Phenology and frugivory of large-fruited species in northern New Zealand and the impacts of introduced mammals.

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Abstract

This thesis investigated the reproductive phenology, fruit features, dispersal and seed predation of native New Zealand fleshy-fruited species, concentrating mainly on fruits larger than 10-mm in diameter borne by trees. There are several species with large tree-borne fruit in New Zealand and they currently only have one seed disperser (kereru, *Hemiphaga novaeseelandiae*). Historical evidence suggests that kereru might have been the sole effective disperser for most of the Quaternary. Thus the New Zealand large-fruited frugivore system is relatively simple. It might, therefore be possible to test whether competition amongst large-fruited species for dispersers has resulted in character displacement in the timing of ripe fruit presentation. With this in mind I examined the timing of ripe fruit presentation – the phenological patterns – and nutrient complementarity of fruit species known to contribute to the kereru diet.

Introduced mammals have impacted significantly on New Zealand forest ecosystems, including fruit production. An experiment was designed to measure the level of mammalian fruit consumption. Three paired forest patches, with similar topography, aspect and forest type, were selected. Mammalian pests were suppressed in three forest patches, but left unchanged at the paired site. This allowed comparison of fruit production and fruit phenology at sites with and without pest suppression. The effects of mammal pests on kereru, other bird species and some insect species were also investigated.

Showing that phenological patterns have statistically significant character displacement has proved difficult in the past. It was considered that significant differences might be obtained if phenological patterns were broken down in to the most important character displacement attributes. These were thought to be: (1) order of ripe fruit presentation amongst species; (2) peak fruit production should be greater than could be expected by chance; (3) synchronicity of fruit production within species; (4) lack of significant overlap between species competing for the same resource.

The two sites with the longest phenological record and best level of pest suppression were used to investigate whether character displacement occurs amongst large-fruited species. The fruiting pattern of large-fruited species in northern New Zealand was more akin to tropical forests with year round fruit supply, than to temperate forest with more seasonal fruiting. The order of fruiting tended to be consistent between years at both sites. Fruit was not produced throughout the year by individual species, but tended to occur in defined peaks. A combination Simpson Index and Monte Carlo parametric bootstrap method was used to confirm that the fruiting peaks were non-random.

The theory of competitive displacement amongst co-existing species requires that little or no overlap should occur in the production of ripe fruits by competing species. This means that the period of ripe fruit presentation for one species should not overlap significantly with ripe fruit production of another species. This was tested by modifying a formula developed by Augspurger (1983) that considers the phenological state of an individual in the context of what all other individuals of that same species (for synchrony) or other species (for overlap) are doing over the same period. A further development was the generation of critical values against which the values for individual species could be compared.

Species tended to be more synchronous than asynchronous in the presentation of ripe fruits but only one species was consistently more synchronous than the calculated critical value at both sites. Two other species at Whitford Bush exceeded the critical synchrony value and several other species from both sites came close to exceeding the synchrony value. Despite synchrony values being generally smaller than expected species tended to not overlap significantly with other species in some or all years. Character displacement, in the form of timing of ripe fruit presentation, was demonstrated for most species. However, it is not possible to conclude that this has come about through co-evolution, solely, with the frugivorous kereru.

Fruit nutritional analysis of a range of (mostly) large-fruited species gave rise to six ‘fruit types’ that clustered on size, lipid content, sugar and moisture content, carbohydrate or protein content. These categories and the nutritional values obtained for New Zealand fruits tended to agree with overseas studies. Compared to overseas fruits, a generalist description of New Zealand fruits could be “relatively small, moist, fibrous but nutritionally poor fruits”. In the forests of Auckland, fruit is available throughout the year. Reasonable quantities of high-lipid fruits are available throughout most

of the year, except for parts of summer, and there is little overlap between lipid-rich species. High-sugar fruits are most common during summer and autumn.

Kereru were shown to use fruit species as they become seasonally available. However, they preferred large lipid-rich fruits, which can amount to 40% or more of the diet at one time and possibly up to 80% of the diet fed to chicks. Taraire (*Beilschmiedia tarairi*) and nikau (*Rhopalostylis sapida*) were the most preferred of the lipid-rich fruits. Nikau is also a calcium-rich fruit. Puriri (*Vitex lucens*), a large sugar-rich fruit, was a common dietary item, eaten throughout the year, even when the fruit was relatively scarce. Kahikatea (*Dacrycarpus dacrydioides*; small and sugar-rich) was eaten by kereru when large quantities of ripe fruit were available. The timing and nutrition of the fruiting species was generally complementary, with different nutritional components available from species fruiting simultaneously. Observational data indicate that kereru generally prefer large-fruits over small fruits. The greatest numbers of feeding observations were of kereru taking fruits that were too large to be taken by other extant bird species.

Fruit species were available and eaten throughout the period that foliage (e.g. kowhai *Sophora* spp.) was also eaten. Kowhai leaves and other sources of foliage have higher concentrations of nitrogen than most fruits. Thus perhaps a switch to utilizing foliage is not so much due to a lack of food but more an issue of nutrient complementarity, during the periods of egg development and nesting.

Possum (*Trichosurus vulpecula*) and rodent (*Rattus* spp., *Mus musculus*) control was reflected in the number of possums and/or rodents caught in forest patches at the end of the study. Long-term pest mammal suppression resulted in no trappable possums, rats or mice. Sites lacking mammal suppression had moderate to high numbers of possums and rodents. Possum numbers were lower at one site with partial possum suppression but lacking rodent suppression. Rodent (rats and mice) numbers were generally too low to make valid comparisons but appeared somewhat elevated at the site with partial possum suppression.

Possum droppings were more frequent in seedfall traps at sites with no systematic possum suppression. Rodent droppings had less clearly defined patterns and showed more seasonal variability than possum droppings. The data for number of pest-mammal droppings in seedfall traps generally support the mammal trapping data.

Possums and rodents had adverse effects on fruit production at sites without pest suppression. Suppression of possum and rodent numbers resulted in more fruit production, less fruit damaged, more fruits maturing and more fruits consumed by birds that void the seed unharmed. Pest suppression also ensured that ripe fruits were available throughout the year, supporting resident native frugivores. Partial possum control resulted in both the production of more fruits and proportionally more possum and rodent damaged fruits. Mammal pests showed preference for energy rich fruits such as taraire, and nikau, which are also preferred by kereru.

Pest suppression generally increased the number of traps with insect or kereru droppings, except at the site with partial pest suppression where the occurrence of insect droppings was relatively low. It is not possible to determine whether the benefits to these species are solely through a reduction in possum numbers or through a combination of reduced possum and rodent numbers.

Bird encounter rates were generally greater at sites where pest-mammals were suppressed, especially for frugivorous birds. This increased encounter rate is unlikely to be solely due to behavioral changes in the bird population since the proportion of consumed fruits also increased. Other factors, such as forest patch size and forest patch isolation, are also thought to be important in determining bird numbers. Some forest patches seemed to have insufficient kereru to consume and disperse available crops of large fruit.

The timing of fruit production and the nutrient content of the fruits resulted in some fruits being more attractive (e.g. high energy food source, or important seasonal nutritional component) to frugivores than others. These fruits were consumed more often by both seed dispersers (kereru) and seed predators (possums and rodents). Predation of fruits has negative consequences for the survival and fecundity of the kereru and long-term implications for the survival of these large-fruited tree species.

The interrelationships between ripe fruit production, disperser availability and predator impact has implications for managing forests and pest and kereru populations. Management will also need to consider the plant species composition since there are fewer large-fruited species at southern latitudes and higher altitudes. At northern latitudes pest suppression may be less successful because fruit is available virtually throughout the year and pest species may not be not food limited. Fewer large-fruited species are found at more southerly or higher locations and might result in ‘windows’ of food shortage that can be utilized for delivering toxic baits. Being able to predict unusually large or small fruiting events would thus be very useful for conservation management.

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[1] Kereru eating a tawa fruit, one of the large-fruited species studied (Photo courtesy B.W. Thomas)

1 Introduction

1.1 History of frugivore studies

During the 1960s and 1970s it was pointed out that, although much information existed on fruit[2] structures and foods eaten by vertebrates, little was known about interactions between fruiting plants and frugivores in an evolutionary context (e.g. McKey 1975; Snow 1962, 1965). The authors suggested various aspects of plant and frugivore interaction that required further research to elucidate proposed co-evolutionary relationships. These initial ideas resulted in a set of themes in frugivory research that have underpinned much of the research into fruit and disperser co-evolution.

Fleshy fruits were taken to be an evolutionary development to enhance the dispersal of the propagule. One central notion was that of 'fruit syndromes' for different suites of dispersers. Amongst the fleshy fruits, black, red, or blue coloured fruits, or a combination of the three colours, were shown to be the most preferred by birds (Snow 1971; Willson and Whelan 1990). Mammalian fruits were described as scented, often with a fetid smell, dull in colour, and in many cases very large. Reptile fruits were suggested to have an attractive odour and be borne basally on the trunk (Snow 1971). Some non-fleshy 'fruits' were noted to be successfully bird-dispersed by mimicking the bird-fruit colouration (McKey 1975). These syndromes were assumed be constant throughout the world (e.g. Armesto and Rozzi 1989). Plant species that produce bird-fruits will be dispersed by birds even when translocated to a different continent, as shown by the dispersal of the Australian species *Acacia cyclops* that has become a major bird-dispersed weed in South Africa (Glyphis *et al.* 1981).

Within the bird-fruits, large lipid rich fruits were thought to be associated with bird species whose diets consisted solely or mostly of fruits, often called specialist frugivores. Fruits eaten by a larger entourage of birds were described as more sugar-rich, with smaller seeds, which could be swallowed by a whole range of small and large birds. These species of bird usually had a varied diet that also included insects, and were therefore called generalist frugivores. Specialist were postulated to provide a better service to the plant by dispersing the seed unharmed to sites more suitable for germination than generalist birds would, or they would enhance the rate or success of germination. Specialist frugivores could exist only where fruits were available year-round, being mainly in the tropical forests (McKey 1975; Snow 1965, 1971).

A trade-off was postulated between producing highly nutritious, but energy expensive, fruits that would attract specialist frugivores (high quality dispersers) and attracting a wider range of lower quality dispersers by producing copious, but less nutritious, fruits. Toxins, structural protection or access (including ease of fruit removal) could further differentiate between preferred disperser and less specialised species (McKey 1975; Snow 1971). For instance, in a more recent example, structurally protected fruits were solely or mostly consumed by particular suite of birds (birds of paradise), while unprotected fruits were consumed by a wider range of species (Beehler and Dumbacher 1996).

Other mechanisms presumed to have evolved to maximise seed dispersal by preferred species included staggering fruiting times (seasonal displacement), fruiting for long periods and providing different nutrients during different seasons (McKey 1975; Snow 1965). The size of the seed(s) often also limits the range of species that can ingest the fruits and hence disperse the propagule. Large fruits tended to be associated with 'specialist' frugivores, and were thought to be only produced by canopy, late successional, tree species, that required ample provision of the embryo while it awaited a canopy gap. However, there had to be a compromise between the size, or number, of seeds in a fruit and the quality of the fruits, since the ingested seeds would essentially be useless ballast for the bird disperser (McKey 1975; Snow 1971).

Evolutionary adaptations in the disperser suite included developing specialised gut systems and ways of handling the fruits to prevent seed damage. The passage of the seed through a gut or particular seed

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[2] Note that throughout, unless otherwise stated, the term fruit is used in a functional sense rather than as a technical botanical description.

handling techniques by preferred dispersers were thought to increase seed germination rates, or deposition of seed in preferred sites (McKey 1975).

However, as more studies were undertaken on fruit and frugivore relationships it became clear that the current relationships had not arisen merely through interactions and co-evolution between plants and their vertebrate, often bird, dispersers (e.g. French 1992; Howe and Smallwood 1982; Janzen 1983). Obligate frugivore systems appeared rare or hard to quantify (Howe and Estabrook 1977; Snow and Snow 1988; Wheelwright 1985a), in contrast to the infrequent but definitely obligate systems recorded in pollination biology (e.g. the *Ficus* species and their pollinating wasps (e.g. Ramirez 1970; Walsby and Early 1997)). Most plant-frugivore interactions involve many species of plants and animals (e.g. Coates-Estrada and Estrada 1988; Wheelwright 1985a), or could not be separated from the influence of evolutionary and palaeontological events (e.g. Armesto and Rozzi 1989; Ehrlén and Eriksson 1993; Fleming *et al.* 1987; Herrera 1989; Willson and Whelan 1990).

Thus it was suggested that plant-frugivore co-evolution was more diffuse than initially postulated, with a number of factors contributing to the noted interactions (e.g. Herrera 1982; Janzen 1980; Snow and Snow 1988; Stiles and Rosselli 1993) and that plants had evolved to attract as many species of disperser as possible, compatible with other ecological constraints affecting fruit quality (Primack 1987; Snow and Snow 1988; Traveset 1994). Furthermore, utilising more than one disperser reduced the chance that losing a single ‘specialist’ disperser would result in the loss of dispersal capabilities, and consequent risk of extinction of the plant species (Snow and Snow 1988). The case for diffuse co-evolution was further strengthened by the life-histories of the species, since plant species appear to have slower rates of evolutionary change than frugivorous species (Janzen and Martin 1982; Snow and Snow 1988; Stiles and Rosselli 1993).

Many plant species appear to have undergone little, if any, change compared with their fossil ancestors, while the suites of potential disperser species undoubtedly have exhibited major changes in form (Herrera 1986; Jordano 1989, 1993; Snow and Snow 1988). Thus, if co-evolution between frugivores and plants exists, it is probably weak and mostly one-sided, with frugivores undergoing most of the morphological and/or physiological modifications or adaptations (Snow and Snow 1988) (but see Keeler-Wolf 1988, who argues for strong selection pressure and rapid plant species modification in isolated situations such as Trinidad and Tobago). Aspects of plant evolution that might lend themselves to modification by frugivore selection are timing of flowering and fruiting, and nutritional constitution, rather than gross morphological structures (Snow and Snow 1988). These modifications, along with fruit or flower colour, cannot be tracked through the fossil record.

It is also possible that frugivores have affected historic plant distribution patterns by selection and spread of those plant species most suited to frugivores. Birds have in some cases been shown to make hierarchical decisions in fruit selection (Herrera *et al.* 1994; Sallabanks 1993), which might have affected the distribution of bird-dispersed fruits through Europe after periods of glaciation (Snow and Snow 1988). The manner by which fruits are disseminated could also modify the habitat, such as clumped distributions of seedlings, with subsequent inter-seedling competition, under favoured perching sites (Loiselle 1990) or discarding excessively large fruits beneath the parent tree (Wheelwright 1985b). The preference of birds for or against the utilisation of canopy gaps or particular habitat types could also influence forest composition by favouring light demanding or shade tolerant seedlings or changing seed loadings at those sites (Ferguson and Drake 1999; Herrera *et al.* 1994; Moles and Drake 1999; Schupp *et al.* 1989).

The theory of ‘diffuse co-evolution’ has been subject to criticism. Jordano (1993) lists three key points that need to be addressed in any critical evaluation of the diffuse selection hypothesis for a particular proposed plant-frugivore system:

- determine the variation in space and time (annual rather than historical, such as migration patterns) of the size, composition and numbers of plant and frugivorous species interacting in local areas;
- evaluate the outcomes of their interactions (e.g. outcome of fruit removal by different species, how that affects post-dispersal seed predation and seedling establishment);

- test the hypothesis that the effects of the interaction outcomes, of all the different species involved, are not opposed (which would negate selection pressure) but additive or compensatory.

However, these criteria do not take into account other aspects of fruit set and fruit development, such as pollination history (e.g. Milton *et al.* 1982), percent fruits set or percent fruits with viable embryos (e.g. Jordano 1989) or climatic conditions (e.g. Brockie 1986; Herrera 1998; Sallabanks and Courtney 1993; van Schaik *et al.* 1993) which can also affect 'apparent disperser success' as measured by distribution of dispersed seedlings.

In short, many factors contribute to, and need to be considered in, most frugivore-fruit bearing plant systems. These multiple factors interrelate and interact in ways that vary in space and time and thus become hard to predict.

The field of frugivory and seed dispersal is searching for new directions. The paradigm that co-evolution of vertebrate frugivores and fruit bearing plants would produce a suite of characters, matched pairs, or group species on morphological, physiological or ecological aspects, did not eventuate (Herrera 1998; Levey and Benkman 1999). Herrera (1998) suggests that viewing plant disperser systems as non-equilibrial and using the conceptual tools associated with that idea could stimulate renewed research in this field. Alternatively, computer modelling of the evolutionary ecology of dispersal and ecological complexity modelling are gaining more momentum and could provide new insights on speciation, evolution, extinction and patterning on various scales (Dieckmann *et al.* 1999; Earn and Rohani 1999) which might help in defining further parameters to test in plant-frugivore systems.

1.2 New Zealand situation

As discussed above, the postulated co-evolution of frugivores and fruit-bearing plants seems to have been overly simplistic, possibly due to the many biotic and abiotic factors that need to be considered. Most studies investigating apparently mutualistic systems have to deal with

- multiple frugivorous species, that consume greater or lesser amounts of fruit in their diet (e.g. Herrera 1985a; Snow and Snow 1988; Thompson and Willson 1979; Wright *et al.* 2000b);
- frugivorous species of many different clades, such as reptiles, birds, large, small or winged mammals (e.g. Charles-Dominique 1993; Ganesh and Davidar 1999; Gorchov 1990; Gorchov *et al.* 1993; Hamann and Curio 1999; Willson 1993; Wrangham *et al.* 1994);
- large fluxes in frugivore populations due to migration (e.g. Lefebvre and Poulin 1996; Thompson and Willson 1979; Whelan and Willson 1994);
- different frugivore suites utilising the same, or similar, floras on a geographic level (e.g. Fuentes 1992, 1995; Jordano 1993; Keeler-Wolf 1988; Wheelwright 1988);
- or a combination of the above (e.g. Herrera 1998; Jordano 1989).

The suite of native frugivores in New Zealand is considerably simpler from that found in most other locations. This is mostly due to the early isolation of New Zealand from other landmasses, which restricted the influx of more "modern" species such as mammals.

1.2.1 General history of NZ

New Zealand is one of the few substantial non-polar landmasses to have never been occupied by large land mammals (Caughley 1989; Cooper and Millener 1993; Holdaway 1989, 1990; Stevens *et al.* 1995; Webb and Kelly 1993). New Zealand became isolated about 80 million years ago (m.y.a.) with the break-up of the vast supercontinent Gondwana (Cooper and Millener 1993; Poole and Adams 1994; Salmon 1980; Stevens *et al.* 1995), and therefore did not share in the evolution and dispersal of monotremes or marsupials and the later evolution and dispersal of terrestrial mammals (Cooper and Millener 1993; Holdaway 1989, 1990; Poole and Adams 1994; Salmon 1980; Stevens *et al.* 1995)

New Zealand originated on the vast super-continent Gondwana, initially as part of the ocean floor. The most active colonisation by terrestrial life probably took place between 140 million years ago, when New Zealand arose from the ocean, and 80 m.y.a. During this time New Zealand was part of a large landmass, that extended from New Caledonia to the edge of the Campbell Plateau (South of the Campbell and Auckland Islands) (Stevens *et al.* 1995) and many plant species with Gondwanan roots probably arrived during this period, including ferns, Podocarps, Araucarian pines, *Nothofagus*, *Protea* and *Metrosideros* ancestors (Daugherty *et al.* 1993; Poole and Adams 1994; Salmon 1980; Stevens *et al.* 1995; Wright *et al.* 2000a) (but also see Craw 1985; Winkworth *et al.* 1999).

Since 80 m.y.a. plate tectonics, changing sea-levels, erosion, glaciation, mountain building, volcanic activity and fluctuating climate have all impacted on the New Zealand landscape. At times New Zealand was reduced to an elongated, narrow low-lying archipelago and a few scattered islands, in total two-thirds of its present size (Cooper and Millener 1993; Poole and Adams 1994; Salmon 1980; Stevens *et al.* 1995). These geological and environmental changes resulted in extinction of some of New Zealand's flora and fauna, but also presented opportunities for species to radiate out to, or disperse into, new niches or sites (Cooper and Millener 1993; Stevens *et al.* 1995). For most of the Tertiary the New Zealand biota experienced subtropical to warm temperate conditions (Cooper and Millener 1993). The low-lying archipelago would have supported extensive forests containing numerous species with fleshy fruits.

Throughout these times New Zealand also saw the arrival of new species on ocean and wind currents and contributed in turn to biota of other countries, a process that still continues to this day (Cooper and Millener 1993; Stevens *et al.* 1995; Wright *et al.* 2000a).

1.2.2 New Zealand Flora [3]

The New Zealand flora has Gondwanan roots (e.g. the podocarps, beeches (*Nothofagus*), Winteraceae, many ferns and bryophytes), overlaid with plants of more recent tropical origins (e.g. *Cordyline*, *Rhopalostylis*, *Avicennia*, *Beilschmiedia*, *Dysoxylum*, *Litsea*, *Vitex*, *Corynocarpus*) and even more recent immigrants (but also see Lord 1999; Webb and Kelly 1993). Different species dominated New Zealand during different geological epochs, due to their varying tolerances for cold or competitiveness during warm eras. Many species did not make it through the various geological bottlenecks (Cooper and Millener 1993).

The late Miocene saw reductions in temperatures and the glacial epochs during the Pliocene, possibly coupled with tectonic upheavals, greatly reduced forest diversity in New Zealand, especially amongst the woody species with high temperature requirements. The changes contributed to disjunct plant and animal distributions, and the localised endemic populations that exist in New Zealand today (Cooper and Millener 1993; McGlone 1985). The current climate sees most of the species with tropical affinities clustered on the North Island, particularly in the northern parts.

The New Zealand flora has many unusual features. Flowers are often small, greenish in colour, and simple in structure, with the sexes on separate plants (Lloyd 1985; Webb and Kelly 1993). The flora has many woody plants; most are evergreen, and relatively few annuals. This probably contributes to the high proportion of the flora with fleshy fruits; 250 species from 50 families, including about 70% of woody mainland forest plants (Burrows 1994a; Burrows 1994c; Clout and Hay 1989; Webb and Kelly 1993). These ratios are similar to other tropical rainforests (Willson *et al.* 1989) or South American temperate forests (Armesto and Rozzi 1989) and not unusual compared to some other temperate forests (Lord 1999).

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[3] Nomenclature for the plants follows Parsons *et al.* Parsons, M. J., Douglass, P. and Macmillan, B. H. (1998). "Current names list for wild gymnosperms, dicotyledons and monocotelydons (except grasses) of New Zealand as used in Herbarium CHR Version, to 31 Dec 1995." Lincoln, New Zealand, Manaaki Whenua Press. 206 pp., with corrections and updates from the New Zealand plant names database at http://nzflora.landcare.cri.nz/plantnames/.

Fleshy-fruited species dominate amongst the coniferous trees (75%) with smaller portions of the dicotyledonous (14%) and monocotyledonous (6%) trees bearing fleshy fruits (Lee *et al.* 1991). New Zealand has greater than expected numbers of genera, and tree species, with Gondwanan roots bearing fleshy-fruits (Lord 1999).

The majority of fleshy fruits are reddish (67%), white (18%) or black (15%) (Lee *et al.* 1991), though it does depend on how the colours are grouped, especially for bi-coloured fruits (e.g. Burrows 1994a; Willson *et al.* 1989). Most fruits are small, with 90% being less than 10 mm in diameter[4] (Burrows 1994a; Lee *et al.* 1991). The large fruits (> 10 mm) are usually oblong or elliptical in shape, and may reach 40 mm in length. Spherical fruits have a maximum diameter of about 20 mm (Lee *et al.* 1991)

Fruit availability varies seasonally, annually, latitudinally and according to altitude. Lowland forests in northern regions may produce fruit the entire year (mostly because of a wider range of species), but peak fruit abundance and diversity occurs from late summer to late winter (Lee *et al.* 1991; Wardle 1978). A high proportion of plant species have considerable year-to-year variation in fruit production (often referred to as mast fruiting), including species producing fleshy fruits (Webb and Kelly 1993) (but also see Herrera *et al.* 1998).

1.2.3 New Zealand Fauna

Like the New Zealand flora, the fauna has seen successive waves of species colonisation.

New Zealand features a number of ‘ancient’ animal species that must have colonised New Zealand during the ‘land-bridge’ stage (140 to 80 m.y.a.) and fossil records indicate that they have survived relatively unchanged to the present day. The extant native frogs (*Leiopelma*), tuatara (*Sphenodon*), *Peripatus* (link between annelids and arthropods), large native land snails (e.g. *Paryphanta*) and earthworms (e.g. *Spenceriella gigantica*), and some of the flightless insects such as weta (Orthoptera) could not have dispersed across the seas once New Zealand became isolated (Stevens *et al.* 1995).

The ancestors of the moa (*Dinornithidae*) probably inhabited the New Zealand landmass before it became isolated from Australia and Antarctica, but kiwi (*Apteryx* spp.) ancestors appear to have arrived about 40 million years ago (Cooper and Millener 1993; Daugherty *et al.* 1993; Stevens *et al.* 1995). Successive waves of colonisation presumably occurred, depending on the wind flows and ocean currents (Cooper and Millener 1993; Daugherty *et al.* 1993). Periods of high extinction rates are associated with global sea-level rises, significant erosion of land area and various ice ages (Cooper and Millener 1993).

Those species that arrived here found a land with no mammalian predators, and few other predators (Holdaway 1989; Stevens *et al.* 1995), although there were predatory birds, lizards and insects (Daugherty *et al.* 1993). The absence of mammalian predators is commonly associated with a set of morphological and life history traits amongst the endemic fauna such as flightlessness, gigantism and low reproductive rates. For instance, among the avifauna many species lost their power of flight (e.g. kiwi, takahe *Notornis manteli*, kakapo *Strigops habroptilus*), became giants of their families (e.g. Haast’s eagle *Harpagornis moorei*, *Cnemiornis* goose, moa), had small clutches (most species), cryptic plumage or melanism (e.g. kiwi, kakapo, kokako *Callaeas cinerea*) and show reduced predator responses (most species) (Daugherty *et al.* 1993; Stevens *et al.* 1995).

Ecological roles typically taken by mammals on other continents are filled by insects, reptiles and birds in New Zealand (Clout and Saunders 1995; King 1998). The large flightless weta (Orthoptera) developed lifestyles and habits similar to those of small rodents, sheltering during the day and

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[4] Unless otherwise stated fruit diameter refers to the average transverse distance through the smallest axis of the fruit. Generally, this distance would have been obtained by measuring multiple fruits of the same species.

emerging at night to feed on vegetation. They even produce rodent-like droppings. Birds such as the takahe, kakapo, various sized moa, kokako, and kereru took on ecological roles similar to mammalian browsers, feeding on plants in various strata (Clout and Hay 1989; Daugherty *et al.* 1993; Stevens *et al.* 1995).

The postglacial fauna of New Zealand was not diverse and populations were small and vulnerable to mammalian invasion. The arrival of humans, both Polynesians and Europeans, with their associated pets and pests, saw the New Zealand fauna lose 40 to 50% of its avifauna, 50% of its frogs and unknown proportions of lizards and invertebrates within about 1000 years (Holdaway 1989; Stevens *et al.* 1995; Towns *et al.* 1997b). Some species are extinct on the main islands but cling to existence on predator-free offshore islands. Many introduced species appear to be more efficient competitors. They are more vigorous in their breeding habits and may prey on both the food sources of the native species and the species themselves. The New Zealand species are struggling (and sometimes failing on the mainland) to survive (e.g. Brown *et al.* 1993; Clout *et al.* 1995b; Cowan and Moeed 1987; Innes 1994; Innes *et al.* 1996; O'Donnell *et al.* 1992; Saunders 1990; Velben and Stewart 1982).

1.2.4 New Zealand frugivore systems

Though New Zealand had a reasonably diverse terrestrial fauna, it currently has (and historically had) a limited suite of frugivores, especially for the larger (>10 mm) fruits. Many of the frugivorous bird species were flightless and unable to utilise fruits produced by the taller tree species, unless fruits fell to the ground or the lower branches were accessible. There have never been any medium or large terrestrial mammals capable of swallowing and dispersing larger fruits. There are no large-scale migrations of frugivorous vertebrates, such as seen in Europe and the Americas (e.g. Izhaki and Safriel 1985; Malizia 2001; Whelan and Willson 1994), which could take advantage of peak fruiting periods and might affect co-evolutionary patterns. There are some local migrations, often up slope as the weather warms, to take advantage of different food sources throughout the year (e.g. Clout *et al.* 1991; Lee *et al.* 1991).

Native frugivores in New Zealand mainly comprise bird and lizard species. The contributions from insects and invertebrates to fruit dispersal is largely unknown. Lee *et al.* (1991) notes that all of the c. 45 species of terrestrial native bird are frugivorous to some extent, but for most species fruits are a minor component of the diet. The diet of the native pigeon (kereru, *Hemiphaga novaeseelandiae*) is somewhat different in that it is comprised mainly of fruits, although it also feeds on foliage and flowers.

Table 1.1 lists extinct and extant native forest species that were browsers, folivores, and/or frugivores, based on data from various sources. (Data on diets from Clout 1990, Clout pers. comm.; Clout and Hay 1989; Daugherty *et al.* 1993; Falla *et al.* 1979; Holdaway 1989; Jamieson and Bishop 1994; MacKenzie 1995; Powlesland 1987; Szabo 1993; Whitaker 1987)

Gape sizes can be used as an approximate guide to the size of the fruit that could be consumed in its entirety by birds and therefore dispersed. The gape sizes listed in the Table 1.1 are mainly from Clout and Hay (1989) who measured these on museum specimens as mean external distance between commissural points. Some gape sizes are from Burrows (1994a) and A. Tennyson kindly measured the gape of the New Zealand raven (*Corvus moriorum*). Gape size is only a rough index of bill capacity, since some species have a distensible gape (e.g. kereru can swallow fruits up to 25-mm in diameter Gibb 1970), while others use force to swallow fruits bigger than their measured gape size, for instance a small silvereye (*Zosterops lateralis*) forcibly engulfing a mistletoe (*Peraxilla colensoi*) fruit by banging the beak-full on a branch (Ladley and Kelly 1996).

Moa were the largest potential avian seed dispersers (Table 1.1). The eleven species were flightless and are thought to have been mainly browsers of shrubs and lower stature trees (Burrows *et al.* 1981). There are suggestions that moa browsing has contributed to the high proportion (10% of woody flora) of woody species with divaricating habits in a relatively mild climate (e.g. Cooper *et al.* 1993; Greenwood and Atkinson 1977). Others (e.g. McGlone and Clarkson 1993) argue for a climatic origin for the growth form. Moa had maximum reach of about 3-m, and would not have been able to browse or eat fruits from the tops of the canopies (Lee *et al.* 1991). However, sub-fossil gizzard contents

Table 1.1: Extinct and extant terrestrial forest seed dispersers of New Zealand, with some indications of size, gape width and postulated or known diet.

(Data from Atkinson and Greenwood 1989; Burrows 1994a; Clout 1990; Clout and Hay 1989; Daugherty *et al.* 1993; Falla *et al.* 1979; Gill and Whitaker 1998; Heather and Robertson 1996; Holdaway 1989; Jamieson and Bishop 1994; MacKenzie 1995; Powlesland 1987; Szabo 1993; Whitaker 1987; Wildlife Service 1985)

[*1] from Atkinson and Greenwood (1989), [*2] Mandible depth not gape width, [*3] from Daugherty *et al.* (1993).

Species (e) = now extinct	Latin name(s)	Weight/size (estimates)	Gape (mm)	Presumably ate/ Does eat
11 species of moa (6 genera) (e)	*Anomalopteryx,* *Megalapteryx,* *Euryapteryx,* *Emeus,* *Pachyornis,* *Dinornis*	41 kg [*1] 24 kg 96 kg 75 kg 1.8 m, 146 kg 1.71 m-2.85 m, 96-1778 kg	11 mm [*2] 8 mm 12 mm 8 mm 13 mm 14-20 mm	Browsed on twigs, leaves, fruits within reach, fallen fruits - smaller species more omnivorous, incl. invertebrates
Flightless 'goose' (e)	*Cnemiornis calcitrans*	(10-15 kg)		Grazed herbs under open canopy and on riparian strips
New Zealand swan (e)	*Cygnus sumneresnis*	(Up to 3.5 kg)		Aquatic plants, and terrestrial herbs
Finsch's duck (e)	*Euryanas finschi*		20 mm?	Invertebrates, fallen fruits
New Zealand raven (e)	*Corvus moriorum*	(900-1000 g)	25 mm	Omnivore, fruit, large insects, carrion, lizards, tuatara, nesting petrels
Huia (e)	*Heteralocha acutirostris*	♀ 480 mm ♂ 450 mm	15 mm	Insects, fruit
Piopio (e)	*Turnagra capensis*	260 mm	11 mm	Invertebrates, fruits, seeds, foliage
New Zealand wrens (7 species) (5e)	*Acanthistidae*	80 mm to 100 mm 16 to 20 g	>5 mm	Insectivorous, some fruit taken
Kakapo	*Strigops habroptilus*	630 mm ♀ 2.0 kg ♂ 2.5 kg	20 mm?	Fruits, flowers, nectar, foliage, roots, ferns, mosses, fungi, ***Seed predator***
Takahe	*Notornis mantelii*	630 mm 3 kg		Foliage, roots, insects? Fruits? seeds?
Weka	*Gallirallus australis*	530 mm ♀ 700 g ♂ 1000 g	13 mm	Insects, vegetation, fruits
New Zealand pigeon (kereru)	*Hemiphaga novaeseelandiae*	510 mm 550 to 850-gr	14 mm	Fruits, young leaves
Pukeko	*Porphyrio melanotus*	510 mm ♀ 850 g ♂ 1050 g		Wetland vegetation, fruits?
Kiwi (3 species?) (?e)	*Apteryx australis, A. owenii, A. haastii*	300 mm to 500 mm 1150 g to 3.3 kg	21 mm to 24 mm	Invertebrates, fallen fruits
Kea	*Nestor notabilis*	460 mm ♀ 800 g ♂ 1000 g	20 mm?	Leaves, buds, fruits, insects, nectar, ***Seed predator***
Kaka	*Nestor meridionalis*	450 mm ♀ 425 g ♂ 475 g	20 mm?	Fruits, insects, nectar, ***Seed predator***
Blue duck	*Hymenolaimus malacorhynchos*	530 mm ♀ 750 g ♂ 900 g		Mainly aquatic invertebrates, occ. fruits
Long-tailed cuckoo	*Eudynamys taitenis*	400 mm 125 g		Insects, occ. fruits

Species **(e) = now extinct**	**Latin name(s)**	**Weight/size (estimates)**	**Gape (mm)**	**Presumably ate/ Does eat**
Kokako	*Callaeas cinerea*	380 mm 230 g	13 mm	Fruits, leaves, insects, buds, flowers, nectar
Yellow- and red-crowned parakeets (2 species)	*Cyanoramphus auriceps, C. novaezelandiae*	♀230 to 250 mm ♂250 to 280 mm 40 to 80 g		Fruits, seeds, leaves, buds, flowers, ***Seed predator***
Saddleback	*Philesturnus carunculatus*	250 mm ♀ 70 g ♂ 80 g	8 mm	Invertebrates, fruits, occasionally nectar
Bellbird	*Anthornis melanura*	♀ 190 mm, 26 g ♂200 mm, 34 g	6 mm	Nectar, insects, fruits
Stitchbird - hihi	*Notiomystis cincta*	♀ 180 mm, 30 g ♂190 mm, 40 g	7 mm	Nectar, insects, fruits
Tui	*Prosthemadera novaeseelandiae*	♀ 290 mm, 90 g ♂310 mm, 120 g	9 mm	Nectar, fruits, insects
Robin	*Petroica australis*	180 mm 35 g	5 mm	Invertebrates, some small fruits
Fantail	*Rhipidura fuliginosa*	160 mm 8 g	<5 mm	Insects, some small fruits
Whitehead	*Mohoua albicilla*	150 mm ♀ 14.5 g ♂ 18.5 g	<5 mm	Insects, small fruits
Yellowhead	*Mohoua ochrocephala*	150 mm ♀ 25 g ♂ 30 g	<5 mm	Insects, (small fruits?)
Tomtit	*Petroica macrocephala*	130 mm 11 g	<5 mm	Invertebrates, some small fruits
Brown creeper	*Mohoua novaeseelandiae*	130 mm ♀ 11 g ♂ 13.5 g	<5 mm	Insects, some small fruits
Silvereye	*Zosterops lateralis*	120 mm 13 g	<5 mm	Insects, nectar, some small fruits
Warbler	*Gerygone igata*	110 mm 6.5 g	<5 mm	Insects, some small fruits
Non-bird species				
Lizards (60 extant spp *[3]) (?e)	e.g. *Hoplodactylus, Naultinus, Cyclodina, Oligosoma*	Max. snout vent length 55 to 160 mm		Small fruits, invertebrates
Greater short-tailed bat (e)	*Mystacina robusta*			Insects, (nectar? small fruits?)
Short-tailed bat	*Mystacina tuberculata*	Head to tail length 100 mm		Insects, nectar, small fruits
Long-tailed bat	*Chalinolobus tuberculatus*	Head to tail length 100 mm		Insects, (fruits?)

showed that they did eat fruits (Burrows *et al.* 1981) and they could have been important dispersers of fallen fruits for some species. Perhaps, they performed a similar role to that of cassowaries (*Casuarius casuarius*) in North Queensland and Papua New Guinea, which consume great quantities of fallen fruits and can move several kilometres during a day (R. Holdaway pers. comm. Clout and Hay 1989; Stocker and Irvine 1983). However, some of the large-fruited species with thin seed coats (e.g. *Beilschmiedia* species) would not have survived well in the stone filled gizzards of some moa species (Clout and Hay 1989, R. Holdaway pers. com).

The diets of other extinct bird species are equally hard to establish. Huia (*Heteralocha acutirostris*) were reported eating medium-sized fruits; 4 mm up to about 10 mm in diameter e.g. hinau (*Elaeocarpus dentatus*), pigeonwood (*Hedycarya arborea*) and *Coprosma* spp. (Buller (1888) cited in Clout and Hay (1989). The extreme sexual dimorphism of the huia bill (males had a stout arched bill while females had a slender scimitar-shaped bill) appears better suited to foraging for insects and could have posed some problems in fruit handling. Moorhouse (1996), suggested that the most likely explanation for the dimorphism was the foraging method, as unrelated wood-probing species show similar sexual dimorphism, though to a lesser extend. They were, in fact, avid consumers of insects and grubs from rotting wood (Falla *et al.* 1979) and seem unlikely candidates to have been major dispersers of large fruits.

Piopio (*Turnagra capensis*) were known to have eaten the smallish (5 mm in diameter) *Fuchsia* fruits (Clout and Hay 1989; Falla *et al.* 1979). The piopio reportedly had a variable diet and spent much of its time grubbing the forest floor (Falla *et al.* 1979), not unlike present day introduced thrushes (*Turdus philomelos*). It probably was predominantly an invertebrate eater and its gape was insufficient to deal with the largest fruits (>14 mm in diameter).

The postulated diets of the flightless 'goose', New Zealand swan (*Cygnus sumneresnis*), Finsch's duck (*Euryanas finschi*), and New Zealand raven (*Corvus moriorum*) are based on general knowledge of the ecology and life history of related species elsewhere in their natural environments (Holdaway 1989). The first three species probably lived close to water-body margins and grazed the surrounding areas, consuming fallen fruits in an opportunistic manner (Holdaway 1989). They would not have foraged in trees for food and can be discounted as major fruit dispersers.

The New Zealand raven had a gape size larger than that of New Zealand pigeons and could probably take items much larger than the pigeon could handle (R. Holdaway pers. com.). Its diet is still unknown, since raven subfossils are found mainly in coastal sites, although a very small number have been found inland. Ravens tend to be omnivorous and some species specialise in hunting the littoral zone (R. Holdaway pers. comm.).

Kea (*Nestor notabilis*), kaka (*N. meridionalis*), kakapo, red and yellow-crowned parakeets (*Cyanoramphus auriceps, C. novaezelandiae*) are primarily seed predators since they tend to chew and crack larger seeds with their relatively powerful bills. They do however disseminate some of the smaller seeds intact (Clout and Hay 1989) and tend to scatter fruits close to the parent tree.

Kiwi species, although they do take fruits from the ground opportunistically (Lee *et al.* 1991), are physically not be able to forage and disperse fruits from plants greater than 1 metre in height. The extant kokako consumes many different species of fruit, but is unable to swallow the larger fruits (>10-mm in diameter, Clout and Hay 1989; Powlesland 1987), although it will pluck tawa fruits from the tree and drop the seed after pecking at the pulp (R. Hay pers. comm. in Knowles and Beveridge 1982). The blue duck (*Hymenolaimus malacorhynchos*) is known to eat fruits occasionally (Heather and Robertson 1996), however it is restricted to aquatic habitats and unlikely to forage in trees.

The long-tailed cuckoo (*Eudynamys taiteni*) is a migratory visitor that breeds in New Zealand during the summer. This species is mainly insectivorous, although fruits are occasionally taken (Heather and Robertson 1996). Given the body size, and probable associated gape size, long-tailed cuckoo probably do not consume fruits larger than those eaten by kokako (<10 mm in diameter). Any bird species with a gape smaller than 13 mm in diameter will not be able to handle the largest fruits (>14 mm in diameter).

Birds feed only on about 50% of the native fleshy-fruited species, principally those with medium to large (4 mm to >14 mm in diameter) reddish fruits. Lizard species may be important for some of the smaller plant species (fruits <3 mm) (Webb and Kelly 1993). Fruits of divaricating shrubs or divaricating vines may have evolved primarily for dispersal by lizards, many having pale (white or light blue) fruits, often cryptically positioned in the middle of the plant canopy where the fruits may be out of reach for bird species (Clout and Hay 1989; Whitaker 1987; Willson *et al.* 1989). The gapes of extant lizard species are generally insufficient to deal with large fruits, although the largest known gecko (Hoplodactylus delcourti, 370-mm head and body length (SVL) Bauer and Russel 1987) may have eaten sizeable fruits before it became extinct (Webb and Kelly 1993). There is a report of

Hoplodactylus duvaceli eating a karaka fruit approximately 20 mm diameter and 39 mm long (Whitaker 1987).

The three New Zealand species of bat (*Mystacina robusta*, *M. tuberculata*, *Chalinolobus tuberculatus*) are small and would have been incapable of swallowing a large fruit. Weta (*Denacrida* and *Hemideina* spp.), and other invertebrates also feed on fruits and foliage, but none are large enough to carry off the large fruited species (>10 mm in diameter) of interest.

A review of New Zealand frugivores therefore indicates that the kereru is the only current (and possibly the only historic) disperser of tree-borne large fruited species.

