

Feeding ecology of kererū (*Hemiphaga novaeseelandiae*) in podocarp–hardwood forest, Whirinaki Forest Park, New Zealand

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Published on-line: 23 July 2009

Abstract: The diet and food preferences of the kererū (*Hemiphaga novaeseelandiae*) were studied in Whirinaki Forest Park, central North Island, New Zealand, during February 2000–March 2001. The study was carried out in two areas of podocarp–hardwood forest, Oriuwaka (1750 ha) and Otupaka (1830 ha). Fruit dominated in the diet at both sites (65% in Oriuwaka, 87% in Otupaka), but there were seasonal changes. Foliage and flowers were more important in the diet in winter and spring, but the timing of the switch from fruit to foliage differed between the areas. The main fruit eaten also changed seasonally from tawa (*Beilschmiedia tawa*) in early summer to miro (*Prumnopitys ferruginea*) in late summer and autumn. Variation in diet partly reflected seasonal phenology of the plants and differences in vegetation between the two areas, but when food-type availability is considered, kererū showed selective preference for some food types at some times. Miro and tawa fruits were highly preferred food types in both areas. This study highlights the likely need of kererū to have access to various vegetation types in order to meet their seasonally changing nutritional requirements in a podocarp–hardwood forest where the availability of food, especially fruits, can differ markedly both in time and space. Thus, large forest blocks that contain a variety of habitat types, or landscapes containing patches of various habitat types, are needed for the long-term conservation of kererū populations.

Keywords: diet; fruit pigeon; phenology

Introduction

The endemic kererū or New Zealand pigeon (*Hemiphaga novaeseelandiae*) is a large fruit pigeon (weight range: 510–850 g; Clout 1990; Higgins & Davies 1996). It inhabits the North, South and Stewart islands, and some offshore islands (Robertson et al. 2007), in a variety of habitats, including extensive tracts of podocarp–hardwood forest, *Nothofagus* forest, forest remnants, exotic plantations, farmland, and urban parks and gardens.

Kererū feed on leaves, flowers and fruits, including buds of these, from a wide variety of species, both native and exotic (Higgins & Davies 1996). However, when available, fruit is preferred over other food types (Clout 1990; Mander et al. 1998). About 70% of New Zealand's native trees and shrubs produce fruit that is dispersed by vertebrates (Clout & Hay 1989), but few of New Zealand's bird species are able to swallow intact large fruit (>10-mm diameter). Many species capable of doing so are now extinct, for example moa (*Dinornithiformes*), or greatly restricted in distribution, such as kiwi (*Apteryx* spp.), weka (*Gallirallus australis*) and kōkako (*Callaeas*

cinerea) (Robertson et al. 2007). The kererū, therefore, is now the only widespread consumer of large fruits, and as a result a number of plants may depend on kererū for seed dispersal (Clout & Hay 1989; Lee et al. 1991). While the movements of individual kererū can be quite limited for several days or weeks (Clout & Hay 1989; Bell 1996), generally their movements create home ranges of >100 ha (Pierce & Graham 1995). Occasionally, kererū home ranges consist of two or more discrete areas several kilometres apart (Clout et al. 1986; Hill 2003), and individuals may make long flights of more than 50 km between areas (Harper 2003), providing the potential for some seeds to be widely dispersed. Thus, kererū perform a vital ecological role in New Zealand forests, maintaining community diversity through seed dispersal (Clout & Hay 1989; Lee et al. 1991).

Kererū diet has been studied in various regions and habitats from Northland to Otago (Table 1). These studies have been concentrated mainly in the northern North Island and in modified landscapes throughout the South Island. In 1998, the Department of Conservation began a study of the effects of an aerial 1080 (sodium

Table 1. Regions of New Zealand and habitat types where diet studies of kererū have been carried out.

| Region | Habitat type | Reference |
|-----------------------|--|--------------------------|
| Northland | Farmland, exotic plantations, and podocarp– hardwood forest remnants | Pierce & Graham 1995 |
| Northland | Podocarp–broadleaved forest remnant | Innes et al. 2004 |
| Little Barrier Island | Podocarp–beech–broadleaved forest | Taylor 1996 |
| Auckland | Coastal broadleaved forest | James 1995; Bell 1996 |
| Auckland | Urban gardens and podocarp–broadleaved forest remnants | Karan 2000; Harwood 2002 |
| Hawke's Bay | Farmland, forest remnants | Langham 1991 |
| Nelson | Podocarp–hardwood and beech–podocarp forest | Clout et al. 1986 |
| Marlborough | Tawa–podocarp forest | Clout et al. 1991 |
| Canterbury | Podocarp–hardwood remnant containing exotics | Ridley 1998 |
| Banks Peninsula | Urban–rural habitats, mixed hardwood forest patches | Schotborgh 2005 |
| Banks Peninsula | Beech forest, second-growth hardwood forest and scrub, urban–rural areas | Campbell 2006 |
| South Westland | Podocarp–hardwood and silver beech forests | O'Donnell & Dilks 1994 |
| Otago | Podocarp–broadleaved forest, exotic plantations, urban habitats | Dunn 1981 |
| Otago | Urban areas | Baker 1999 |

monofluoroacetate) possum (*Trichosurus vulpecula*) control operation on kererū and kākā (*Nestor meridionalis*) in podocarp–hardwood forests of Whirinaki Forest Park, central North Island (Powlesland et al. 2003). During this study, the diet of kererū was recorded separately for two study areas, one at an elevation of 600–900 m a.s.l. (Otopaka), and the other at 475–600 m a.s.l. (Oriuwaka). Here we report on the diet of kererū in these two study areas for February 2000 – March 2001 in relation to the availability of the main foods. This information fills a gap in our knowledge of kererū ecology because podocarp–hardwood forest includes some important mast-fruiting species, e.g. rimu (*Dacrydium cupressinum*) and kahikatea (*Dacrycarpus dacrydioides*), and was once much more widespread over the central North Island (McGlone 1983), thereby providing a significant influence on kererū distribution.

