit intake and energy budgets for frugivorous bats. *Physiological Zoology* 57: 457-467.
- Tisdall, C.J. 1992. Feeding ecology of parea (*Hemiphaga novaeseelandiae chathamensis*) and impacts of possums (*Trichosurus vulpecula*) on parea food plants. Unpublished MSc thesis. University of Otago, Dunedin .
- Traveset, A., Riera, N. and Mas, R.E. 2001. Ecology of fruit-colour polymorphism in *Myrtus communis* and differential effects of birds and mammals on seed germination and seedling growth. *Journal of Ecology* 89: 749-760.
- Uma Shaanker, R., Ganeshaiah, K.N. and Bawa, K.S. 1988. Parent-offspring conflict, sibling rivalry and brood size patterns in plants. *Annual Review of Ecological Systematics* 19: 177-205.
- Van Schaik, C.P., Terborgh, J.W. and Wright, S.J. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24: 353-377.
- Voight, D.R. and Tinline, R.R. 1980. Strategies for analysing radio tracking data in Amlaner, C.J., MacDonald, D.W., editors. A handbook in biometry and radiotracking. Pergamon Press, Oxford.

- Ward, P. 1969. The annual cycle of the Yellow-vented Bulbul *Pycnonotus goiavier* in a humid equatorial environment. *Journal of Zoology* 157: 25-45.
- West, C.J. 1986. Population ecology of *Beilschmedia tawa* at Pureora forest. *Botany*. Auckland, University of Auckland.
- Wheelwright, N.T. 1988. Fruit-eating birds and bird dispersed plants in the tropics and temperate zone. *Trends in Ecology and Evolution* 3(10): 270-274.
- Whelan, C.J., Schmidt, K.A., Steele, B.B., Quinn, W.J. and Dilger, S. 1998. Are bird-consumed fruits complementary resources? *Oikos* 83: 195-205.
- White, S.C. 1975. Ecological aspects of growth and nutrition in tropical fruit-eating birds. Dissertation. University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.
- Williams, C.K. 1982. Nutritional properties of some fruits eaten by the possum *Trichosurus vulpecula* in a New Zealand broad-leaf podocarp forest. *New Zealand Journal of Ecology* 5: 16-20.
- Willson, M.F. 1991. Birds and fruits: how does this mutualism matter? *Acta XX Congressus Internationalis Ornithologica*. New Zealand Ornithological Congress Trust Board.
- Wilson, P.R., Taylor, R.H. and Thomas, B.W. 1988. Effect of topography on seasonal distribution of forest birds in the Ohikanui, Lower Buller and Inangahua Valleys, North Westland. *Notornis* 35: 217-243.
- Witmer, M.C. 1998. Do seeds hinder digestive processing of fruit pulp? Implications for plant/frugivore mutualisms. *Auk* 115(2): 319-326.
- Witmer, M.C. and Van Soest, P.J. 1998. Contrasting digestive strategies of fruit-eating birds. *Functional Ecology* 12(5): 728-741.
- Wray, S., Cresswell, W.J., White, P.C.L. and Harris, S. 1992. What if anything is core area? An analysis of the problems of describing internal range configurations in Wildlife Telemetry – Remote Monitoring and Tracking of Animals. Friede, I.G. and Swift, S.M., editors. Ellis Horwood Limited, Great Britain.
- Wright, A.E. 1984. *Beilschmedia* trees (Lauraceae) in New Zealand. *New Zealand Journal of Botany* 22: 109-125.
- Wright, S.J., Zeballos, H., Dominguez, I.G., Gallardo, M.M., Moreno, M.C and Ibanez, R. 1999. The El Nino southern oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80(5): 1632-1647.

Appendix

Index of common and scientific plant names

Broom	<i>Carmichaelia aligera</i>
Five-finger	<i>Pseudopanax arboreus</i>
Hinau	<i>Elaeocarpus dentatus</i>
Hoho	<i>Pseudopanax chathamicum</i>
Horopito	<i>Pseudopanax colorata</i>
Houndstongue	<i>Phymatosorus pustulatus</i>
Kotukutuku	<i>Fuchsia exorticata</i>
Kahikatea	<i>Dacrycarpus dacrydioides</i>
Kamahi	<i>Weinmannia racemosa</i>
Karamu	<i>Coprosma robusta</i>
Kowhai	<i>Sophora tetraptera</i>
Mahoe	<i>Melicytus ramiflorus</i>
Maire	<i>Mida salicifolia</i>
Matai	<i>Prumnopitys taxifolia</i>
Makomako	<i>Aristotelia serrata</i>
Miro	<i>Prumnopitys ferruginea</i>
Mahoe wao	<i>Melicytus lanceolatus</i>
New Zealand Jasmine	<i>Parsonsia heterophylla</i>
Nikau	<i>Rhopalostylis sapida</i>
Putaputaweta	<i>Carpodetus serratus</i>
Ribbonwood	<i>Plagianthus regius</i>
Rimu	<i>Dacrydium cupressinum</i>
Supplejack	<i>Ripogonum scandens</i>
Tawa	<i>Beilschmedia tawa</i>
White Maire	<i>Nestigis lanceolata</i>