McEwen (1978) postulated that the genus *Hemiphaga* is an old endemic and has probably been in New Zealand since the late Tertiary after its ancestors arrived from Australia or Melanesia. Cladistic analysis by James (1995) reached a similar conclusion and also proposed that the New Zealand pigeon, or kereru, represents an early stage in the evolution and radiation of Pacific fruit-pigeons and could have resided in New Zealand for as long as 2 million years.

1.2.5 Effect of introductions to New Zealand

King (1984) and Holdaway (1989) describe at least two pulses of extinction in New Zealand, linked to immigration by humans. The first began about 1000 years ago with the arrival of Polynesians, who hunted the native fauna, reduced the forest cover and brought with them kiore (*Rattus exulans*) and dog (*Canis domesticus*). This immigration affected those native species most vulnerable to hunting and mammalian predation. Further native species extinctions were associated with European exploration in the mid 18th century and colonisation in the mid 19th century, the latter of which resulted in further wide-scale habitat destruction. The Europeans introduced cats (*Felis catus*), mustelids (*Mustela erminea*, *M. furo*, *M. nivalis*), two more rats and a mouse (*R. norvegicus* and *R. rattus*, *Mus musculus*), mammalian herbivores (bovids, ovids, lagomorphs, cervids and marsupials), omnivores (*Sus*) and a whole range of European birds (Clout and Saunders 1995; Holdaway 1989; King 1984).

The result of these various introductions, hunting and habitat loss, has not only been extinction of some of the species mentioned above (i.e. 1.2.3 and 1.2.4), but drastic reductions in the populations of other species, including the frugivorous birds. Kereru populations are greatly diminished from pre-human settlement and even pre-European times, and in places they are still hunted illegally (Pierce *et al.* 1993). Tui and bellbirds vary in abundance throughout the country (e.g. low or missing bellbird populations in the north of the North Island, although the cause has never been firmly established for that extinction and could be related to disease rather than predation). Kokako and yellowhead are now restricted to a few places on the mainland, kakapo and stitchbird to offshore islands (Castro and Robertson 1997; Clout and Craig 1995; Davidson 1992; Halkett 1985; Leathwick *et al.* 1983; O'Donnell *et al.* 1992), and other bird species, such as kaka, the native parakeets, robin and whitehead, are rare but can be locally common.

Burrows (1996) suggests that the phenomenon of drawn-out fruit displays noted in some New Zealand plant species could be exaggerated by the local or total extinction of important frugivores and seed dispersers. Even where the main dispersers are still present they are often reduced in number and rarely consume the entire amount of fruit or nectar on display (Burrows 1996).

Possums (*Trichosurus vulpecula*), cats (*Felis catus*), rats (ship rat *Rattus rattus*, Norway rat, *R. norvegicus*, and the Polynesian rat -kiore, *R. exulans*), and stoats (*Mustela erminea*) are thought to be the main predators causing the reduction of native bird numbers (Brown *et al.* 1993; Brown *et al.* 1998; Clout and Saunders 1995; Murphy 1992; Wilson *et al.* 1998). Possums, deer (Cervids) and goats (*Capra hircus*) have altered the structure and composition of native forest communities, which evolved in the absence of mammalian browsers, through selective browsing (Clout and Saunders 1995; Jane 1994; King 1984; Ogden and Buddenhagen 1994). Possums not only compete directly with birds for food, they also eat eggs and chicks and disturb nesting adults of even large species such as kereru (Brown *et al.* 1993; Innes 1994). Rats appear to depress bird populations in a similar way but to a lesser extent (Brown *et al.* 1998). The effects directly attributable to either possums or rats are often hard to separate, since (on the mainland) there are few areas that have one and not the other. Stoats eat eggs and chicks, and even nearly full-grown kiwi chicks are no match for a stoat (Best and Bellingham 1990; Murphy 1992; O'Donnell *et al.* 1992; Wilson *et al.* 1998).

1.3 The stimulus for this study

In New Zealand there appears to be currently only one frugivorous species, the native fruit-pigeon or kereru, which can swallow large fleshy-fruits (>14 mm) and disperse the seeds intact. This also tends to be true historically if one considers which species were capable of reaching fruits in the tops of tall trees (refer to section 1.2.4). Moreover, there are few native arboreal frugivores that can successfully disperse fruits between 10 mm and 14 mm in diameter (refer to section 1.2.4), and not all of these are capable of sustained flight (Clout and Hay 1989). Despite the scarcity of such frugivores there seem to be several tree species in the native New Zealand flora with fruits exceeding 10 mm in diameter (refer Table 1.2).

Table 1.2: Larger-fruited tree species presented by minimum transverse fruit diameter classes

modified from Clout and Hay (1989).

Minimum transverse fruit diameter class (mm)		
>14 mm	>10 mm to 14 mm	>6 mm to 10 mm
Karaka# - *Corynocarpus laevigatus*	Miro$ - *Prumnopitys ferruginea*	Supplejack$@ - *Ripogonum scandens*
Puriri# - *Vitex lucens*	Swamp maire - *Syzygium maire*	Black maire - *Nestegis cunninghamii*
Taraire# - *Beilschmiedia tarairi*	Kohekohe# - *Dysoxylum spectabile*	Nikau$ - *Rhopalostylis sapida*
Tawa# - *Beilschmiedia tawa*	Mangeao - *Litsea calicaris*	Titoki$ - *Alectryon excelsus*
Tawaroa* - *Beilschmiedia tawaroa*	Hinau$ - *Elaeocarpus dentatus*	Matai - *Prumnopitys taxifolia*
Tawapou# - *Pouteria costata*	Pigeonwood$ - *Hedycarya arborea*	

* Contentious classification, see 2.4 Tawa.
# Focus species for this study.
$ Other species partially investigated.
@ Vine, not tree species.

This list does not include all possible species with large fleshy-fruits in New Zealand. Ground cover species, such as *Colensoa physaloides* (fruits 10 mm to 25 mm diameter), *Fuchsia procumbens* (fruits can be > 20 mm diameter), and the iris *Libertia ixioides* (fruits 15 mm to 20 mm diameter), have been excluded because these lower stature species could have been dispersed by several species, including moa (Allan 1961; Ogle 1997). The native passionfruit, *Passiflora tetrandra* (capsule 25 mm to 30 mm diameter with 4-5 smaller seeds), is often a canopy component but was excluded as the fruit is probably not swallowed entire, but pecked open to obtain the seeds (Allan 1961; Ogle 1997).

The species listed in the table above as producing fruits with diameters greater than 10 mm belong to tropical families (refer Chapter 2), with the exception of the podocarp, *Prumnopitys ferruginea* (miro).

Presented below (Table 1.3) are the ‘first appearance dates’ in the fossil record as far as is known for the genera of interest (D. Mildenhall, Institute of Geological & Nuclear Sciences Ltd., pers. comm.). It is unlikely that the species stayed constant over geological time and the genera likely represent the minimum durations.

Table 1.3: First appearance dates in fossil records for large-fruited genera of interest
(D. Mildenhall pers. comm.).

Genus	Example	First appearance date (million years ago)
Dysoxylum	Kohekohe *D. spectabile*	Early Eocene, Bortonian (53→37)
Prumnopitys	Miro *P. ferruginea*	Only identified as such in the Pliocene and Pleistocene (5→0.01). Probably much older i.e. Eocene (53→37) but not yet recognised as macrofossils
Hedycarya	Pigeonwood *H. arborea*	Only recognised in the late Pleistocene (2→0.01); a potential, but disputed, record of the genus *Hedycarya* from the late Cretaceous (ended 65 m.y.a.)
Litsea	Mangeao *L. calicaris*	Very rare as fossil pollen in the Pleistocene; one Pliocene macrofossil record (5→0.01)
Vitex	Puriri *V. lucens*	Very rare as fossils in the Pleistocene (2→0.01)
Pouteria	Tawapou *P. costata*	Very rare as fossils in the Pleistocene (2→0.01)
Beilschmiedia	Tawa -B. *tawa* Taraire – *B. tarairi*	Does not preserve as pollen, very rare in Holocene (0.01→0); one macrofossil record in the early Pleistocene (2→0.01) (Taraire - not recognised in the fossil record)
Corynocarpus	Karaka *C. laevigatus*	Pollen only found immediately under existing trees, but a recent study (Byrami *et al.* 2002/ M. Byrami pers. comm.) found karaka pollen in a stratum less than 700 years old.

The large-fruited plant species have probably been in New Zealand for at least 2 million years and have probably co-existed with kereru throughout this time (refer section 1.2.4). The key fruiting species discussed can all have large crops of fruit (A. Dijkgraaf pers. obs.) and reducing the possibility that the total crop was dispersed even when kereru were abundant (Best 1977; Pierce *et al.* 1993). Thus there would have been competition amongst trees within species and amongst species for the services of the key disperser. This scenario provides the opportunity of at least 2 million years (and probably longer) of competition between tree species and for co-evolution between these large-fruited species and kereru.

It is therefore postulated that, given a single disperser for the largest fruits, and only a few dispersers for fruits greater than 10 mm, there is likely to have been inter-specific competition amongst co-existing large fleshy-fruited species (fruits >10 mm diameter) for dispersers.

Co-evolution of frugivores and fruiting species is difficult to establish, let alone prove (refer to section 1.1). Yet, the long association between kereru and the endemic large-fruited species competing for their dispersal services could have resulted in differences in ‘fruiting behaviour’ that may have arisen through co-evolution. There are several characters associated with fruiting that could have changed over time (also known as character displacement) to achieve maximal dispersal by frugivores. These include variations in timing of fruit presentation, variations in fruit colouration, size and presentation, and alterations in fruit nutritional composition. These, and other, characters that may have been modified through high inter-specific competition are discussed in more detail in Chapter 4.

The impetus to undertake this study arose from the observation that many of the co-existing tree species with large fleshy fruits appeared to have non-overlapping fruiting phenologies. Such fruiting phenologies would ensure that each tree species had maximal opportunity to entice the chief dispersal agent, kereru, and thus achieve maximum dispersal of its seeds.

Thus it is therefore postulated that, the timing of ripe fruit presentation might have evolved, through high inter-specific competition, so that co-occurring species have distinct and non-overlapping annual fruiting periods.

Data on phenological patterns for New Zealand species is often scare and/or contradictory and requires clarification and defining. There are alternative hypotheses for the seasonal timing of fruiting that relate to the evolutionary history of the tree species. These hypotheses will be further discussed in Chapters 5 and 6.

It was also noted that amongst these species with large fleshy fruits there were a number of different fruiting strategies. Some species presented small amounts of ripe fruit for most of the year, but also carried abundant fruits for part of the year. Other tree species had very short and well-defined periods of ripe fruit and none throughout the rest of the year (refer to Chapter 2 for more details). It seemed likely that the variability in fruiting effort might also be reflected in the quality of the fruits produced. Trees with short periods of ripe fruit presentation could allocate more resources on fruit production than trees fruiting nearly continuously throughout the year; it might be expected that the former species would carry higher quality fruits than the latter. Moreover, species with large fleshy fruits may have different nutritional composition according to the level of competition with co-existing tree species (i.e. more nutritional fruits required to successfully compete with multiple competitors), or depending on whether generalist or specialist frugivores are the main dispersers (refer Section 1.1).

It is therefore postulated that the different fruiting strategies of species with large fleshy fruits have resulted in fruits of differing nutritional quality.

Fruit phenologies can vary with locality and soil quality. It was therefore decided to record fruit phenology at several sites with similar geology to ensure that the observed phenologies would not simply reflect site selection.

A further aspect that must be taken in to account in present-day forest systems is the impact on fruit phenologies that introduced mammalian, arboreal, fruit predators might be having. These fruit predators include the Australian marsupial brushtail possum, the European rodents (ships rat, Norway rat, and house mouse, *Mus musculus*) and the Polynesian rat -kiore. They are all known to have significant impacts on fruit production (refer to Chapter 2) and fruit abundance, and therefore apparent fruiting phenologies, could be considerably changed in areas where these fruit predators are abundant. Such changes in fruit production would make interpretation of phenological patterns more difficult. Furthermore, altered fruit abundances could have considerable adverse impacts on the native frugivore system, and could potentially have significant long-term impacts on forest regeneration and the maintenance of healthy ecosystems.

It is therefore postulated that introduced mammalian fruit predators, such as possums, rats and mice, have significant adverse impacts on fruiting phenologies and availability of large fleshy fruits of some species.

To quantify the impact of fruit predators, numbers of introduced mammals were experimentally modified to give high and low density treatment areas. Low-density sites were paired with proximal high-density sites. This allowed comparison of the amount of fruit produced, the predation rate on the fruit, and any gross changes in observed phenological patterns.

1.4 Focus, thesis structure and aims

1.4.1 Focus

The focus of this thesis is on tree species with large, fleshy fruits and the principle consumer of these fruits, the kereru. Large fruits are classified as those with mean transverse diameters[5] of 10 mm or more. The fieldwork concentrates primarily on the fruiting patterns (phenology) of these tree species. Introduced arboreal mammals, such as possums and rodents, compete directly with kereru for large fleshy fruits, thus the effects of these fruit predators on fruit phenology are examined. Since the nutritional attributes of the various species of fruit could have direct impacts on some of the animal behaviours observed nutritional values of samples of fruit are analysed.

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[5] Where the diameter of the fruit is measured through the smallest axis (refer to footnote 4 for diagram).

1.4.2 Thesis structure and aims

Chapter 1: Introduction

Brief literature review of co-evolution and description of New Zealand flora, fauna, frugivore system and introduced mammals.

Chapter 2: Review of key native and exotic species in the current frugivore system

Detailed descriptions of focus tree species, principle disperser (kereru), and main arboreal fruit predators.

Chapter 3: Methods and site description

Selection and description of methods, description of sites, testing validity of some of the methodology.

Chapter 4: Validation of site selection and methods

Comparing sites selected and testing the robustness of some of the methodology.

Chapter 5:Fruiting patterns of indigenous species

Hypothesis 1

The timing of ripe fruit presentation has been altered, through inter-specific competition amongst large-fruited tree species for dispersal, so that co-occurring species have distinct and non-overlapping annual fruiting periods.

Aims

1. Describe the fruiting phenologies of large-fruited species (for focus species refer to Table 1.2).
2. Determine if the fruiting phenologies of those species are distinct and non-random.
3. Test whether the timing of fruiting phenologies of focus species overlap significantly.
4. Decide if character displacement in fruiting phenologies might have occurred for the focus species.

Chapter 6: Nutritional characteristics, utilisation by kereru and success in attracting dispersers for various fruiting species

Hypothesis 2

The different fruiting strategies of species with large fleshy fruits have resulted in fruits of distinctive nutritional qualities and disparate attractiveness of fruits to frugivores.

Aims

1. Determine the nutritional attributes of a range of species, including the focus species.
2. Quantify the annual availability of food and nutrients for frugivores.
3. Compare the nutritional ‘attractiveness’ of these species to frugivores.
4. Decide if character displacement in fruit nutrition might have occurred for the species analysed.

Chapter 7: Impacts of possums and rodents

Hypothesis 3

Introduced mammalian fruit predators, such as possums, rats and mice, have significant impacts on fruiting phenologies of species with large fleshy fruits.

Aims

1. Describe and quantify the fruiting phenologies of focus (and other species) at sites with ‘normal levels’ of mammalian fruit predators.
2. Compare the fruiting phenologies of these sites to sites with suppressed levels of mammalian fruit predators.
3. Illustrate the impacts that mammalian fruit predators might be having on native frugivores and continued ecosystem health.

Chapter 8: Discussion and conclusions

Statement

Given a single disperser for the largest fruits, and only a few dispersers for fruits greater than 10 mm, has there has been inter-specific competition amongst the co-existing large fleshy-fruited species (fruits >10 mm diameter) for dispersers?

Aims

1. Comment on and discuss the above question.
2. Comment on and discuss the significance of the phenological fruiting patterns for native and introduced frugivores
3. Discuss the impacts of the mammalian fruit predators on northern New Zealand forest ecosystems and the conservation implications.
4. Highlight future areas of study

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[1] Kereru eating nikau fruit, one of the smaller fruits studied (Photo courtesy Geoff Moon)

Chapter 2 Key native and exotic species in the current frugivore system.

This Chapter provides a brief literature review on the plant and animal species of interest. Each of the large-fruited species is described and additional details are provided. There is a brief overview of what is known about the main disperser of these fruits, the kereru (*Hemiphaga novaeseelandiae*). Two further sections deal with the mammalian fruit predators: rodents (rats and mice) and possums. Nomenclature for the plants follows Parsons *et al.* (1998), with corrections and updates from the New Zealand plant names database at http://nzflora.landcare.cri.nz/plantnames/.

2.1 Karaka

Taxonomy

Karaka, *Corynocarpus laevigatus* J.R. et G. Forst., belongs to the family Corynocarpaceae, which contains one genus, *Corynocarpus*, with currently five recognised species and two subspecies (Dawson 1997). The other species occur in Australia, Papua New Guinea, Aru Islands, Solomon Islands, New Caledonia, and Vanuatu (Dawson 1997; Molloy 1990). There are some suggestions that two of the species (*C. dissimilis* from New Caledonia and *C. similis* from Vanuatu) are conspecific with karaka, or that at least *C. similis* should be assigned infraspecific rank with karaka (Stevenson 1978). However, Molloy (1990) considered that the fruit characters distinguish karaka from the other taxa.

The taxonomic position of the family Corynocarpaceae is uncertain and it has been placed near various families on the basis of many characters (e.g. floral morphology, pollen morphology, wood anatomy, and biochemistry). For instance, Dawson (1997) tentatively placed the family Corynocarpaceae in the one of the suggested families, Celastraceae, on the basis of chromosome number ($2n = 46$), but Savolainen, *et al.* (1997) suggested on the basis of the sequence of a noncoding region of DNA on the chloroplasts that karaka is not related to Celastraceae. The most recent paper on the subject (Wagstaff and Dawson 2000) compared coding and noncoding regions on the chloroplast and found that the Corynocarpaceae were most closely aligned with the Cucurbitaceae. The sequence data also suggested two radiations from a Palaetropical centre of origin, the second of which reached New Zealand through New Caledonia, probably several million years ago.

Distribution, description and growth habit

The species occurs throughout the North Island, mostly along the coast at margins or interiors of mixed forest, and near the coast in the South Island to c. latitude 44°, that is about Banks Peninsula on the east coast and Jackson Bay on the west coast (Burrows 1996; Eagle 1978; Poole and Adams 1994). It is believed to have been moved to many locations by the Maori but has subsequently naturalised in unmanaged vegetation (Burrows 1996). The Maori have a tradition that karaka was introduced into New Zealand by their forebears on one of the earliest founding canoes (Best 1977). Its distribution tends to be at pa sites or other places of habitation, and in intact forest it is rarely found far from such sites or from mature trees (Dijkgraaf pers. obs., Best 1977). Coastal groves were planted and maintained by Maori (Eagle 1978), since the fruits were very important to them, second only to kumara (Eagle 1978). The fruits had to be carefully prepared to remove the poison, karakin, before storage (Eagle 1978). The species is easily cultivated within its range (Poole and Adams 1994) and prefers deep, rich soils (Cockayne 1923).

Karaka is an evergreen, usually single-stemmed, tree up to about 18 m tall (Burrows 1996; Poole and Adams 1994), although the trees readily sprout from the base of the trunk (Dijkgraaf pers. obs.). If single-stemmed then the smooth, grey, trunk can be up to 600 mm in diameter, and supports stout branches (Eagle 1978; Hamlin 1962).

It has large (70 to 200 mm long), thick, elliptic-oblong leaves, that are glossy dark-green in colour (Burrows 1996; Matthews 1962; Poole and Adams 1994; Salmon 1991)

Phenology

The small (5 mm diameter) creamy-white bisexual flowers are borne in erect 100 to 200 mm long panicles on the ends of the branchlets (Burrows 1996; Matthews 1962; Poole and Adams 1994; Salmon 1991). The flowers have petals, sepals, functional stamens, nectaries and petaloid structures in fives (Eagle 1978; Philipson 1987; Salmon 1991). Flowers occur from August to November (Allan 1961; Salmon 1991).

The fruit is a pendulous, elliptic, yellow-orange drupe, 25 to 43 mm long (Burrows 1996; Matthews 1962; Poole and Adams 1994). Fleshy mesocarp and a fibrous endocarp enclose a non-endospermous seed covered by a papery, veined testa (Bannister *et al.* 1996). Fruits are ripe from January to April (Allan 1961; Salmon 1991), though this varies considerably nationally. Fruits in Auckland are ripe from December to February while a planted specimen in Otago had fruits on the tree as late as April and May (Bannister *et al.* 1996).

Full-grown fruits at different stages of maturity showed no differences in the ability to germinate (Bannister *et al.* 1996). Karaka seeds are considered to be recalcitrant, meaning that they have a high water content, well-developed embryo, no dormancy and are sensitive to desiccation and dry storage (Fountain and Outred 1991). Recalcitrance is often considered to be typical of species of tropical origin with large-seeded fleshy fruits (Bannister *et al.* 1996; Fountain and Outred 1991). Husking the seed or removing the fruit-flesh considerably improves seed germination rate and percentage germination. If the fruit is desiccated germination is delayed and reduced (Bannister *et al.* 1996). There is a suggestion that the outer layers of the embryo, even when husked, reduce desiccation to some extent (Bannister *et al.* 1996).

Karaka seeds collected in early March from trees in Canterbury began germinating a few days after collection, and most had germinated after 2 months (Burrows 1996). Some seeds continued to germinate over winter. Dark treatment reduced germination rate. Karaka had a high germination success on soil and when seeds are shallowly buried, but could be vulnerable to prolonged drought (Burrows 1996).

2.2 Kohekohe

Taxonomy

Kohekohe (*Dysoxylum spectabile* (G.Forst.) Hook. f.) is the only New Zealand member of the Meliaceae, the mahogany family (Cockayne 1967). This is a family of 51 genera and approximately 550 species distributed throughout the tropics and sub-tropics of both hemispheres (Court and Mitchell 1988) mainly in Asia, Polynesia, Malayan and Australian (Cockayne 1967). The genus *Dysoxylum* comprises about 80 species from the Indo-Malayan region through to New Zealand (Braggins *et al.* 1999; Court and Mitchell 1988). The tropical affinities of kohekohe are suggested by its cauliflory, large fruits, pulvini on the leaves, and rapid, epigeal germination (Dawson *et al*., 1969).

Distribution, description and growth habit

Kohekohe is a forest tree species with a mainly northern lowland distribution. North of approximately 38º S the species is found both coastal and inland to an altitude of 600 m a.s.l. South of 38º S the species is mainly restricted to coastal forest generally below 250 m a.s.l. (Court 1985), extending as far south as the Marlborough Sounds and Cape Farewell. In coastal regions it may be a canopy dominant, but further inland it is found associated with many other species, often as a subcanopy component (Court and Mitchell 1988). Cockayne (1958) suggested that kohekohe tended to be found in the more humid and frost-free areas. Court (1988) experimented with the tolerance of the germinating seed; cooler temperature reduced both the rate and final numbers of kohekohe seed to germinate. The tolerance of the seed is more than for kauri seed and could explain why kohekohe penetrates further south than kauri (Court and Mitchell 1988).

Kohekohe trees grow to about 17 m in height (Poole and Adams 1994) and can reach 1 m in diameter (Court 1985). The light green, compound leaves are large (±200 mm long but can be up to 500 mm long) glossy, imparipinnate, with 40 mm long petioles. Leaflets occur in 3 to 4 pairs, they are opposite or sub-opposite with blades that are undulate, slightly leathery and obliquely ovate to obovate-oblong set on 15 mm long petiolules (Allan 1961; Buddenhagen 1995; Eagle 1978).

Phenology

Kohekohe is modified androdioecious. Although the flowers look perfect superficially, some trees carry only female flowers (lacking pollen) while others have male, or rarely, hermaphrodite, flowers (both with pollen) (Braggins *et al.* 1999). The flowers are carried on cauliflorous thyrses of variable length (c. 50 to 530 mm long), have a creamy white staminal tube, pale green calyx and corolla, with nectar produced from a disk around the ovary (Braggins *et al.* 1999). They are visited by insects and birds and possibly bats. The nectar in the flowers contains sufficient energetic value to sustain the smallest of the native nectar-feeding birds, hihi and bellbird, and possibly tui (Castro and Robertson 1997).

The complex fruit is an obovate pendulous capsule up to 25 mm long with 3 to 5 (usually 4) locules each with 0 to 2 or rarely 3 seeds (total per fruit 4 to 7) (Braggins *et al.* 1999, but also see Chapter 5). The fruits have orange to scarlet arils containing a sticky white latex (Braggins et al., 1999). Fruiting occurs from about late April to early August, with the peak generally about May or June (Allan 1961; Court 1985; Court and Mitchell 1988). Young fruits over-winter and are ripe during the following autumn/winter, a year after flowering (Leathwick 1984)

The seed has high viability with no evidence of dormancy. Court (1988) found that seeds germinated successfully in either the light or dark, and seedlings could continue to grow for at least 18 weeks in the dark. Cooler temperatures slowed the rate of germination and seedling development, while a covering of litter was found to be essential for successful establishment (Court and Mitchell 1988). Germination is semihypogeal, that is the cotyledons are exposed at ground level without a developed hypocotyl (Philipson 1989).

2.3 Puriri

Taxonomy

The puriri (*Vitex lucens* Kirk) is the only New Zealand representative of the genus *Vitex* (Allan 1961; Poole and Adams 1990). This genus comprises about 250 mainly tropical and subtropical trees and shrubs, some of which are evergreen and some deciduous (Bryant 1999). *Vitex* was classified as a member of a large varied family Verbenaceae, but reclassified to the subfamily Viticoideae in the Lamiaceae (Cantino 1992; Cantino *et al.* 1992; Dijkgraaf *et al.* 1995 ; Rimpler *et al.* 1992).

Puriri is considered to be an octoploid species, based on $x = 8$ with a chromosome number of $2n = 64$ (Dijkgraaf, Lewis *et al.* 1995).

Distribution, description and growth habit

Puriri is endemic to New Zealand and can be found in the upper half of the North Island from North Cape to the Waikato and Upper Thames, and from thence in small numbers southwards to Mahia Peninsula on the east coast and Cape Egmont on the west (rare south of latitude 37°). Its altitudinal range is from sea level to 800 m (2,500 ft) above sea level (Cheeseman 1906; Cockayne and Phillips Turner 1967; Lidgard 1930). It tends to be associated with fertile or volcanic soils (Cheeseman 1914; Moore and Irwin 1978), and early settlers often sought out and burned puriri-rich areas to obtain good farmland (Dykgraaf 1992).

Puriri is a large handsome tree of somewhat irregular growth that can attain a height of up to 20 m or more with a massive trunk 1 to 2 m in diameter. It has a broad spreading crown (Cheeseman 1906; Poole and Adams 1986), often with flattened branches. Branchlets are tetragonous and glabrous with leaves, flowers and fruits often only towards the extremities (Dijkgraaf 1994). The massive roots lie close to the surface (Laing and Blackwell 1964).

The dark green glossy adult leaves are borne in opposite pairs and consist of long stout petioles terminating digitally in 3 to 5 leaflets, each 50 to 120 mm long, elliptic-oblong or obovate in shape and abruptly acute or almost acuminate with entire, often wavy, margins (Cheeseman 1906; Poole and Adams 1986).

Phenology

There is some confusion in the literature as to the time of flowering and/or fruiting of puriri, with some authors claiming puriri flower in spring (Fisher *et al.* 1985) and fruits in autumn (Pardy and Bergin 1989). However, puriri, unlike most other native New Zealand trees, flowers mainly in winter (May/June to September/October) (Davies 1961; Lidgard 1930; Petrie 1905) and carries most fruit over summer (December to February). Remarkably, both fruits and flowers can be found on the tree in small numbers throughout the year (Dijkgraaf 1994; Laing and Blackwell 1964; Lidgard 1930; Petrie 1905; Salmon 1989) and it is not unusual to see full grown fruits and young flowers on the same branch, even the same panicle (Petrie 1905). Puriri is not deciduous, but leaf flush and accompanying shedding of old foliage, occurs shortly after flowering finishes and before fruits starts ripening (Dijkgraaf 1994).

The flowers are unusually large and colourful for the New Zealand flora, being 25 mm long irregular bell-shaped flowers that range in colour from dull red (most common occurrence) to white (Dijkgraaf 1994; Lidgard 1930). Lidgard (1930) describes puriri flower colour as “mostly a dull rich red with a fine golden pubescence which gives a regally magnificent effect. The colour is lighter inside the flower than outside.” The flowers are abundantly produced in 4 to 15 flowered dichotomously branched axillary panicles (Cheeseman 1906; Crookes 1926; Poole and Adams 1994). The flower bears four stamens and a style that grows to be as long as the stamens once pollen has been shed. This is thought to be a mechanism to prevent self-pollination (Petrie 1905), though selfing within the tree produces equally viable progeny as outcrossing (Barrell 1995; Barrell *et al.* 1997).

Puriri flowers are thought to be bird pollinated due to the floral shape, positioning of the anthers and style and the secretion of nectar. Nectar secretion begins once the corolla has fully opened and continues until the corolla begins to wither. Insects are excluded from the nectar at the base of the corolla by a dense plug of hairs, but nectar can on occasion be so abundant that it will drop out of the flower when shaken (Lidgard 1930; Petrie 1905).

Puriri fruit is a bright red (usual) to yellow globose drupe about 20 mm in diameter and consists of a thin layer of flesh surrounding the highly lignified (bony), four celled, flanged endocarp containing up to 4 seeds (1 or two live seed most common) (Cheeseman 1906; Lidgard 1930; Poole and Adams 1990). The four apertures are guarded by woody doors similar to that found in teak (*Tectona grandis*) (Godley 1971; Hill 1933), and the flanges of the puriri drupe are only found on the doors.

It is generally believed that puriri fruit is bird-dispersed (Clout and Hay 1989). The fleshy tissue surrounding the stone is taken to be an adaptation to attract vertebrate dispersers (e.g. Krefting and Roe 1949; McKey 1975; Snow 1971), while the size and red coloration of the fruits is regarded as typical for bird dispersal (e.g. Willson *et al.* 1989). The heavily lignified stone inside the puriri is thought to be adaptive for passage through the stone filled gizzard of birds (e.g. Clout and Hay 1989) and the curious plug like structure of the lids could indicate the requirement for mechanical disruption (Fountain and Outred 1991). Puriri seeds germinate more quickly if the fruit-flesh is removed, but overall percentage germination stays the same. There was no statistical difference between fruits collected from the ground and picked from the tree, thus presumably ripe fruits on the tree contain fully matured embryos. Seeds started germinating after about 29 days, up to 4 seedlings could emerge from each kernel, but not all emerged at the same time (longest time between emergence of sibling seedlings was 183 days) and germination could take up to a year (Dijkgraaf 1994). Puriri seed did not germinate once it had been allowed to dry out (Dijkgraaf 1994; Godley 1971).

Photomontage of karaka, puriri and kohekohe fruits

Karaka fruits

Kohekohe fruit, flowers and leaf

Puriri fruit (Courtesy New Zealand Geographic)

Photomontage of tawa, taraire, titoki and nikau fruits

Kereru eating tawa fruit (Photo courtesy B.W. Thomas)

Taraire fruit

Titoki fruit

Nikau fruit

2.4 Tawa

Taxonomy

Beilschmiedia tawa (A. Cunn.) Benth et Hook. f. Kirk, commonly known by the Maori name tawa, is a member of the mainly tropical and subtropical family Lauraceae that comprises more than 2500 species in over 50 genera (Christophel *et al.* 1996). New Zealand has four (or five) endemic Lauraceae, three (or four) are forest trees: tawa; tawaroa (*B. tawaroa* A.E.Wright, see below); taraire (*B. tarairi*); and mangeao (*Litsea calicaris*); and the other is a leafless parasitic liane *Cassytha paniculata* R. Br. The genus *Beilschmiedia* Nees comprises approximately 270 species (Kostermans (1964) sensu West (1986)). The genus *Beilschmiedia* is mainly distributed through tropical and subtropical rainforests of eastern Australia, Africa, Asia, America and the islands of Melanesia and New Zealand. (Hutchinson 1964). In New Zealand two *Beilschmiedia* species (tawa and taraire) are widely recognised while a third, proposed by Wright (1984), *B. tawaroa* (tawaroa) is not recognised by all.

Tawaroa was described as very similar to tawa but separated on the basis having broader leaves and being confined to the North Island in northern coastal and offshore island forests. Positive identification of tawaroa is difficult since leaf width and abaxial leaf surface coloration are the only characters that appear to separate the two species. Tawa shows great plasticity of leaf shape according to whether leaves are exposed to the sun (generally small and yellowish in colour) while shade leaves are much broader and could certainly be classified as tawaroa (Knowles and Beveridge 1982, pers. obs). No other differences, such as phenology or differences in fruit shape, have been reliably reported. Gardner (1996) reports that the fruits of ‘tawaroa’ proved anatomically identical with that of tawa. Tawaroa is deemed to be present at some of the sites in this study (Wright 1984), but since it is difficult to positively identify tawaroa in a mixed tawa-tawaroa forest this contentious classification was ignored.

Tawa apparently means “purple” in Maori, probably in reference to the coloration of the fruit (West 1986). Chromosome number of tawa n = 12 (Hair and Beuzenberg 1960).

Distribution, description and growth habit

Tawa can be found throughout lowland and lower montane forests of the North Island and its offshore islands. It is present in the South Island as far west as Takaka Valley (longitude 172 º 49’E) and Kaikoura (about latitude 42 º20’S) on the east coast ((Allan 1961; Poole and Adams 1990; West 1986), also see Knowles and Beveridge (1982) for more details). Tawa at its southern limits is uncommon but often found in small stands. The distribution suggests that tawa was formerly more widespread in the Kaikoura area than it is currently (West 1986). Tawa does not grow above 1000 m above sea level in the North Island and 300 m a.s.l. in the South Island (Eagle 1986). It could also be limited by low rainfall since it is scarce in the Kaimanawa and Kaweka Ranges and only tends to occur where there are seepages (West 1986). However, it seems more likely that tawa is limited by frost given its distribution in forest remnants in the Hautapu Valley (Ogle *et al.* 2000).

Tawa is an evergreen tree capable of reaching 37 m in height but more commonly grows to about 30 m (Poole and Adams 1990; West 1986). The smooth black or dark brown trunk can reach a maximum diameter of around 1 m and becomes more fluted or buttressed in larger trees. Crown shape is variable, young and canopy confined trees have a conical appearance, but larger or more solitary trees tend to have wider crowns (Allan 1961; Poole and Adams 1990; West 1986). Tawa probably has maximum longevity in the range 300 to 400 years (Ogden 1981).

The thin yellowish-green to dark green leaves are opposite to sub-opposite and narrow-elliptic to lanceolate. The under-surface of the leaves can be glaucous, and the young leaves can bear fine hairs scattered over both leaf surfaces. The slender petioles can be up to 10 mm long and mid-rib and main veins are evident in the 50 to100 mm long and 10 to 50 mm broad leaves. The spring flush of new leaves appears pink (Allan 1961; Poole and Adams 1990; West 1986).

Phenology

The small (2 to 3 mm diameter) green flowers are borne in axillary panicles up to 80 mm long on slender glabrous stalks. A floral description is given in West (1986) and Roper (1967). Flowerbuds are present throughout the year and flowering time generally occurs between September and December (Leathwick 1984; West 1986). Flowers are bisexual (Burrows 1999) and wind pollinated. Once pollinated the perianth segments close again and the “flower” ‘over-winters’ in this state. Unpollinated flowers abscise. It is possible that fertilisation proceeds slowly during the winter months and it seems likely that tawa is self-compatible (West, 1986). Because of the small size of the flowers it is hard to tell how many (thousand) flowers the tree bears or their state (bud, open or pollinated).

The time from flowering to fruit maturation is usually 14 months (Leathwick 1984). Fruiting times are erratic but are generally from October to April (Allan 1961; Leathwick 1984; West 1986). Tawa fruits are single-seeded pendulous drupes, 20 to 30 mm long and around 10 mm in diameter, ellipsoid to ovoid in shape with dark purple pericarp (Allan 1961; Gardner 1996; West 1986). The embryo develops during spring and summer, gradually utilising the gelatinous endosperm until, at maturity, the endosperm is no longer evident. The embryo then comprises two massive cotyledons that take up nearly all the space in the fruit, with a plumule and radicle at the stylar end. The fruits ripen from green to red and then purplish-black and are hairless and shiny when ripe (West 1986). The green fruits can be cryptic, often being the same colour and approximate shape as the leaves.

It takes approximately six weeks from fruit fall for germination to commence; germination is hypogeal and improved by burial under litter. Seeds cannot cope with desiccation. Low temperatures keep tawa seeds from germinating. Germination is considerably improved after mechanical removal of the meso and exocarp layers (Burrows 1999; West 1986). After gut passage the seeds resembled smooth olive stones (Dijkgraaf pers. obs.).

Small numbers of tawa, taraire and miro (*Prumnopitys ferruginea*) fruits are parasitised by *Cryptaspasma querula* larvae. This insect is generally associated with *Beilschmiedia* in pan-tropical regions, but is also found in parts of New Zealand where *Beilschmiedia* is currently absent. There is a suggestion that the current New Zealand distribution of *C. querula* reflects past distributions of *Beilschmiedia* and that the larvae have possibly adapted to eating the seed of miro where *Beilschmiedia* is absent (West 1986).

2.5 Taraire

Taxonomy

Beilschmiedia tarairi (A. Cunn.) Benth. et Hook. f. ex Kirk, is one of four or five species of Lauraceae indigenous to New Zealand (see 1.3.1.4 tawa).

Distribution, description and growth habit

Taraire is a warm temperate forest tree of lowland to low montane forests. Beveridge (1974) described taraire as frost-tender, susceptible to severe droughts and shade tolerant. Lidgard (1930) points out that heavy frosts affect even mature trees turning the leaves into sickly yellow paper. Sakai and Wardle (1978) found that the frost resistance of taraire twigs correlated well with the current distribution of the species.

Taraire is confined to the frost ‘free’ northern part of the North Island from North Cape to latitude 37º25' S (Port Waikato) on the west coast and scattered pockets to latitude 37º42' S (East Cape) on the east coast (Myers 1984). Taraire is particularly abundant in parts of Northland (north of Auckland). Myers (1984) in a survey of forests in Northland, noted that 53% of the sites contained taraire and in 18% of those sites taraire was the dominant species. Taraire occurred most frequently between 50 m and 200 m a.s.l. with an altitudinal upper limit of 650 to 700 m a.s.l. Taraire was found predominantly on gentle to moderate slopes with well-drained, fertile soils (Myers 1984).

Taraire is an evergreen tree that can reach 22 m in height with a trunk of about 1 m diameter (Poole and Adams 1994; Wright 1984) and a lifespan estimated at about 400 years (Ogden 1983). The bark is smooth and dark brown, often with a patchy appearance from lichen growth. Taraire has a stout spreading form with robust branches. Branchlets, young leaves, petioles and inflorescence bracts are covered in dense reddish-brown tomentum. The leathery leaves are wide-elliptic to wide-obovate in shape and alternate on the branches, often bunched at the tips. The leaves are glaucous underneath and often bullate in appearance as a result of impressed veins (Poole and Adams 1994; Wright 1984).

Taraire appears to regenerate successfully under a taraire canopy on Little Barrier Island where there are no seed or seedling predators. Slope and altitude were significantly correlated with distribution of taraire; gentle slopes with seedling and sapling abundance and lower altitudes with canopy tree abundance. (Myers 1984).

Phenology

The small greenish flowers are covered in reddish-brown tomentum. The flowers are in axillary panicles that are shorter than the leaves and, therefore, can be rather inconspicuous. Wright (1984) gives more detailed description of the flowers. Flowers occur from about September to December, but most commonly about November (Allan 1961; Myers 1984; Wright 1984). The rate of pollination may be affected by rainfall, with less pollen transfer during heavy rain (Myers 1984).

The fruits are black, erect, ellipsoid to ovoid drupes, with a size range of 25 to 35 mm long and 14 mm to nearly 20 mm wide. The fruit contains one large seed surrounded by a fleshy purple pericarp consisting of 3 distinct layers; a thin black exocarp, a thick fleshy mesocarp and a hard endocarp (a layer of stone cells) surrounding the embryo. The seed itself has a very thin seed coat and a layer of enlarged mucilage-filled cells, “jelly layer”(Gardner 1996), surrounding the two large cotyledons. (Allan 1961; Myers 1984; Wright 1984).

Taraire seedfall occurs predominantly in autumn and early winter (May-August) and possibly occurs slightly earlier on offshore islands than on the mainland (Allan 1961; Myers 1984, Dijkgraaf pers. obs.; Wright 1984). Germination of seed occurs from May to October, which is about 17 weeks. In moist conditions, taraire seeds produce abundant mucilage and can look as if the sprouting seed is surrounded by clear jelly. This might be a way for taraire seed to increase its seed to water contact and retain water during germination (Gardner 1996; Myers 1984). Mucilage production appears to vary from year to year in accordance with rainfall (Dijkgraaf pers. obs.).

Germination rate and percentage are affected by temperature, with higher temperature producing both higher rates and total percentage germination. Plumule emergence is suppressed at low temperatures. Taraire seed lack dormancy and are difficult to store. Storage (especially at cooler temperatures) decreases seed viability, most markedly for seed with exocarp removed because seed germinates in cold storage and the seedlings die through cold. Taraire seed cannot cope with desiccation. Seedling emergence appears to be faster in more shady conditions but total absence of light slows the process down. Leaf litter appears to enhance germination as it creates a moist microclimate beneath the litter but can be problematical for roots trying to penetrate through from above the leaf litter. Removal of the fruit-flesh significantly improves the rate and percentage germination (Myers 1984). After gut passage, the seed looks like a light coloured, olive stone with a netted appearance.

2.6 Mangeao

Taxonomy

Mangeao (*Litsea calicaris* (A. Cunn.) Benth. et Hook. f. ex Kirk) is another member of the Lauraceae family (see under tawa). The genus *Litsea* is a tropical genus of about 180 species of trees and shrubs with the sexes on separate plants. New Zealand has only the one indigenous species (Salmon 1980).

Distribution, description and growth habit

Mangeao is found from sea level to about 600 m a.s.l., from North Cape south to East Cape and south of Mokau. Salmon (1980) describes it as being quite common in forests in this region, but it did not occur at any of my study sites.

It is a much-branched small tree up to 12 m tall with a dark brown trunk up to 800 mm in diameter (Allan 1961; Salmon 1980). In the open, mangeao has a spreading, rounded crown, but produces a more confined crown in forest (Salmon 1980). The leaves are alternate, subcoriaceous, on petioles that are up to 20 mm long. The lamina are 50 mm to 125 m long, ovate to oval or ovate-elliptic, with obtuse to subacute tips. The leaves are glabrous and more or less glaucous underneath (Allan 1961).

Phenology

This is a dioecious species, with yellow-green, sweet-scented flowers borne profusely on umbels arising from axils towards the branch tips. Each umbel carries about 4 or 5 flowers and flowering takes place during September and October (Allan 1961; Salmon 1980).