Methods

Study areas

In Whirinaki Forest Park, we studied kererū in two areas, Oriuwaka (1750 ha) and Otopaka (1830 ha), separated by about 4 km at their nearest points. Habitat between and near the study areas was mainly native forest, but included patches of exotic plantations. Both study areas have undulating to moderately steep topography, and broadly similar forest cover (Nicholls 1966). Powlesland et al. (2003) described the main canopy species in each study area. For our study, differences between the two

areas relate principally to the distribution of kererū food species. Tawa (*Beilschmiedia tawa*) is abundant at Oriuwaka, but is mostly replaced at the higher altitudes of Otopaka by cold-tolerant hardwoods such as kāmahī (*Weinmannia racemosa*), which is not a recognised food species of kererū. Kōtukutuku (*Fuchsia excorticata*) is a common understorey species in Oriuwaka, but in Otopaka, makomako (*Aristolelia serrata*) and hīnau (*Elaeocarpus dentatus*) are more frequent. Kōwhai (*Sophora tetraptera*) is locally abundant only in the Oriuwaka study area. Nicholls (1966), Herbert (1978) and Morton et al. (1984) provide details of Whirinaki forest types and distribution. Aerial possum control was carried out in May 2000 in Otopaka but not in Oriuwaka (Powlesland et al. 2003).

Mean annual rainfall recorded at the Whaeo power station (38°38' S, 176°35' E; 6–8 km west of Oriuwaka and Otopaka) was 1449 mm during 1990–2001. Since greater rainfall has been recorded over the higher altitude ground at the head of the Whaeo River and towards the Whirinaki River (Nicholls 1966), greater rainfall would be expected at Otopaka than at Oriuwaka. Based on data from the Whaeo power station, the mean annual temperature in Whirinaki Forest Park during 1990–2001 was 12°C, with mean annual minimum and maximum of 7°C and 17°C, respectively. The difference in altitude between the two study areas (c. 300 m) would be expected to produce a 1–2°C difference in air temperature, and this was confirmed by opportunistic thermometer readings. Seasons are defined as spring (September–November), summer (December–February), autumn (March–May) and winter (June–August).

Phenology

Between February 2000 and March 2001, timing and duration of leaf growth and fruiting of selected forest species were recorded to determine seasonal variation in food availability. Eleven species were chosen for regular monitoring because they were present in the study areas, and elsewhere are common components of kererū diet (McEwen 1978; Clout & Hay 1989; Clout et al. 1991; O'Donnell & Dilks 1994). Karamū (*Coprosma robusta*), makomako, putaputaweta (*Carpodetus serratus*), white maire (*Nestegis lanceolata*), tawa, kōtukutuku, rimu, kahikatea, and miro (*Prumnopitys ferruginea*) were monitored for fruiting; kōwhai for leaf development; and māhoe (*Melicytus ramiflorus*) for both. In each study area, we established five plots (100 × 100 m) containing all of the fruiting species, and within these a representative of each species was chosen. Kōwhai, however, was absent from Otupaka and only patchily distributed in Oriuwaka where we established five plots for kōwhai in addition to the plots for the fruiting species. The plants monitored within each grid were mature, healthy, of a sufficiently large size that kererū would feed from them, and visible for accurate fruit scoring. Fruit and leaf abundance were given a score from 0 to 5: 0 = absent, 1 = scarce; 2 = below average; 3 = average; 4 = above average; 5 = high. Unripe and ripe (full-sized and consisting of more than 80% of usual ripe colouration) fruits, and actively growing (pale green and less than 80% of mature leaf size) and mature leaves were scored separately. These assessments were carried out using 10 × 50 binoculars and a telescope with ×60 magnification.

Diet

Feeding kererū were observed with binoculars using focal animal sampling (Martin & Bateson 1993). Between February 2000 and March 2001, feeding of 34 radio-tagged kererū, tagged by Department of Conservation staff (Powlesland et al. 2003), and an unknown number of untagged kererū were recorded. Each tagged kererū was located using a receiver (TR-4; Telonics, Inc., Mesa, Arizona, USA) and hand-held Yagi antenna (Sirtrack, Havelock North, NZ) at least once every 10 days and tracked until a feeding observation was obtained or a maximum of 2 hours had elapsed. Additional feeding observations were made of untagged kererū, which were followed until they fed or disappeared. If more than one kererū was using the same food source, only the first individual seen was recorded. A second feeding observation was not recorded for the same bird unless it spent at least 10 minutes in a non-feeding activity, fed on a different food type on the same plant, or moved to feed on a different plant. During each observation, food species and type were recorded.