The fruit is a sub-ovoid drupe, about 15 mm to 20 mm long and sits on a pedicel produced from the lower flower tube. The mesocarp is reddish to purple when ripe. Fruiting occurs from about September to November (Allan 1961; Salmon 1980).

2.7 Tawapou

Taxonomy

Pouteria costata (Endl.) Baehni. (Nicol 1997; Parsons *et al.* 1998) (previously *Planchonella novae-zelandiae* and *P. costata* (Poole and Adams 1994)) belongs to the family Sapotaceae. This family comprises 75 genera and about 800 species, mostly trees and some shrubs that exude white milky juice (latex) when damaged.

Distribution, description and growth habit

Tawapou occurs sporadically in lowland forests to about 450 m a.s.l., mainly along the coast and on rocky headlands from Three Kings Islands to Tolaga Bay in the east and Manukau Harbour in the west. It also occurs on Norfolk Island (Poole and Adams 1994; Salmon 1980). Tawapou appears to require free-draining soil or steep terrain (Dijkgraaf pers. obs.).

It is a medium-sized tree reaching about 15 m with a trunk up to 1 m in diameter. The pubescent branchlets and petioles yield a milky juice. The shiny, thick, leathery leaves are 50 mm to 100 mm long, elliptic-obovate with obvious, almost parallel venation visible from above and below, and alternate along the branch (Poole and Adams 1994; Salmon 1980).

Phenology

The generally perfect, but sometimes unisexual, flowers occur singly or in pairs, usually in the axils but occasionally directly from the branch, and are very small (4 to 6 mm across) (Poole and Adams 1994; Salmon 1980). They look a bit like small upright, and rather more pubescent hinau (*Elaeocarpus dentatus*) flowers. Flowering takes place around January (Salmon 1991)

The fruit is a berry 25 to 40 mm long which ripens from green to yellow to red to black from about March to May (Poole and Adams 1994; Salmon 1980, 1991). Fruits take from 12 to 15 months to ripen (Salmon 1980). The berries contains 1 to 4, almost banana shaped, highly polished brown seed(s).

2.8 Miro

Taxonomy

Prumnopitys ferruginea (D.Don) de Laub. is one of 10 to 12 *Prumnopitys* species (F. Podocarpaceae) spread through Indonesia, South America, Chile, New Caledonia and New Zealand. Miro was previously known as *Podocarpus ferruginea*. *Prumnopitys* "plum-fruits" are distinguished from *Podocarpus* species by the female cones that are borne on scaly stalks and the fruits that lack a fleshy stalk (Poole and Adams 1994). Chromosome number 2n = 36 (Hair and Beuzenberg 1958 cited in Dawson 2000).

Distribution, description and growth habit

Miro is found throughout lowland and montane forests of all three main islands (Allan 1961; Poole and Adams 1994), though distribution within a forest tends to be clumped, often on ridges (Dijkgraaf pers. obs.).

The tree can reach up to 35 m in height and has a dark, almost black trunk of up to 1 m in diameter. The bark has a hammered appearance and falls off in thick flakes that are pale underneath. The juvenile leaves are up to 30 mm long, narrow-linear, falcate, with acute points. The dark-green recurved adult leaves are shorter at 15 to 25 mm long, occur on one plane, either side of the branchlets (Allan 1961; Poole and Adams 1994).

Phenology

Miro is considered dioecious, though in one study most male trees had at least one branch that bore fruit (Leathwick 1984). The male cone is solitary, grows from the leaf axil and is almost sessile. The female cone is also solitary, or rarely paired, on short curved scaly stalks about 10 mm long (Allan 1961; Poole and Adams 1994). Male strobili appear on the trees in autumn and, after over-wintering, shed their pollen in late spring or early summer. The small ovules appear in spring, just before anthesis (Leathwick 1984).

Botanically, the propagule of miro is a "seed", but functionally and ecologically it is a "fruit" and will be referred to as such (Clout and Tilley 1992). The fruit is oblong to sub-spherical, drupaceous (since it has an outer fleshy cover like a drupe), reddish purple in colour with a glaucous bloom and up to 20 mm long and 12 to 15 mm in diameter (Allan 1961; Clout and Tilley 1992; Poole and Adams 1994). They have a fleshy exocarp surrounding a large "seed" with a woody endocarp (Clout and Tilley 1992). Unripe fruits develop slowly with the greatest increase in size during the spring and summer following over-wintering (Leathwick 1984). Ripe fruits are available 18 months after pollination during late summer and autumn (Clout *et al.* 1991; Clout and Tilley 1992; Leathwick 1984; McEwen 1978). Fruit production in miro tends to be more regular than for some other podocarp species (Leathwick 1984).

Fruits of the miro show variable germination success rates. Passage through a pigeon did not seem to affect the germination success. No seeds germinated for 18 months, then germination continued over four years (Clout and Tilley 1992). The seed probably requires a cold period (stratification) for successful germination (Fountain and Outred 1991) and germination is epigeal (Godley 1985). Miro is often considered one of the most shade tolerant of the podocarp species and responds to elevated light levels with an increased growth rate, especially in the forest (Ebbett and Ogden 1998).

2.9 Pigeonwood

Taxonomy

Hedycarya arborea J.R.Forst. & G.Forst. (pigeonwood or porokaiwhiri) is the sole and endemic New Zealand species of the small (20 species) Pacific genus *Hedycarya*. It belongs to the family Monimiaceae, a family of tropical to subtropical trees and shrubs, containing about 30 genera and 450 species (Allan 1961; Salmon 1980). Chromosome number 2 = 57 (Hair and Beuzenberg 1959 cited in Dawson 2000).

Distribution, description and growth habit

Pigeonwood occurs from sea level to 800 m a.s.l. throughout the North Island and as far south as Banks Peninsula in the east. The species favours a wet climate and rich soil (Allan 1961; Salmon 1980). The plant is usually an erect, small (up to 12 m tall), aromatic tree, with a trunk up to 500 mm in diameter. The leaves, set on 20 mm long petioles, are thick, leathery, shining above and duller below, with saw-toothed or plain margins and a distinct venation pattern.

Phenology

Pigeonwood is dioecious. The male flowers (late autumn) are considerably larger and more abundant than the female flowers (winter), though neither is very showy, being rather simple with undifferentiated perianths of green tepals making up the visible flower. The tepals surround many stamen (for the male) or a few carpels (female). The fruit is a bright orange drupe up to 15 mm long. Flowering occurs from September to December, and fruiting from October to February (Allan 1961; Salmon 1980) but the period of fruit ripening is about 18 to 20 months from flowering (Leathwick 1984). The fruits germinate well, generally within 6 to 12 months. Pigeonwood fruits will germinate under dark conditions but have low success when the pericarp is left on (Burrows 1993).

2.10 Other important species

Two other large fruited species, swamp maire (*Syzygium maire*) and hinau (*Elaeocarpus dentatus*), will not be described since neither is very common in the Auckland area, and neither were found at any of the sites.

Other fruits of importance to pigeons but not investigated in detail, because the fruits are eaten by other smaller bird species, are described below.

2.10.1 Nikau

Rhopalostylis sapida H.Wendl. & Drude belongs to the Arecaceae palm family. The genus *Rhopalostylis* contains 2 to 4 species, which are endemic to New Zealand, Kermadec Islands, Chatham Islands and Norfolk Island (Moore and Edgar 1970; Poole and Adams 1994, C. Ogle pers. comm.; Salmon 1980).

Nikau is found in lowland forests throughout the North Island and in the South Island as far south as Banks Peninsula in the east and Greymouth in the west (range from about 35 to 43 S) (Cowan 1991; Enright 1985). The possibly distinct species or subspecies of *Rhopalostylis* growing on the Chatham Islands make this the most southerly occurring species of palm in the world (Moore and Edgar 1970; Poole and Adams 1994; Salmon 1980).

The palm can achieve a height of 10 m or more with a trunk up to 250 mm in diameter. The stem has pronounced leaf-scars. The leaves can be up to 3 m long, with individual leaflets to 1 m long, closely set along the leaf and ascending sharply (Moore and Edgar 1970).

The spathe surrounding the flowering spadix is smooth and pinkish-yellow in colour. It falls off the many branched spadix about the time that the first of the flowers open (Moore and Edgar 1970). The numerous lilac-pink flowers are in groups of three, one female with two large males on either side. Male flowers open almost immediately, and most of the male flowers are open three days after the spathe has fallen. By the seventh day, nearly all of the male flowers have fallen and it is not until the fourteenth day that the stigma of the female flowers start to appear (A.E Esler in Eagle 1986).

By the time the female flowers have opened the ovary has already grown to a third of its ultimate size. The fruits mature in less than a year. Maturity is indicated by a change from green to red (A.E Esler in Eagle 1986). The fruits are about 10 mm long by 7 mm in wide, elliptic-oblong, and seated in a cup of the flower remains and brick red when mature. Flowering has been reported from November to April and fruiting from February to November (Moore and Edgar 1970).

2.10.2 Kahikatea

Dacrycarpus dacrydioides (A.Rich.) de Laub. is one of about nine species belonging to the genus *Dacrycarpus* (F. Podocarpaceae) with a distribution from Burma to New Zealand (Moore and Edgar 1970). Kahikatea is the sole and endemic species in New Zealand and occurs in forests as high as 600 m above a.s.l. (Allan 1961; Poole and Adams 1994; Salmon 1980).

This is New Zealand's tallest tree species, up to 60 m tall, and can be found throughout both Islands and Stewart Island. The trunks can be up to 1.5 m in diameter and are covered in hammer-marked grey bark and often fluted at the base. Branchlets are slender and drooping. Leaves of juvenile and young trees are in two rows, 4 to 6 m long, linear and falcate, while those of adults are 2 to 3 mm long and imbricate (Allan 1961; Poole and Adams 1994; Salmon 1980).

The species is dioecious with separate male and female trees. The male cones are solitary and at the tips of the branches, as are the minute the female cones which also feature a swollen peduncle. Flowering is around November (spring) with ripe fruits appearing three to five months later, mostly in January and February (Leathwick 1984). The fruits are small (4 to 5 mm long) black, nut-like seed seated in a red, swollen, succulent receptacle (Allan 1961; Poole and Adams 1994; Salmon 1980). Kahikatea produces periodic exceptionally heavy crops, and fruits have been observed to remain on the trees for up to two years (Leathwick 1984). Chromosome number 2n = 20 (Hair and Beuzenberg 1958 cited in Dawson 2000).

2.10.3 Titoki

Alectryon excelsus Gaertn. is in the soap-berry family (Sapindaceae), a tropical and subtropical family of about 150 genera and 2000 species of trees, shrubs and lianes (Allan 1961; Poole and Adams 1994; Salmon 1980). Titoki can be found in lowland forests from sea level to 600 m a.s.l., from North Cape to Banks Peninsula in the east and about Bruce Bay in the west (Allan 1961; Poole and Adams 1994; Salmon 1980).

A single, or few stemmed, evergreen, dioecious tree, up to 15 m tall. It occurs in mixed forests, prefers river flats, is often a canopy species and may form groves. Titoki has imparipinnate leaves of about 100 to 400 mm long on about 80 mm long petioles. Each leaf consists of about 4 to 6 pairs of sub-opposite 50 to 100 mm long leaflets. Tiny flowers occur in axillary panicles up to 300 mm long from October to December; they are pleasantly fragrant (Allan 1961; Poole and Adams 1994; Salmon 1980). The paniculate infructescences, at the ends of the branchlets, bear up to 20 large capsules, each containing one (rarely two) seed(s). When the capsule opens, the upper part dehisces, revealing the shining black seed with its lower half embedded in a fleshy scarlet arillode. It is a periodic but very prolific seeder (Burrows 1996). Most fruits germinate within 2 to 9 months, but a small fraction stays dormant and germinates after 10 to12 months. Titoki seed encompassed by fruit-flesh has a low germination rate, but dark treatment only slightly depresses germination (Burrows 1993).

2.11 New Zealand pigeon – kereru

The New Zealand pigeon (*Hemiphaga novaeseelandiae* (Gmelin)) has different Maori names in different parts of New Zealand; kereru, kuku or kukupa (Taylor 1996). Kereru is the most commonly used name for the Auckland region and will be used in this thesis. Kereru belongs to the family

Columbidae, and the subfamily Treroninae, which is found throughout Southeast Asia, Malaya, Africa and New Zealand. The members of this subfamily feed largely on fruits and berries (Falla *et al.* 1979). *Hemiphaga* is a monotypic genus endemic to the New Zealand archipelago and Norfolk Island and recently a *Hemiphaga* bone was found on Raoul Island (Worthy and Brassey 2000). There are three known subspecies of New Zealand pigeon, *H. n. novaseelandiae* of mainland New Zealand is the species featured in this thesis. The other two species are *H.n. chathamensis* of the Chatham Islands and *H.n. spadicea* of Norfolk Island, which is now extinct. The subspecies differ in their plumage colour and physical morphology (James 1995). It has been suggested that the differences between *H. n. novaseelandiae* and *H.n. chathamensis* are sufficient to raise the latter to full species status (Millener and Powlesland 2001).

The kereru is a large (550 to 850 g) arboreal fruit-pigeon (Clout 1990) that is found in forests from Northland to Stewart Island, ranging in habitats from coastal to montane (Clout *et al.* 1986). Its general morphology is that of a typical pigeon, in that it has a relatively small head, a straight soft-based bill and loosely attached feathers. It also displays typical pigeon behaviour, which includes drinking by suction, a wing-threat display, hitting with the wing when threatened, a diving display flight, a ‘bowing’ display, ritualised preening and ‘billing’ during courtship. Kereru build flimsy, shallow, twiggy nests and feed crop milk to hatchlings (Falla *et al.* 1979; James 1995).

Pigeons are important seed dispersers in New Zealand’s forests as they are one of the few historic and only extant frugivores that can swallow the fruits of large-fruited species and void the seeds intact (Bell 1996; Clout and Hay 1989; Clout and Tilley 1992; James 1995; Lee *et al.* 1991; McEwen 1978; Myers 1984; West 1986). However, pigeon populations are under threat from hunting, habitat degradation and poor reproductive success (Clout *et al.* 1995a; Clout *et al.* 1995b; Clout and Saunders 1995). Pigeons were very numerous until about the 1860s and large flocks used to congregate in fruiting trees to feed (Best 1977). Restrictions on the shootings of pigeons were necessary as early as 1864, with total protection since 1921 (Falla *et al.* 1979).

Fruit-pigeons typically inhabit tropical forest (Goodwin 1970; sensu James 1995) where they feed on tropical fruits such as figs (family Moraceae) (James 1995) and the families Lauraceae (Crome 1975b) and Arecaceae (palms) (Firth *et al.* 1976). Kereru also feed on many species with tropical affinities, including the Lauraceae and Arecaceae (Bell 1996; Clout and Hay 1989; Clout *et al.* 1991; McEwen 1978) but live in the temperate forest of New Zealand and also feed on podocarp species, thought to be elements of Gondwana, such as miro and kahikatea (Clout and Hay 1989; Clout *et al.* 1991; Clout and Tilley 1992; McEwen 1978). A complete list of fruits taken by kereru can be found in section 2.11.1. When fruit is scarce kereru feed extensively on leaves, buds and flowers (e.g. kowhai (*Sophora* spp), wineberry (*Aristotelia serrata*), *Coprosma*, *Parsonsia*) and fruits and leaves of some introduced species (Bell 1996; Clout and Hay 1989; Clout *et al.* 1991; James 1995; McEwen 1978).

An important morphological feature of fruit-pigeons is a thin-walled, grit-free gizzard ((Crome and Shields 1992) sensu (James 1995)) that processes fruits without damaging the seed. The gizzard may be cornified as in *Ducula goliath* and *D. latrans*, or uncornified as in *D. pacifica* and *D. rubricera* (James 1995). The gizzard of *Hemiphaga* is thick-walled with a cornified lining, and no grit is present (James 1995; McEwen 1978). The cornified gizzard serves to separate fruit-flesh from the seeds, allowing the pulp to be digested and the seeds to be defecated intact (Bell 1996). Kereru also have a distensible gape, which enables them to eat large fruits up to 26 mm in diameter (Gibb 1970).

McEwen (1978) and James (1995) propose that *Hemiphaga* has been isolated on the New Zealand archipelago since the mid to late Tertiary, and that it represents an early stage in the evolution and radiation of the Pacific wood-pigeons. In that case, it would be an ancient inhabitant of New Zealand (James 1995; McEwen 1978).

2.11.1 Plant species utilised by kereru

The following is a list of other native species recorded or seen eaten by kereru (McEwen 1978, M. Clout unpublished data).

Fruits

Podocarps:
Dacrycarpus dacrydioides, Dacrydium cupressinum, Podocarpus hallii, P. nivalis, P. totara, Prumnopitys taxifolia, P. ferruginea.

Angiosperms:
Alectryon excelsus, Aristotelia serrata, Beilschmiedia tarairi, B. tawa, B. tawaroa, Carpodetus serratus, Coprosma areolata, C. foetidissima, C. grandifolia, C. linariifolia, C. lucida, C. parviflora, C. propinqua, C. pseudocuneata, C. rhamnoides, C. robusta, C. rotundifolia, Coriaria arborea, Corynocarpus laevigatus, Dysoxylum spectabile, Elaeocarpus dentatus, E. hookerianus, Fuchsia excorticata, Gaultheria antipoda, Griselinia littoralis, G. lucida, Hedycarya arborea, Ixerba brexioides, Libocedrus plumosa, Litsea calicaris, Lophomyrtus bullata, L. obcordata, Macropiper excelsum, Melicytus chathamicus, M. lanceolatus, M. ramiflorus, Mida salicifolia, Muehlenbeckia australis, M. complexa, Myoporum laetum, Myrsine australis, M. divaricata, M. salicina, Neomyrtus pedunculata, Nestegis cunninghamii, N. lanceolata, Passiflora tetrandra, Pennantia corymbosa, Pouteria costata, Pseudopanax arboreus, P. chathamicus, P. colensoi, P. crassifolius, P. edgerleyi, P. simplex, Pseudowintera axillaris, P. colorata, Rubus australis, R. cissoides, Schefflera digitata, Solanum aviculare, S. laciniatum, S. nodiflorum, Streblus heterophyllus, Syzygium maire, Tupeia antarctica, Vitex lucens.

Monocotyledons:
Astelia banksii, Cordyline australis, Rhopalostylis sapida, Ripogonum scandens.

Foliage

Calystegia spp, *Carpodetus serratus, Coprosma rotundifolia, Fuchsia excorticata, Melicytus ramiflorus, M. lanceolatus, Nothofagus menziesii, N. truncata, Parsonsia heterophylla, Phyllocladus trichomanoides, Sophora microphylla*.

Fungi and other food types

Cyttaria gunnii

Kereru also feed on many exotic plant species, especially in urban areas but, since these were introduced within the last 200 years or so, co-evolution is unlikely to have manifested itself yet.

2.12 Fruit predators

This section provide background details on two groups of introduced mammals that are having an impact in New Zealand native forest systems: the Australian marsupial brushtail possum (*Trichosurus vulpecula* Kerr) and the introduced European rodents (ship rat *Rattus rattus* Linnaeus, Norway rat, *R. norvegicus* Berkenhout, and house mouse, *Mus musculus* Linnaeus). The introduced Polynesian rat (kiore, *R. exulans* Peale) will be mentioned in passing, but kiore are generally confined to offshore islands, and were not present at the study sites.

2.12.1 Possums

The possum was first introduced into New Zealand from Australia in 1837 to establish a fur trade (Clout and Ericksen 2000; Cowan 1998; Pracey 1974). The first successful liberation in 1858 in forest behind Riverton presaged many liberations of possums, especially between 1890 and 1900 (Pracey 1974). The consequent spread of possums throughout the country was accelerated by additional liberations of New Zealand bred progeny (see Bennett 1992; Clout and Ericksen 2000; Cowan 1998; Poole 1969; Pracey 1974). Legislation regarding and the protection status of, possums varied over time with changing views on the destructive behaviour of the animal versus the value of its fur (Clout and Ericksen 2000). The possum is no longer a protected species in New Zealand, and is actively eradicated or suppressed in many habitats to reduce vegetation damage to acceptable levels and eliminate possums as sources of re-infection of bovine tuberculosis (Atkinson and Wright 1993; Cowan 1998; Green 1984).

These nocturnal animals are well adapted for climbing, with opposing digits on both hands and feet and a prehensile tail, but they are also mobile on the ground (Cowan 1998). They are generally 650 to 930 mm long including a 250 to 405 mm thick bushy tail. Possums weigh from 1.4 to 6.4 kg, have a pointed snout and a darkly stained sternal gland on the chest. The ears are long and narrow, tapering towards their tips, nearly naked on the inside and the outer tips. The fur is thick and woolly, generally either grey or black and is currently becoming popular as a fibre (Cowan 1998; Poole 1969).

The home range sizes of possums vary between males (mean 1.9 ha, range 0.7 to 3.4 ha, length 295 m) and females (mean 1.3 ha, range 0.6 to 2.7 ha, length 245 m) and are also affected by season, and available food sources (Cowan 1998).

Possum sign in the field includes runs or pads (the tracks made by possums), bark biting, bark scratching (mainly from climbing), partially eaten fruits and flowers and partially eaten leaves to wholly defoliated trees (Cowan 1998; Payton *et al.* 1997b). Possum droppings may be found singly or in groups and are usually about 15 to 30 mm long, 15 to 14 mm wide, oval with a slight crescent curve and slightly pointed at the ends. The colour and texture vary according to diet, but the pellets often have a distinctive smell (Cowan 1998, A. Dijkgraaf pers. observ.).

Possums are opportunistic herbivores, feeding mainly on foliage, but they also take fruits, flowers, ferns, bark, fungi, invertebrates, eggs, small birds and commercial crops (Allen *et al.* 1997; Cowan 1990, 1998; Mason 1958). More recently, possums have been described as ‘reluctant folivores’ since their success in maintaining population densities, and subsequent damage of forests, probably largely depends on the non-foliar components of the diet (Nugent *et al.* 2000). Foliage tends to be a low energy and low nutrient source, which must be supplemented by other food items (Nugent *et al.* 2000).

Extensive dietary studies show that although the total diet spectrum over the whole country is wide, the bulk of the diet relies on only 4 to 7 species locally or seasonally (e.g. Cowan 1990; Mason 1958). In New Zealand, this selective browsing leads to tree death, dietary switches to less preferred species, and changes in forest composition as preferred species are reduced in numbers (Allen *et al.* 1997; Campbell 1984, 1990; Coleman *et al.* 1985; Green 1984; Nugent 1994; Poole 1969; Rogers and Leathwick 1997; Rose *et al.* 1993).

Unlike damage by insects, leaves browsed by possums are torn, rather than cut, and often the midrib and part of the lower leaf remains (Cowan 1998; Payton *et al.* 1997b; Poole 1969). Feeding sign depends on the species of tree, possums feeding on five-finger (*Pseudopanax arboreus*) eat only the base of the petioles and discard the remainder (Cowan 1998). Similarly for the juvenile spadex of nikau (*Rhopalostylis sapida*), the covering spathe is shredded and only the base of the spadex is eaten with the rest discarded below the palm tree (Cowan 1991, A. Dijkgraaf pers. obs.)

Among the species most impacted by possum browse of the foliage (in no particular order) are northern rata (*Metrosideros robusta*), southern rata (*M. umbellata*), kohekohe, fuchsia (*Fuchsia excorticata*), tawa, five-finger, kamahi (*Weinmannia racemosa*), toro, (*Myrsine salicina*), titoki, mahoe (*Melicytus ramiflorus*), tutu (*Coriaria arborea*), totara (both *Podocarpus totara* and *P. hallii*) mountain cedar (*Libocedrus bidwillii*), various species of indigenous mistletoe, woodrose (*Dactylanthus taylori*) and the tree fern mamaku (*Cyathea medullaris*) (Allen *et al.* 1997; Anonymous 1983; Brockie 1992; Campbell 1984, 1990; Leutert 1988; Pekelharing and Batcheler 1990).

Tree fuchsia has become extinct or very rare in many parts of the country as a result of possum damage (e.g. Anonymous 1983; Batcheler 1983; Brockie 1992). Areas of extensive dieback, tree death and local extinction have also been recorded for the other tree species (e.g. Allen *et al.* 1997; Atkinson 1985; Batcheler 1983; Brockie 1992; Campbell 1990; Court 1985; Kean 1951; Kean and Pracey 1953; Leutert 1988; Pekelharing and Batcheler 1990; Rogers and Leathwick 1997). Less preferred species, such as supplejack (*Ripogonum scandens*) and scarlet rata (*Metrosideros fulgens*), are becoming more heavily browsed in the Orongorongo Valley by possums as northern rata and kamahi decline (Allen *et al.* 1997). Protection of individual trees, or the control or eradication of possums has resulted in marked recovery of susceptible species (Atkinson 1985; Brockie 1992; Cowan and Waddington 1990; Meads 1976; but also see Payton *et al.* 1997a).

Damage to forests and trees within a forest by possums are by no means uniform (e.g. Meads 1976; Sweetapple and Nugent 1999) or always predictable (e.g. Cowan *et al.* 1997). Floristic composition and a variety of site and climatic factors may lead to several possum induced damage scenarios, including complete canopy collapse, reducing plant vigour and triggering damage episodes, or accelerating the rate of vegetation change (Payton 2000).

Possums also compete with native animals, especially birds, for the fruits, seeds, flowers and nectar of native trees and shrubs (e.g. Anonymous 1983; Cowan 1990; Cowan 1991; Cowan and Waddington 1990; Fitzgerald 1978; Mason 1958). Fruits of most species are eaten to a greater or lesser extent by possums (Brockie 1992). Poole (1969) noted that the actual destruction and waste of fruits was greater than stomach contents analyses indicate. Frequently only part of the fruits was taken, as with tawa where the half-grown fruits were destroyed by extracting the soft seed kernels from holes chewed at one end of the fruits. Other fruits, such as hinau, miro, etc. were eaten while only small and green. Waste of fruits was considerable since undamaged fruits were knocked to the ground in large numbers as possums forage in a tree (Poole 1969).

A range of animal species are known to be preyed on or killed by possums. Birds, including the kokako (*Callaeas cinerea wilsoni*), brown kiwi (*Apteryx australis mantelli*), kahu (*Cirus approximans*), fantail (*Rhipidura fuliginosa*), North Island saddleback (*Philesturnus carunculatus rufusater*) and kereru (*Hemiphaga novaeseelandiae*) are predated as eggs, chicks or adults. Large insects such as stick insects, weta, cicadas and beetles, *Powelliphanta* snails and possibly lizards are also consumed by possums (Cowan and Moeed 1987; Innes 1994; Innes *et al.* 1994; James and Clout 1996; Sadleir 2000).

Possums in Australia mature earlier and have better breeding success than in New Zealand, perhaps indicating that populations in New Zealand are often food-limited (Green 1984). Cowan (1990) noted that hinau fruits comprise a significant component of the possum diet during autumn and winter and their abundance affects possum reproduction and body weight.

2.12.2 Rodents

Nowhere in New Zealand are the four introduced species of rodent (three species of rat and one mouse species, *Mus musculus* Linnaeus) known to be sympatric (Innes 1998; Moors 1998). The two most widely distributed rats are the Norway rat (*Rattus norvegicus* Berkenhout) and the ship rat (*R. rattus* Linnaeus), while the kiore (*R. exulans* Peale) is restricted to offshore islands or parts of South-Westland. Where the two widespread rat species coexist, the larger Norway rat usually remains on the ground whilst ship rats occupy trees and the upper canopy, though ship rats do descend to the forest floor (Innes 1998; Moors 1998). Norway rats tend to be commensal with human habitation and are found more commonly in and around cities, towns and farms, with isolated populations in wetlands and along watercourses (Moors 1998). Unlike Norway rats, ship rats are unwilling swimmers and more likely to be found in forests than Norway rats (Innes 1998). Mice are essentially ground dwelling, but can swim and also climb well (Murphy and Pickard 1998, and references therein).

All rodent species, with the exception perhaps of kiore, arrived in New Zealand as unwanted stowaways on European ships (Innes 1998; Moors 1998; Murphy and Pickard 1998). The exact arrival time for Norway rats is not known, but they were apparently well established on both the North and South Islands by the middle of the 1800s, with a rapid decline in numbers by the end of that century (Moors 1998). Ship rats spread through North and South Islands after 1860 and 1890 respectively (Atkinson and Bell 1973) and are now the dominant rat species throughout most of New Zealand (Innes 1998). Mice probably arrived in the North Island as early as 1830 (Guthrie-Smith 1969) and by the mid 1850s in the South Island (Gillies 1877; sensu Murphy and Pickard 1998) and probably occupied most suitable habitats in both islands by the turn of the 20th century (Murphy and Pickard 1998).

Male Norway rats are usually larger than females, but sizes can vary considerably. Animal lengths from various studies listed in Moors (1998) range from 138 mm to 246 mm. Most Norway rats weigh between 150 g to 300 g (Moors 1998). Ship rats also vary greatly in length and weight according to location and time of the year. The range for head plus body lengths listed in Innes (1998) is 108 mm to 230 mm, with a weight for wild ship rats of 160g for males and 137g for females (Innes 1998). Mice weigh on average 20.7g with a mean head to body length of 89.3 mm (references in Murphy and Pickard 1998).

Home ranges of Norway rats can vary considerably in size. A New Zealand study showed that three male rats on Motuhoropapa Island had home ranges of 0.8 to 1.8 ha (average 1.2 ha) and that on average males travelled 113 m and females 49 m between successive live captures. The longest recorded distance was 330 m in 48 hours, and distances travelled increased as food became more scarce (Moors 1985). On Kapiti Island, radio-tracked Norway rats had minimum average home range convex polygon of 5.8 ha (range 1.6 to 21 ha), while average range lengths were around 450m (Bramley 1999). Overseas studies have shown that Norway rats could travel considerably further than thus far recorded for animals in New Zealand (Moors 1998).

Ship rat home ranges vary with habitat, season and breeding (Dowding and Murphy 1994). Adult males in the Orongorongo Valley moved on average 55.4 m (range 0 to 190 m) and females 38.8 m (range 0 to 117) between successive cage captures (Daniel 1972). In similar habitat near Palmerston North the figures were 38 m (0 to 67 m) for males and 36 m (range 0 to 45 m) for females (Innes 1977).

Mice in the Orongorongo Valley had minimum home ranges of 0.6 ha, and ranged widely within that territory every night, but one animal covered 2.62 ha in three nights (Fitzgerald *et al.* 1981).

Faecal pellets from Norway rats can be distinguished by their length, usually being twice the length of other rat pellets. They are cylindrical and stubby, sometimes tapering to a point and on average about 16 mm long (Moors 1998). Ship rat pellets average 8.6 mm long (range 6.8 to 13.8) and 3.6 mm wide (range 2.7 to 5.0) (Daniel 1969). Mice produce dark brown or black 5 to 7 mm long pellets (Murphy and Pickard 1998).

Rats and mice are mainly nocturnal, omnivorous and opportunistic feeders that eat a wide range of foods including grains, foliage, fruits, flowers, invertebrates, eggs, birds and lizards (Beveridge 1964; Innes 1998; Moors 1985; Moors 1998; Murphy and Pickard 1998 and references therein). Norway rats are known to hoard food including large fruits such as tawapou (Moors 1985), and have been implicated in the lack of beech (*Nothofagus menziesii* and *N. solondri* var *cliffortioides*) seedling recruitment on Breaksea Island (Allen *et al.* 1994). They have been reported to eat various types of insects (especially weta), aquatic and terrestrial molluscs, and crustacea and bird feathers have also been found in stomach contents (Moors 1985)

Plant matter comprises about 80% of ship rat diets. They are known to collect seeds of miro and hinau into large caches (Beveridge 1964; Innes 1998). Other important fruits in the diet of ship rats relevant to this study include karaka, pigeonwood, miro, and nikau (Best 1969; Beveridge 1964; Daniel 1973;

Innes 1979). Ship rats also eat the fruits of the native passionfruit (*Passiflora tetrandra*), puriri and taraire (Lowe and Clout 1994).

Ship rats are known to prey on eggs and chicks of kereru (Clout *et al.* 1995a; James 1995), kokako (Innes *et al.* 1995), robins (*Petroica australis*), tomtits (*Petroica macrocephala*) and kaka (*Nestor meridionalis*) and the decline, or disappearance, of many other bird species coincides with the rate of ship rat colonisation (Atkinson 1973; Brockie 1992; Brown *et al.* 1998). They also eat lizards (Whitaker 1978) and invertebrates.

In a comparison between adjacent forest sites, the site with pest suppression, Wenderholm Regional Park, had a greater abundance and diversity of insects, especially beetles, weta, and cockroaches (Craddock 1997). Snap trapping of animals illustrated that rats appeared to eat more invertebrates (average 24.0% of diet) than mice (13.7%), and also a wider range of invertebrates. Rats concentrated on invertebrates greater than 3 mm in size, while mice ate insects between 3 mm and 12 mm (Craddock 1997).

Mouse diet consists largely of adult arthropods, lepidopteran larvae and small seeds (Badan 1986). Mouse numbers are known to increase greatly during beech seed mast years, but it is unclear if this is because the mice eat the abundantly available beech seeds, or the greater than average number of moth larvae (*Tingena epimylia*) associated with mast years (Fitzgerald *et al.* 1996; Murphy 1992).

Rat populations can be successfully suppressed using aerial application of pollard baits containing 1080, but they recover within about 6 months (Innes *et al.* 1995; Innes and Williams 1991). It has been noted in several studies that mouse numbers increase after rats are controlled, possibly because of reduced competition and/or predation by ship rats (Clout *et al.* 1995a; Craddock 1997; Innes *et al.* 1995).

[1]

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[1] Kereru resting in tawapou tree at Wenderholm Regional Park

Chapter 3 Sampling design, methods and study site descriptions.

3.1 Introduction.

This chapter describes the main methods used to monitor fruiting events, pest presence and other community aspects, describes and compares the experimental sites (pest suppressed and 'non-treatment'), and compares and contrasts the methods used to record fruiting and flowering.

3.2 Sampling design.

The main aims of the fieldwork for this study were to describe the fruiting phenologies of a range of large-fruited co-existing species (large fruits have diameters >10 mm) and to quantify the impacts of introduced arboreal mammalian fruit predators (for more detailed aims refer to Section 1.4). It was decided that several sites should be studied simultaneously to eliminate the possibility of atypical phenologies being recorded from a single site. All the selected sites should have the same type of native forest cover, in this case hardwood (mainly taraire, *Beilschmiedia tarairi*) podocarp forest, on typical Auckland clay soils (derived from Waitemate Group sandstones and mudstones, Ayres *et al.* 1986; Thornton 1999). The sites north of Auckland were all identified in the 1983/84 Protected Natural Areas Survey as classification "D" type forest; where taraire is the only species with a cover abundance greater than 25% (Ayres *et al.* 1986). The sites south of Auckland have similar vegetation types and soils.

A second aspect dictating the sampling design was the aim of comparing forested sites that had the usual high levels of mammalian fruit predators with areas where these species were suppressed or absent. The pairs of sites should be situated as close as possible (but preferably further apart than the home range lengths of pest species) to ensure similar environmental cues were operating at each site.

It proved rather difficult to locate forested areas where no pest suppression was being undertaken, or where the owner was amenable to not treating the area for the duration of the study. Time, logistics and equipment further limited the sites that could be used.

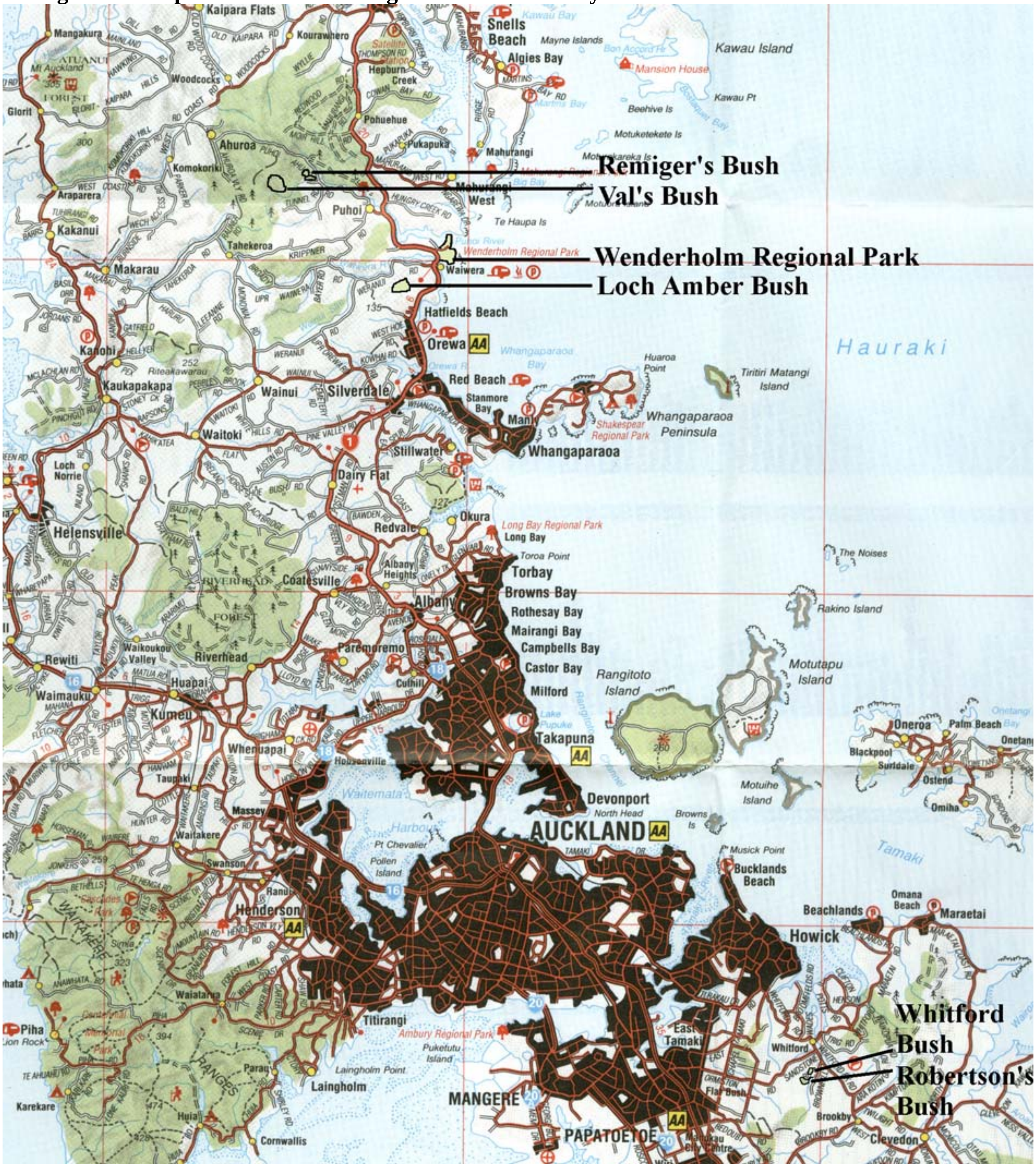
The final design consists of three pairs of sites, spatially separated by up to 50 km. Individual sites in a sample pair are separated by less than 5 km. One site in each pair was undergoing treatment to suppress pest numbers, whilst the other site was left untouched. Sampling methodology was identical at all sites, and as were the species monitored.

Table 3.1: Sample design; summary of site pairs and levels of pest suppression.

Site	Pest suppressed	Location	Paired with
Wenderholm Regional Park	Possums & rodents	North & coastal	Loch Amber
Loch Amber Bush	*No poisoning*	North & coastal	Wenderholm
Whitford Bush	Possums & rodents	South & inland	Robertson's
Robertson's Bush	*No poisoning*	South & inland	Whitford
Remiger's Bush	Possums (rodents?)	North & inland	Val's
Val's Bush	*No poisoning*	North & inland	Remiger's

Toxins were used to suppress pests at the treatment sites. At Remiger's Bush the toxin was provided within the range length of possum, but outside the range length of rodents, however, the toxin was available in such a manner that would not have completely excluded rodent access. Four of the sites were located north of Auckland City, one of the pairs was in a coastal situation and the other pair located further inland. The remaining two sites were south of Auckland and situated away from the coast.

Figure 3.1 Map of Auckland showing location of the study sites



3.3 *Phenological sampling methods.*

There are numerous ways of quantifying fruiting or flowering patterns. A selection of the most commonly used methods are considered below.

3.3.1 Presence/absence classification.

The simplest methods note the presence or absence of ripe fruits or flowers (French 1992; Nakagoshi 1980; Smith-Ramirez and Armesto 1994). Usually, various aspects of the phenology are scored, such as the presence of flower buds, flowers, green and ripe fruits (Milton *et al.* 1982; Murali and Sukumar 1994; Nakagoshi 1980; Smith-Ramirez and Armesto 1994). In this approach a plant or species is added to the tally even if only one flower or fruit is spotted. In some cases phenology information is obtained from herbarium samples (e.g Poulin *et al.* 1999).

These methods provide a basic description of seasonal fruiting patterns, but yield little quantitative, comparable data (Blake *et al.* 1990). The durations of different phenological stages are quantified, but no data are obtained on quantities of fruits produced, or the ripening rates of fruits. The size of the fruit crop might vary from year to year, and provide different feeding opportunities for frugivores (e.g. Herrera 1988; Herrera 1998; Herrera *et al.* 1994; Sallabanks 1992; Sallabanks and Courtney 1993; Welch *et al.* 1997). Similarly, the degree of ripeness can affect rate of fruit take by frugivores (e.g. White 1994b).

In addition, some species produce or carry small numbers of fruits throughout the year. Using a presence/absence system would not distinguish between periods of low and peak fruit production. Examples in New Zealand include, puriri (*Vitex lucens*), which produces small amounts of fruit nearly continuously (Dijkgraaf 1994), kohekohe (*Dysoxylum spectabile*), whose fruits take a year to ripen (Leathwick 1984), and tawa (*Beilschmiedia tawa*), which has overlapping 18-month periods (Knowles and Beveridge 1982; Leathwick 1984). Other species have cryptic fruits that are not readily visible until they start ripening (e.g. tawa), which would reduce observed length of fruiting.

3.3.2 Intensity scales.

Intensity scales record not only when fruiting occurs, but also some measure of how much fruit each tree carries. These scales can vary from subjective, such as; none, some, many (Lee *et al.* 1997), to categorical such as; 0, 1 to 10, 11 to 100, >100 fruits (Ehrlén and Eriksson 1993), or; 0%, 1 to 25%, 26 to 75%, 76 to 100% of canopy area bearing fruit (Wheelwright 1985a). Or they can be a mixture of these, such as a combination of the proportion of the tree that carries fruit, and the proportion of that fruit that is ripe (Patel 1996).

Subjective scales inherently have considerable error, since scoring relies on observer experience. In New Zealand for instance, fruit production on pest free offshore islands can be several magnitudes greater than that observed for the same species on the mainland where possums and rodents predate the fruit (e.g. Lee *et al.* 1997). An observer would not be aware of the potential magnitude of fruiting unless they had experienced fruiting events in predator free environments. Wheelwright (1985a) found that percent of the canopy carrying ripe fruit correlated with actual counts, and was repeatable. Scoring intensity in this manner also provided an estimate of relative crop size regardless of tree size (e.g. small tree with lots of fruits or the same number of fruits on a large tree).

Wheelwright (1985a) combined the percentage class scores with the developmental stage of the most advanced fruits (scored as stages 1 to 4: recently fertilised, swollen and growing, mature size but still unripe, or ripe) to provide an unambiguous indication of phenological state (Wheelwright 1985a). This method is quick and easy to use, and provided that the ‘canopy’ is the ‘observable canopy’, and that the same part of the canopy is surveyed each time, then direct comparisons can be made between trees. This eliminates the need to determine the proportion of canopy being surveyed. Scores are likely to be comparable across species with different sized fruits and flowers and the categories are sufficiently broad to absorb most of the potential observer variation/error.

3.3.3 Direct counts.

Authors have used different methods to count or estimate fruits abundance in trees. On small trees with few fruits it is possible to count all fruits or flowers, (e.g. Coates-Estrada and Estrada 1988; Herrera *et al.* 1994; Primack and Lloyd 1980), or estimate to the nearest 100 fruits, (e.g. Sallabanks 1992; Sallabanks and Courtney 1993). Others have counted accessible fruits, e.g. below 3 m (Wheelwright 1993) or up to 10 m (e.g. Loiselle and Blake 1991; Stiles and Rosselli 1993). More detailed studies mark branches and follow the fate of individual fruits (e.g. Guitián 1998; Herrera *et al.* 1994; Jordano and Herrera 1995; Thompson and Willson 1979; Whelan and Willson 1994).

Blake, *et al.* (1990), favour the use of direct counts of fruits as these are more relevant to disperser populations and allows statistical comparisons between trees, studies, sites and years. Direct counts of fruits allow conversion to index scales at a later time, but the reverse is not true. Where numbers of fruits are too large to count (i.e. >1000) they suggest estimating the crop size on a logarithmic scale (e.g. 100 to 1000, 1000 to 10 000 etc).

The logarithmic scale method was trialed in this study, but the differences between the scaled value and the actual size of the fruit crop were considered to be unacceptably large at the higher end of the scale (e.g. 1000 to 10000 fruits, when the actual number was closer to 5000). Marking individual branches can provide misleading results due to high fruiting variability (e.g. Janzen 1976; West 1986). All target species, for this study, were medium to large canopy trees that could, seasonally, produce in excess of 1000 fruits. Direct counts for the entire canopy of all target trees would therefore be difficult to conduct (if only due to lack of time) at two-week intervals for several years in succession. Direct counts do not necessarily take into account the different sized canopies of the target trees (e.g. a large canopied tree with a moderate crop would be given the same score as a small canopied tree with an exceptionally heavy crop).

The canopy area over which frugivores forage, or over which fruits are presented, has in some cases shown to be a significant as an attractant, or relevant to the rate of fruit consumption (e.g. Bell 1996; Sallabanks 1993). Thus an ideal would use a direct count and include some measure of spatial distribution.

3.3.4 Seedfall traps.

Catching fruits and flowers as they fall from the tree is probably the most precise measure of phenological output, since all individual items can be identified, counted, weighted and assessed for dispersal or predation. Many authors use this method either by placing trays on the ground (e.g. Herrera *et al.* 1994) or more sophisticated raised traps to prevent rotting or seed removal by animals (e.g. Setterfield and Williams 1996; Wright *et al.* 1999; Zagt 1997). Some sample the ground directly (e.g. Howe and Schupp 1985; Jordano and Herrera 1995), but this can be biased as rotted, predated or consumed fruits are unlikely to be collected (e.g. Blake *et al.* 1990; Forget 1993; Forget and Milleron 1991; Ganesh and Davidar 1999) or fruits from more than one season could be collected (e.g. Short 1981; White 1994a; Wright *et al.* 2000b).

Sampling fallen fruits underestimates fruit production, since it does not account for fruits removed from the tree by frugivores or eaten by insects (Blake *et al.* 1990; Ganesh and Davidar 1999), or moved away from the tree by wind. How patterns of fruit fall relate to absolute fruit abundance is still unclear. Fruits can remain on trees long after it is acceptable to frugivores, and this will cause the seedfall phenology to lag behind the actual phenological event. Or in some cases, where fruits are rare, or only a few ripen each day, all fruits may be removed quickly (e.g. Catterall 1985; Howe 1984) and never collect in the seedfall traps. Further, seedfall traps can overestimate the annual variation, since a larger portion of the crop will be removed when ripe fruits are scarce than in years of abundant fruits (e.g. Blake *et al.* 1990; Terborgh 1983). Moreover, seedfall traps sample a small, often undefined, three-dimensional proportion of the canopy (Blake *et al.* 1990). Seedfall traps are also more likely to sample large-seeded, capsulate, dry arillate, and canopy fruits and under-estimate small seeded sub-canopy shrubs (Blake *et al.* 1990). This should not pose a problem in this study since the focus is on large-fruited canopy species.

3.4 Forest sampling methods.

The way in which trees are selected for a phenological study can significantly influence the results obtained. A number of commonly used sampling methods are discussed below.

3.4.1 Random sampling.

Random sampling is the preferred method statistically, but if target species are rare or clumped in distribution there is a likelihood that not enough trees will be located. This method is suitable when sites are relatively uniform and have large numbers of the target species (e.g. Martínez del Rio *et al.* 1996). Random sampling is more likely to allow extrapolation on the production of the whole forest, especially if the sample size is large (e.g. Burrows 1994b; Zagt 1997). However, my study was focussed on the year-round phenology of selected species rather than the overall production of the forest communities.

3.4.2 Transects.

Following fixed transects allows the repeated surveillance of the phenology of the same individuals along the transect (e.g. Ehrlén and Eriksson 1993; Thompson and Willson 1979; Wheelwright 1986). A fixed width transect will also allow the estimation of fruit production per unit area (e.g. kg/ha). However, the total area in which fruits are counted can still vary according to species (different architecture or patchiness of species) and conspicuousness (bright coloured fruits versus dull fruits) (Stiles and Rosselli 1993).

Some of the species of interest to this study were known to be highly clumped spatially (e.g. kohekohe, tawapou (*Pouteria costata*), mangeao (*Litsea calicaris*)) and were likely to be missed by randomly located transects. However, following a fixed route, connecting the various patches, seemed feasible.

3.4.3 Marked trees.

Many studies use individually marked trees to record phenological events (e.g. French 1992; Herrera *et al.* 1994; Jordano 1989; Milton *et al.* 1982; Murali and Sukumar 1994; Patel 1996; Thompson and Willson 1979). This enables repeated and detailed surveillance of individuals, including seasonal, annual and supra-annual variation in phenology for each tree and species. Following the fate of individual trees is the preferred method and recommended by Janzen (1976).

Frankie, *et al.* (1974) recommended a minimum of five individuals per species for tropical phenological studies, while Wheelwright (1986) suggested at least 10 individuals per species. The number of trees selected per species depends to some degree on the rarity of the species and the philosophy behind the sampling (e.g. maximisation of the number of species sampled rather than the number of individuals of each species Thompson and Willson 1979). Number of trees selected per study varies from 3 to 5 (e.g. Keeler-Wolf 1988) upwards and ten trees is a common sample size (e.g. Setterfield and Williams 1996).

3.4.4 Selection of phenology methods for this study.

For this study it was decided to follow a route along which individuals of target species were located and individually identified. This enabled semi-random sampling of common or widely spread species, and the identification of patches of clustered species or individuals of rare species. The aim of this study was to measure the seasonal and inter-annual phenological variation of key large-fruited species. A minimum of 5 to a maximum of 10 individuals per species were located and marked at each site. The regular route also allowed less formal observation of other (non-target) species.

Phenological observations were conducted using four different methods. More detailed descriptions of these methods are provided in the appropriate sections below. The methods were;

1. Indexing fruit fall on the ground (refer section 3.5.2);
2. Identifying the most common developmental stage on the sample trees (refer section 3.5.3).
3. Recording the average number of fruits per cubic metre for each tree (refer section 3.5.4);
4. Collecting plant material using seedfall traps (refer section 3.5.5)

3.5 Description of methods.

Each fortnight the phenology of up to 10 individual trees of each large-fruited species was scored at all six sites (see 3.8 for site descriptions). Five of the species, karaka (*Corynocarpus laevigatus*), kohekohe, puriri, taraire, and tawa (and in one instance pigeonwood (*Hedycarya arborea*) rather than tawa), also had seedfall traps placed beneath six of the phenology trees. These traps were emptied each visit. At Wenderholm Regional Park, phenology trees monitored in previous studies were included wherever possible (e.g. Bell 1996; James and Clout 1996).

3.5.1 Selection of trees.

Janzen (1976) notes that sub-adult or sub-canopy trees can often behave differently from mature canopy trees, and thus misrepresenting phenology. Weak or injured trees may also differ significantly from the ‘normal’ phenological pattern. Conversely, all these trees are part of a community, which can show marked variability between individuals and between years, and this variability is itself biologically important (Janzen 1976). Karaka, kohekohe, puriri, taraire, and tawa were selected as focus species for this study, since they had large fruits (>10 mm diameter) and were the most commonly occurring of the big-fruited species.

Mature trees were included in the study if a good proportion of the canopy was visible, preferably in the range of 0 to 12 m from the ground. The subset of trees that acquired seedfall traps also had to be relatively easily accessible on foot to allow seedfall to be collected. Seedfall traps were placed beneath that part of the canopy that was most visible. This resulted in selecting trees that were generally located near forest edges or canopy gaps.

An additional constraint on seedfall placement at Wenderholm Regional Park was the necessity to place seedfall traps away from the main tracks and out of sight of the public. This was to prevent tampering with samples and to preserve the enjoyment of the bush for the public. Part of Whitford Bush was also excluded for this reason.

3.5.2 Ground fall.

The ground beneath the phenology tree was briefly scanned for numbers of fruits out to the canopy edge. Number of fruits beneath the canopy were recorded in categories; 1 to 10, 11 to 25, 26 to 75 and more than 76 fruits on the ground. This was a rough guide to the number of fruits produced, and served to alert observers to the presence of fruits for species with cryptic fruits or low fruit numbers. The area under most trees was reasonably clear, but occasionally understorey shrubs or grass, partially obscured the search area.

3.5.3 Maturity scale.

This scale was based on the categories used by Wheelwright (1985a) and describes the development and growth of the fruits. The developmental categories were (1) recently fertilised (e.g. flower dropped off, but ovary still present), (2) swollen and growing, (3) mature size but still unripe, (4) ripe. Stage (2) covers a wide range of phenological stages, but the main interest was fruit availability as food source (stage 3 and 4). The rate at which fruits ripened was of interest but the intermediate stages, as fruits ripen, were not relevant to the scope of this thesis.

When approximately equal proportions of fruits were at different stages more than one category was selected and the results were averaged. More detailed descriptions of developmental stages for various species can be found in Appendix 3.1

3.5.4 Number per cubic metre.

The average number of fruits per cubic metre of canopy was recorded for each tree. This method reduces problems with asynchronous fruiting within a tree, differences in tree size and provides some measure of foraging effort required by frugivores.

This current study uses average number of fruits per cubic metre of canopy volume as the measure of fruit phenology. Sallabanks (1992) approximated fruit densities by counting fruits, measuring the shrub dimensions and assuming the shrub was a rectangular box. The method in this study was different in that it used a smaller area of the canopy to estimate the average fruit densities for the entire canopy. This was done mainly to reduce sampling time, yet still retain a relatively quantitative measure of fruit production. The method was flexible and could be used on trees, shrubs and climbers, but it was easier to count the larger-fruited species than small-fruited species.

When assessing fruit density, the actual shape or size of the canopy assessed does not matter, provided the final volume could be expressed per cubic metre (m^3). The easiest shape to assess is 1 metre on each side (i.e. 1 m x 1 m x 1 m). However, 1 m^3 can also enclose a volume of 1 by 2 metres and 0.5 m deep, or 2 m by 2 m and 0.25m deep, or 4 cubes of 0.5 m to a side. For low numbers of fruits a much larger volume (e.g. 4 m^3), or for extremely plentiful fruits a smaller volume (e.g. ¼ m^3), can be counted provided, that the total volume assessed is noted and final average fruit abundance is expressed per m^3. Since tree canopies are not regular, symmetrical or straight edged shapes the 1 m^3 volume was estimated.

Most New Zealand tree species carry fruits, flowers and leaves at the outer extremities of the branches (see note 5 for exceptions). Thus a cubic metre generally only included the volume where leaves occurred and where fruits were likely to occur. The distribution of fruits was not necessarily even across the canopy. To take account of this the selection of counting volumes varied as follows:

1) **Fruits numerous and evenly distributed across the canopy;** Select any 1 m^3 area and count fruits.
2) **Fruit density uneven, areas of the canopy with abundant fruits or sparse fruits;** Count fruits in a half-cubic metre in the ‘dense area’ and the other half in the ‘sparse area’.
3) **Fruits sparse across the entire canopy;** Count fruits in larger volume of canopy, for instance 2 or 4 m^3, note total volume counted and express as fruits/ m^3.
4) **Fruits extremely abundant across the entire canopy;** Count fruits in smaller area of the canopy, (e.g. ¼ m^3), note total volume counted and multiply to fruits/ m^3.
5) **Fruits found throughout interior canopy;** (e.g. kohekohe) count fruits in a larger volume, including interior, note total volume counted and express as fruits/ m^3.

Number of ripe fruits (by colour and size) and total fruits per average cubic metre were assessed for each tree. Ripe fruits were counted as a separate category since the focus of this study was ascertaining whether ripe fruit presentation of co-existing tree species overlapped. This method was also used for scoring flower abundance.

A sample data collection sheet for phenological observation is provided in Appendix 3.2. An analysis was undertaken comparing the results obtained by scoring average fruits per cubic metre with the results obtained from other methods used in this thesis (refer Section 4.3).

3.5.5 Seedfall traps.

Description.

To allow comparison with other studies, the seedfall traps were built so that catch area was same as for traps used by the Forest Research Institute to sample and classify seedfall (e.g. Beveridge 1964; Norton and Kelly 1988). Thus the mouth of the trap was a square yard (0.528 m to a side). The traps were made of green plastified canvas (Cambercon 7000 SS) and raised off the ground by wooden stakes at the corners. The angle between the horizontal (catch plane) and the sides of the trap was intended to be 45°, so that any seed hitting the side would not easily bounce out. However, the first 60 traps made by the contract manufacturers had a shallower angle (35°). Subsequent traps were made correctly. This inadvertent change in design necessitated switching traps between sites at a later date (see section 4.2, which also includes a photograph of the two ‘designs’).

The traps funnelled all leaf litter, fruits and flowers to the removable cup suspended at the bottom of the funnel. The cup had a diameter of 90 mm with a 2 mm stainless steel mesh circle wedged in the bottom to allow water to drain out. The cup was attached to the funnel by a pin inserted through the top of the cup and through the holding ring at the bottom of the funnel. Schematics of the design are provided in Appendix 3.5.

Positioning of seedfall traps.

Seedfall traps were placed below six individuals of each of the following large fruited species; kohekohe, karaka, puriri, taraire, and tawa (but see section 3.8.6 Remiger's Bush). Each trap was positioned midway between the drip line of the canopy and tree trunk, underneath that part of the canopy that was scored visually for phenology. Care was taken to avoid trees, or positions beneath the tree, where conspecific trees might overhang the seedfall trap.

At the beginning of the study 60 seedfall traps were available. These traps were split equally over the two initial study sites (Whitford Bush and Wenderholm Regional Park). Other sites were added as traps were manufactured and suitable sites were found (see section 3.8.1 Site selection). Six sites were set up by the end of the study, with 30 seedfall traps at each site.

Table3.2 gives the dates that seedfall trap placement was completed at each site and the dates of first sample collection.

Table 3.2: Set up dates of phenology sites

Site	Date set up	Date first collection
Whitford Bush	20 October 1994	3 November 1994
Wenderholm Regional Park	2 November 1994	16 November 1994
Loch Amber Bush	8 January 1996	22 January 1996
Robertson's Bush	23 July 1996	22 August 1996
Remiger's Bush	3 September 1996	18 September 1996
Val's Bush	1 November 1996	14 November 1996

Each trap was individually labelled with a 2-letter code (Kh = kohekohe, Kr = karaka, Pr = puriri, Tr = Taraire, Tw = tawa, Pw = pigeonwod) and a number between 1 and 6. These codes were also used to identify collection bags and subsequent samples.

Sample collection.

The first set, of 30 samples, was collected from Whitford Bush on 3 November 1994 and every fortnight thereafter. The first set of samples from Wenderholm Regional Park was collected on 16 November 1994 to coincide with the Whitford Bush collection dates and every fortnight thereafter. As further sites were set up sample collection was synchronised to coincide with sample collection at Whitford Bush and Wenderholm Regional Park.

Each fortnight the seed fall traps at all sites were emptied. Each pair of sites (pest suppressed and pests left untouched refer Table 3.1) was assigned a day of the week for collection, and this was adhered to as much as possible (e.g. Wenderholm Regional Park & Loch Amber Bush every second Tuesday). Collection of samples and phenological scoring of trees generally took about half a day per site.

Prior to the removal of the collection cup the sides of the trap were vigorously brushed down, using a stiff bristled brush, to ensure that the entire sample was in the cup. The contents of the cups were decanted into pre-labelled cloth bags, these were allowed to air-dry, analysed and weighed as soon as possible in the same week.

Categorising seedfall litter.

Samples were processed by identifying and weighing fruits and flowers according to species. Fruits (ripe, immature, fresh and predated), and flowers (larger-flowered species) were counted and weighed (including small-flowered species). The classifications are presented in table 3.3.

Seedfall collection occurred every two weeks, thus most of the fruits and flowers caught were often desiccated or past their best, however, occasionally freshly fallen material was found and this was noted as a separate category. Seeds were found in the seedfall traps after passing through vertebrate guts and these were classified as consumed. Both mature flowers and fruits were preyed on, meaning that their condition in the seedfall trap indicated that they could not be successfully pollinated or dispersed respectively. Immature fruits and flowers were also found in the seedfall traps, in either an intact or predated state. Total immature fruits/flowers include any predated immature fruits/flowers; hence predated immature fruits/flowers was not summed separately in the total number or weight of fruits or flowers caught.

Table 3.3: Classification of fruits and flowers, within species, in samples collected from seedfall traps.

Weight of fruits or flowers			
Categories			**Explanation**
Total			Sum of fresh, consumed, predated and immature total (fruits or flowers)
Sum of these categories	***Fresh***		Fruits or flowers that looked fresh
	Consumed		Fruits only, fruit flesh removed by gut passage
	Predated	Destruction of embryo, or fruit/flower unavailable for legitimate dispersers or pollinators	Damaged fruits or flowers, damaging agent noted in separate file
	Immature total	Sum of predated and unpredated immature fruits or flowers	Unripe fruits or unopened flowers
Except →		***Immature predated***	Damaged unripe fruits or damaged unopened flowers, agent noted in separate file

Number of fruits or flowers			
Categories			**Explanation**
Total			Sum of fresh, consumed, predated and immature total (fruits or flowers)
Sum of these categories	***Fresh***		Fruits or flowers that looked fresh
	Consumed		Fruits only, fruit flesh removed by gut passage
	Predated	Destruction of embryo, or fruit/flower unavailable for legitimate dispersers or pollinators	Damaged fruits or flowers, damaging agent noted in separate file
	Immature total	Sum of predated and unpredated immature fruits or flowers	Unripe fruits or unopened flowers
Except →		***Immature predated***	Damaged unripe fruits or damaged unopened flowers, agent noted in separate file

More detailed categorisation of fruits and flowers, including degrees of maturity and types of predation, for each species is provided in Appendix 3.3. Identifiable animal droppings in a trap were recorded as present per trap. All weights and sample sizes were entered directly into the computer (Microsoft Excel Macintosh version 3.2). Weighing of samples was done on a Mettler Toledo PB3002 electronic balance, weight range 0.01 g. to 3100 g. ± 0.03 g.

3.6 Mammalian seed predator numbers.

The presence of mammalian seed predators was recorded in various ways. Throughout the study the presence or absence of animal faeces in the seedfall traps was noted and faeces identified to species. Fruits and flowers were also examined for signs of predation. Generally if the bite marks were incisor-like and wider than 5 mm the damage was assigned to possums, if teeth-marks were between 5 and 2 mm than rats were deemed the culprit, and less than 2 mm was assigned to mice (refer to Chapter 7 for more detail). Often it was difficult to establish if rats or mice were the causal agent, and in that case damage was attributed to rodents. Small holes with frass protruding were assigned to insect damage. At sites where bait-stations were used to suppress pest numbers the rate of bait take was recorded, and used to infer animal abundance.

At the end of the study possums and rodents (mostly rats) were trapped to extinction in the small study sites (Whitford, Remiger’s and Robertson’s Bush), or sections of the larger sites (Wenderholm Regional Park, Loch Amber and Val’s Bush, refer to Chapter 7 for more detail). Though both possum and rodent numbers would have fluctuated throughout the study, earlier trapping was not warranted since that would have modified animal numbers, especially in the smaller study sites.

3.7 Bird counts.

Bird presence, heard or seen, was noted for every 15 min time-block while walking the route between traps, or servicing traps. During the last 6 months of this study, Sandra Anderson recorded bird presence using the distance sampling method (e.g. Cassey 1997) and five minute bird counts (as per Dawson and Bull 1975), in addition to the 15 min block count.

3.8 Site selection and description.

3.8.1 Site selection.

Lowland and coastal broadleaf podocarp forests, with a predominantly taraire canopy, were selected as study sites, since these sites contained sufficient numbers of target species. We obtained agreement from all landowners to maintain the status quo in pest control (or lack of it) for the duration of the study.

Study sites were paired, where one site had possum and rodent control while the other site had no systematic pest control; there were three such replicates (i.e. 6 sites in total). Pairs were located within the same valley and had similar aspects. It proved difficult to find sites in the greater Auckland area that did not have some measure of possum control.

Structurally, the vegetation of these forests featured an uneven canopy 15 to 30 m high with emergent podocarps, relatively simple layering, medium-sized woody lianes, tree ferns, palms and vascular epiphytes that are characteristic of New Zealand lowland mesophyll forest.

Photo 3.1: Aerial view of location and relationship of the 4 northern sites.
All sites are in or adjacent to the same river valley. Val’s and Remiger’s Bush are in the Puhoi River valley. Wenderholm Regional Park is between the Puhoi River and the Waiwera River, and Loch Amber Bush is on the ridge overlooking the Waiwera River. Val’s Bush includes most of the forest in the foreground and adjoins Arthur’s Bush at the left of the picture.

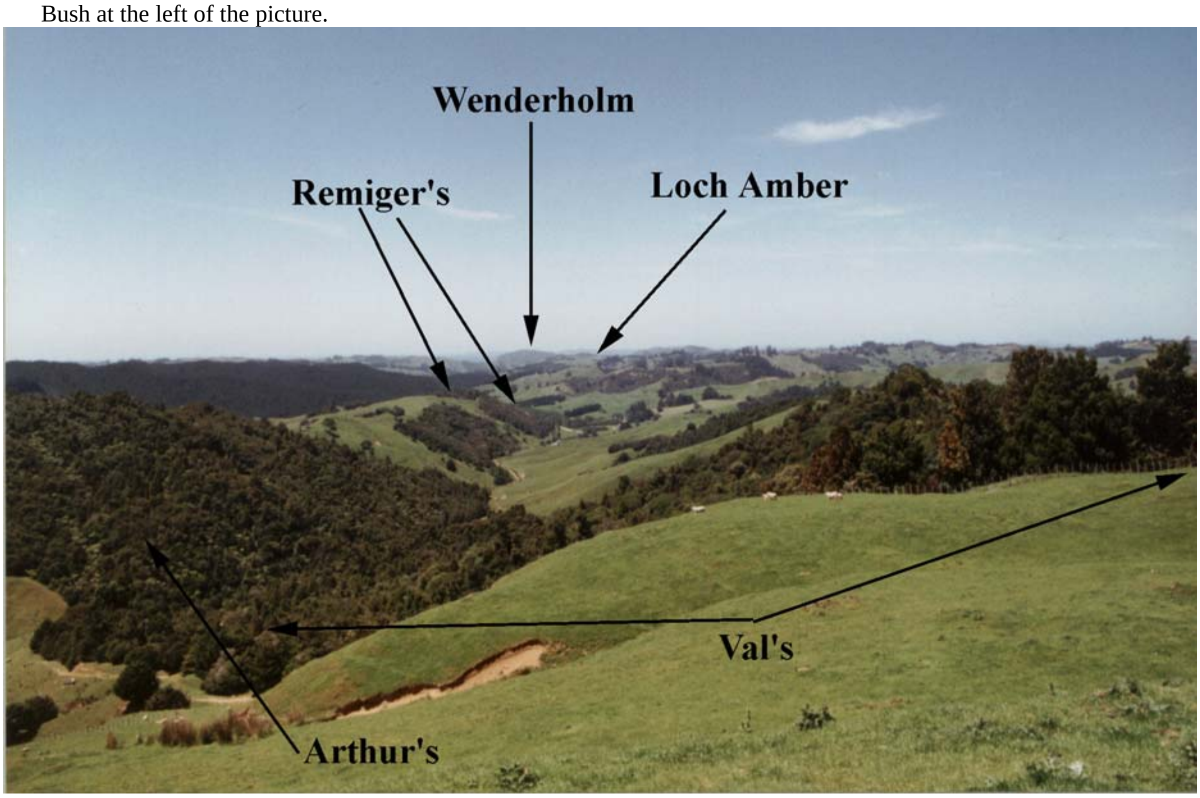
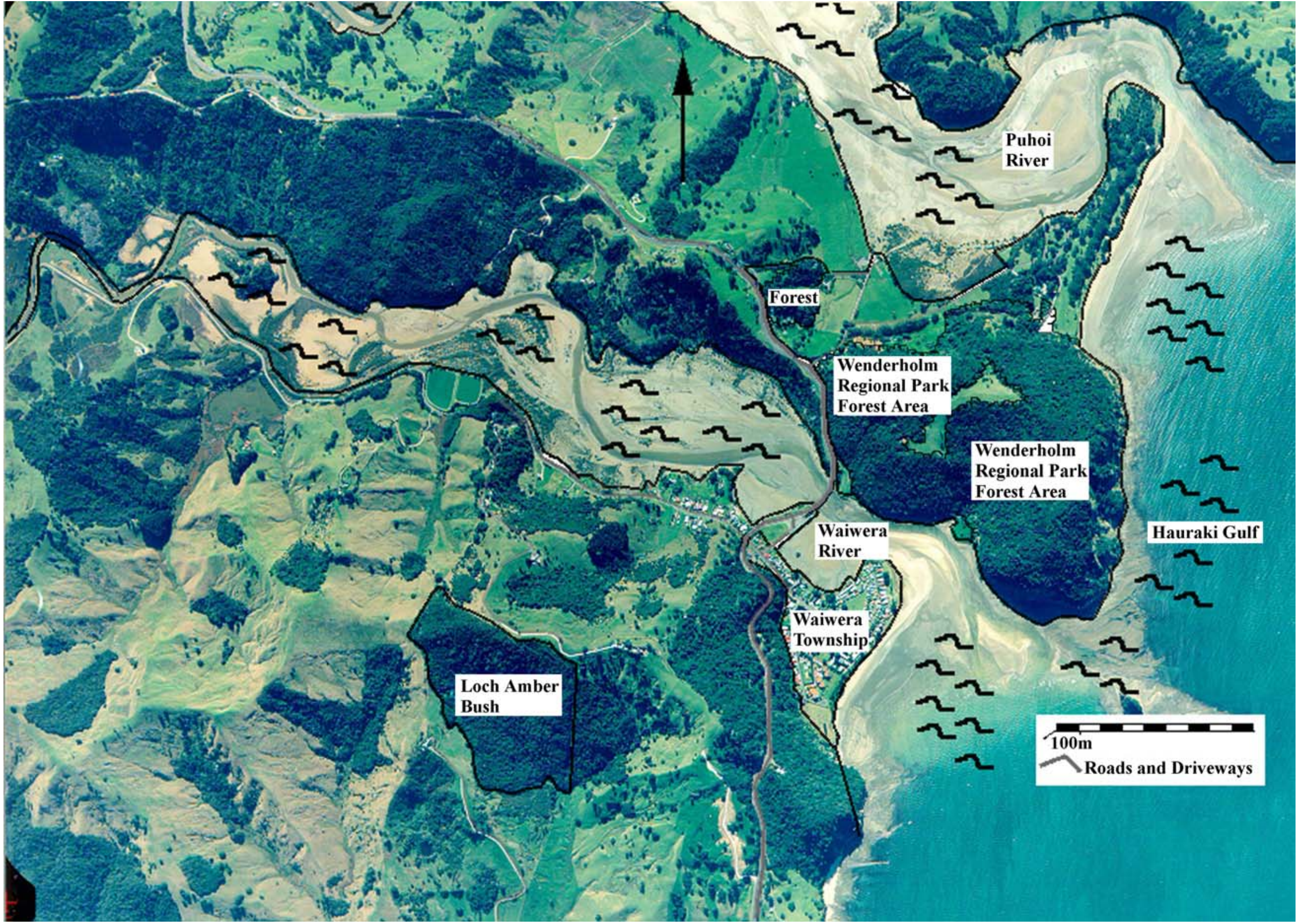


Photo 3.2: Aerial photograph showing forested headland at Wenderholm Regional Park the kohekohe patch at Wenderholm Regional Park and the non-treatment site Loch Amber Bush.

Photo 3.3: Site map of Wenderholm Regional Park and Loch Amber Bush, and their relationship to each other.



3.8.2 Wenderholm Regional Park.

Wenderholm Regional Park is one of 16 Parks administered by the Auckland Regional Council Parks Service and is 55 km north of Auckland (36°32' S lat, 174°42' E long). Wenderholm Regional Park is about 154 ha in size and includes a long sandy beach backed by a planted strip of pohutukawa (*Metrosideros excelsa*), but the dominant geographical feature is a steep forested coastal headland. The 50 ha headland achieves an altitude of 150 m above sea level. Wenderholm Regional Park is bordered to the north by the Puhoi River, to the south by Waiwera River, to the east by the Hauraki Gulf and to the west by State Highway 1. This has made pest control easier, since reinvasion (especially for possums) is generally only possible across State Highway 1, thus it is virtually an island on the mainland (commonly known as a 'mainland island' in pest control parlance, Saunders 1990). The Auckland Regional Council now manages the site as a mainland island.

The forest is predominantly coastal taraire broadleaf with an area of pasture grass on the main ridge, and on the river flats between the headland and the Puhoi River. Dominant trees include taraire, pohutukawa, puriri, and tawa. Tawapou was common along some bluffs. Other common species are karaka, kowhai (*Sophora microphylla*), nikau (*Rhopalostylis sapida*), rewarewa (*Knightia excelsa*) and kohekohe. There are patches of secondary kanuka (*Kunzea ericoides*) forest and scattered podocarps (Bell 1996; Greene 1994). Wenderholm Regional Park has one female miro (*Prumnopitys ferruginea*) and one non-fruiting male miro. Kahikatea (*Darcycarpus dacrydioides*) are clustered below the knoll that has the majority of mature kohekohe while titoki (*Alectryon excelsus*), pukatea (*Laurelia novae-zelandiae*), and totara (*Podocarpus totara*) are occasional throughout the forest. Pigeonwood (*Hedycarya arborea*) is scarce and no mangeao (*Litsea calicaris*) could be located.

Wenderholm Regional Park was selected because pest control was guaranteed to continue and access posed no problems. Possum control at Wenderholm Regional Park was begun in 1987 (Wotherspoon 1994) and staff at Wenderholm Regional Park arranged for annual cyanide poisoning or trapping of possums during winter. Rodent control began in 1992/93 and used Novacoil tunnels in a 50 x 100 m grid on the forest headland. Bait type was changed annually to reduce bait-shyness, and varied between Shell Agricultural 'Storm Rodenticide' one year and Talon 50WB the following.

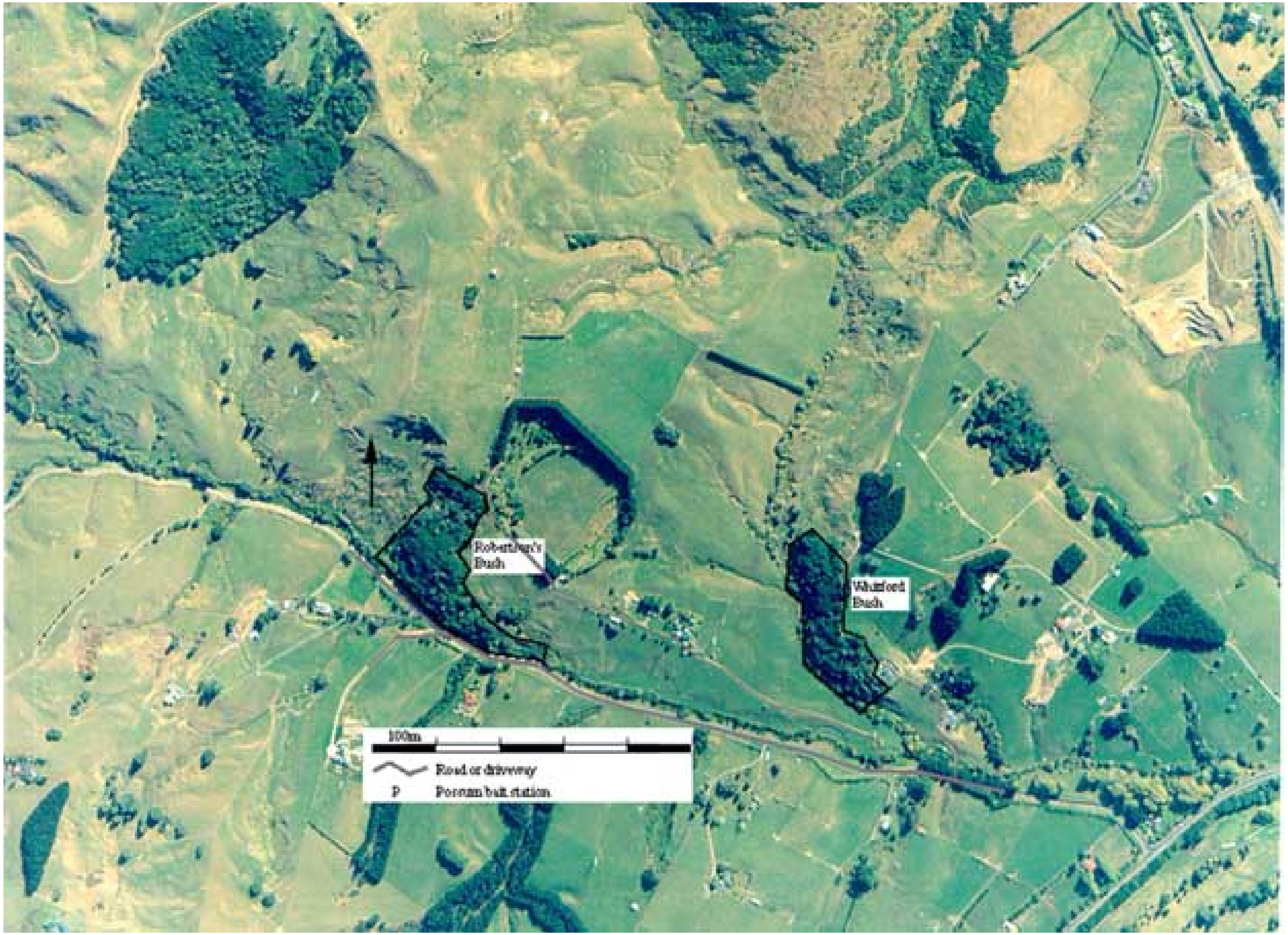
3.8.3 Loch Amber Bush.

This 16 ha site (36°33' S lat, 174°42' E long, paired with Wenderholm Regional Park) is privately owned and no possum or rodent control was undertaken. The site was also accessible to cattle and occasionally feral goats were sighted. The forest was not in good condition due to browse at various levels. Seedfall traps were first emptied at Loch Amber Bush on 22 January 1996.

Loch Amber Bush was chosen because it is close to Wenderholm Regional Park (about 2 km) and is of a similar forest type. It straddles the ridge of the Waiwera River valley while Wenderholm Regional Park abuts the Waiwera River. Most importantly, the site did not have any pest control, the owner was willing to forgo pest control for the duration of the study and thus this site could be used as a comparison for Wenderholm Regional Park. It was agreed to assist with reducing pest numbers upon completion of the study. Access was easy, either through the property of the owner, or via the access road of neighbours.

The forest at Loch Amber Bush does not contain some of the coastal components seen at Wenderholm Regional Park, such as, ngaio (*Myoporum laetum*), whau (*Entelea arborescens*), tawapou and pohutukawa, but has northern rata (*Metrosideros robusta*) instead. It contained a wider range of podocarp species than Wenderholm Regional Park. In addition to those found at Wenderholm Regional Park this site had matai (*Prumnopitys taxifolia*), kauri (*Agathis australis*), and celery pine (*Phyllocladus trichomanoides*). Taraire was the predominant canopy with puriri, kowhai, tawa, supplejack (*Ripogonum scandens*), nikau, rewarewa and kohekohe throughout. Titoki was common on the main ridge, pukatea in some of the gullies. Many species, including most of the podocarps, seemed to be confined to particular patches or ridges. Mangeao could not be found, but white maire (*Nestegis lanceolata*) and three hard beech trees (*Nothofagus truncata*) were noted.

Photo 3.4: Site map of Whitford Bush and Robertson's Bush and their relation to each other.



3.8.4 Whitford Bush.

This was a small (2 ha) privately owned site on the rural outskirts south of Auckland (36°56’ S lat, 174°56’ E long). The forest was located on a southeast-facing moderate to steep slope. The canopy varied from old growth kanuka forest at the northeastern end to kohekohe dominant at the southwestern end with taraire, puriri, tawa, and rewarewa throughout. The forest also contained karaka, nikau, kahikatea, pigeonwood, supplejack, the occasional titoki, pukatea and totara, and various smaller-fruited understorey species. Due to the small size of the site, scarcely more than half a dozen of each species were available to sample. The site had no mangeao or tawapou and only two male (non-fruiting) miro trees.

The forest was in good condition with little sign of possum or rodent browse and only infrequent ground browsing mammal damage (an occasional escaped deer from the neighbours and the occasional rabbit). The understorey was rather sparse because stock had access to the forest up until about 3 years before the study.

Whitford Bush was selected because pest control had already been initiated, was guaranteed to continue, and access posed no problems. The owner had placed bait-stations in trees throughout the patch and had been filling these stations with Talon® cereal or Pindone pellets (for more detailed description of toxins refer to Appendix 3.4). At the beginning of the phenological study, bait supply was increased to ensure that all possums were eradicated from the forest. Subsequent to that, bait-stations were filled when possum sign was noted. This method of control was continued for the duration of the study.

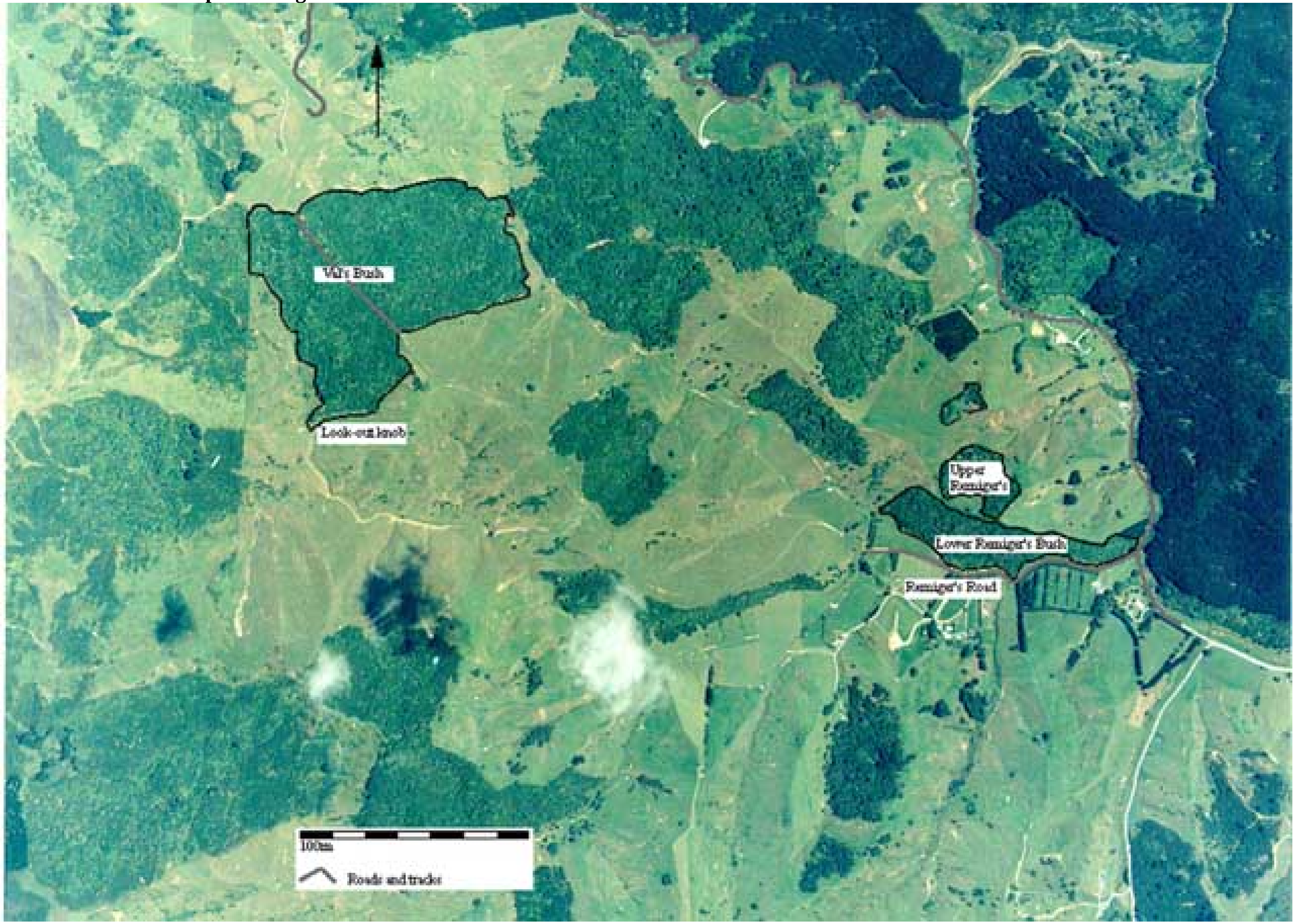
Ground-based rodent bait-tunnels were installed along two lines within the site. These tunnels were 600 mm lengths of Novacoil, staked to the ground by wire, in which 4 Talon 50WB baits were placed once a month. As bait take reduced, the tunnels were stocked less frequently.