Principal components analysis was used to explore patterns of food-type usage by kererū over the 14 months

in the two areas. Food types used were the five most common foods, miro fruit, tawa fruit, makomako fruit, kōwhai foliage, white maire fruit, with other food types categorised as 'other fruit', 'other foliage' and 'flowers'. Counts of feeding observations were transformed to proportions of total observations in each area at each time. The covariance matrix was factored so that the ordination reflected absolute (rather than relative) importance of each food type. To test for significant differences in food-type usage between areas and over time, we used Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson 2005). Seven 2-month time categories were used to allow replication within cells of the two-factor crossed design and 9999 permutations of the raw data were used for all permutation tests.

Food preference

A monthly index of food preference was calculated by the Manly–Chesson Index (Manly et al. 1993) using data from the plant phenology (food available) and kererū diet investigations. A yearly mean preference was also calculated by pooling all values obtained over the year. The proportion of a particular food in the diet (d_i) was divided by the availability of that food on the trees (phenology observations) (N_i). This ratio was then normalised so that the sum of all ratios equalled one. The formula applied was:

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

where P_i = kererū preference values for food type i when foraging in a habitat with k food types available; d_i = the proportion of food of type i in the diet; and N_i = the proportion of food of type i available in the habitat. A preference value above $1/k$ indicates a preferred food; values below $1/k$ indicate avoidance (Manly et al. 1993).

Statistics

Differences in diet between months and in food types used between months were tested statistically using contingency tables (χ^2 test) and PROC GENMOD command in SAS Version 8.e (SAS Institute Inc. 1990).

Results

Phenology

In both Oriuwaka and Otupaka, immature foliage of māhoe began forming in winter, and continued to do so through to summer, although the growing season started a month later and finished a month earlier in Otupaka (Fig. 1). Kōwhai at Oriuwaka grew new foliage during November–February (Fig. 1).

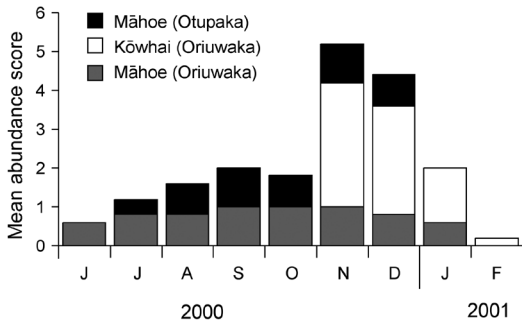


Figure 1. Abundance of immature foliage of māhoe (*Melicytus ramiflorus*) in Oriuwaka and Otupaka study areas, and kōwhai (*Sophora tetraptera*) in Oriuwaka study area, Whirinaki Forest Park, June 2000 – February 2001. Abundance scores: 0 = absent, 1 = scarce, 2 = below average, 3 = average, 4 = above average, 5 = high.

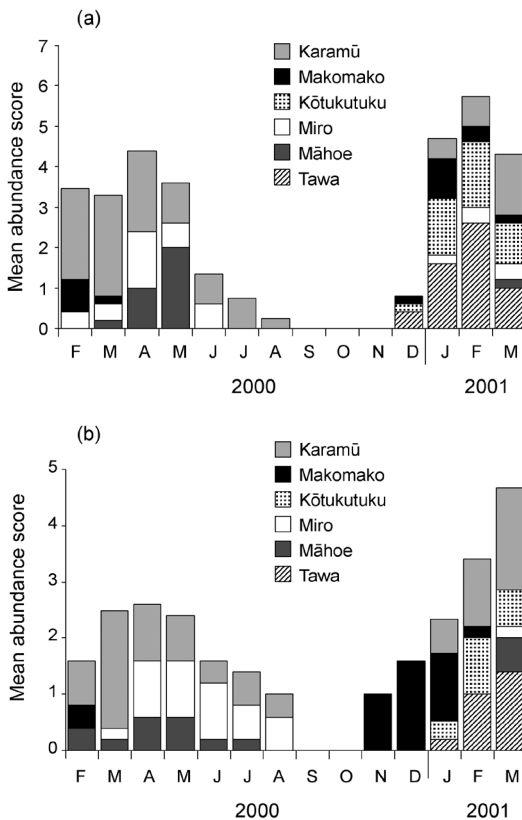


Figure 2. Abundance of ripe fruit of tawa (*Beilschmiedia tawa*), māhoe (*Melicytus ramiflorus*), miro (*Prumnopitys ferruginea*), kōtukutuku (*Fuchsia excorticata*), makomako (*Aristotelia serrata*) and karamū (*Coprosma robusta*) in Oriuwaka (a) and Otupaka (b) study areas, Whirinaki Forest Park, February 2000 – March 2001. Abundance scores as for Fig. 1.