3.8.5 Robertson’s Bush.

Forest remnants in the Whitford area, that had the required tree species, but no possum control, were rare. Eventually, the neighbours to the Whitford block were approached and permission obtained to use Robertson's Bush (36°57’ S lat, 174°56’ E long). This small (2 ha) privately owned bush remnant is less than 1 km from the Whitford site, and did not have regular mammal control. The owners were willing to forgo pest control for the duration of the study, provided pests were eradicated at the end of the study. Robertson’s Bush has a similar range of plant species to Whitford Bush, is on the same side of the valley with a similar aspect and slope and has year-round easy access.

The dominant canopy was taraire. Mature kohekohe was clustered at the north end of the site. Puriri, tawa, rewarewa and nikau could be found throughout, but mature karaka was rare. Supplejack and kaikomako (*Pennantia corymbosa*) was found in patches. No mangeao or tawapou was found, only two non-fruiting miro were seen and totara was occasional. The forest has been fenced since 1973 and stock kept out, this has resulted in dense nikau regrowth in places. The forest is in generally good condition, with some possum browse in the upper canopy.

Photo 3.5: Site map of Remiger's Bush and Val's Bush and their relation to each other



3.8.6 Remiger’s Bush.

Remiger’s bush was located inland from Wenderholm Regional Park, 9.5 km up the Puhoi River valley. The forest was in two parts, the larger part situated on a steep east-facing slope adjacent to Remiger’s Road (36°30’ S lat, 174°38 E long), while the smaller 3.5 ha remnant, used in this study was on the flat at the top of the slope. Both blocks have been gifted to the Department of Conservation, and the previous owner intermittently controlled possums using bait-stations in the lower block and by shooting in the upper block.

This small upper block was chosen because it was at the same latitude as the Wenderholm-Loch Amber pair, it would match Val’s Bush for location and it was small enough that pest suppression could be undertaken on a limited budget. The larger block of Remiger’s Bush was too steep to provide year round access. The site was not ideal in that no tawa and only 5 karaka trees could be located during the initial survey. Later, another karaka and one tawa were located and were included in the phenology observations. In other respects the forest was similar to previously described forests, being dominated by taraire, with puriri, kohekohe, rewarewa, nikau, and supplejack in the canopy and totara, two northern rata, pukatea, and kahikatea as emergents. There were a large number of pigeonwood trees and various small-fruited *Coprosma* shrubs. No tawapou, mangeao or miro was located.

The lack of adequate numbers of tawa and karaka meant that there were 7 ‘additional’ traps that had to be reassigned to species not used in other sites in order to maintain 30 traps per site. Just prior to setting up it became apparent that kohekohe was dioecious (pers. comm. J. Braggins, Braggins *et al.* 1999), and not monoecious as was generally assumed (e.g Allan 1961); female trees carry significant quantities of fruit and have sterile anthers, whereas male trees have pollen loaded anthers and can carry small quantities of fruit (Braggins *et al.* 1999). Therefore the opportunity was taken to assign 4 traps to male and 4 traps to female kohekohe to enable comparison between sexes. Usually only 6 traps were used for kohekohe, without selecting for the sex of the tree.

The remaining 5 traps were placed beneath pigeonwood trees, though 4 of the 5 proved to be male once flowering started. The forest had been fenced and stock kept out since 1983. There was copious nikau regeneration in light gaps, and the canopy was generally in good condition. The pest control history of this site was somewhat unusual, and only possum numbers were systematically controlled (refer to section 7.2 for further details).

3.8.7 Val’s Bush.

The matching site for Remiger’s bush was the 36 ha Val’s bush (36°30’ S lat, 174°36 E long) at the top of the Puhoi River valley, 3.5 km further inland from Remiger’s Bush, and 12 km inland from Wenderholm Regional Park. This forest is part of two contiguous conservation covenanted (Queen Elizabeth II Trust) blocks, situated at the end of J. Tolhopf Road. The east-facing block was used in order to maintain aspect similarity with Wenderholm Regional Park and Remiger’s Bush. The forest was fenced and stock excluded although feral goats sometimes encroach into parts of the forest. Possum and rodent control was non-existent, though during July and August 1997 spotlight hunting on the perimeter of adjacent forest destroyed more than 400 possums, including 44 in one night. It is not certain what effect that would have had on possum densities in Val’s Bush (refer section 7.2).

The forest was primarily taraire, with puriri, tawa, nikau, and rewarewa in the canopy. Mature kohekohe was restricted to a steep valley in the upper part of the forest, and karaka was mostly found (planted?) around two prominent spurs. Several species of podocarp were present as canopy or emergent species, including totara, kahikatea, rimu (*Dacrydium cupressinum*) and miro, and there was evidence of kauri (*Agathis australis*) logging in the past. This site was particularly rich in *Metrosideros* species, including emergent northern rata, orange rata (*M. fulgens*), common white rata (*M. perforata*), diffuse white rata (*M. diffusa*) and the relatively rare carmine rata (*M. carminea*). No tawapou or mangeao could be found. Access was good, though the sampling route had to be located to avoid the steepest parts. The canopy showed signs of possum browse, and parts of the forest understorey were noticeably grazed by goats.

[2]

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[2] Seedfall traps used throughout the study. Two ‘types’ were used. The trap on the left has the collection cup attached.

Chapter 4 Validation of site selection and methods

4.1 Plant species similarity between sites.

Visually the six study sites appeared to have similar tree species composition. To more accurately compare species composition a limited Point Centred Quarter (PCQ) survey of each site was undertaken. Random numbers were generated for each site with minimum distances between points of 10 paces for small sites and 50 paces for large sites. At least 10 PCQ points were located in each site. Pace length was measured and found to be on average 0.75 m per step. Transects followed the route taken to clear the seedfall traps, since that was where the species and individual trees were observed during this study. Once a point was located the nearest tree in each of the 4 quarters was identified, and the distance to it was measured with a tape measure from the centre point.

4.1.1 Results

The small size of some of the forest fragments (i.e. Whitford, Remiger's and Robertson's Bush), and the near random route taken, restricted the number of PCQ points that could be located without sampling the same trees repeatedly. Therefore, the resulting data set is perhaps not as robust as preferred (refer to Table 4.1).

For instance, some species that were important components of the forest (e.g. puriri at Loch Amber and Val's Bush) were not sampled during the survey, whilst other species were sampled in excess to their presence in the forest (e.g. 2 of the 3 titoki at Whitford Bush). The PCQ data are summarised in Table 4.1, presenting the number of trees of each species that were sampled during the survey, the average diameter for each species and standard error of the mean for the diameter (for 2 or more trees). Those species that were present at a site but were not sampled are indicated by an asterisk '*'.

However, it is possible to obtain some idea of similarity (or lack of) between the sites by using a similarity coefficient such as the Czekanowski similarity coefficient. Complete similarity will be indicated by a score of 1 and complete dissimilarity by a score of 0 (Kent and Coker 1996). Similarity coefficient values around 0.7 can be expected for presence/absence data when re-sampling the same site and a coefficient of around 0.6 when using species proportion data. Any values greater than these indicate good similarity in species composition between pairs of sites, (J. Ogden pers. comm.).

The Czekanowski coefficient is calculated as follows:

$$\mathrm{S_c} = \frac{2\sum_{i=1}^{m}\min(X_i, Y_i)}{\sum_{i=1}^{m}X_i + \sum_{i=1}^{m}Y_i}$$

Where: Xi and Yi = the abundances of species I, from site X and Y respectively

=the sum of the lesser scores of species I where it occurs at both sites

m =the number of species

(Kent and Coker 1996)

The Czekanowski similarity coefficient was calculated between pairs of sites, either from presence absence data, or species proportion data (e.g. # trees spp A/total trees at site), to determine how similar those sites were. An arbitrary value of 0.5 was assigned to those species known to be present at a site, but not sampled during the PCQ survey. The results are presented in Table 4.2. Values for *a priori* paired sites (sites set up as matched pairs of pest suppression versus no poisoning) are in bold font.

Table 4.1: Summary of species found during Point Centred Quarters surveys at each site

	Canopy trees																	
Site	Wenderholm			Loch Amber			Whitford			Robertson's			Remiger's			Val's		
Species[4]	Count[1]	dbh (cm)[2]	Std err[3]	count	dbh (cm)	Std err	count	dbh (cm)	Std err	count	dbh (cm)	Std err	Count	dbh (cm)	Std err	count	dbh (cm)	Std err
Hawthorn							1	27.30		*								
Kahikatea	*			1	0.80		4	51.68	8.75	3	36.43	3.17	1	91.10		3	17.47	7.07
Kanuka	14	19.85	3.51	8	23.45	4.38	*			1	11.80							
Karaka	14	28.62	4.51	2	29.10	0.28	3	37.13	14.42	2	31.85	7.85	1	40.10		*		
Kohekohe	1	38.90		2	20.85	18.31	14	23.31	3.17	2	13.35	5.02	4	15.35	4.31	2	33.60	14.99
Kowhai	24	21.41	3.74	7	14.16	4.03												
Lacebark				2	18.55	4.17												
Lemonwood	1	28.90																
Northern rata				*									*			1	146.50	
Maire				3	10.23	0.47	1	13.10					*			1	36.70	
Ngaio	1	43.50																
Pigeonwood							1	20.30					1	17.30		3	14.83	3.33
Pohutukawa	1	46.10																
Pukatea	*			*			1	58.90		*			*			*		
Puriri	6	63.36	13.77	*			3	87.20	0.56	2	53.40	31.68	3	57.00	26.71	*		
Rewarewa	1	21.80		1	9.80		1	26.80		1	51.00		2	31.90	4.81	2	35.00	3.68
Rimu				1	11.00					2	63.65	14.64	1	74.30		*		
Taraire	9	25.09	3.94	10	23.25	3.38	3	57.10	6.86	4	36.60	10.38	11	31.02	3.24	14	29.58	3.59
Tawa	1	29.00		1	17.50		2	38.75	8.27	*			(1*)			*		
Tawapou	1	3.70																
Titoki	1			*			2	50.10	18.53									
Totara	1	10.20		*			*			*			2	19.70	1.13	2	35.45	34.86
	Sub-canopy or shrubs																	
Cabbage tree	6	13.68	3.83	2	3.35	3.04							*					
Coprosma	16	5.26	1.83	5	39.08	8.22	*			*			2	3.50	0.28	*		
Hangehange	2	3.10	3.26				*			*			1	4.50		*		
Kaikomako										6	16.35	3.64						
Lancewood	*			*			*						*			1	5.60	
Mapou	9	3.43	0.71	2	18.95	0.49	1	9.20		1	13.30		*			*		
Nikau	13	16.05	0.70	11	16.47	1.00	15	15.61	0.43	8	16.85	0.79	14	16.05	0.65	33	16.24	0.32
Putaputaweta							2	13.15	5.02							2	18.80	9.76
Milk tree	*			1	10.40													
Wharangi	1	1.50		*														
Whau	2	4.20	0.99															
Whiteywood	10	8.54	1.84	1	13.80		6	18.62	3.47	12	18.97	4.88	6	8.55	3.31	*		
Wineberry	*												1	5.50				

[1]Count = total in sample, [2]dbh = average diameter at breast height, [3]Std err = standard error of the mean dbh, * = present at site but not picked up in sample. [4]Latin names provided in Appendix 4.1.

Table 4.2: Czekanowski similarity coefficients for species composition for all sites.
The upper part of the table was generated using presence-absence data, and the lower half of the table using species proportion data. Values for *a priori* paired sites (pests suppressed, no poisoning) are in bold font.

	Site	Wenderholm	Loch Amber	Whitford	Robertson's	Remiger's	Val's
Site	Pest regime	Pest suppressed	No poisoning	Pest suppressed	No poisoning	Pest suppressed	No poisoning
Wenderholm	Pest suppressed		**0.78**	0.71	0.67	0.71	0.64
Loch Amber	No poisoning	**0.63**		0.76	0.67	0.80	0.77
Whitford	Pest suppressed	0.39	0.43		**0.77**	0.81	0.88
Robertson's	No poisoning	0.42	0.51	**0.59**		0.74	0.72
Remiger's	Pest suppressed	0.41	0.56	0.65	0.58		**0.93**
Val's	No poisoning	0.24	0.48	0.64	0.42	**0.68**	

Presence absence data >0.7 =good similarity

Species proportion data >0.6 =good similarity

All of the sites pairs have exceeded 0.7 with the similarity coefficient for presence/absence data (top right quadrant of Table 4.2) and all but one site have exceeded 0.6 for the species proportion data (lower left quadrant of Table 4.2) indication good similarity in the species found at those sites. Even the Robertson's Bush –Whitford Bush pairing for species proportion data gives a reasonable degree of similarity. Furthermore, many of the sites, even if they were not *a priori* pairs, have similarity coefficients greater than 0.7 for presence/absence data or 0.6 for species proportion data, indicating that most sites have similar vegetation types.

4.1.2 Effect on further work

These data show that with regards to forest composition the sites are very similar, thus any differences in fruit production will largely be due to factors other than species composition. These factors could include the control of pest species and environmental factors such as aspect, latitude, distance from the coast, soil substrate, etc.

4.2 Switching traps at Wenderholm Regional Park.

As mentioned in 3.5.5 the seedfall traps used were of two slightly different designs due to manufacturer's error (Photo 4.1). There was some concern that the shallow trap (the earlier design) might catch less fruits, flowers and leaf litter than the deeper design. To test this deep traps were set up immediately adjacent to shallow designs (Photo 4.1) at Whitford Bush and the quantities caught by both traps were compared over the next 5 collection periods (7 March 1996 to 2 May 1996).

4.2.1 Results.

Data were combined into totals for three categories per trap type; weight of leaves caught, weight of fleshy fruits caught and number of fleshy fruits caught. The totals were compared for the two trap designs by sampling week. The shallow traps were designated as the expected values (Table 4.3) , but analysis with deep traps as expected values yields the same results. The Chi-square value for some of these pair-wise comparisons gave a significant result: $P(\chi^2>3.841)_{1d.f} < 0.05$. A summary of the results is presented in Table 4.3. Values significantly greater than the critical value are indicated by '*'.

Photo 4.1: The two trap 'designs'.
The new deeper version (without the cup) on the right and the shallow version on the left (with cup attached).

Table 4.3: Summary of Chi-square comparisons between trap designs for bulked samples.

Date	07-Mar-96	22-Mar-96	05-Apr-96	17-Apr-96	02-May-96	Average difference ± Std error.
Weight leaves shallow	263.01	144.77	350.21	118.68	173.75	
Weight leaves deep	278.5	167.57	440.3	138.27	229.51	
Difference (deep-shallow)	15.49	22.8	90.09	19.59	55.76	
Chi square	0.91	**3.59 ***	**23.18 ***	3.23	**17.89 ***	
Percentage difference (shallow/deep)	5.56	13.61	20.46	14.17	24.30	15.62 ± 3.59
Weight fleshy fruits shallow	76.34	17.78	24.09	13.74	11.51	
Weight fleshy fruits deep	105.68	18.99	28.06	10.67	23.44	
Difference (deep-shallow)	29.34	1.21	3.97	-3.07	11.93	
Chi square	**11.28***	0.08	0.65	0.69	**12.37***	
Percentage difference (shallow/deep)	27.76	6.37	14.15	-28.77	50.90	14.08 ± 14.66
Number fleshy fruits shallow	152	78	63	61	42	
Number fleshy fruits deep	272	106	90	91	46	
Difference (deep-shallow)	120	28	27	30	4	
Chi square	**94.74***	**10.05***	**11.57***	**14.75***	0.38	
Percentage difference (shallow/deep)	44.12	26.42	30.00	32.97	8.70	28.44 ± 6.44

For most weeks the deep traps caught more leaves (by weight) and fruits (by number) than the shallow traps and about half the time the total 'weight fleshy fruits' was greater for deep traps. This difference amounts to about 14% to 28% of the total material caught. Other data (not shown) indicated that differences in catch rates appeared to be most marked when species were producing large fruit crops. Thus the trap design was contributing to different catch rates.

4.2.2 Conclusion.

The change in trap design did affect the amount of material caught. Unfortunately, we did not have the resources to purchase an additional 60 seedfall traps to replace the ‘shallow design’. At this stage both Whitford Bush and Wenderholm Regional Park were set up with shallow traps, whilst Loch Amber Bush had the deep traps. There were 120 deep traps available and only 60 shallow traps. The decision was therefore made to replace the shallow traps at Wenderholm Regional Park with deep traps so that the four northern sites (Wenderholm Regional Park, Loch Amber, Remiger’s and Val’s Bush) had the same deep trap designs, while the two southern sites (Whitford and Robertson’s Bush) could be compared using the shallow traps. The shallow traps were replaced with deep seedfall traps at Wenderholm Regional Park on 15 May 1996.

4.2.3 Effect on further work

The above analysis did not distinguish between the trapability of particular species by the different ‘trap designs’. Chapter 5 tests for character displacement of fruit phenology, including amplitude of fruit production, using data from the seedfall traps. Therefore, it was important to ascertain whether any adjustments to the data, for the focus species, were required to compensate for the changing ‘trap design’.

At the conclusion of the study, analysis of variance of number of fruits to fall into traps before (41 sampling periods) and after (45 sampling periods) the trap switch at Wenderholm Regional Park showed that there was no significant difference in number of puriri, karaka, kohekohe or tawa fruits caught, although fewer fruits were caught post-switch for some of these species (Table 4.4). Significantly more taraire (F=16.71, P<0.0001, df=2548) and nikau (*Rhopalostylis sapida* F=20.49, P<0.0001, df=2548) fruits were caught after the switch (refer to Table 4.4). An analysis of variance over the same 5-week period for the three sample years also did not reveal any differences.

It is unclear whether these differences (significant or not) were due to the change in trap design or due to annual and intra-annual variation in fruit production. Given the lack of significant change for most species, it is probably reasonable to assume that trap design did not affect numbers of fruits caught to such an extent that it significantly masked seasonal variability. Hence, the change in trap design will be ignored in the analysis of periodicity.

Table 4.4: Average number of fruits from focus species per seedfall traps per sampling occasion before and after trap switch at Wenderholm Regional Park.

	Mean ± Standard error	
Species	**Before switch**	**After switch**
Karaka	0.173±0.047	0.161±0.055
Kohekohe	0.918±0.444	0.389±0.113
Nikau	0.324±0.043	0.733±0.076
Puriri	0.465±0.057	0.403±0.047
Taraire	0.048±0.009	0.162±0.025
Tawa	0.018±0.006	0.012±0.004

4.3 Comparison between methods.

This study used four different methods to assess the phenological state of the species of interest. This section compares three of those methods; mature fruits in seedfall traps, maturity scale and counts of ripe fruits per cubic metre (referred to as seedfall, maturity and counts respectively hereafter). Groundfall, the fourth method, was used more as a warning for the presence of cryptic or rare fruits than a quantitative measure.

Comparisons were made for two reasons. It was known (as mentioned in 3.3.4) that seedfall traps can lag behind the phenology observed in the tree, and this lag period would affect further analysis. It would also be useful to know how the various methods relate to each other and whether one method was more ‘representative’ of the phenology than the other methods.

4.3.1 Method.

Various sets of data from Wenderholm Regional Park (a site with a long sequence and minimum fruit predation) were combined in Excel (Excel 97 SR-1 © 1985-1997 Microsoft Corporation) and pair-wise combinations plotted as paired x-y plots. A linear regression was fitted to each plot and the R^2 value and regression equation noted. One of the variables was then advanced or delayed in time with respect to the other variable, and the new R^2 value and regression equation was noted. This method was repeated to a maximum of 5 sampling period lags (5 fortnights) or maximum advance of 2 sampling periods (2 fortnights).

The R^2 values for various comparisons are shown in Figure 4.1, and maximum R^2 values and associated regression equations are given in Tables 4.5 and 4.6. The largest R^2 values indicated the best linear fit for those two variables, and also indicated what lag period occurred between that pair of variables (see Figure 4.1). Once the lag period for each pair of variables was determined the correlation function of Excel was used to calculate the correlation coefficient between the variables. Those correlations are also presented in Tables 4.5 and 4.6.

4.3.2 Results.

Various mathematical transformations were tried, including forcing the linear regression through zero (since at zero counts one could expect zero fruits in the seedfall traps) and plotting the variables after log+1 transformations, but the best fit proved to be the untransformed data without forcing the regression through zero. Initially, comparisons were made between average amount of fruits per trap per week and average counts of ripe fruits per tree per week for the five main species. These comparisons are called ‘site averages’ on the graphs (Fig 4.1) and are presented in Table 4.5.

e.g. Site average for week 10
total amount of karaka fruit in seedfall traps plotted versus total number of ripe fruit counted in karaka trees
30 (seedfall traps) 10 (phenology trees)

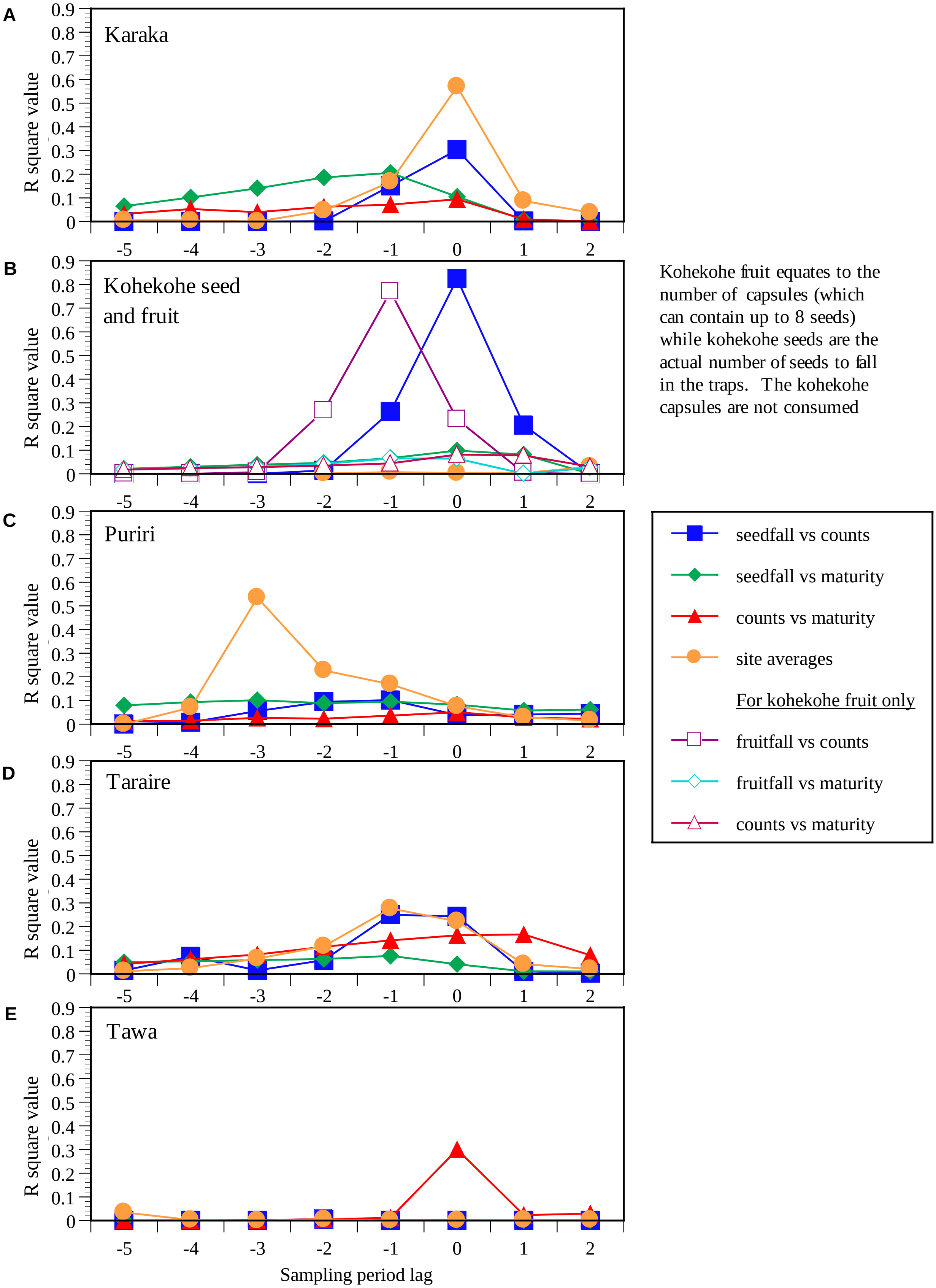
Table 4.5: Comparisons of average seedfall numbers versus counts per cubic metre.
The lag period at which maximal R^2 was achieved is presented with associated regression equations for linear relationships between these two methods. The correlation of the two variables at this lag is significant (*) if it exceeds 0.217 (p=0.05, df>80).

Species	comparison	Method 1		Method 2	by	R^2	Linear equation	Correlation
karaka	site averages	seedfall	lags	counts	0	0.5698	y = 0.0924x + 0.0933	0.754852*
kohekohe seed	site averages	seedfall	lags	counts	-1	0.0076	y = 0.0009x + 0.0072	0.087293
puriri	site averages	seedfall	lags	counts	-3	0.5346	y = 0.1078x + 0.2027	0.731176*
taraire	site averages	seedfall	lags	counts	-1	0.2762	y = 0.0839x + 0.0636	0.525515*
tawa	site averages	seedfall	lags	counts	-2	0.0049	y = 0.0156x + 0.0129	0.069932

Statistically it is necessary to differentiate between fruits caught in traps that were deliberately placed beneath a species, and fruits caught accidentally by other traps (e.g. karaka fruits caught in a trap under a karaka tree is deliberate, but caught in a kohekohe trap is accidental). The analysis of averages uses mixed data, some deliberate catches and some accidental catches, but also mixed phenology data where some trees have seedfall traps placed beneath them, while other don’t. To avoid this problem the data were further analysed by comparing the performance of specific traps (hereafter referred to as target traps) with the tree under which it was placed (hereafter called target tree). These comparisons were made between the three different methods (seedfall, maturity and counts) for each target species. Results are presented in Table 4.5 and Figure 4.1.

e.g. Individual tree for week 10
total amount of karaka fruit in seedfall trap Kr1 plotted versus total number of ripe fruit counted in karaka 1

Figure 4.1: R-square values from linear correlations between various phenology methods to determine the degree of lag between methods. Comparisons were between individual trees and their target traps, except for the site averages, which compare number of fruits per cubic metre for all 10 phenology trees for each species with the average number of fruits for each species over all 30 traps.



Kohekohe fruit equates to the number of capsules (which can contain up to 8 seeds) while kohekohe seeds are the actual number of seeds to fall in the traps. The kohekohe capsules are not consumed

Table 4.6: Comparisons of different phenological methods for individual trees with target traps. The lag period at which maximal R^2 was achieved is presented with associated regression equations for linear relationships between these two methods. The correlation of the two variables at this lag is significant (*) if it exceeds 0.321 (p=0.001, df>100).

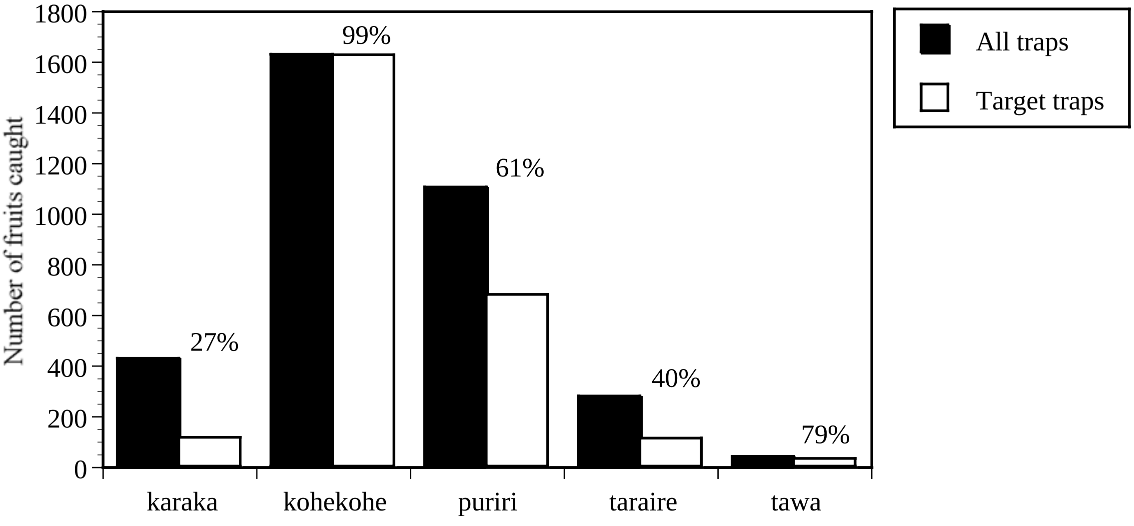
Species	comparison	Method 1		Method 2	by	R^2	Linear equation	Correlation
karaka	individual trees	seedfall	lags	counts	0	0.303	y = 0.4939x - 0.0013	0.550458*
karaka	individual trees	seedfall	lags	maturity	-1	0.2055	y = 0.1188x + 0.3212	0.453313*
karaka	individual trees	counts	lags	maturity	0	0.0943	y = 0.0903x + 0.3667	0.307155
kohekohe fruit (1)	individual trees	seedfall	lags	counts	-1	0.77	y = 1.1749x + 0.1148	0.877503*
kohekohe fruit	individual trees	seedfall	lags	maturity	-1	0.0649	y = 0.0662x + 1.5486	0.254936
kohekohe fruit	individual trees	counts	lags	maturity	0	0.0813	y = 0.0553x + 1.5457	0.285197
kohekohe seed(2)	individual trees	seedfall	lags	counts	0	0.8241	y = 3.4415x - 0.0376	0.907797*
kohekohe seed	individual trees	seedfall	lags	maturity	0	0.0984	y = 0.1636x + 1.5299	0.313618
kohekohe seed	individual trees	counts	lags	maturity		As for kohekohe fruit		
puriri	individual trees	seedfall	lags	counts	-1	0.1021	y = 3.6514x + 1.1094	0.509821*
puriri	individual trees	seedfall	lags	maturity	-3	0.1012	y = 0.2402x + 1.6285	0.317413
puriri	individual trees	counts	lags	maturity	0	0.0506	y = 0.0204x + 1.7468	0.351868*
taraire	individual trees	seedfall	lags	counts	-1	0.2497	y = 0.3639x + 0.4372	0.499619*
taraire	individual trees	seedfall	lags	maturity	-1	0.0759	y = 0.0809x + 1.0402	0.275221
taraire	individual trees	counts	precedes	maturity	1	0.1665	y = 0.2189x + 0.9646	0.40809*
tawa	individual trees	seedfall	lags	counts	-2	0.006	y = 0.0123x + 0.0146	0.077101
tawa	individual trees	seedfall	lags	maturity	-2	0.0047	y = 0.0774x + 0.3104	0.068783
tawa	individual trees	counts	lags	maturity	0	0.3001	y = 3.5941x + 0.1611	0.547774*

(1) Kohekohe fruit equates to the number of capsules (which can contain up to 8 seeds), (2) kohekohe seed are the actual seeds to fall in the traps.

For three of the species (karaka, puriri, and taraire) 'site averages' produced the largest R^2 values and significant correlation coefficients of any of the analysis. This was probably attributable to the distribution of the species within the park and the fruit production over the duration of the study.

These three species have a fairly 'even' spread through the mature forest and thus have a higher chance of fruit fall in an 'accidental' manner than kohekohe, which was more clumped with the largest proportion of mature trees on the knoll behind the rangers house (indicated in photos 3.2 and 3.3). This can be partially seen from Figure 4.2 since only 27% of karaka, 40% of taraire and 61% of puriri fruits were caught by target karaka, taraire and puriri traps respectively, whereas 99% of kohekohe fruits were caught by kohekohe traps. Tawa was also reasonably 'evenly' spread through the forest, but fruit production was so low for the duration of the study (39 fruits total, 31 of which fell in target traps) that no meaningful analysis was possible.

Figure 4.2: Number of target fruits caught in all and in target traps at Wenderholm Regional Park.



For the individual pair-wise comparisons, seedfall traps most commonly lag behind counts per cubic metre by a sample period (kohekohe fruit, puriri and taraire; Figures 4.1 B, C and D) but karaka (Figure 4.1 A) and kohekohe seed (Figure 4.1 B) did not lag. For karaka and kohekohe these patterns could reflect rates of consumption and dispersal. Kereru (*Hemiphaga novaeseelandiae*) does not seem to favour karaka (kereru was the only consumer able to consume the fruits) and most fruits fell directly below the tree, including the trap, without being consumed and/or dispersed. Thus, when there was ripe fruit to count in the tree there was a good probability that there were also mature fruits in the trap.

Kohekohe (Figure 4.1 B), on the other hand, was very much favoured by birds (kohekohe was also taken by tui (*Prosthemadera novaseelandiae*) and blackbirds (*Turdus merula*)) and it was rare to find fresh uneaten fruits in the traps or in the tree. Ripe fruit was scored as open capsules (whether they still contained fruits or not). So, there was a good probability that when large numbers of capsules were ripe (i.e. open) the seedfall traps contained a lot of consumed mature seeds. The ripe capsules fell from the tree not long after opening (a week or two), thus producing the lag between ripe fruit counts and seedfall counts for ‘fruits’.

Rates of consumption and dispersal are harder to apply to taraire (Figure 4.1 D). Mature uneaten fruits appeared in seedfall traps one or more sampling periods earlier than consumed fruits; a similar lag to the comparison between counts and seedfall. Perhaps the earliest fruits were misclassified as ripe, in the cubic metre counts, while it was not quite ripe (i.e. kereru did not consider the fruits palatable yet). Or perhaps there was a degree of overlap with a more preferred species (e.g. kohekohe) and the first fruits fell into the trap, uneaten but ripe, a few weeks after ripening while the kereru fed on the preferred species.

Consumption and dispersal does not seem immediately applicable to the two-week (1 sampling period) lag for puriri (Figure 4.1 C), since it virtually had fruits throughout the year in various degrees of ripeness (refer to Chapters 5 and 6). Counts, would therefore, target different ‘cohorts’ of ripe fruits in any one period. About half of the fruits in seedfall traps were consumed and the other half desiccated.

It could well be that the patterns observed are caused by several factors, other than rates of consumption. Perhaps the rate or timing of abscission of different species has produced different lag periods. Maybe the different architecture or epiphyte loadings of the different species delays fruit fall to different degrees if fruits are caught up in these epiphytes (puriri and taraire tend to have more epiphytes). The weight and presentation of fruit could have a bearing on the lag period. Karaka is a heavy pendulous fruit, puriri is a smaller pendulous fruit, both taraire and kohekohe are presented erect, but the heavier taraire were not eaten as quickly as kohekohe. Storm or bad weather conditions may also have affected fruit fall and the observed lag periods. More research is needed on the rates of fruit development, abscission, attrition and consumption to clarify these issues.

The correlation coefficient between seedfall and counting tended to be around 50%, except for kohekohe, closer to 90%, and tawa (7%) (Table 4.6). This probably reflected the architecture of the different species. The kohekohe trees sampled were of relatively short stature (10 to 12 m), the cauliflorous capsules were large, not too numerous, conspicuous and it was relatively easy to count all, or a large part of the canopy, thus giving more accuracy. The other species tended to have larger numbers of more concealed fruits in taller trees, and thus were harder to count accurately. Tawa fruits in particular could be very cryptic and often only became noticeable when ripe or in large numbers.

The lags between the maturity index and mature fruit in the seedfall traps were interesting. They varied from no lags to 6 weeks lag (3 sampling periods). Kohekohe fruits and seed (Figure 4.1 B) had no lag. Maximum maturity (stage 4) was assigned to open capsules, from which the seeds often already been consumed by birds. Kohekohe capsules opened relatively synchronously over a short period of time and they fell from the tree shortly after opening (see Appendix 3.1). Mature karaka and taraire fruits in seedfall traps showed a lag behind maturity of two weeks (one sampling period). Both these species coloured up over a relatively short synchronous time, the fruits stayed on the tree for a period after ripening, but then fell to the ground, usually in a desiccated state. Puriri fruits ripened much more asynchronously, often with several ‘cohorts’ of fruit at different stages of ripeness. This made it difficult to determine how long an individual fruit stayed on the tree, but the impression was that they did stay on the tree for considerable time, perhaps even for the 6 week lag (3 sampling periods) shown in this comparison.

The correlation coefficients between seedfall and maturity ranged from 7% (tawa) to 45% (karaka), with the majority of species around 30% (Table 4.6). The degree of ripeness had a relatively low correlation with the amount of fruit that ended up in the seedfall trap, but it could also reflect that at any one time only a portion of the crop is ripe, or that as fruit ripened it was eaten and dispersed away from the trap.

Usually, there was no lag between number of ripe fruits per cubic metre and the maturity scale, except for taraire where maximum counts tended to precede the maturity scale by one sampling period (2 weeks, Figure 4.1 D). I am unsure why taraire had this tendency, but it might be related to fruit ripening somewhat asynchronously over a month and the proportional nature of the maturity index score. Correlations varied from 28% to 55% (for tawa) with most around 30% (Table 4.6). The higher correlation for tawa probably reflected the cryptic nature of the fruit, and that frequently a fruit wasn’t seen until it was ripe.

4.3.3 Conclusions.

The three different methods (seedfall, maturity and counts) measure different aspects of phenology and thus produce somewhat different results. The distribution of trees throughout a forest and amount of fruit produced appears to affect accuracy of seedfall scores. The tree architecture, size and placement of fruits probably impacted on the accuracy of counts per cubic metre; the rates of ripening, fruit-fall or fruit-take probably reduced the accuracy of maturity scores.

The suggestions presented above, to explain some of the observed trends, are tentative at best. More work needs to be done on the rates of fruit ripening, how long ripe fruits remains on the tree, and the rate and amounts of fruits taken by dispersers.

Of the three methods, seedfall traps are the most accurate measure of fruit production. Seedfall traps encompass aspects of the other two methods. The traps show when fruit is ripe and the number of fruits in the trap tends to be proportional to the number of fruits in the tree. Data from seedfall traps seemed to be more robust with regards to sampling error (unequivocal counts of fallen material) and generally resulted in the highest correlations with the other methods, especially with direct counts. Therefore most of the data in this thesis will be based on seedfall trap data, supplemented with count data where this is appropriate.

[1]

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[1] Time of fruiting

5. Fruiting patterns of large-fruited native species.

5.1 Introduction.

Timing of fruit production varies according to species and locality. Fleshy fruits in temperate regions predominantly ripen in late summer to early winter (Snow 1971; Thompson and Willson 1979) and often coincide with migration patterns of bird species (Thompson and Willson 1979) (but also see Gorchov 1990). In some seasonal tropical forests the number of animal-dispersed fruiting species peaks during the rainy season (Milton *et al.* 1982; Murali and Sukumar 1994; Stocker and Irvine 1983), (but see French 1992) when migratory frugivores are present in abundance (Loiselle and Blake 1991; Murali and Sukumar 1994). Other seasonal tropical forests have greatest fruit production during the dry seasons (Crome 1975a, b; Wheelwright 1985a). In aseasonal tropical forests, such as those in Malaysia, fruiting occurs throughout the year; usually without defined peaks in fruit or frugivores abundance (Putz 1979; sensu Rathcke and Lacey 1985). Some tropical dipterocarp-dominated forests exhibit supra-annual fruiting cycles (Fleming *et al.* 1987).

These temporal patterns of fruit production could be interpreted as co-evolution of fruiting phenologies by plant species to take advantage of resident or migratory frugivores, or to avoid seed predators. In many cases the patterns could equally be regulated by abiotic factors such as climate (Rathcke and Lacey 1985; Smith-Ramirez and Armesto 1994). Some of the patterns described above can be attributed to short growing seasons in temperate regions, more advantageous growing seasons during the rainy or dry season in tropical areas, the effects of the annual solar cycle (van Schaik *et al.* 1993) or Southern Oscillation patterns (Wright *et al.* 1999). Masting of rimu (*Dacrydium cupressinum*) in New Zealand was shown to be correlated with cool temperatures two years prior to, and warm temperatures during, the summer of super-abundant fruit production (Norton and Kelly 1988).

Phylogenetic constraints will also influence fruiting patterns (Gorchov 1990). Some current fleshy structures probably evolved long before the current frugivores utilised them (Fischer and Chapman 1993; French 1991; Herrera 1982, 1985b). A large fruit probably takes longer to grow and ripen than a small fruit, and seed size is likely to be constrained by seedling energy requirements and germination strategies (Janzen 1977). Timing of ripe fruit production might also depend on the environmental factors that trigger flowering (van Schaik *et al.* 1993), and these cues could in turn be constrained by evolutionary history (Gorchov 1987, 1990). Genetic variation within a species can also influence fruiting patterns. It is known in some flowering species, for instance, that late flowering individuals translocated from their normal population into an earlier flowering population continue to flower in synchrony with the parent population (Rathcke and Lacey 1985); i.e. there is an genetic component which may override environmental ‘triggers’.

It is usually difficult to attribute causal relationships to observed correlations between fruiting patterns and frugivorous animals. Did selection by the frugivore assemblage cause species to overlap or separate in time, or are the frugivores there because the fruit is available at that specific time (Rathcke and Lacey 1985)? Frugivore interaction with fleshy-fruited species is based on the, generally accepted, underlying assumption that the production of fleshy fruits has arisen to attract the attention of frugivores because consumption, and subsequent dispersal, of fruits by frugivores contributes to the reproductive success of an individual (French 1991; Howe and Smallwood 1982; Stiles and Rosselli 1993).

Evolutionary history and extinction of animal species should also be considered, since some of the phenomena seen today might be due to selection pressures exerted by frugivores now extinct. Janzen and Martin (1982) illustrated this for large-fruited species still found in Central America that have characteristics similar to African large-mammal dispersed fruits. There are no extant large native mammals capable of dispersing these fruits and the Gomphotheres (related to North American mastodonts) died out 10,000 years ago, yet these large fruited species have persisted in the flora.

As far as is known, the only large terrestrial animals to have lived on the New Zealand archipelago were dinosaurs (Molnar and Wiffen 1994; Molnar *et al.* 1998; Wiffen 1996), and moa (*Dinornithidae*). Dinosaurs have been extinct since end of the Cretaceous (Cooper and Millener 1993; Stevens *et al.* 1995). The moa were hunted to extinction some 700 years ago and are unlikely to have had a significant impact on fruit production of tall trees (refer Section 1.2.4).

Chapter 1 briefly reviewed the frugivores known to have existed in New Zealand since the demise of the dinosaurs and concluded that the native pigeon, kereru (*Hemiphaga novaeseelandiae*) was probably the only non-seed predator species capable of accessing treetops and swallowing large-fruits intact. It has been postulated that attractive, high-quality dispersers move the seed, unscathed, away from its parent to sites that are available, and/or suitable, for colonisation by the plant species (e.g. Coates-Estrada and Estrada 1988; Glyphis *et al.* 1981; Hoppes 1988; Howe and Primack 1975; Snow 1971). Is kereru a high quality seed disperser of large-fruits?

Kereru have gapes large enough to swallow intact the fruits of the native large-fruited species (Clout 1990; Clout and Hay 1989; Lee *et al.* 1991) and a digestive system that results in defecation of the seeds without damage (Bell 1996; Clout and Tilley 1992; James 1995; McEwen 1978). They also move between con-specifics and trees of different species after a feeding bout, although this depends to some extent on the food plant utilised, and juvenile birds range further than adult birds (Bell 1996). Deposition of seed by kereru was more common in the interior of the forest, rather than on edges or in gaps (Bell 1996). Moreover, most of the large fruited species germinate and establish in shady conditions (refer Chapter 2) provided by the forest interior. Thus, kereru would appear to be disseminating seed of most large fruited species into suitable conditions for germination.

Another proposed advantage to plant species, endeavouring to entice frugivores, is that seeds that pass through a frugivore gut system could achieve more rapid or consistent germination, while seeds that are not passed through the appropriate vertebrate gut may have retarded germination (McKey 1975; Snow 1971) (but also see Krefting and Roe 1949). Is there any evidence for this amongst the large-fruited species of interest to this study?

Tawa (*Beilschmiedia tawa*: Burrows 1999; West 1986), taraire (*Beilschmiedia tarairi*: Myers 1984), puriri (*Vitex lucens*: Dijkgraaf 1994), karaka (*Corynocarpus laevigatus*: Bannister *et al.* 1996; Burrows 1996), and kohekohe (*Dysoxylum spectabile*: Burrows 1999) all germinated more readily when the fruit tissue was removed. In some cases (kohekohe and karaka) germination failed when fruit flesh was not removed (Burrows 1996, 1999). However, Clout and Tilley (1992) could not detect any difference in germination rates of miro (*Prumnopitys ferruginea*) that had passed through kereru guts.

Given the constraints outlined above there are probably a number of ways in which plant species could compete with each other and amongst themselves for the attention of frugivores, with subsequent dispersal of fruit (Howe and Estabrook 1977). Various fruit or plant characteristics that could have been modified by competition from co-occurring species are each illustrated with an example(s) below, followed by an explanation of how relevant the hypotheses are to current New Zealand conditions.

1. **Trees could attract dispersers by varying the number of fruits on display**
   Large fruiting displays, and increased synchrony within individuals and populations, may facilitate dispersal if increases in fruit availability attract more frugivores (French 1991; Janzen 1977; Rathcke and Lacey 1985). For instance, smaller fruit displays are sufficient during summer months to attract resident frugivores familiar with local resources, but larger fruit displays are required during autumn months to attract transient frugivores (Thompson and Willson 1979). Sallabanks (1993; Sallabanks and Courtney 1993) illustrated flexible foraging behaviour in relation to crop size, fruit size, fruit pulpiness and climate, but Traveset (1994) concluded that avian foragers had a negligible effect on crop size or number of viable seeds produced. Or, extended and constant periods of ripe fruit availability might attract a better ‘class’ of frugivore (e.g. a highly specialised obligate frugivore) than species that have short and unpredictable

fruiting seasons (Howe and Estabrook 1977).
Most of the native, large-fruited species have sub-tropical origins, and thus fruit could be available throughout the year, as in the tropics, rather than most prevalent in the autumn, as is more common in temperate climates. However, currently New Zealand does have a seasonal temperate climate and fruiting could be expected to correlate with seasonal changes in temperature. New Zealand does not experience large migrations of frugivorous birds, thus fruiting phenologies will probably not be similar to those noted by Thompson and Willson (1979) but perhaps the native species exhibit extended fruiting seasons if kereru acts as a good disperser.

2. **Attract particular dispersers by use of fruit colour regimes.**
   Red, pink, blue, black and purple fruits tend to be more attractive to birds, while fruits consumed by mammals generally tend to be large, mechanically protected, and green, brown, orange, or yellow in colour (Howe 1986; Willson and Whelan 1990). Red *Rubus spectabilis* fruits are chosen more frequently by bird dispersers than orange fruits (Gervais *et al.* 1999).

   Most fleshy fruits in New Zealand are reddish (67%) with white (18%) and black (15%) being other significant colours (Lee *et al.* 1991). Of the 17 large-fruited species listed in Table 1.2 most are red or purple-black when ripe and only three species had fruits tending more towards orange colouration (refer to Chapter 2). Thus the largest proportion of large-fruited species and New Zealand fruits are probably attractive to birds.

3. **Exclude some frugivores through changes in fruit size or accessibility.**
   Beehler and Dumbacher (1996) showed that structurally protected fruits (fruits in dehiscent capsules) had visits from a small number of specialist frugivores, while unprotected fruits had a diverse frugivore assemblage. Fruit diameter was hereditary in *Ocotea tenera* (Lauraceae), and birds preferred larger than average fruits, thus the potential exists for an evolutionary response through fruit selection (Wheelwright 1993). Fruit size was one of the few variables that showed greater covariance with disperser-type (birds only, birds and mammals, or mammal only) than could be accounted for by phylogeny (Jordano 1995).

   In New Zealand, the tree-borne fruits of the focus species for this study are too large to be swallowed intact by any present-day native species other than the native pigeon, kereru. This situation has changed little for at least the last 2 million years and possibly longer. There are few, if any, native fleshy fruits that require special adaptations by frugivores to gain entry. Even encapsulated kohekohe fruits become accessible when the capsules open.

4. **Provide rewards, or methods of presentation, that are more attractive to all or part of the frugivore assemblage.**
   McKey (1975) proposed that plant species that attract high-quality dispersers tend to have more nutritious fruits than species with more generalist dispersers. Whelan, *et al.* (1998) found that in general fruits consumed by migrant passerines in North America complemented each other in nutritional values. Jordano (1995) found that particular nutritional components (e.g. lipids, or carbohydrates) tended to be associated with particular suites of frugivores (birds only, birds and mammals or mammals only).

   The nutritional characteristics of some native fruits will be discussed more in Chapter 6

5. **Vary timing of fruit display to avoid or satiate seed predators.**
   Annual variability in seed production by woody plants, commonly known as masting, is a world-wide phenomenon found in fleshy-fruited and dry-fruited plant species (Herrera *et al.* 1998). A range of theories have been proposed to explain the phenomenon including; resource matching, i.e. plants vary their reproductive output to match variable resources; predator satiation, i.e. losses to predators are reduced by varying the seed crop; differential pollination success for wind pollinated species; variable success of animal pollination; climatic prediction by plant species of favourable years for seedling establishment; attracting animals for dispersal of fruits; pulsed seed production due to high accessory costs of reproduction and large seed size (Kelly 1994). Of these,

wind pollination, predator satiation and environmental prediction are important in a number of species, but the other theories have less support (Kelly 1994).

In New Zealand most of the podocarps have supra-annual cycles and masting is also common amongst the flowering species. The New Zealand masting species exhibit a range of growth forms, pollination and dispersal mechanisms, habitats and different masting behaviour altitudinally (Allen and Platt 1990; Burrows and Allen 1991; Webb and Kelly 1993). Different masting strategies have been proposed for some of the New Zealand species; satiation of the seed predator *Diplotoxa similis*, a chloropid fly, seems to favour masting in the alpine tussock *Chionochloa pallens* (Kelly *et al.* 1992; Webb and Kelly 1993); the effect of wind pollination might mediate the masting of *Dacrydium* (Podocarpaceae) and *Nothofagus* (Fagaceae) (Allen and Platt 1990; Norton and Kelly 1988; Wardle 1984; Webb and Kelly 1993); the ability to attract birds to disperse fruit crops, or the need to satiate bird predators might have influenced the size of fruit crops of podocarp species (Beveridge 1973; Norton and Kelly 1988); and the amount of effort to produce large (2 to 3m tall) floral spikes combined with the attraction of birds to a massed floral display may have resulted in supra-annual flowering cycles in New Zealand flax, *Phormium* (Brockie 1986; Webb and Kelly 1993). Mast years often coincide in unrelated genera, and can be regional or national in scope (Beveridge 1964; Knowles and Beveridge 1982; Leathwick 1984; Webb and Kelly 1993).

Of the large fruited species investigated in this study only tawa was known to mast, and West (1986) concluded that masting in tawa was unlikely to have evolved to satiate invertebrate or vertebrate predators since only a relative small proportion of the crop was affected in any one year.

6. **Vary timing of fruit display to coincide with preferred migratory or patchily distributed frugivores.**
Convergent or synchronous phenologies are thought to be adaptations to take advantage of seasonal changes in animal vectors, or satiate seed predators (Fleming and Partridge 1984). Thompson and Willson (1979) concluded that it was advantageous for plant species to produce most of their fruit during late summer and fall to take advantage of the greater numbers of frugivores present due to migratory patterns.

In New Zealand few frugivorous birds would have been available to disperse the fruits of the large-fruited native species. These bird species were probably non-migratory, present day kereru on average move less than 20 km (Clout *et al.* 1991), with a reasonably even distribution of wholly or partially frugivorous birds throughout the forest. Kereru was probably the only species capable of accessing canopy borne fruits. Thus it seems unlikely that forest tree species would have competed for preferred migratory frugivores.

7. **Vary timing of fruit display to avoid competition with other fruiting species vying for the same frugivores.**
Interspecific competition in sympatric species relying on the same frugivore could be expected to have evolved fruiting patterns that do not overlap significantly (Fleming and Partridge 1984; McKey 1975; Rathcke and Lacey 1985) and these fruiting patterns should be fairly consistent between years (Gorchov 1987; Rathcke and Lacey 1985). Such patterns were first postulated by (Snow 1965), but often the evidence appeared to be weak or the observed phenologies could not be distinguished from random patterns (e.g. Gleeson 1981). In some cases, such postulated asynchrony did not occur, for instance, in a study of multiple Lauraceaous tree species sharing similar avian frugivores in Monteverde, Costa Rica. However, fruit removal rates did decline when multiple tree species fruited, indicating the presence of ecological competition for frugivores (Wheelwright 1985a).

Casual observation of sympatric large-fruited tree species in New Zealand shows an asynchronous pattern.

The four hypotheses (numbers 1, 5, 6 and 7) discussing variations in numbers of fruit and timing of fruit are inter-related since the timing of fruiting relies on the number of fruits presented. The amount of fruit produced can vary considerably, and deciding which year is a mast fruiting year often has no objective basis, unless additional cues such as pollination success are available (Norton and Kelly 1988).

Thus there are a range of hypotheses that can be proposed for the New Zealand situation for large-fruited species. Colour and fruit presentation (tops of tall trees) indicate that the fruits of these native tree species are bird dispersed. The sizes of the larger fruits restrict the suite of potential arboreal frugivores to kereru. Furthermore, the lack of migrating species, and other clades, such as mammals or reptiles, capable of consuming fruits whole and dispersing them, further reduces the number of hypotheses to be tested.

The remaining questions are;

1. Do New Zealand plant species with large-fruit have defined fruit phenology patterns, or is fruit produced randomly or throughout the year?
2. Do these large-fruited species have overlapping fruit phenologies, or are they segregated in time? Divergent, or asynchronous, fruiting or flowering patterns of species have been postulated as a consequence of historical competition amongst co-existing plant species for limited high quality animal vectors (e.g. Fleming and Partridge 1984; Snow 1965).
3. Have the nutritional components of the different fruit been ‘tailored’ to suit dispersal by avian frugivores?

This chapter will investigate the displacement of fruiting periods in time and the next chapter will address nutritional differences.

5.2 Statistical testing for character displacement.

Phenological data are generally analysed using non-parametric tests since often the nature of the distribution of the population is not known or cannot be calculated. None of the non-parametric tests has received wide-spread acceptance (Zar 1996).

In comparisons of phenology, authors have used various methods. Wheelwright (1985a) used the Kendall’s coefficient of concordance in association with the Friedman’s chi-square test, but could not demonstrate that competition-induced character displacement did or did not occur. Gorchov (1987) used a similar analysis to show that the order of fruit ripening for different species was similar over 5 years, but could not make any conclusions about the degree of overlap in fruit production between species.

Phenological overlap was tested by Fleming and Partridge (1984) using pair-wise Pianka’s symmetrical indices and population total overlap comparisons. They reported significant differences from random expectations, but there was greater overlap between species than would be expected for character displacement. This result contradicted the earlier analysis by Pleasants (1980). Pleasants (1990) noted that there were flaws in the analysis by Fleming and Partridge (1984) but concurred that species should be analysed in the context of sympatric species. Within-species synchrony of flower phenology was tested by Primack (1980) and Augspurger (1983), both of whom found considerable differences in flowering phenology within and between species.

Phenological character displacement (i.e. alteration in timing of fruit phenology to reduce competition for frugivores) in a community of co-occurring species appears to be hard to quantify, let alone prove statistically. One of the reasons why statistical significance in phenological character displacement may have been difficult to pinpoint is because this phenomenon appears to be composed of several different attributes. Generally these attributes are not tested individually, often with the result that one or several attributes can obscure the significance of other attributes. The most important of these character displacement attributes appear to be;

1. The presentation of ripe fruit changes among species within a year. The order and timing should not change significantly from year to year. Data presented in Sections 5.5 and 5.6.
2. Ripe fruit displays of a particular species vary in magnitude (quantity) between years. However, the peak quantity of fruit produced within a year (regardless of its magnitude) should still be proportionally greater than could be expected by chance. Tested in Section 5.7.
3. A species should have synchronous fruit production amongst individuals. If a species is asynchronous then fruit may be available throughout the year leading to ill-defined fruiting peaks (violating point 2 above) or fruiting times (probably negating point 1 above). Synchrony within a species will be tested in Section 5.8.
4. Different species should not overlap significantly with species competing for the same resources. This attribute comprises parts of all of the above aspects but also needs to be tested for directly. Tested in Section 5.8.

This study will attempt to illustrate the significance, or otherwise, of the above character displacement attributes.

5.3 Chapter structure

This chapter will explore the four character displacement attributes identified above. Different sections will address particular attributes, utilising various datasets. The origin and acquisition of the data is explained in the relevant section. Therefore, most sections include some methodological and data descriptions, followed by a description of the analysis and results obtained. All character displacement attributes are discussed in the penultimate section, followed by a conclusions section.

Section 5.5 dealing with observed fruiting phenologies describes the fruiting patterns of the five focus species. Section 5.6 checks whether the order of fruit presentation among the different species is the same from year to year. Section 5.7 ascertains whether the observed phenologies are distinguishable from random patterns. The last data section (5.8) investigates within species synchrony and overlap between species at the same site.

5.4 Data used in this Chapter

Co-evolutionary patterns can only be detected from sites with minimal impact from mammalian predators on fruiting phenologies. The data used in this Chapter come from the two sites with the longest phenological data set and best pest suppression; Wenderholm Regional Park and Whitford Bush. Both seedfall data and observational data (counts per cubic metre) will be used.

The large-fruited species found at both sites were karaka, kohekohe, puriri, taraire and tawa; these are therefore the focus species. Generally, only the availability of ripe, or mature, fruit will be considered when testing hypotheses. Ripe fruits are most likely to be consumed by kereru and will therefore be the variable experiencing the greatest degree of inter-specific competition for a single disperser, if competition is part of the system. Mature, or ripe, fruits are those that are both full-sized and ripened, as indicated by fruit colour and often softening of the pericarp. Fruit that had passed through a digestive system was included as being ripe, as were predated fruits that appeared fully-grown and appropriately coloured.

The seasons in New Zealand are conventionally given as; spring; September to November, summer; December to February, autumn; March to May, and winter; June to August (Godley 1979). In most cases calendar years, rather than seasons, are delimited on the graphs.

5.5 Observed fruiting phenologies.

The fruiting patterns of the five focus species (karaka, kohekohe, puriri, taraire, tawa) will be introduced and discussed by species in this section. Figures 5.1 and 5.2 illustrate the total number of mature and immature fruits, of large-fruited species, to fall in the seedfall traps at Wenderholm

Regional Park (30 traps) and Whitford Bush (30 traps). Immature fruits were those that were not full-sized nor fully ripened, as indicated by fruit colour. Flower phenology is also indicated as a dotted line; large flowers were counted, small flowers were bulked by species and weighed.

5.5.1 Results.

Tawa.

The greatest weight of tawa flowers (79% to 87%) fell into seedfall traps during spring and summer (October to February). Small numbers of fruits were sporadically dropped throughout the year (Figures 5.1 and 5.2). No consistent fruiting pattern was apparent at Wenderholm Regional Park, but Whitford Bush produced moderate numbers of fruit during the early part of the calendar year (83% of fruit fell during January and February). A large number of ripe tawa fruit were found on the ground at both sites during September and early October prior to the start of this study, but such a heavy crop did not repeat itself during this study.

Karaka.

Karaka flowers fell mostly during spring and early summer (61% to 86% of flowers fell during October and November) and ripe fruits were available 3 to 4 months later (95% of fruit fell during January to March). Trees at Wenderholm Regional Park tended to have peak production of both flowers and fruits about a month earlier than at Whitford Bush (Figures 5.1 and 5.2). Ripe fruit was available at Wenderholm Regional Park from January to February, while ripe fruit occurred from January to March at Whitford Bush. Flowering was followed by the abortion of large numbers of immature fruit. The numbers of fruits produced appear to show biennial fluctuations (more so at Whitford than Wenderholm), though a 3-year study is in adequate for assessing inter-annual variation.

Puriri.

Puriri showed an extended winter flowering season (April/May to September/October, 48% to 54% from April to June), but some flowers could be found in seedfall traps throughout the year (Figures 5.1 and 5.2). Fruit was most common in seedfall traps during summer and autumn (December/January to April/May, 68% to 78% January to May), but again some fruit could be found throughout the year. Immature fruits fell in seedfall traps throughout the year. The ‘start’ and the peak periods of both fruiting and flowering varied somewhat in consecutive years. The amount of fruit produced also showed variation within and between years.

Kohekohe.

Flowers occurred during June, July and August (63% to 91% during June and July), while fruits were predominantly found in seedfall traps during April and May (98% of fruit) (Figures 5.1 and 5.2). Kohekohe shows a biennial pattern in both fruiting and flowering. The fruiting and flowering pattern of kohekohe is somewhat complicated since at the time that the sites were set up kohekohe was thought to be monoecious (Allan 1961; Poole and Adams 1994) and trees were selected without regard for sex. Partway through the study it became apparent that kohekohe was modified androdioecious and that the female and male trees behaved quite differently (Braggins *et al.* 1999).

Every other year the female trees either have abundant flowers or abundant fruits, and these years are offset (Braggins *et al.* 1999; Court and Mitchell 1988, A. Dijkgraaf pers. obs.). That is, when trees carry copious fruit they tend to have few flowers and vice-versa. This pattern of inter-annual variation is somewhat obscured on the Figures because male/hermaphrodite trees tend to flower every year and can be prolific flower producers. They carry more, longer and more complex inflorescences, with more flowers per inflorescence than female trees (Braggins *et al.* 1999, A. Dijkgraaf pers. obs.). For instance, during 1995 male kohekohe were extremely prolific in flower production at Wenderholm, hence the relatively large flower and ‘immature fruit’ (aborted flower pedicels) peaks in that year (Figures 5.1 and 5.2). Very few fruit abort once they have started to enlarge.

Figure 5.2: Number of fruits, from large-fruited species, caught in seedfall traps at Whitford, with an indication of flower phenology

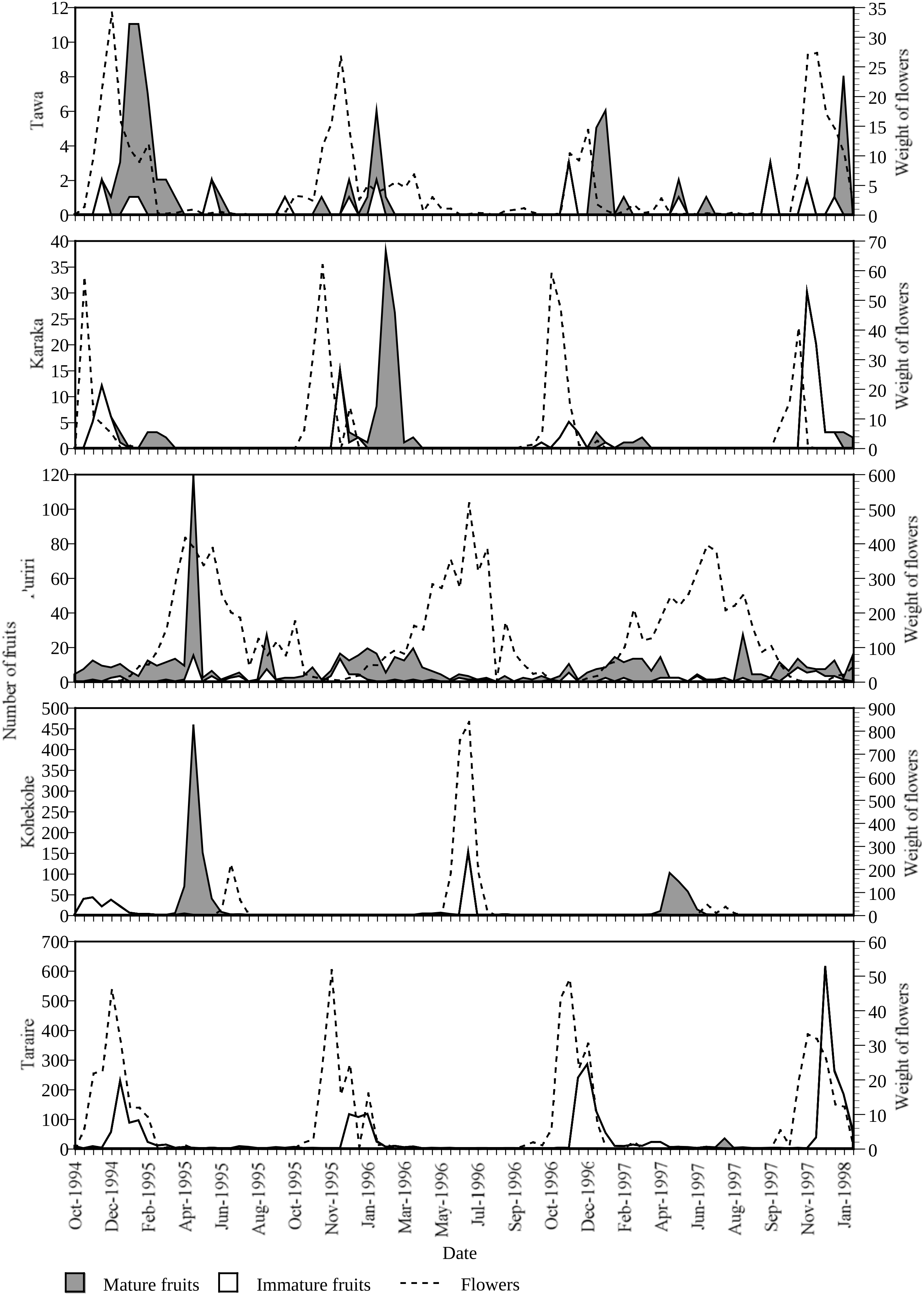
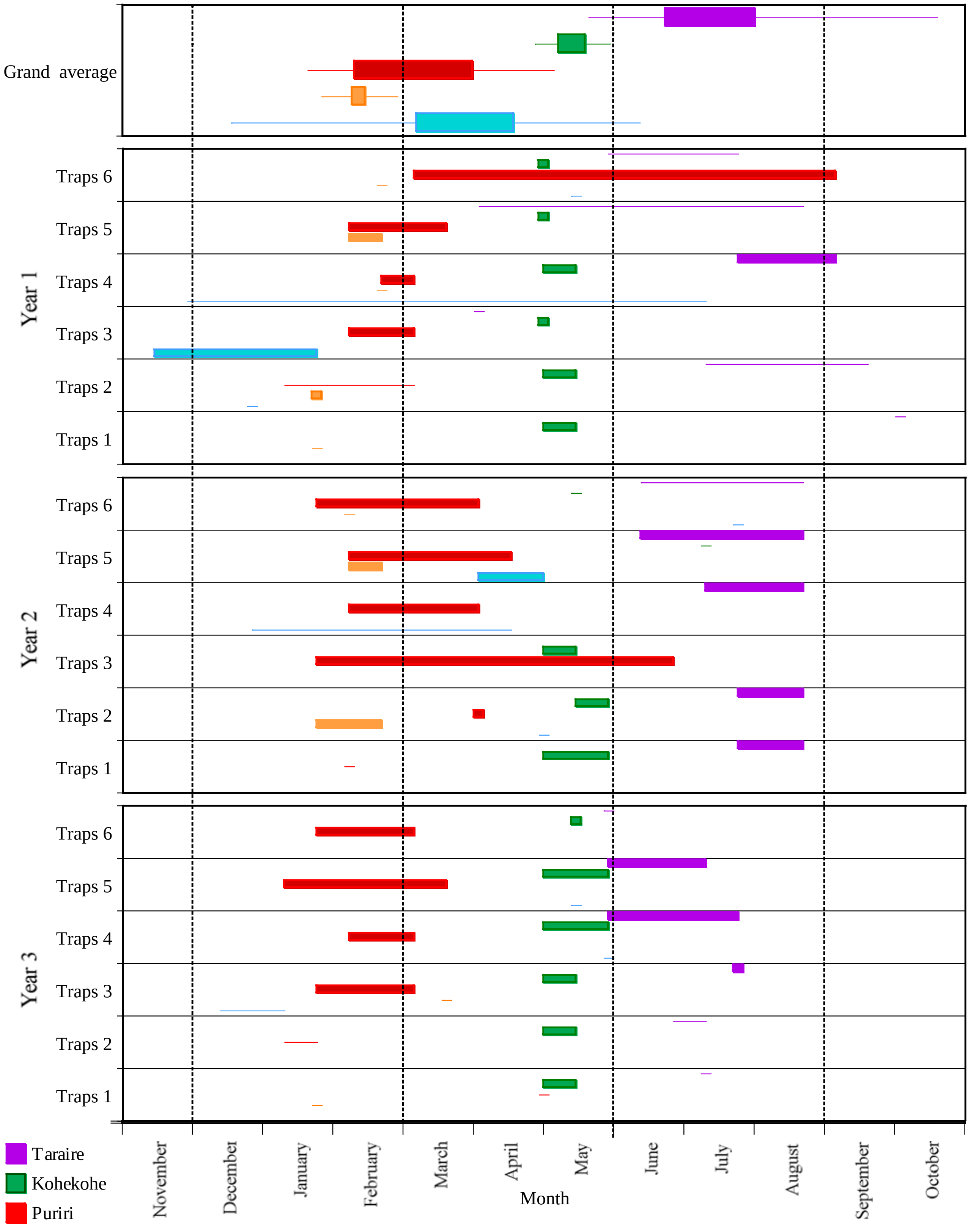
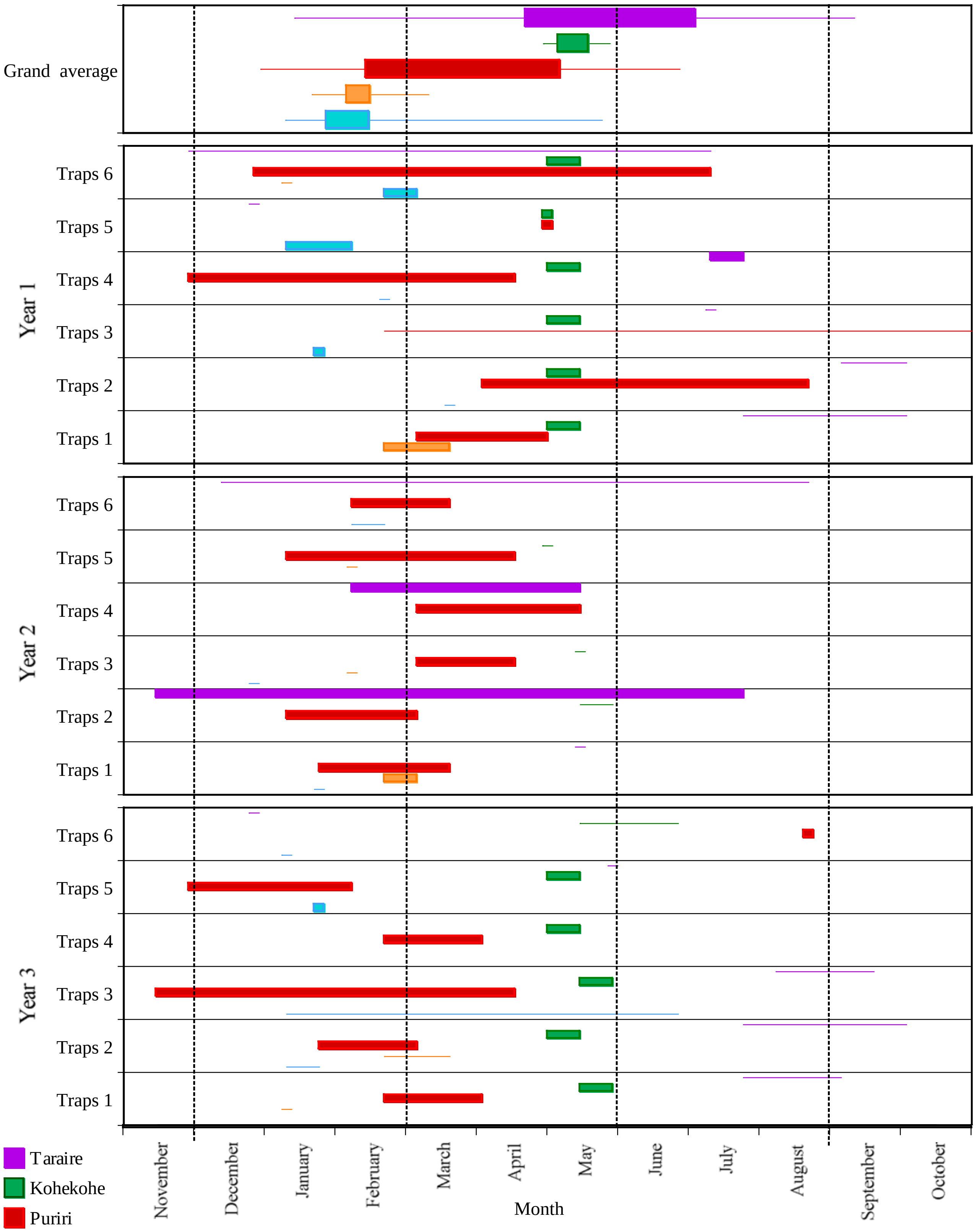


Figure 5.3: Fruitfall timing for individual trees during three consequetive years at Wenderholm (25th to 75th percentiles) and average fruit-fall over three years (Grand average). Error bars top graph = average absolute differences from mean for 25th (left most) and 75th (right most) percentiles respectively. Thin lines on lower graphs indicate that less than 5 fruits fell into the trap that year.



Note: Each bar plotted against a 'traps' label represents the contents of one trap under a specific tree. For instance, 'Traps1' can have up to five bars representing the traps beneath trees Tawa-1, Karaka-1, Puriri-1, Kohekohe-1, and Taraire-1 respectively.

Figure 5.4: Fruitfall timing for individual trees during three consequetive years at Whitford (25th to 75th percentiles) and average fruit-fall over three years (Grand average). Error bars top graph = average absolute differences from mean for 25th (left most) and 75th (right most) percentiles respectively. Thin lines on lower graphs indicate that less than 5 fruits fell into the trap that year.



Note: Each bar plotted against a 'traps' label represents the contents of one trap under a specific tree. For instance, 'Traps1' can have up to five bars representing the traps beneath trees Tawa-1, Karaka-1, Puriri-1, Kohekohe-1, and Taraire-1 respectively

Taraire.

The majority of flowers were found in seedfall traps from spring to early summer (October to December, 78% November to December) with peak fruiting about 6 months later, from May to October (Wenderholm 78% May to August, Whitford 69% July to October). Ripe fruits were approximately a month later at Whitford Bush than at Wenderholm Regional Park. More juvenile and fewer mature fruits were found at Whitford Bush than at Wenderholm Regional Park (Figures 5.1 and 5.2), which could be due to greater exposure of individual trees to wind in the small Whitford forest fragment. Juvenile fruits appeared in seedfall traps over a 2 to 3 month period, shortly after peak flowering. There was some anecdotal evidence that dry periods during early fruit ripening reduce the number of fruits set (B. Green pers. comm.). The amount of fruit varied annually, as it did in the study of taraire in 1982 and 1983 by Myers (1984).

Comparison between the sites.

The sequence of ripe fruit production among the species appears to be consistent between the two sites and among years, though tawa at Wenderholm Regional Park was too variable and sporadic to show any identifiable patterns. The overall order of fruit production amongst the species was tawa, karaka, puriri, kohekohe and taraire.

5.5.2 Discussion.

Karaka.

Latitudinal differences can apparently be marked for karaka. West (1986) noted that the fruiting season of karaka on Tiritiri Matangi Island, which is at a similar latitude to Wenderholm Regional Park, was from January to April. While ripe fruit was collected by Bannister, *et al.* (1996) from April to June in Otago, who attributed the late maturing to the tree being south of its natural distribution limit.

Burrows (1996) noted that ripe fruit of karaka were displayed on the trees at Kaikoura for periods of at least 3 months (sometimes more). He suggested that such long fruiting periods were achieved by extended consecutive flowering and resultant consecutive ripening of fruit on any one plant, and differences in flowering and fruiting times within the plant population. Flowering and fruiting periods at both Wenderholm Regional Park and Whitford Bush were more contracted than those noted by Burrows (1996), thus perhaps extended fruiting seasons are also a function of latitudinal differences.

Kohekohe.

The marked biennial pattern in both the fruiting and flowering of kohekohe can be explained in terms of tree energetics. If a tree has a large fruit crop, it is unable to divert enough energy to produce large quantities of flowers simultaneously. While in years with small fruit crops, more resources are available to produce flowers. This hypothesis was supported by several other observations in the field. Sub-canopy kohekohe produced noticeably fewer flowers, often none at all, and considerably more flowers and fruits were produced in that part of the canopy that was most exposed to sunlight. Male trees were much more prolific in flower production than female trees. In areas where possums were prevalent, and kohekohe canopies nearly denuded, only male trees produced any flowers.

Fruits in the Auckland region take less than one year to ripen, and flowers open after all the fruits are gone. Further south, ripe fruits and open flowers occur on the tree at the same time (A. Dijkgraaf pers. obs.).

Puriri.

These observations generally agree with the current literature (also see Chapter 2). The timing of flowering and fruiting were similar in Best and Bellingham's (1990) study of kokako habitat in Puketi, Northland. It is difficult to tell from the data provided in that paper, but it is possible that the fruiting seasons there might be somewhat more extended than in the Auckland area, or the difference could be due to inter-annual variation. Like karaka, it could be that the fruiting season varies with latitude, which could explain some of the confusion about fruiting and flowering times noted in Chapter 2. Auckland collection dates for puriri fruit in Godley's (1971) paper agree with the data from this study, but fruit was collected later in the year from sites further south.

Taraire.

There was some anecdotal evidence that dry periods during early fruit ripening reduce the number of fruits set (B. Green pers. comm.). The amount of fruit varied annually, as it did in the study of taraire in 1982 and 1983 by Myers (1984).

Tawa.

The literature records both biennial and masting patterns for tawa. Limited observations of tawa by Wright (1984) suggested heavy fruiting in alternate years. West (1986) found that some trees seemed to have alternately good and poor fruiting years.

Other authors imply a more complex fruiting pattern for tawa. Knowles and Beveridge (1982) stated that tawa fruit are borne annually but fluctuate in abundance. In good seed years there may be 100 or more fallen fruits per square meter below some parent plants. In the central North Island 1970/71 produced a heavy tawa crop, while the following years saw a virtual failure of the crop. This pattern recurred with a heavy crop in 1978 followed by a light crop in 1979. Leathwick (1984) found the same in his 1979-1980 study of four central North Island forests. Burrows (1999) recently noted that fruit production of tawa was low in the Marlborough area during 1996 and 1997, but that a slightly bigger crop occurred in 1998. The Maori were also aware of good and bad seed years, and that some trees fruited more heavily than others (Best 1977).

5.6 Fruiting sequence.

This section investigates the order of fruiting phenologies amongst co-existing species and timing of capture of mature, large-fruits in seedfall traps at both sites.

5.6.1 Data used.

The data comes from seedfall traps at Wenderholm Regional Park and Whitford Bush for the entire sampling period (from November 1994 to February 1998). Only conspecific fruit to the target tree are included. For instance, only karaka fruits falling into the seedfall traps beneath karaka trees were included, all other species of fruit were removed from the analysis. Restricting the data in this way gives a more accurate picture of the phenological behaviour of the target trees since it reduces the impact of 'accidentally introduced fruit' (i.e. dispersed by frugivore or dropped from overhanging tree) from conspecific trees with different phenological behaviour.

For instance, if the entire dataset was used it might include karaka fruits, from a tree with an exceptionally early fruiting phenology, dropped in seedfall traps under several puriri trees. This would skew the phenology for karaka as a species. We cannot, of course, avoid including 'accidentally introduced karaka fruit' if it happens to be dispersed to a seedfall trap beneath a karaka tree. Thus, 'target catches' are those fruits found in seedfall traps underneath conspecific species (e.g. karaka fruit in karaka seedfall trap) while 'accidental catches' are those fruits caught by seedfall traps under different species (e.g. karaka fruit in puriri seedfall trap).

5.6.2 Analysis.

The beginning and end of fruit-fall can be somewhat erratic and drawn out, thus the decision was made to use only the period between which 25% to 75% of the fruit fell (i.e. only 50% of the fruit-fall was included in the analysis). Other authors (e.g. Augspurger 1983; Wheelwright 1985a) also truncated their data to reduce the effect of phenological tails (protracted but small volume fruit production at the beginning or end of a fruiting season). The data were analysed on a calendar year from November to October, since that was when data collection started, and November is the middle of spring.

The sampling fortnights were numbered from 1 to 26 within each year. The number of the fortnight, in which either the 25th or 75th percentile fell, was noted for each trap in the three complete years. These start (25th %) and finish (75th %) times are illustrated in the lower three graphs of Figures 5.3 and 5.4, one graph for each year.

Note that on the graphs (Figures 5.3 and 5.4) all 30 traps per site are shown for each of the 3 years. Each bar plotted against a ‘Traps’ label represents the contents of one trap under a specific tree. For instance, ‘Traps 1’ can have up to 5 bars representing the traps underneath karaka 1, puriri 1, kohekohe 1, taraire 1 and tawa 1 respectively. Periods where traps received less than 5 conspecific fruits during a year are denoted by thin lines, while the thicker bars illustrate the period over which more than 5 fruits were caught.

The mean start of fruiting (top graphs in Figures 5.3 and 5.4) was calculated by averaging the sampling period numbers (1-26) for the 25th percentile for those three years. The mean finish of fruiting was averaged over the 75th percentile numbers. The error bars in the top graph represent the average absolute difference between sampling period numbers and the mean for the 25th (left most) and 75th (right most) percentiles. These graphs illustrate the duration of fruiting without considering the magnitude (number of fruits to fall into the traps) of fruiting.

5.6.3 Results.

Figures 5.3 and 5.4 illustrate that most species tend to have identifiable fruiting season. Karaka generally fruits during the latter half of summer (January to February). Puriri mostly fruits from mid-summer (January) into winter (May) and is more variable at Whitford than at Wenderholm. Kohekohe has a very well defined and tight fruiting phenology during late autumn (May). Taraire tends to fruit mostly in the winter (June to August) but is more variable at Whitford Bush than at Wenderholm Regional Park. Tawa fruits fell sporadically throughout the seasons, but the majority of fruit occurred in summer and early autumn (January to March).

Fruit phenology of individual trees is very variable; they can have quite different fruit phenologies from one year to the next. For instance, puriri trap-5, at Whitford Bush (Figure 5.4), collected 113 mature fruits in one fortnightly sampling period in year one, in year two 17 mature fruits fell into the seedfall trap over a period of 7 fortnights (approx 3 ½ months), and the following year only 6 fruits were deposited over 5 fortnights (approx. 2 ½ months) (refer to Figure 5.4 and Table 5.1). Most other trees showed similar variability.

There also appears to be considerable inter-annual variation within the species. Kohekohe trees produced hardly any fruit during year two, while taraire tended to have more protracted fruiting phenologies, but not necessarily more fruit, during that same year.

For most species there is considerable overlap with one or more species at the site (top graph in Figures 5.3 and 5.4). However there are a few species that show little or no overlap at one site e.g. kohekohe and taraire show little overlap at Wenderholm Regional Park (Figure 5.3), but at Whitford Bush taraire has considerable overlap with kohekohe. Puriri has limited overlap with other species at

Whitford Bush, but considerable overlap with both karaka and tawa at Wenderholm Regional Park. This illustrates that the phenological behaviour of the species also differs between sites.

Table 5.1: Total number of target species fruits to fall into conspecific seedfall traps at Wenderholm Regional Park and Whitford Bush for each of three years.
Thirty seedfall traps, at each site, were monitored from November 1994 to October 1997.

	Wenderholm Regional Park					Whitford Bush				
	Karaka	**Kohekohe**	**Puriri**	**Taraire**	**Tawa**	**Karaka**	**Kohekohe**	**Puriri**	**Taraire**	**Tawa**
Year 1										
Trap 1	1	235	0	1	0	7	50	16	3	0
Trap 2	11	47	2	2	1	0	53	25	2	1
Trap 3	0	117	53	1	8	0	43	5	2	8
Trap 4	1	106	64	15	3	0	41	58	6	1
Trap 5	5	9	55	4	0	0	287	113	1	7
Trap 6	1	577	14	3	1	1	7	16	4	10
Year 2										
Trap 1	0	11	1	5	0	71	0	11	1	1
Trap 2	26	9	11	6	1	0	3	17	6	0
Trap 3	0	8	41	0	0	1	1	18	0	1
Trap 4	0	0	46	8	3	0	0	24	5	0
Trap 5	40	1	53	7	5	1	1	17	0	0
Trap 6	3	3	27	2	2	0	0	37	2	3
Year 3										
Trap 1	1	137	1	1	0	4	10	16	3	1
Trap 2	0	25	2	2	0	3	23	18	2	2
Trap 3	1	51	21	5	4	0	20	13	2	4
Trap 4	0	109	76	38	1	0	14	26	0	0
Trap 5	0	15	117	10	1	0	97	6	1	5
Trap 6	0	164	27	1	0	0	3	38	1	1

5.6.4 Discussion

Both graphs (Figures 5.3 and 5.4) illustrate that plant species tended to have identifiable fruiting seasons at one or both of the sites (well defined fruiting periods for puriri, kohekohe, taraire and karaka at Wenderholm Regional Park, and kohekohe and tawa at Whitford Bush). However, most species show a great deal of variability, within the tree, within the species, between years and also between sites. In some instances, little reliability can be placed on some data due to small seed counts but overall the average pattern is probably a fair reflection of community patterns.