Ripe karamū fruit was scarce (abundance score = 1) or of below-average abundance (score = 2) in both areas during February–August 2000 (Figs 2a & b). Ripe fruit of makomako, miro and māhoe were scarce during autumn–winter 2000, except for the latter in May 2000 at Oriuwaka (Fig. 2a), and with miro and māhoe bearing fruit for two months later in Otupaka (Fig. 2b) than in Oriuwaka. Several species bore ripe fruit during January–March 2001, particularly karamū, makomako, kōtukutuku and tawa (Figs 2a & b). For most of these species, fruit abundance was scarce to below-average, although tawa fruit was of average abundance in Oriuwaka during February (Fig. 2a). The two mast-fruited species (Kelly 1994), rimu and kahikatea, bore little fruit during this study. Overall, there was much ripe fruit available during February–May 2000, little in June–August, and then almost none during the following four months, before it became readily available again in January 2001, especially in Oriuwaka (Figs 2a & b).

Diet

Kererū in Whirinaki Forest Park were seen to feed on 21 plant species in total, 19 in Oriuwaka and 14 in Otupaka (Hill 2003). From these species, kererū fed on 32 combinations of food-type (foliage, flower buds and flowers, and fruits) and species (Hill 2003). Twelve species provided one food type, seven provided two, and only two (kōtukutuku, māhoe wao (*Melicytus lanceolatus*)) provided all three. Only one exotic species, broom (*Cytisus scoparius*), was recorded as food of kererū. Most of the diet consisted of a few species in each study area (Table 2). The top five species, ranked as a percentage of feeding observations, at Oriuwaka were tawa, kōwhai, miro, maire and makomako (77.7% of 302 observations), and at Otupaka were miro, makomako, māhoe, tawa and karamū (85.0% of 262). There is quite a difference in ranking of food species between the two study areas, partly due to the near absence of kōwhai in the Otupaka study area. Makomako and miro foods were four and two times, respectively, more prevalent in the diet at Otupaka than at Oriuwaka, but tawa was three times more abundant in the diet at Oriuwaka than at Otupaka.

During 2000–2001, the use of fruits, flowers and foliage varied significantly throughout the 14 months ($\chi^2 = 1022$, d.f. = 26, $P < 0.001$). Fruit predominated in the diet of kererū in both study areas; in Oriuwaka diet consisted of 65.4% fruit, 26.5% foliage, and 8.1% flowers (including flower buds) ($n = 302$ feeding observations), and in Otupaka these food types contributed 86.5%, 7.9% and 5.6% to the diet, respectively ($n = 262$), the difference between sites being significant ($\chi^2 = 7$, d.f. = 2, $P < 0.05$).

In Oriuwaka, the diet consisted of 100% fruit during March, April and May 2000, and February and March 2001 (Fig. 3a). Fruit consumption was less than 30%

Table 2. Top 10 food species, expressed as a percentage of feeding observations, of kererū in Oriuwaka and Otopaka study areas, Whirinaki Forest Park, February 2000 – March 2001.

| Species ¹ | Oriuwaka (n = 302) | | | | Otopaka (n = 262) | | | |
|----------------------|--------------------|--------|-------|-------|-------------------|--------|-------|-------|
| | Foliage | Flower | Fruit | Total | Foliage | Flower | Fruit | Total |
| Miro | | | 14.8 | 14.8 | | | 34.9 | 34.9 |
| Makomako | | | 7.4 | 7.4 | 1.6 | | 28.6 | 30.2 |
| Tawa | 0.6 | | 23.5 | 24.1 | | | 7.1 | 7.1 |
| Kōwhai | 18.5 | 4.3 | | 22.8 | 0.8 | | | 0.8 |
| Maire | 0.6 | | 8.0 | 8.6 | | | 3.2 | 3.2 |
| Māhoe | 1.9 | | 0.6 | 2.5 | 4.8 | | 4.0 | 8.8 |
| Karamū | | | 3.1 | 3.1 | | 0.8 | 3.2 | 4.0 |
| Kōtukutuku | 1.2 | 0.6 | 1.9 | 3.7 | | | | 0.0 |
| Māhoe wao | | 1.2 | | 1.2 | | 2.4 | 0.8 | 3.2 |
| Hīnau | | | | 0.0 | | | 3.2 | 3.2 |

¹Miro (*Prumnopitys ferruginea*), makomako (*Aristotelia serrata*), tawa (*Beilschmiedia tawa*), kōwhai (*Sophora tetraptera*), maire (*Nestegis lanceolata*), māhoe (*Melicytus ramiflorus*), karamū (*Coprosma robusta*), kōtukutuku (*Fuchsia excorticata*), māhoe wao (*Melicytus lanceolatus*), hīnau (*Elaeocarpus dentatus*).

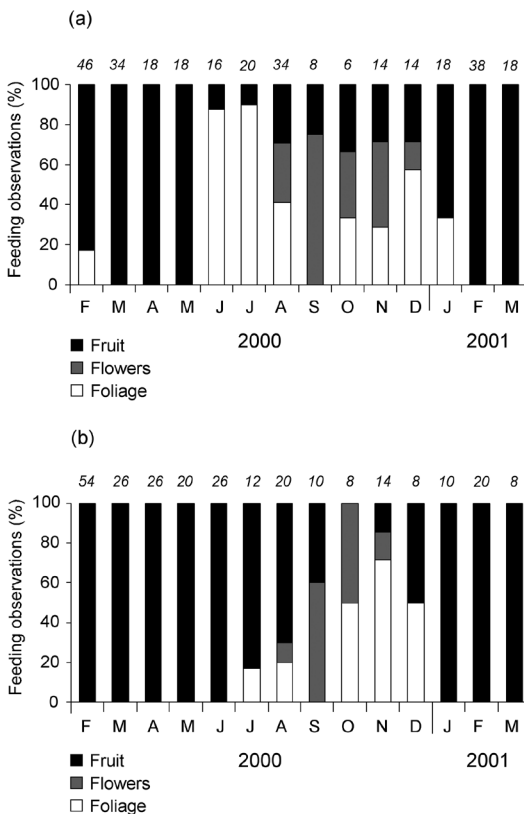


Figure 3. Monthly trend in the composition (percentage of feeding observations) by food type (foliage, flowers/buds, fruit) of the diet of kererū in Oriuwaka (a) and Otopaka (b) study areas, Whirinaki Forest Park, February 2000 – March 2001. Figures above columns are sample sizes.

of feeding observations during June–December 2000, kererū taking mainly foliage in June and July, flowers in September, and fairly equal proportions of the three food types during August, and October–November. In contrast, Otopaka kererū fed entirely on fruit during eight of the 14 months, and only in spring did foliage and flower consumption exceed that of fruit (Fig. 3b).

The ordination of feeding observations by principal components analysis is shown in Fig. 4, with component loadings displayed in Fig. 5. The first two axes account for 38% and 21% of the variance, respectively. Despite the differences in species availability in Oriuwaka and Otopaka, the ordination shows broadly similar patterns in the two areas over the 14 months. Figure 4 shows a roughly triangular dispersion of points reflecting the transitions between three main diets. In autumn of 2000, miro fruit was the dominant food source in both areas. In winter and spring, foliage and flowers dominated the diet but the change from miro fruit occurred abruptly in June at Oriuwaka, being later and more gradual at Otopaka, with miro still being consumed there in September. In summer 2000–2001, there was an abrupt change in both areas back to a fruit-dominated diet, this time predominantly of tawa or makomako. Apart from the difference in timing of the shift to foliage feeding, the main differences between the two areas were the particular species of foliage consumed (mostly kōwhai at Oriuwaka, other species and flowers at Otopaka) and the main summer fruit source (tawa arrived later at Otopaka and more makomako was eaten there than at Oriuwaka).

There was a significant difference in food-type usage between areas ($F = 4.17$, d.f. = 1,14, $P = 0.0046$) and with season ($F = 5.77$, d.f. = 6,14, $P = 0.0001$) but the interaction was not significant ($F = 1.51$, d.f. = 6,14, $P = 0.0848$). Pairwise comparisons of the levels of the season factor indicate a gradual change in diet because adjacent time

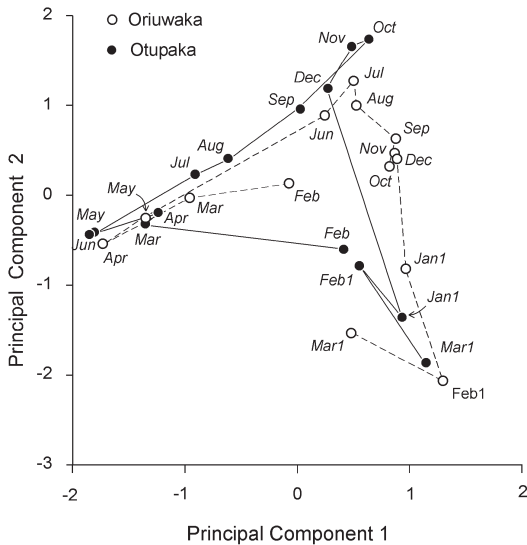


Figure 4. Ordination by principal components analysis of kererū feeding observations on eight major foods over 14 months in Oriuwaka and Otupaka study areas, Whirinaki Forest Park, February 2000 – March 2001.

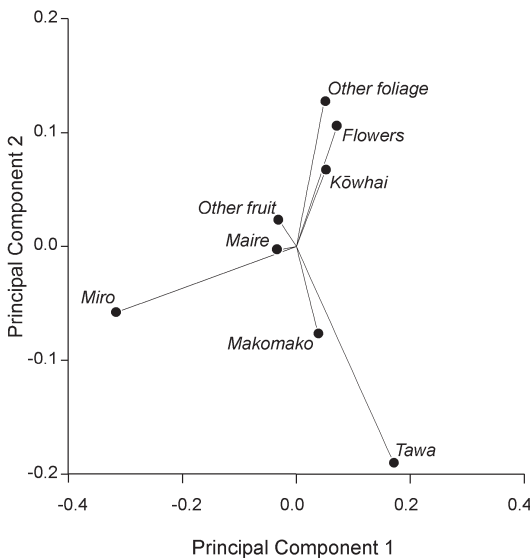


Figure 5. Factor loadings of the eight foods used in the ordination (see Fig. 4) of kererū feeding observations over 14 months in Oriuwaka and Otupaka study areas, Whirinaki Forest Park, February 2000 – March 2001. Species scientific names as for Fig. 2.

periods were not significantly different. However, diets more than two months apart were generally significantly different. The most distinctive period was February–March 2001 when the diet was dominated by tawa fruit.