Some of the lengthy fruit phenologies could have arisen through lack of fruit consumption by birds, or having two fruiting peaks in one calendar year. The impression at Whitford Bush was that considerable quantities of taraire fruit remained on the trees long after ripening, only falling off when dried and shrivelled (but still classed as mature). At Wenderholm Regional Park taraire fruit disappeared (presumed eaten) generally as soon as it was ripe. This shortened the period of fruit presentation in the trees and the period over which fruit was caught in the seedfall traps.

Tawa fruit production was very small and rather erratic. Fruit production was more seasonally predictable at Whitford Bush than at Wenderholm Regional Park. The fruiting order amongst the species appears to be (tawa), karaka, puriri, kohekohe and taraire.

As noted in Section 5.6.1, a proportion of fruit for some species was caught ‘accidentally’ in non-target traps. At times this could amount to quite a large proportion of the total annual fruit caught. The total fruit catch from all traps, including ‘accidental’ fruits caught, was also analysed using 25th to 75th percentiles (data not shown). None of the results were significantly different from those presented in Figures 5.3 and 5.4. Thus, the pattern presented above is representative for all the trees at the sites.

5.7 Testing for randomness.

The first step in evaluating whether apparently divergent or non-overlapping fruiting-phenologies of sympatric species might have evolved to fulfil some function, such as reduced competition for seed-dispersers, is to determine if the observed phenological patterns differ significantly from random expectations (Fleming and Partridge 1984). A Simpson diversity index, coupled with computerised resampling methods, can determine whether observed phenological patterns are uniform or random (A. Rodrigo pers. comm.).

Simpson diversity analysis is one of a number of non-parametric procedures that are commonly used as measures of species diversity. This study uses the Simpson index to test whether the diversity of large-fruited species, as measured by the number of fruits to fall in target traps, is different from random patterns. The Simpson index, in comparison to Species Richness and the Shannon Information indices, is unbiased, even with small sample sizes and has the smallest standard deviation of the three methods (Lande 1996).

In this section the Simpson index will be used to illustrate the diversity of fruits, both in numbers and as total weight of fruits, at Wenderholm Regional Park and Whitford Bush. This is followed by a more detailed analysis of the large-fruited species, using parametric bootstrapping to estimate parameters with Monte Carlo simulation to generate the expected patterns. These analyses will indicate whether the observed phenological patterns differ significantly from random patterns (Fleming and Partridge 1984).

The equation used to calculate the Simpson index at time ‘t’ was;

$$S = \sum_{t=x} P_i^2 \quad \text{where} \qquad P_{i,\, t=x} = \frac{\text{fruit weight or number for species } i}{\text{total weight or number of fruit for all species}}$$

and x = sampling occurrence 1 to 85 sampling fortnights.
Species ‘i’ could be any of the fleshy-fruited species that deposited more than 5 fruits in the seedfall traps over the duration of the study.

The index was calculated for each fortnight and plotted against time. The index ranges from 0 to 1, with lower values indicating greater diversity.

5.7.1 Fruit weight and numbers for all traps and all fleshy fruits.

This section introduces the Simpson index and illustrates how individual species contribute to the index for a particular site. Both number of fruits and weight of fruits caught are presented for each site to illustrate the difference between large-fruited species and small-fruited species.

5.7.1.1 Data used.

The data used for Figures 5.5 to 5.8 were the total number (Figures 5.5 & 5.7) or total weight (Figures 5.6 & 5.8) of all mature fleshy fruits to fall in all 30 seedfall traps at each site. No distinction was made between ‘accidental’ and ‘target’ catches of fruit (refer to Section 5.6.1 Data used.).

5.7.1.2 Analysis.

The equation in Section 5.7 was used to generate the Simpson index (dashed line), which is the sum of the Simpson transformed proportions for the various species (coloured lines). The closer a peak is to 1 the more dominant that species is at that time. The lower the overall Simpson index is, the more species contribute to the total for that week.

5.7.1.3 Results and discussion.

For both sites, the species that were most prominent in the Simpson index plots changed depending whether number, or weight, of fruits was used. The large-fruited species dominated the weight graphs, while smaller fruits dominated numerically. This is logical since species with small, and generally lighter, fruits have a tendency to produce greater numbers of fruit than species with large heavy fruits. The numerical difference can be several orders of magnitude (refer to Figures 7.11 to 7.16).

The lower graphs on each page show the actual number or weight of fruits to fall in all 30 seedfall traps at each site. The total weight or number of fruit does not necessarily influence the Simpson proportions for each species, since this index is one of *relative* and not absolute diversity. However, on several occasions the large peaks on the weight or numbers graphs are dominated by one fruit type in the traps, prominent peaks for that fruit type on the Simpson plot reflect this.

In the weight graphs (Figures 5.5a and 5.7a), the large-fruited species of interest (karaka, kohekohe, puriri, taraire and tawa) all approach 1 on several occasions, indicating that on those occasions there were few fruits from other species that contributed to the weekly total. Also notable is that the peaks of the large-fruited species do not generally overlap with the peaks of other large-fruited species.

Numerically, more species contributed to the weekly totals, as shown by the generally smaller overall Simpson index, and the peaks that only approach 0.8 to 0.9, rather than 1 (Figures 5.6a and 5.8a). Nikau and kahikatea (*Dacrycarpus dacrydioides*) produced the largest numbers of fruit at both sites, but all the large-fruited species made noticeable numerical contributions to the index. At Whitford Bush the large-fruited species were more noticeable numerically than at Wenderholm Regional Park, reflecting the greater species diversity at Wenderholm Regional Park (greater diversity depresses the Simpson index value).

A species that contributed significantly to the index at Whitford Bush, but not Wenderholm Regional Park, was putaputaweta (*Carpodetus serratus*). This species was virtually the sole contributor to the ‘Other’ peak from June 1996 to October 1996 and a significant contributor from June 1997 to October 1997. A mature putaputaweta overhung one of the seedfall traps at Whitford Bush, and the large peaks are not necessarily a reflection of a putaputaweta rich forest.

5.7.2 Number of target fleshy fruits to fall into target traps.

Fruit production of the five target species (karaka, kohekohe, puriri, taraire, and tawa) is tested for randomness and evenness. If a species produces fruit randomly throughout the year this will add up over time, or with a large enough sample, to having equal probabilities of picking up a fruit from that species at any point during the year. Thus with randomly produced fruit the probability of picking up a fruit is constant throughout the year.

This probability will be similar to the proportion that this species contributes to the total number of fruits collected. Thus it is possible to test whether the chance of picking up a fruit of a specific species is smaller or greater than its total proportion over three years. The graphs at the top of Figure 5.9 illustrate what is meant by the total proportion.

5.7.2.1 Data used.

The data used in this section are number of mature target species fruits that fell into target seedfall trap at Wenderholm Regional Park or Whitford Bush. That is, any mature karaka fruit that fell into karaka traps, or puriri fruit to drop into puriri traps, etc. All other species and ‘accidental catches’ were removed from the data. Mature fruits did include those that had passed through a gut or had been preyed on when mature. Numbers of fruit were used in preference to weights of fruit because numbers allowed direct comparison, while weights would have to be scaled (since different species have different average fruit weights). Also, the weights of consumed or predated fruit would be different from entire mature fruit.

Figure 5.5a: Simpson plot of weight of all fleshy-fruits falling in to seedfall traps at Wenderholm

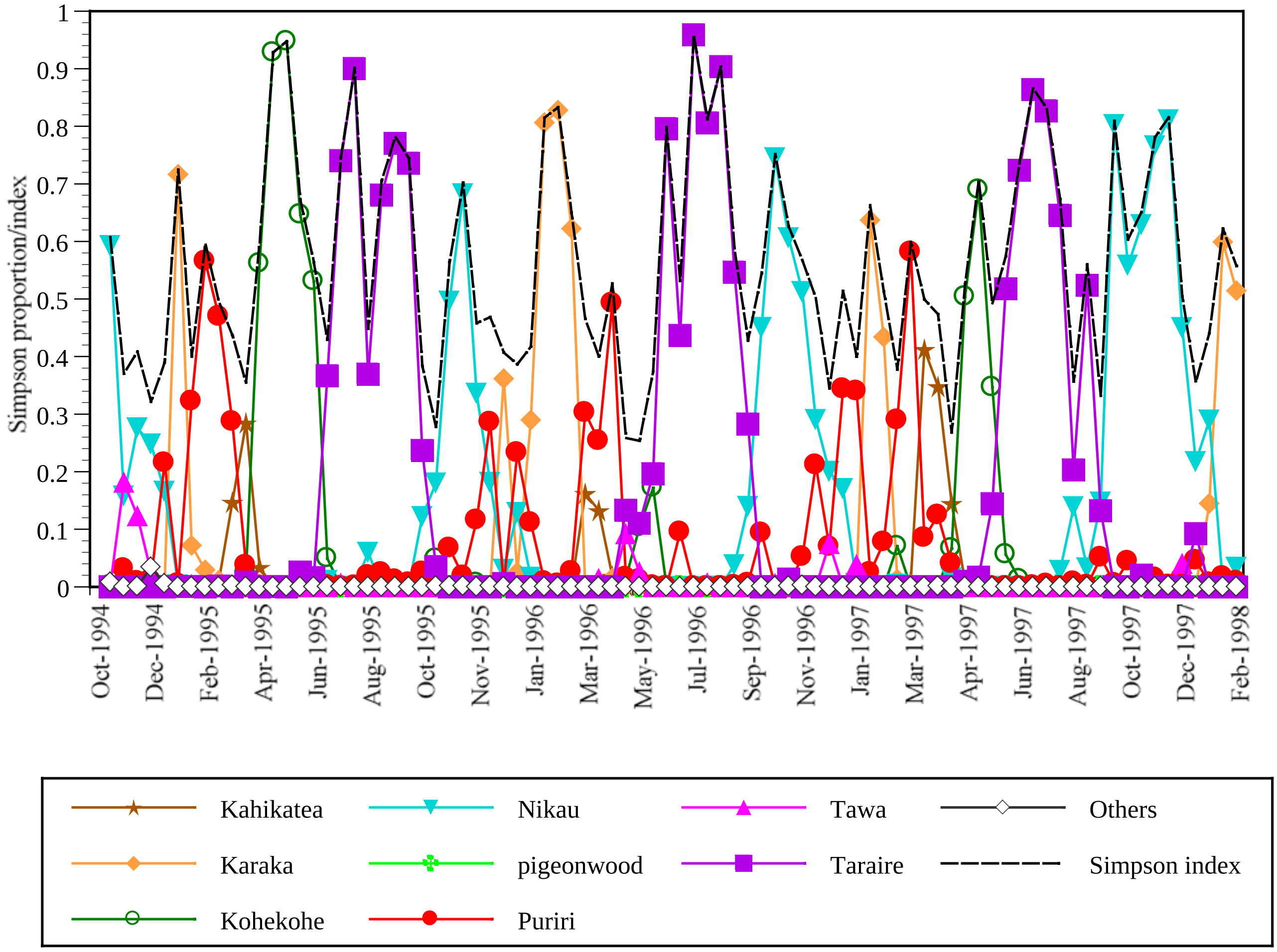
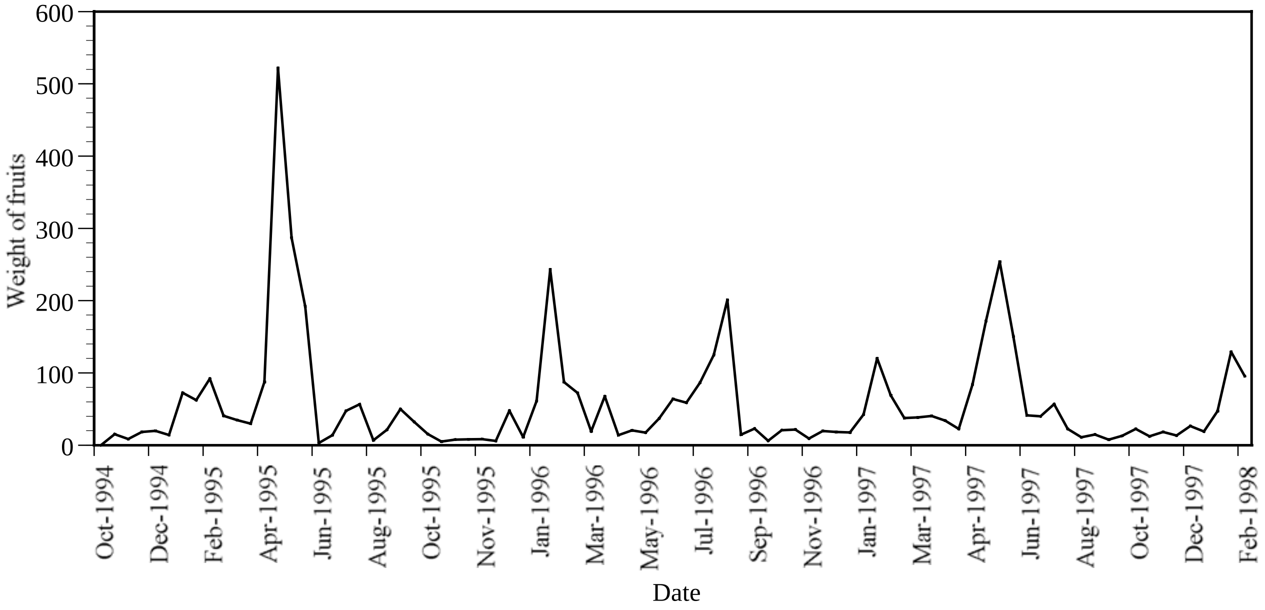


Figure 5.5b: Total weight of all fleshy-fruits falling in to seedfall traps at Wenderholm



A Simpson proportion or index approaching 1 equates to low species diversity. On occasion the large peaks on the bottom graph coincide with large peaks (often approaching 1) on the top graph, this indicates that nearly all the fruit to fall in to the seedfall traps was comprised of a single species.

Figure 5.6a: Simpson plot of number of all fleshy-fruits falling in to seedfall traps at Wenderholm

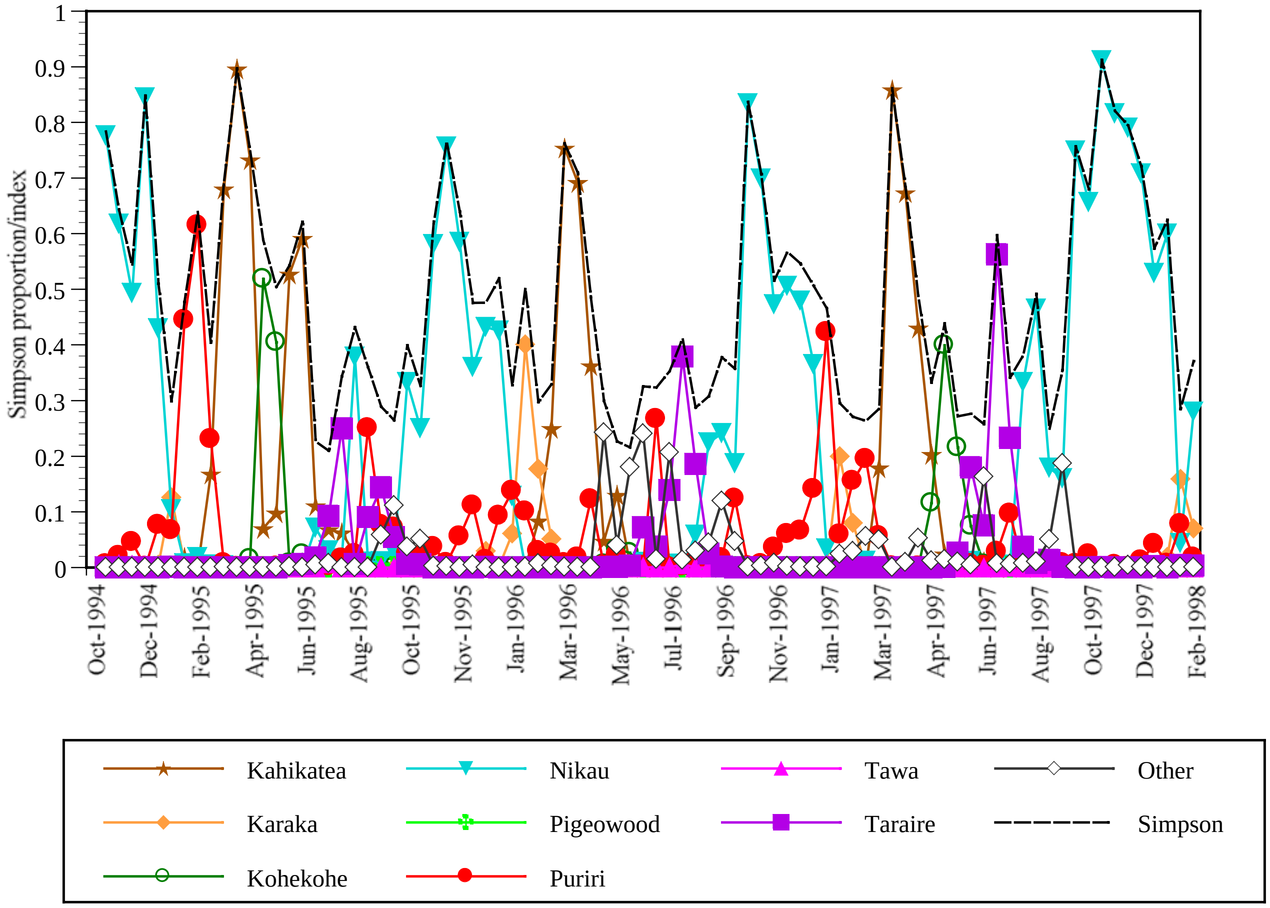
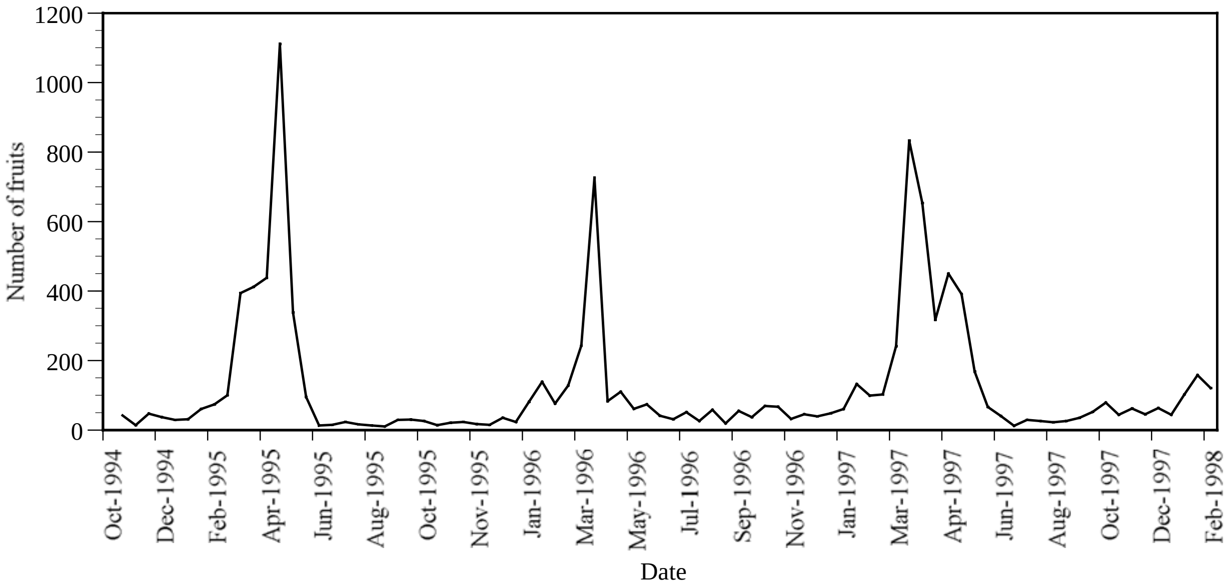


Figure 5.6b: Total number of all fleshy-fruits falling in to seedfall traps at Wenderholm



A Simpson proportion or index approaching 1 equates to low species diversity. On occasion the large peaks on the bottom graph coincide with large peaks (often approaching 1) on the top graph, this indicates that nearly all the fruit to fall in to the seedfall traps was comprised of a single species.

Figure 5.7a: Simpson plot of weight of all fleshy-fruits falling in to seedfall traps at Whitford

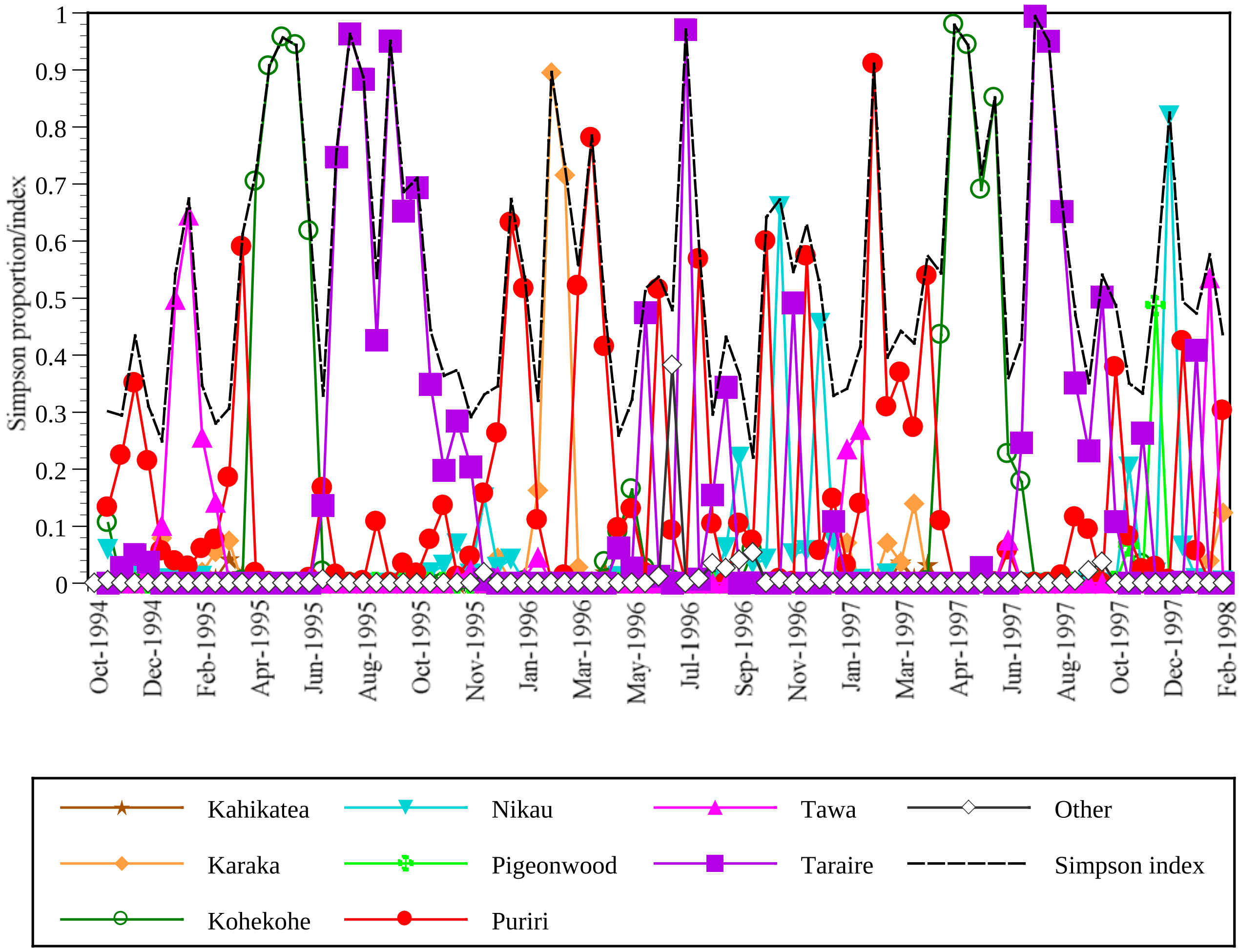
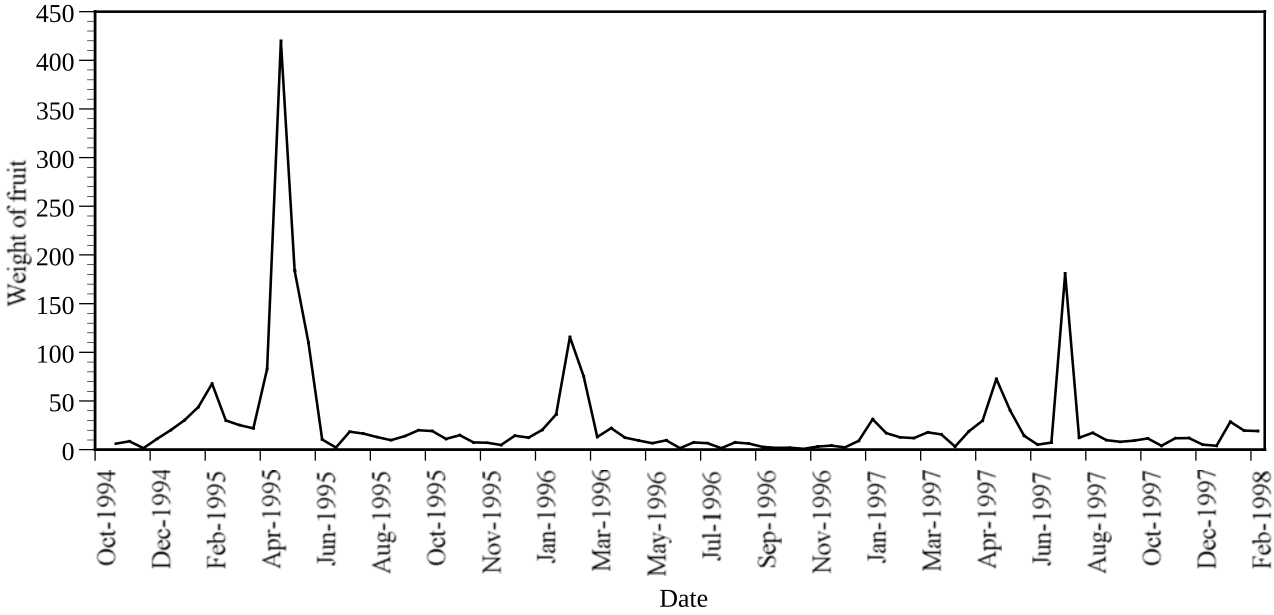


Figure 5.7b: Total weight of all fleshy-fruits falling in to seedfall traps at Whitford



A Simpson proportion or index approaching 1 equates to low species diversity. On occasion the large peaks on the bottom graph coincide with large peaks (often approaching 1) on the top graph, this indicates that nearly all the fruit to fall in to the seedfall traps was comprised of a single species.

Figure 5.8a: Simpson plot of number of all fleshy-fruits falling in to seedfall traps at Whitford

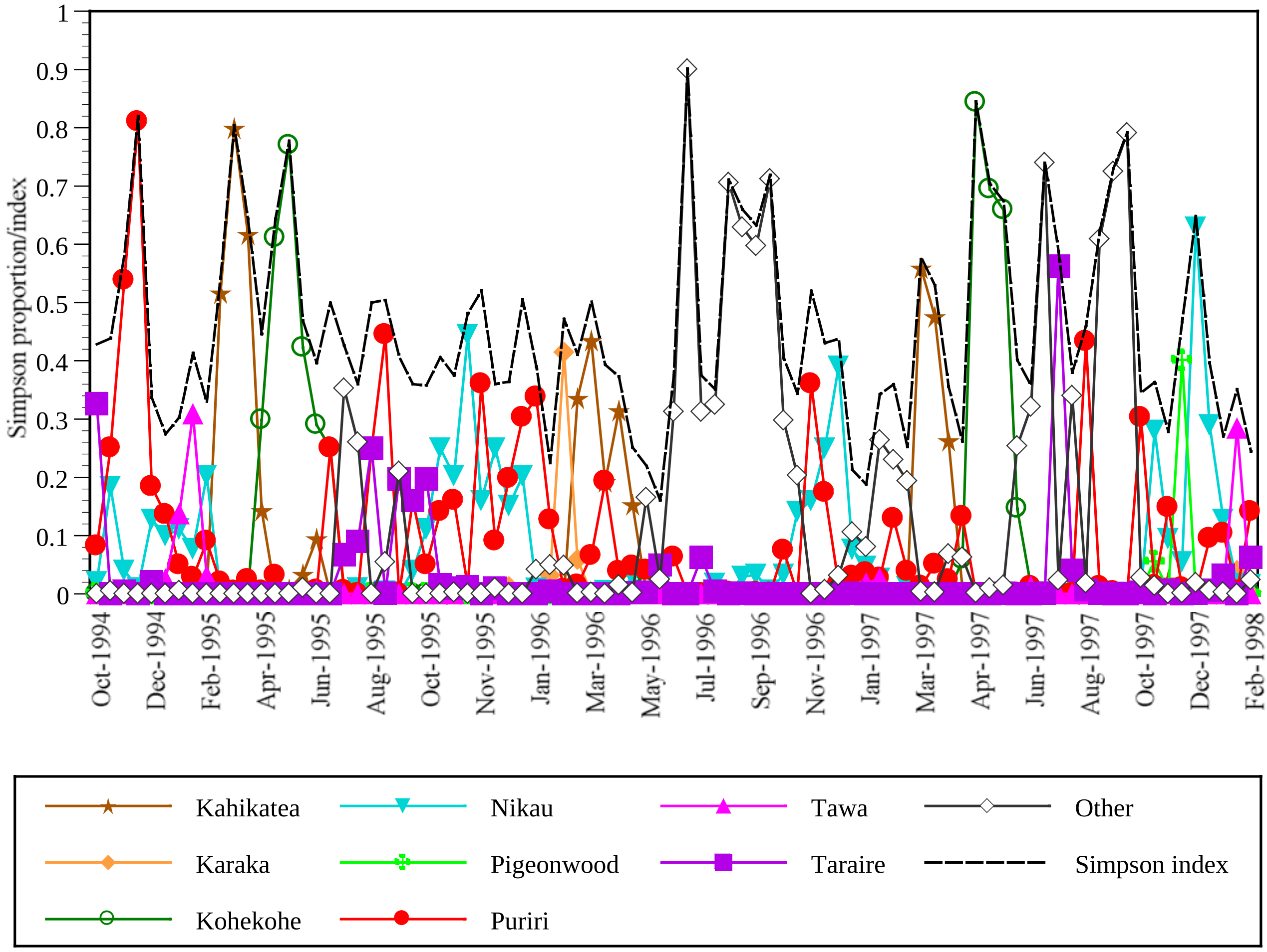
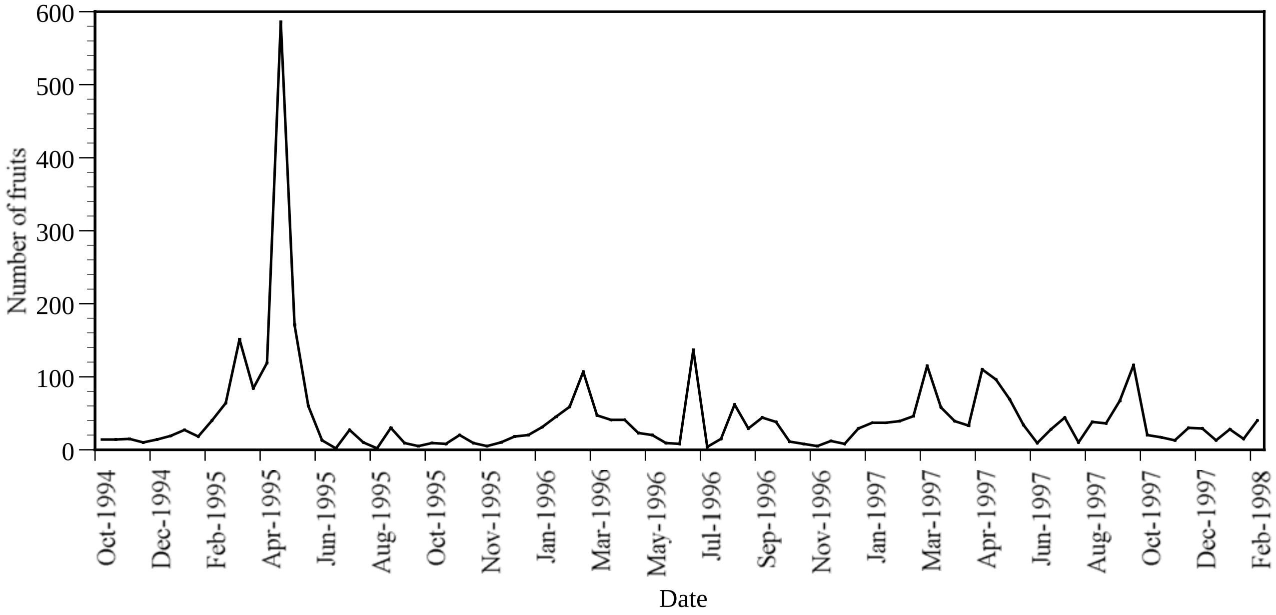


Figure 5.8b: Total number of all fleshy-fruits falling in to seedfall traps at Whitford



A Simpson proportion or index approaching 1 equates to low species diversity. On occasion the large peaks on the bottom graph coincide with large peaks (often approaching 1) on the top graph, this indicates that nearly all the fruit to fall in to the seedfall traps was comprised of a single species.

5.7.2.2 Analysis.

A Simpson index was calculated for each of the target species by taking the square of the proportion that that species contributed to the total number of target fruits per week (refer equation in Section 5.7). This essentially equates to the plot for an individual species (the coloured lines) such as shown in Figures 5.5 to 5.8, but, for this analysis, the total fruit number only included target fruit species to drop in target seedfall traps. These indices are plotted as dotted lines in Figures 5.10 and 5.11 for Wenderholm Regional Park and Whitford Bush respectively. When the index approaches 1 then that particular species comprises the total sample, regardless of how many fruits are in the sample. The index drops when more species contribute to the total number.

The grey areas on Figure 5.10 and 5.11 represent the simulated Monte Carlo expected values generated by resampling the data 1000 times for each of the 85 sampling periods (refer to flow diagram in Figure 5.9). This is the area in which we would expect the Simpson Index values to fall if fruit fall for the species was randomly spread throughout the year. If Simpson Index values exceed the upper limits of the grey area then the fruiting peak for that species is greater than could be expected by chance ($p<0.001$).

The parametric bootstrap method randomly sampled the total number of fruits available each week in the proportions that these fruit occurred in seedfall traps over the entire sampling period (presented diagrammatically in Figure 5.9). For instance, 63% of all fruit caught, over all sampling periods at Wenderholm Regional Park, were kohekohe and 4% was karaka fruit, thus for each sampling period there was 63% chance of a randomly ‘picked’ fruit being kohekohe and 4% of it being karaka.

The total number of fruits available was set to the total number caught at that site for that sampling period, e.g.177 fruits were caught in sampling period 77, 16 October 1997, at Wenderholm Regional Park, therefore 177 fruits were ‘picked’ for that week using random resampling. The SAS syntax is supplied in Appendix 5.1.

The probability of the Simpson index (dotted line) for a particular species exceeding the bootstrap boundaries by chance are $P<0.001$.

The following null hypothesis was tested.
<u>Null hypothesis</u>: The probability of finding a fruit of a particular species is constant over time. Since, a random distribution of fruit over time will approximate a constant distribution given a large enough sample size or sufficient length of time.

<u>Alternative hypothesis</u>: The probability of finding a fruit of a particular species has defined peaks that are comprised of greater than expected numbers of fruit.

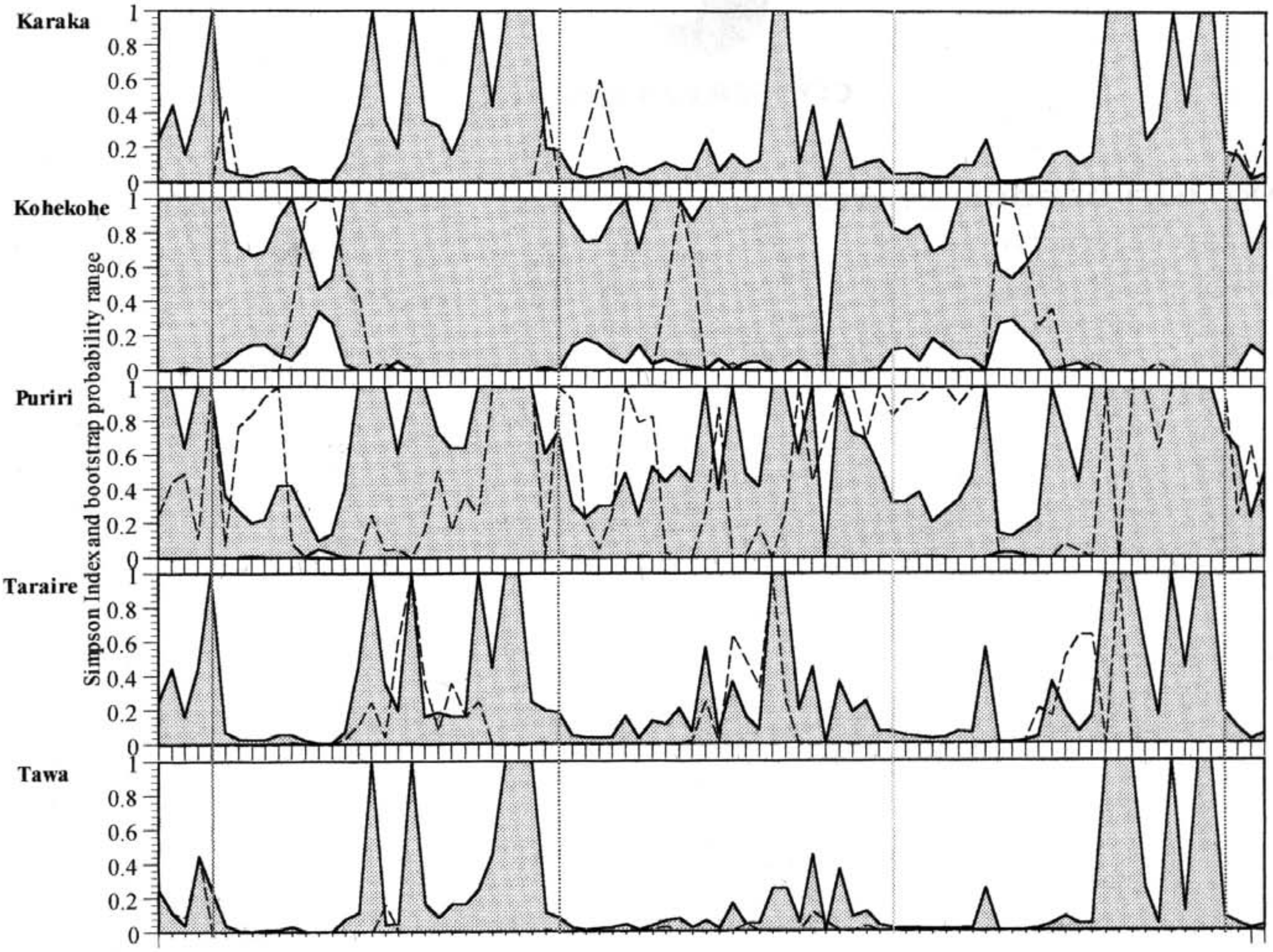
5.7.2.3 Results.

The results are presented for each species individually below, and in Figures 5.10 and 5.11.

Karaka

The null hypothesis can be rejected for karaka at Wenderholm Regional Park (Figure 5.10) and Whitford Bush (Figure 5.11). At Whitford Bush the small number of karaka fruit, caught during three of the four summers (February-March), meant that the chance of picking up a karaka fruit was no greater than the proportion in which karaka was caught over the entire sampling period. That is, the Simpson index for number of karaka fruits found did not exceed the Monte Carlo bootstrap boundaries (the grey area on the graphs in Figures 5.10 and 5.11) most years. However, the second summer (1996) at Whitford Bush had a significantly greater proportion of mature karaka fruits in the seedfall traps than could be expected by chance. The karaka at Wenderholm Regional Park produced significantly greater proportions of fruit than expected most summers.

Figure 5.10: Simpson analysis for number of target fruits to fall in target traps at Wenderholm Regional Park
The probability limits ▨, generated by resampling the original data 1000 times are shown.
The probability of the Simpson index – – – exceeding the bootstrap boundaries by chance is $p<0.001$



Number of fruits produced by target species at Wenderholm
shown in two graphs; for those species that produced low numbers of fruits, and those species that numerically dominated the total fruit production amongst the target species.