Food preference

Fruits of two plant species, miro and tawa, were highly preferred by kererū in both Otupaka and Oriuwaka, and the preference for tawa was more pronounced in the latter (Fig. 6). Makomako fruit was preferred in Otupaka, but not in Oriuwaka. Of the other fruit sources, māhoe, kōtukutuku and karamū, each was taken by kererū in both study areas far less than would be expected if taken in proportion to their occurrence. Kōwhai foliage was taken in proportion to its occurrence in Oriuwaka, while māhoe foliage was avoided in Oriuwaka, but was taken only slightly less than at random in Otupaka.

When food preference of kererū was analysed on a monthly basis at Oriuwaka (Fig. 7a) and Otupaka (Fig. 7b), tawa fruit was preferred during all months when available. Similarly, miro fruit was preferred in all months when available, except for February 2001 at Oriuwaka. Notably, kererū preference for miro fruit in Otupaka declined slightly from when ripe fruit first became available (March 2000) to when fruiting ceased (August 2000). Even more dramatic was the decline in preference for young kōwhai foliage at Oriuwaka, from being one of the most preferred foods in November 2000 to a slightly preferred food two months later (Fig. 7a). Makomako fruit was always a preferred food when available in Otupaka, but in Oriuwaka it was preferred only in February 2001. Although kererū showed an aversion to karamū fruit in both study areas on an annual basis (Fig. 6), on a monthly basis it was actually a preferred food in April and August 2000 at Otupaka (Fig. 7b). In Oriuwaka, karamū fruit was not sought after when ripening in February–March, but became highly preferred four months later in July and August 2000 (Fig. 7a). Similarly, kererū at Otupaka showed a slight preference for eating young māhoe foliage in July 2000, but it became a highly sought-after food three months later in October and November (Fig. 7b). In Oriuwaka, kererū shunned feeding on māhoe foliage when it first became available in June 2000, showed a preference for it in July, but ate very little one month later (Fig. 7a).

Discussion

Phenology

Most tree and shrub species at Whirinaki displayed highly seasonal and synchronous patterns of fruiting, most doing so in summer or autumn. Makomako, kōtukutuku and tawa were summer fruiters, while miro, maire, māhoe, putaputaweta and karamū were predominantly autumn

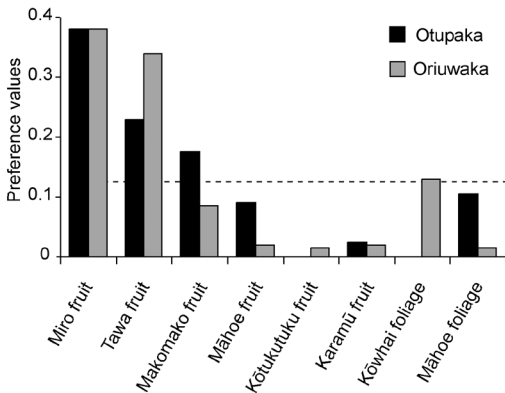


Figure 6. Mean preference values for eight foods eaten by kererū in Otupaka and Oriuwaka, Whirinaki Forest Park, February 2000 – March 2001. The dashed line at 0.125 represents random preference; values above this line reflect a positive preference, while those below reflect a negative preference based on a random encounter rate. Species scientific names as for Fig. 2.

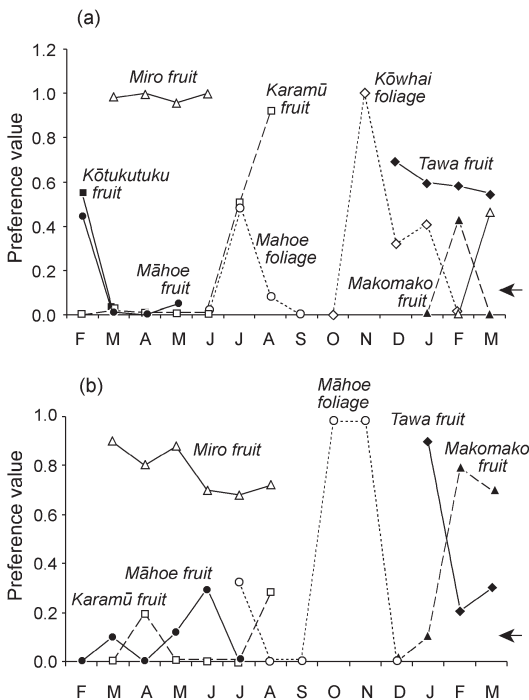


Figure 7. Monthly preference index for eight foods in Oriuwaka (a) and Otupaka (b), Whirinaki Forest Park, February 2000 – March 2001. The arrow indicates random preference of $1/k$; values above the arrow indicate foods preferred by kererū. Breaks in the line for a species indicate months when that food was not available. Foliage values are for immature foliage only. Species scientific names as for Fig. 2.

fruiters. As a result, the peak of ripe fruit abundance occurred in autumn, following the November–February peak in ambient temperatures and in solar radiance. Similarly, Ting et al. (2008) found that high-latitude sites in both hemispheres had annual peaks in fruit production, typically in late summer or autumn, 2–4 months after annual peaks in solar energy and water availability.

Extended fruiting of some tree species has been observed in some New Zealand species (Burrows 1996; Dijkgraaf 2002), so that ripe fruits can be found on some individual trees for over three months, and even all year round in the case of pūriri (*Vitex lucens*) (Dijkgraaf 2002). At Whirinaki this extended period of ripe fruit availability was most apparent among autumn fruiters, such as māhoe and miro.

There were marked differences in fruit production at Whirinaki by rimu, kahikatea, makomako, kōtukutuku and tawa between the 1999/2000 and 2000/01 fruiting seasons. Annual variations in fruit production have also been seen in other studies (e.g. Clout 1990; Cowan 1990; James et al. 1991). Tawa can have annual, biennial and irregular patterns of fruit production (Burrows 1999; Knowles & Beveridge 1982; Wright 1984). Rimu and kahikatea are typical masting species, producing a superabundance of fruit at irregular intervals, with little or no fruit produced in the intervening years (Norton & Kelly 1988; Kelly 1994). Thus, the amount of fruit available to kererū can vary markedly with season and year, and this affects pigeon diet and breeding effort (Clout 1990; Powlesland et al. 2003). Had either of these two species fruited during our study it would have been interesting to determine which dominated kererū diet in autumn, rimu and kahikatea, or miro.

The phenology of the individual plants selected for observations may not be representative of fruit abundance throughout Whirinaki Forest Park. Because of the prevalence of old logging sites and roads, a high proportion of the randomly placed phenology plots were situated at these relatively open sites deep in the forest and at forest edges. This may have influenced the degree of fruiting of the subcanopy species because plants that had greater access to direct sunlight appeared to carry more fruit than those below a canopy (MTE pers. obs.).

Another factor influencing foliage and fruit availability may have been feeding by birds, including kererū, as well as by possums and rodents. Birds and mammals are known to remove unripe fruit of a variety of species. This feeding activity was noted at four of the monitored miro trees, one in Oriuwaka and three in Otupaka. Possums caused varying degrees of defoliation of several māhoe, which is one of their preferred food species (Nugent et al. 2000). Severe defoliation was apparent on one māhoe in Otupaka, and less severe defoliation was noted on another in Otupaka and one in Oriuwaka (MTE pers. obs.). Kererū fed on young māhoe leaves to a greater degree in Otupaka than in Oriuwaka (Table 2),

perhaps as a result of the rarity of kōwhai in the former. Kōwhai are considered to be semi-deciduous, particularly in colder climates (Poole & Adams 1990). However, this does not explain the almost complete defoliation of some kōwhai trees; this can probably be attributed to the heavy browsing of its foliage by kererū in winter and early summer, as occurs elsewhere (Clout & Hay 1989; Medway 2006). While kōwhai moth caterpillars (*Uresiphitz polygonalis maoralis*) also defoliate kōwhai trees (Somerfield 1984), their distinctive feeding sign of dead leaves left on the trees (RGP pers. obs.) was not apparent in Oriuwaka.

Food preference

Although kererū are known to feed from many species ($n = 138$; Higgins & Davies 1996), during this study in Whirinaki Forest Park they exhibited a preference for fruit, and fed on the fruits of a few species almost exclusively when they were available. Tawa and miro fruits were keenly sought even when little remained. Miro fruit was also sought by kererū in Pelorus Bridge Scenic Reserve, Marlborough, where an individual defended a fruiting miro from other kererū (Clout & Hay 1989). Kererū numbers increased markedly in Otupaka during late autumn and winter when ripe miro fruit was abundant there, and few other fruit sources were available elsewhere in the park (MTE pers. obs.). Such tree species that fruit when few or no others do are particularly important in sustaining frugivore populations (Anderson 1997).

Other fruit sources did not appear to be as important to kererū at Whirinaki. Some species, such as karamū, māhoe, maire and kōtukutuku, were eaten when readily available, but not as much as tawa and miro. Likewise, studies by Dunn (1981) and Baker (1999) indicated that karamū fruit was not a preferred food of kererū about Dunedin. Anderson (1997) found that during periods when there were few high-reward foods available or when these were restricted to particular areas, birds utilised lower value resources. Fruits not commonly eaten in large amounts, even when readily available (such as that of kōtukutuku), would fall into this category. However, such fruit was important in providing a continuous food supply. It is also possible that these fruits, although inferior sources of proteins, lipids and carbohydrates compared with tawa and miro (Hill 2003), may have been eaten in small quantities because they contained complementary nutrients, such as vitamins and minerals (Whelan et al. 1998).

Foliage formed a significant component of kererū diet at Whirinaki during the study, more so in Oriuwaka (26.5%) than in Otupaka (7.9%). Kererū fed selectively on the leaves from only a few species, in particular kōwhai and māhoe. Kōwhai appeared to have two functions in the kererū diet. Over the winter months, when little fruit was available, kōwhai appeared to be a subsistence food, forming a larger component of the diet than any other food (Hill 2003). In addition, during November–January

(kererū breeding season at Whirinaki; Powlesland et al. 2003) in Oriuwaka, when tawa and makomako fruits were eaten, young kōwhai foliage was eaten also. Fruit pulp is considered nutritionally inadequate for frugivorous birds because of its low protein content (Bosque & Pacheco 2000), while some foliage sources contain relatively high protein levels (Williams 1982; Powlesland et al. 1997; Nelson et al. 2000). Protein is important for egg and nestling development, and the growth of feathers during the moult (Fisher 1972; Payne 1972; Poulin et al. 1992). Thus, it appears that young kōwhai foliage was eaten because it contained important nutrients required by breeding kererū in Oriuwaka. In Otupaka, where kōwhai was scarce, young māhoe foliage was eaten, which was a better protein source (43.8%) than kōwhai foliage (27.9%) (Hill 2003).

The differences in diet of kererū in Oriuwaka and Otupaka reflect, to some extent, the differences in forest composition between the two areas as a result of the higher elevation (colder temperatures, greater rainfall) of Otupaka. There was a greater abundance of miro (and the later ripening of its fruit) and a scarcity of kōwhai in Otupaka than in Oriuwaka. Likewise, the occurrence of hīnau fruit in the diet of Otupaka kererū reflects a difference in abundance of hīnau between the two areas. Whether possum control in Otupaka in May 2000 and not in Oriuwaka had a confounding effect on the results of our study of kererū diet in the two study areas is unknown. Given that māhoe leaves and miro fruit are favoured foods of possums (Nugent et al. 2000), the possum kill may have contributed to both foods remaining in the diet of Otupaka kererū for several months longer than of those in Oriuwaka.

Because of the unpredictability of fruit sources in a temperate climate (Banack 1998), frugivorous animals, such as kererū, diversify their diet when required. Kererū behave as fruit specialists when a preferred fruit is readily available. For example, individuals have been seen feeding almost entirely on miro fruit for up to three months in both Whirinaki Forest Park (Hill 2003) and Pelorus Bridge Scenic Reserve (Clout & Hay 1989). However, kererū were more generalist feeders when tawa or miro fruit was unavailable in Whirinaki, taking food from a variety of species involving a combination of food types: fruits, foliage, flower buds and flowers. Among frugivorous birds, this differential use of food sources has been evident in fruit pigeons (Crome 1975), some species of tanagers, honeycreepers (Snow & Snow 1971), and saltators (Jenkins 1970). A lack of fruit has been postulated as the reason for the switch in kererū diet from fruit to foliage in late winter and early spring (Clout et al. 1986; Baker 1999). Such a lack of fruit appears pertinent at some sites, such as Pelorus Bridge Scenic Reserve (Clout et al. 1986, 1991), and Invercargill, Southland (RGP pers. obs.), but in Auckland (Dijkgraaf 2002) and during late spring–summer at Whirinaki, fruit was available and eaten when foliage

was eaten. Likewise, parea (*Hemiphaga chathamensis*) on Chatham Island during the breeding season acquired supplementary protein by feeding on herb foliage and flower buds when much fruit was available (Powlesland et al. 1997). Therefore, the switch from a mainly fruit diet to one of fruit and foliage by kererū and parea may be an issue of nutrient complementarity during periods of egg and chick production.

While the actual species of foods or their timing in the diet differed between the two study areas, the principal components analysis showed that there was much similarity in these diets with regard to food type. During summer–autumn, kererū in both study areas fed mainly on fruits and changed to a foliage–flower bud–flower diet in either spring (Otuwaka) or winter (Oriuwaka). Subsequently, kererū in both areas fed mainly on fruits in summer. The timing of the shift to inclusion of foliage in the diet during winter–spring by kererū populations is likely to differ regionally and from year to year in relation to availability of preferred fruits, but it is also likely to relate to nutrient requirements in relation to breeding.

Unripe fruit and mature foliage appear not to be preferred forms of food, even though studies have shown nutrient levels to be similar between unripe and ripe fruit, and young and mature foliage (Nelson et al. 2000). Suggestions for this lack of appeal include secondary compounds in such foods making them unappetising and/or inhibiting protein digestion. Also, unripe fruit may be indigestible, owing to its hard pericarp and high fibre content. The preference for young leaves of māhoe may reflect the bird's ability to include the midrib in the diet, which contains most of the lipid in the leaf structure (Williams 1982).

Conclusion

The variability of kererū food availability, both in time and space, evident from our study, suggests that large areas of New Zealand's temperate podocarp–hardwood forests (1000s of hectares), or several patches of forest that contain different habitat types and therefore species mixes, need to be managed for the long-term conservation of the kererū. The various patches of forest or food trees need not be in close proximity to each other, given the kererū's ability to fly tens of kilometres over inhospitable country, or the sea, to reach seasonal food sources (Clout et al. 1991; Harper 2003). Even small patches of native species in exotic forest can benefit kererū, such as hardwood species along stream and river margins, and the availability of some shrub species in the understorey of mature plantations.

Acknowledgements

We thank Dave Wills, Claude August and Andrew August who provided logistical support to MTE while carrying out an MSc study of which some of the results form the basis of this paper. The Department of Conservation, Massey University Research Fund, Julie Alley Bursary, Waikato Branch of the Royal Forest & Bird Protection Society, Coombs Memorial Bursary, and the New Zealand Federation of University Women provided financial support to MTE. We also thank Astrid van Meeuwen-Dijkgraaf, Sue Hallas and two referees for constructive comments on a draft of the manuscript. This project was funded by the Department of Conservation (investigation 3158), and was carried out with Department of Conservation Animal Ethics Committee approval (AEC 54).

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Editorial Board member: Kay Clapperton

Received 15 December 2008; accepted 17 June 2009