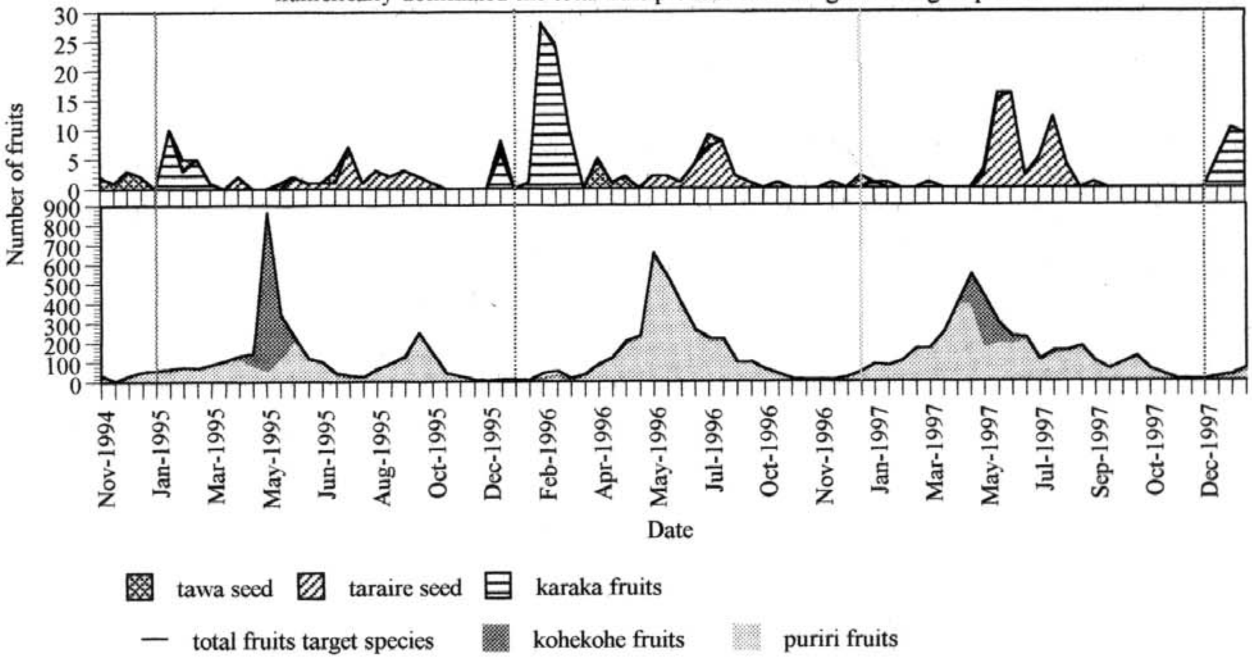
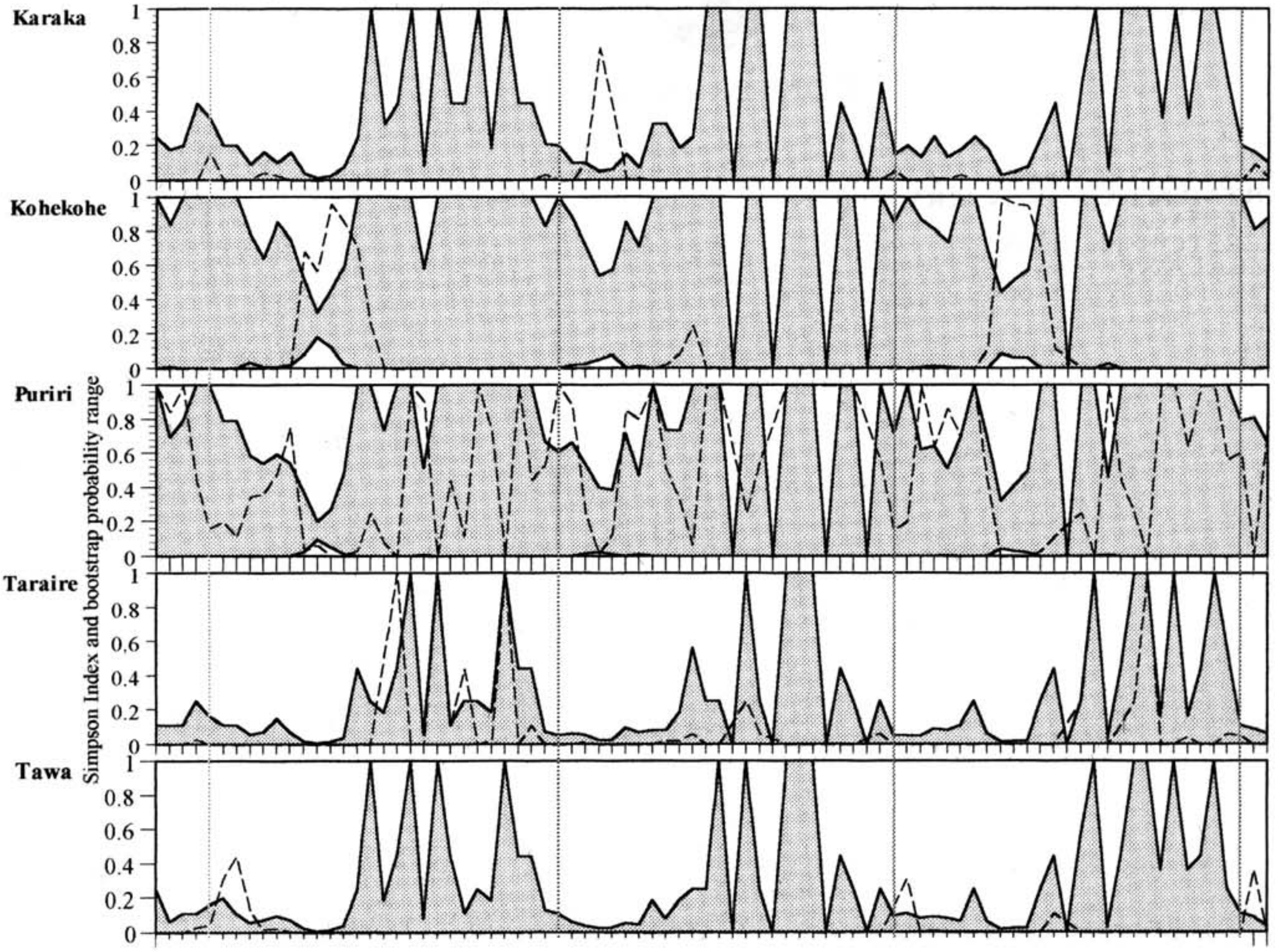
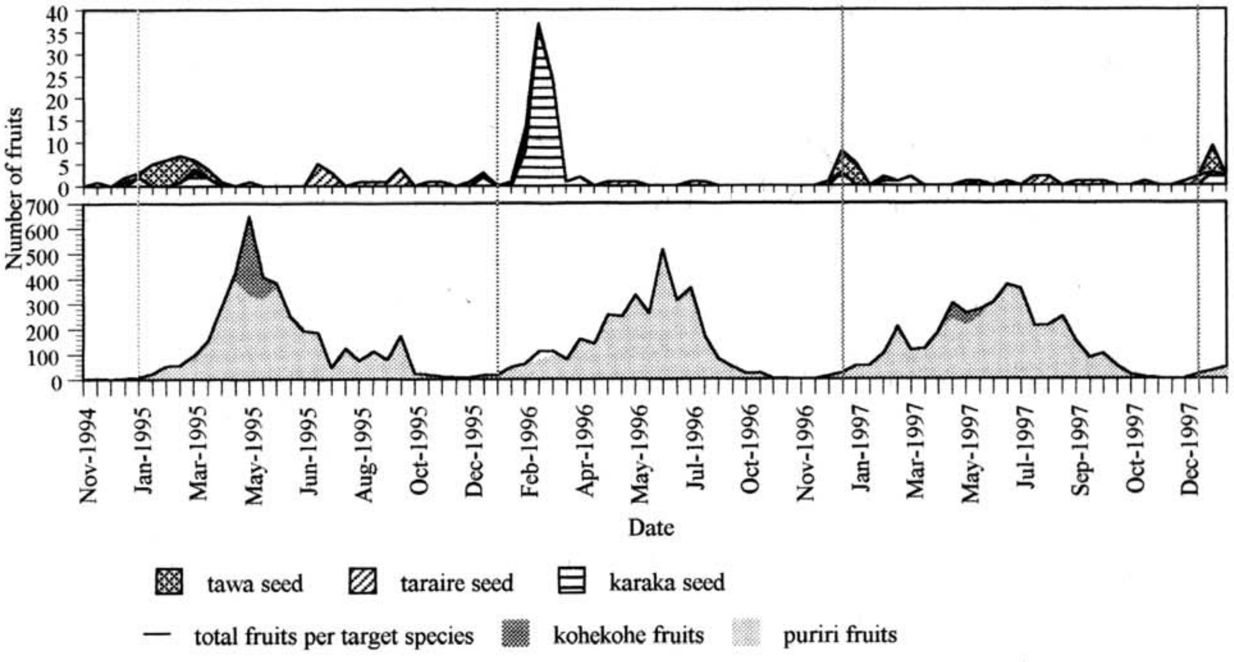


Figure 5.11: Simpson analysis for number of target fruits to fall in target traps at Whitford Bush

The probability limits ▨, generated by resampling the original data 1000 times are shown.
The probability of the Simpson index – – – exceeding the bootstrap boundaries by chance is $p<0.001$



Number of fruits produced by target species at Whitford,
shown in two graphs; for those species that produced low numbers of fruits, and those species that numerically dominated the total fruit production amongst the target species.



Kohekohe

Kohekohe also produced larger proportions of fruit, every other year during May/June at both sites, than could be expected if fruit production was, on average, constant over time (refer to null hypothesis for explanation of constant fruit production). The phenomenon of biennial fruit production by kohekohe has already been explained (Section 5.5.2 Kohekohe.) and is possibly related to the energetic constraints of female trees.

Puriri

Puriri was sporadically available at both sites in proportions significantly greater than expected, especially at Wenderholm Regional Park. This analysis does not reveal any clear seasonality for puriri, but fruiting proportions tended to exceed expected values (Monte Carlo bootstrap values) from about February to May. The lack of clear seasonality is probably due to the deposition of small numbers of fruit into seedfall traps virtually throughout the year.

Taraire

Taraire occurred in significantly greater numbers than expected every year at Wenderholm Regional Park. Numbers of taraire fruit were generally too small at Whitford Bush to be able to distinguish fruit fall from a constant fruit fall pattern, however, there was a significant peak for taraire in the first year at Whitford Bush.

Tawa

Tawa fruit generally fell in insufficient numbers to be able to distinguish it from a random, or constant pattern, at Wenderholm Regional Park. At Whitford Bush, significant peaks occurred during the early summer (December-January) in three of the four years.

5.7.2.4 Discussion

The null hypothesis of constant fruit production (since a random distribution of fruit over time will approximate a constant distribution given a large enough sample size or sufficient length of time) can be rejected for all species and for both sites, except for tawa at Wenderholm Regional Park. The peak quantities (regardless of magnitude) of fruit produced were proportionally greater than could be expected by chance for at least some of the time for all species.

5.8 Fruiting synchrony.

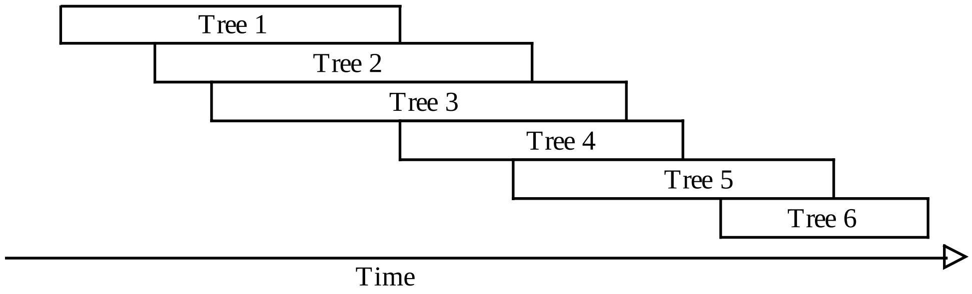
The theory of competitive displacement amongst co-existing species requires that little or no overlap occurs in the production of ripe fruits by competing species. This means that the period of ripe fruit presentation for one species should not overlap significantly with ripe fruit production of another species (refer for example to Figures 6.7 and 7.11 to 7.16). It also requires that the individuals within a species fruit synchronously.

Analyses of synchrony and overlap are often conducted in pair-wise fashion, comparing two species with nearly contemporaneous phenologies with each other for both synchrony and overlap. Primack (1980) used such pair-wise analysis to describe the overlap of flowering individuals within three montane species in New Zealand. Murali and Sukumar (1994) used Hulbert's general overlap, followed by Chi-square analysis, to describe the behaviour of species in different guilds (flowering and various types fruiting guild, such as fleshy fruited, dry fruited).

However, Fleming and Partridge (1984) noted "In the case of plants competing for a limited supply of pollinators, it clearly does not benefit a pair of species to diverge temporally from each other if by doing so they experience increased competition from other guild members. Divergence must be considered in the context of the entire guild simultaneously rather than in a pair-wise fashion." Despite this statement Fleming and Partridge (1984) found no significant difference between their total overlap simulation and Pianka's symmetrical index computed for all pairs.

Nevertheless, the point made regarding comparing entire guilds simultaneously is still valid. Therefore the method used to analyse synchrony and overlap in this study uses a formula developed by Augspurger (1983). This formula (equation 1a) considers the phenological state of an individual in the context of what all other individuals of that same species are doing over the same period. Essentially, the index for a species is the average number of occasions that individuals within the species of interest have fruit simultaneously (Figure 5.12 and equation 2a).

Figure 5.12: Species synchrony sums the occasions that individual trees have fruit simultaneously

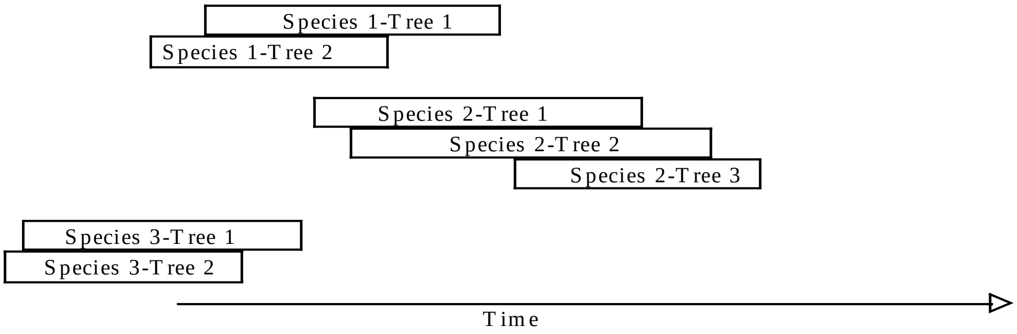


Species synchrony = ((overlap Tree1 with Tree2 + Tree3+ Tree4) + (overlap Tree2 with Tree1 + Tree3 + Tree4 + Tree5)+ …… + (overlap Tree5 with Tree6))/ (Number of trees-1)

The formulae developed by Augspurger (1983) have been modified further to elucidate synchrony (overlap) between species. To calculate the degree of overlap between species, the index sums the number of occasions that individuals of the species of interest have fruit simultaneously with individuals of other species (Figure 5.13 and equation 1b). The individual indices are then averaged for the species (equation 2b).

The SAS code used to sum the number of fruiting occurrences in common (from which to calculate synchrony and overlap values) for each tree is provided in Appendix 5.2.

Figure 5.13: Species overlap sums the occasions that individuals from one species overlap with fruiting occasions of other species



Species1 overlap = ((Species1_Tree1 overlap with Species2_Tree1 + Species2_Tree2 + Species2_Tree3 + Species3_Tree1 + Species3_Tree2) + (Species1_Tree2 overlap with Species2_Tree1 + Species2_Tree2 + Species2_Tree3 + Species3_Tree1 + Species3_Tree2))/ Number of trees

5.8.1 Synchrony and overlap formulae.

In each case let all individuals be numbered 1, 2, 3, … , n

Let n_s = the number of individuals of species s that had fruit
Let sp(i) = the species to which individual i belongs
Let f_i = number of occasions (fortnightly observations) that individual i has ripe fruit

Equation 1a) Synchrony of a given individual with its conspecifics:

$X_i^{(sp)}$ the index of synchrony for individual i, from species s is defined as:

$$X_i^{(sp)} = \left(\frac{1}{n_s - 1}\right)\left(\frac{1}{f_i}\right)\sum_{\substack{j:\,sp(j)=s \\ j \neq i}} e_{ji}$$

Where, e_{ji} = number of occasions (fortnightly sampling periods) that both individuals i and j have one or more ripe fruit synchronously, $j \neq i$, and j is the same species as i, sp(j)=s;

Note that the term $n_s - 1$ is required because individual i cannot overlap with itself.

Equation 1b) Overlap of a given individual with other species:

Let $n_{\neq s}$ = the number of individuals of species other than species s

$X_i^{(o)}$ the index of overlap for individual i, from species s, with other large fruited species at the site is defined as:

$$X_i^{(o)} = \left(\frac{1}{n_{\neq s}}\right)\left(\frac{1}{f_i}\right)\sum_{j:\,sp(j)\neq s} e_{ji}$$

Where, e_{ji} = number of occasions that both individuals i and j have one or more ripe fruit synchronously, and j is not of the same species as i, $j \neq s$;
f_i = number of occasions individual i has ripe fruit;

Note that the term $n_s - 1$ from equation 1a) has changed to $n_{\neq s}$ because individual i is not included in the total since j is not of the same species as i, $j \neq s$.

For all instances of X:

When X = 1.0, perfect synchrony occurs, i.e. all fruiting days of individual i overlap with fruiting occasion of each other individual, $j \neq i$, in the selected population.

When X = 0.0, no synchrony occurs, i.e. no overlap occurs among any of the fruiting occasions of individual i and any other individual, $j \neq i$, in the selected population.

Equation 2a) Synchrony of a species population is defined as:

$$Z_s^{(sp)} = \frac{1}{n_s}\sum_{i:\,sp(i)=s} X_i^{(sp)}$$

Where $X_i^{(sp)}$ is the synchrony of individual i as calculated in part 1a) (above).

Equation 2b) Overlap of a species population with other species is defined as:

$$Z_s^{(o)} = \frac{1}{n_s}\sum_{i:\,sp(i)=s} X_i^{(o)}$$

Where $X_i^{(o)}$ is the overlap of individual i with other species as calculated in part 1b).

The above equations take account of trees that did not produce fruit in any one calendar year, since the total population includes all trees monitored (n_s), regardless of whether ripe fruit was produced or not.

Equation 3a) Within-species critical value:

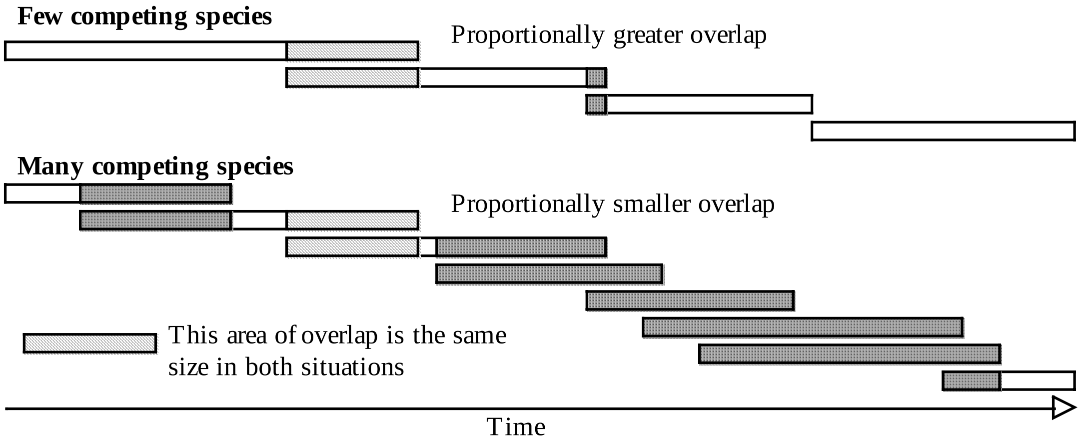
A species is considered synchronous if the fruiting periods of individuals overlapped with other individuals, of the same species, for at least half the duration of their fruiting periods. For instance, an individual that had fruit on 8 occurrences should overlap with other con-specifics for at least 4 of those occurrences.

Using equation 1a), and substituting the above assumption, generates a critical value for within-species synchrony of 0.5. Any species that exceeds this value is more synchronous than asynchronous. Any species that has a within-species synchrony less than 0.5 is more asynchronous than synchronous. That is if the critical value $Z_s^{(sp)} < 0.5$ then that species is more asynchronous than synchronous.

Equation 3b. Critical value for overlap between species:

Pianka (1974) found that the degree of overlap between co-existing species was closely related to the number of competing species and the intensity of the competition, rather than environmental variability. Stronger competition resulted in greater niche separation (less overlap) and the amount of overlap had to be viewed in proportion to the number of competitors. For instance, low overlap in a situation with many competitors might be of similar magnitude to high overlap with few competitors (refer to Figure 5.14). He further found that the total overlap (sum over all species of lizard) increased with increased lizard species density, even though the average amount of overlap between pairs of species decreased (Pianka 1974).

Figure 5.14: The magnitude of overlap with other species should be viewed in proportion to the number of competing species (Pianka 1974).



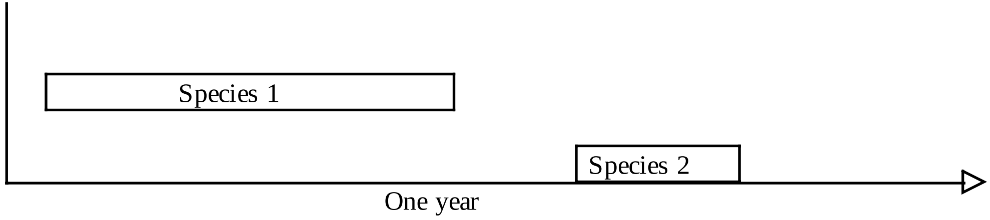
Thus the overlap between fruiting species is likely to be proportional to the number of sympatric species.

The longer a particular species carries ripe fruits the greater the possibility that its fruiting phenology will overlap with that of other species. Moreover, the more species that produce ripe fruit, within the defined location, the greater the chance that long-fruiting species will present ripe fruit simultaneously with other species (Figure 5.15).

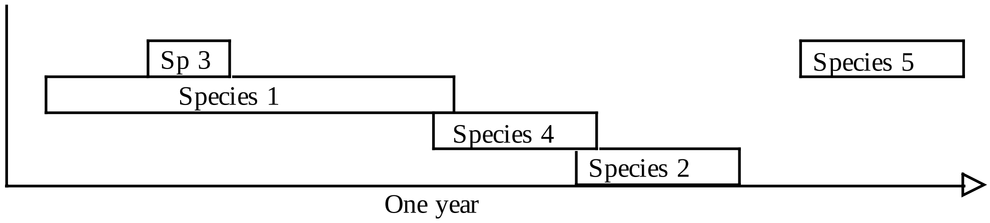
Let's therefore assume that the average overlap in fruiting phenology experienced by one species is proportional to the length of time this species fruited and proportional to the number of co-existing species that fruit within the same habitat.

Figure 5.15: Illustration of the chance of overlap between species in the same habitat. *Both the number of species fruiting and the length of fruiting contribute to the possibility of overlap for any particular species.*

Few fruiting species within the habitat - reduced chance of overlap between species



More fruiting species - more overlap. Long fruiting season (Species 1) more chance of overlap



In each case let all individuals be numbered 1, 2, 3, … , n

Let n_s = the number of individuals of species s
Let $n_{\neq s}$ = the number of individuals of species other than species s
Let sp(i) = the species to which individual i belongs
Let $N_{\neq s}$ = the number of co-existing species other than species s
Let $\overline{F}_s$ = the period that trees within species s had ripe fruit

Mean overlap events ($\overline{E}_s$) for species s are the sum of the number of occasions that each individual tree within species s overlapped with other species (e_{ji}), divided by the total number of trees that could have fruited and were not the same as species s ($n_{\neq s}$).
This is expressed mathematically as:

$$\overline{E}_s = \frac{\sum_{n_s}\left(\sum_{j:\,sp(j)\neq s} e_{ji}\right)}{\sum_{N_{\neq s}} n_{\neq s}}$$

Where, e_{ji} = number of occasions that both individuals i and j have one or more ripe fruit synchronously, and j is not of the same species as i, $j \neq s$;

By substituting the above species parameters into equation 1b) we can calculate the critical overlap values for each species

The critical index of overlap value $C_s^{(o)}$ for species s with other large fruited species at the site is defined as:

Equation 3b. Critical value for overlap between species:

$$C_s^{(o)} = \left(\frac{1}{N_{\neq s}}\right)\left(\frac{1}{\overline{F}_s}\right)\overline{E}_s$$

Where, $N_{\neq s}$ = the number of co-existing species other than species s
$\overline{F}_s$ = the period that trees within species s had ripe fruit.

If the mean overlap value for species s (including 95% confidence intervals), calculated by equations 1b) and 2b), is smaller than the overlap critical value $C_s^{(o)}$ then we can be 95% certain that the species showed less overlap with other species than might be expected. This is interpreted to mean that the fruiting phenology of this species does not overlap significantly with the phenology of other species. It is therefore probably optimally spaced in time with regards to other large-fruited species in the same population and is experiencing no, or reduced, competition for the services of a disperser. Any species with overlap values greater than the critical value are not optimally spaced in time, and are therefore not displaying character displacement in fruiting phenology.

Note that there is an issue with defining how the period of ripe fruit production ($\overline{F}_s$) should be calculated. Various population statistics were tried, and each produced slightly different results. It was felt that modelling these various population statistics to determine the best fit was outside the scope of this thesis. However, rather than skew the outcomes by presenting only one type of population statistics, all five parameters are presented in the overlap results to allow more objective comparisons.

5.8.2 Hypotheses to be tested.

The following two null hypotheses were tested pertaining to the synchrony within species and the overlap between species.

Nu**ll Hypothesis 1**: There is no synchrony of fruiting within a species.
Fruit is available throughout the year because individuals within a species can have ripe fruit at any time of the year.
Alternative Hypothesis 1: There is synchrony of fruiting within a species.
When one individual of a species is fruiting there is a good probability that other individual trees of the same species are fruiting simultaneously.

Null Hypothesis 2: Fruiting patterns of different species overlap substantially.
Given that species, and individuals, can have ripe fruit at any time of the year it follows that fruit production between species will overlap and will therefore be synchronous.
Alternative Hypothesis 2: There is little or no overlap between fruiting seasons of different species.
When one species is fruiting there are no or few other species with ripe fruit simultaneously.

5.8.3 Data used.

The data used were observations of the phenology trees at Wenderholm Regional Park and Whitford Bush. The counts of ripe fruit were converted to presence or absence of ripe fruit. Figures 5.16 and 5.17 illustrate the presence of ripe fruit on each of the trees at Wenderholm Regional Park and Whitford Bush respectively. Three calendar years were analysed.

At each site some of the phenology trees were not added until the middle of the second calendar year (1995). Thus the data for that year (year 2) was analysed using only the 6 original phenology trees for each species, with the exception of tawapou at Wenderholm Regional Park for which 10 trees were scored throughout all years. Whitford Bush only had a total of 6 observable puriri and 9 observable taraire throughout, but the equations presented above take account of this.

5.8.4 Results for Wenderholm Regional Park.

Species on average had ripe fruit on 4.81±1.52 (mean ± 95% confidence interval of the mean) fortnightly visits per calendar year. Puriri trees had ripe fruit on significantly more visits (refer Tables 5.2, 5.3 and Figures 5.16, 5.18 and 5.19) than any other species. This was a reflection of the length of time that individual puriri trees had one or more ripe fruits, which was significantly longer than any

Figure 5.16: Occasions that phenology trees at Wenderholm had one or more ripe fruits

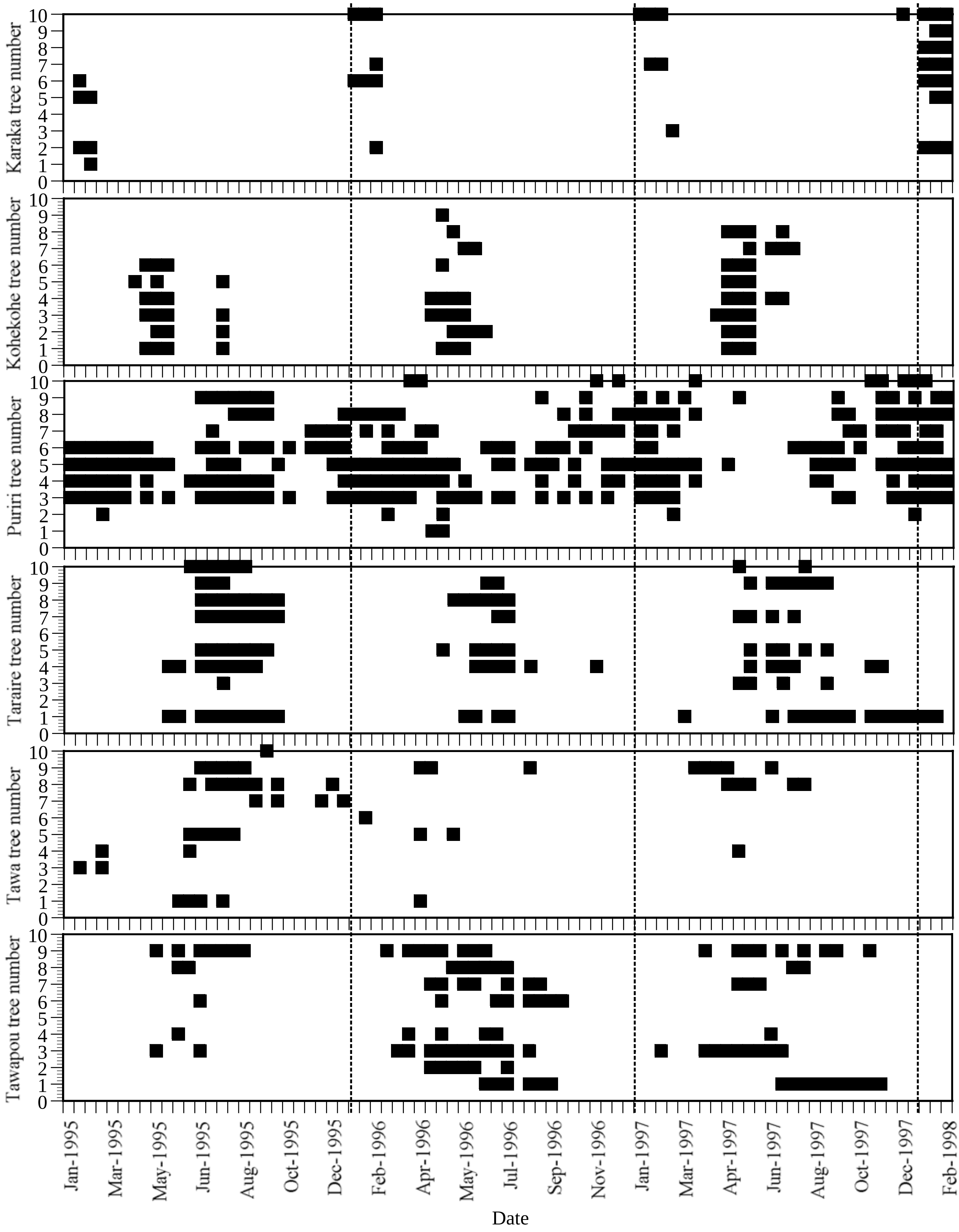
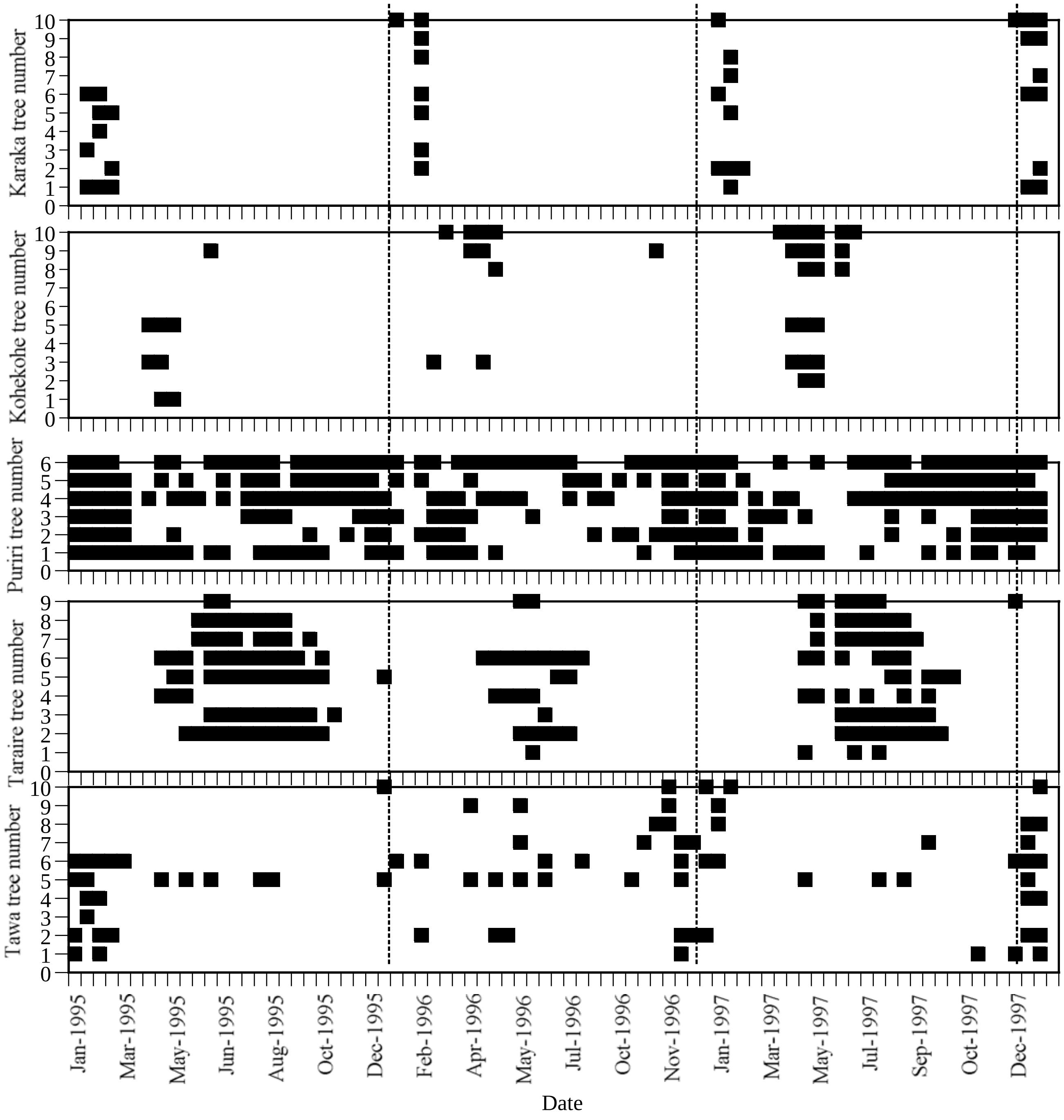


Figure 5.17: Occasions that phenology trees at Whitford had one or more ripe fruits



other species (ANOVA F=6.62, P<0.0001, df=17, refer Appendix 5.3 Wenderholm DURATN for population duration, and F=6.62, P<0.0001, df=17, for fruiting trees only Wenderholm DAYS)[2]. A specific puriri tree could have ripe fruit on up to 19 visits of 26 fortnights per calendar year (Table 5.3). Only 9 of 81 sampling periods (11%) over the entire study did not have any ripe puriri fruit (Table 5.2). The number of visits when ripe fruit was seen in other species varied greatly. Tawapou (52%), taraire (47%) and tawa (36%) tended to have trees with fruit on more visits than either kohekohe (22%) or karaka(16%).

Table 5.2: Number of visits when ripe fruit was sighted at Wenderholm Regional Park. Each visit is one fortnightly sampling period. Percentage (%) of trees/visit is the average percentage, over the entire study, of sample trees seen fruiting per visit. These averages can be quite small for species with short fruiting seasons. Population duration is the average number of visits that individual trees within the population, including trees that did not produce fruit, had ripe fruit. This differs from **fortnights** in Table 5.3 which only includes those trees that had fruit on at least one or more occasion.

Species	Visits* with ripe fruit	% visits*	% trees/visit (± 95% conf. int#)	Population duration (± 95% conf. int#)
Karaka	13	16.05	5.43±3.40	0.81±0.47
Kohekohe	18	22.22	9.84±5.10	2.65±0.61
Puriri	72	88.89	36.26±5.18	8.96±2.44
Taraire	38	46.91	15.02±4.80	3.54±1.44
Tawa	29	35.80	6.38±2.32	1.19±0.71
Tawapou	42	51.85	12.59±1.83	3.40±1.37

* *Number of visits when ripe fruits were seen on* ***any*** *individual of a specific species. This differs from fortnights (e.g. Table 5.3), which is the mean number of sampling days that* ***individual*** *trees had ripe fruit.*

\# *95% confidence interval of the mean*

The population duration of fruiting, for species other than puriri, varied from short periods (e.g. karaka = 0.81 fortnightly visits) to somewhat longer periods (e.g. taraire = 3.54 fortnightly visits) (refer Table 5.2).

The proportion of trees with ripe fruit, within the sample population, varied greatly between species. Puriri again had a significantly larger proportion of trees (36%) with at least one ripe fruit throughout the study (ANOVA F=29.63, P<0.0001, df=5, refer Appendix 5.3 Wenderholm PROP, and Figure 5.18) and few periods when no fruit was available. Karaka, tawa and kohekohe were on average available in smaller proportions over the period of the study (5, 6 and 10% respectively; Table 5.2). This was partially attributable to the short fruiting phenology of these species, but also in part to the relatively small number of individuals fruiting in any calendar year (e.g. in year 4 seven trees of both karaka and tawa never bore any ripe fruit; Table 5.3). However, most kohekohe trees produced fruit in every year, including at least some fruits on the male trees (trees 2, 5, 9 and 10).

5.8.4.1 Within-species synchrony.

For population synchrony ($Z_s^{(sp)}$), values approaching one (1) indicate perfect synchrony (within-species overlap) between trees of that species. Synchrony values approaching zero (0) indicate no synchrony (within-species overlap) between trees of that species. In several instances the critical synchrony values ($C_s^{(sp)}$) were included within the 95% confidence limits of the mean species synchrony values ($Z_s^{(sp)}$). These instances are indicated by “Yes?” in Table 5.3.

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[2] Critical values and degrees of freedom for each test can generally be found in the Appendices mentioned in the text.

Table 5.3: Duration of fruiting and synchrony of trees with one or more ripe fruits at Wenderholm Regional Park.
Data collected by observation of marked trees. Mean synchrony index and synchrony critical value for each species are shown. "Yes?" means that the 95% confidence interval includes the critical value.

					Fortnights* of ripe fruit		**Synchrony ($Z_s^{(sp)}$) within species**		**Critical value $C_s^{(sp)} = 0.5$**
Year	Species	# individs.	Not fruiting	Visits with ripe fruit	Mean ± 95% confidence interval	Range	Mean ± 95% confidence interval	Range	Species synchronous? ($Z_s^{(sp)}$)>0.5
2	Karaka	6	2	2	1.50±0.58	1-2	0.67±0.00	0.67-0.67	**Yes**
3	Karaka	10	6	3	2.00±1.16	1-3	0.78±0.41	0.55-1.00	Yes?
4	Karaka	10	7	5	2.33±1.76	1-4	0.25±0.62	0.00-0.05	Yes?
2	Kohekohe	6	0	5	3.33±0.42	3-4	0.74±0.11	0.53-0.80	**Yes**
3	Kohekohe	10	2	6	2.50±1.00	1-4	0.48±0.09	0.32-0.57	Yes?
4	Kohekohe	10	2	7	3.63±0.52	3-5	0.75±0.16	0.36-0.90	**Yes**
2	Puriri	6	1	24	13.60±6.40	1-19	0.70±0.22	0.57-1.00	Yes?
3	Puriri	10	0	25	8.80±3.94	2-19	0.39±0.05	0.32-0.56	No
4	Puriri	10	1	20	8.56±2.42	2-15	0.54±0.08	0.40-0.75	Yes?
2	Taraire	6	2	9	6.50±3.88	1-10	0.71±0.32	0.53-1.00	Yes?
3	Taraire	10	4	9	4.17±1.50	2-6	0.67±0.16	0.28-0.50	**Yes**
4	Taraire	10	3	10	5.86±2.68	2-13	0.45±0.11	0.21-0.57	Yes?
2	Tawa	6	2	7	3.25±1.50	2-5	0.32±0.22	0.17-0.50	Yes?
3	Tawa	10	6	5	1.75±0.96	1-3	0.31±0.44	0.00-0.67	Yes?
4	Tawa	10	7	9	3.67±2.66	1-5	0.27±0.52	0.10-0.50	Yes?
2	Tawapou	10	5	8	2.60±2.24	1-7	0.36±0.18	0.14-0.40	Yes?
3	Tawapou	10	2	16	6.88±1.44	4-11	0.49±0.05	0.31-0.43	Yes?
4	Tawapou	10	4	14	5.67±3.34	1-10	0.30±0.10	0.16-0.40	No
			Never fruited	Average over all years					
All	Karaka		3	3.33	1.91±0.62	1-4	0.59±0.19	0.00-1.00	Yes?
All	Kohekohe		1	6.00	4.14±0.46	1-5	0.65±0.08	0.32-0.90	**Yes**
All	Puriri		0	23.00	9.71±2.34	1-19	0.51±0.07	0.32-1.00	Yes?
All	Taraire		2	9.33	5.41±1.50	1-13	0.59±0.10	0.21-1.00	Yes?
All	Tawa		1	7.00	2.82±1.00	1-5	0.30±0.13	0.00-0.67	No
All	Tawapou		2	12.67	5.37±1.50	1-11	0.39±0.06	0.16-0.55	No

* Number of days sampled on which ripe fruit was seen on **individual trees**. Each of these days is a fortnight apart. Trees that did not fruit during any one year were excluded from the averages for that year. The synchrony calculation does not include non-fruiting trees either, only trees that fruited are included in equation 1a)

There were significant differences between species, with kohekohe and karaka and taraire generally being more synchronous and tawa less synchronous than other species (Table 5.3, Figures 5.18 and 5.19). Kohekohe achieved the highest mean population synchrony value ($Z_s^{(sp)} = 0.78$) in any one year and was the only species for which the mean synchrony over all years exceeded the synchrony critical value ($C_s^{(sp)} = 0.5 >$ kohekohe $Z_s^{(sp)}{}_{\text{all years}} = 0.65 \pm 0.08$; Table 5.3). For kohekohe we can reject Null Hypothesis 1, since the estimate of the population mean, including the 95% confidence level is greater than the critical value $C_s^{(sp)} = 0.5$.

Kohekohe, taraire and puriri all had individual trees with high within-species synchrony ($X_i^{(sp)} = 1.0$) during some years, but species averages ($Z_s^{(sp)}$) were lower (Table 5.3). Karaka and taraire each had one year where the population synchrony value exceeded the critical value with 95% confidence, and two years where the population synchrony value exceeded the critical value although it was still included in the 95% confidence interval of the mean. This resulted in an overall critical value that was greater, but not significantly so, than the critical value (karaka $Z_s^{(sp)}{}_{\text{all years}} = 0.59 \pm 0.19$, taraire $Z_s^{(sp)}{}_{\text{all years}} = 0.59 \pm 0.10$). Thus we fail to conclusively reject Hypothesis 1 for karaka and taraire.

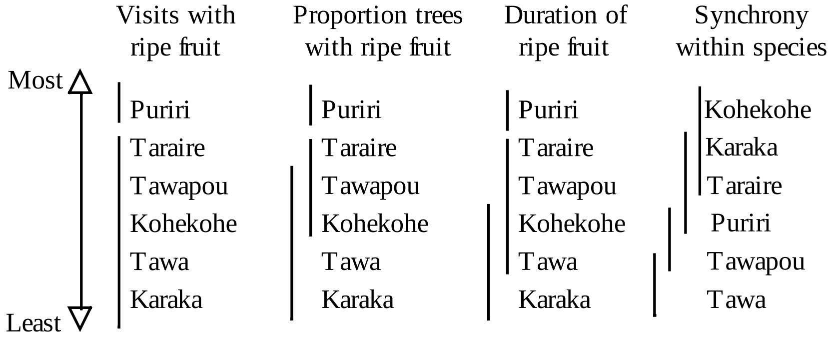
It was also not possible to conclusively reject Hypothesis 1 for puriri. Interestingly enough, puriri just exceeded the overall critical value (puriri $Z_s^{(sp)}{}_{\text{all years}} = 0.51 \pm 0.07$) despite having one year where the species failed to exceed the critical value. Tawapou ($Z_s^{(sp)}{}_{\text{all years}} = 0.39 \pm 0.06$) and tawa ($Z_s^{(sp)}{}_{\text{all years}} = 0.30 \pm 0.13$) on average showed less internal synchrony than the critical level ($C_s^{(sp)} = 0.5$) and less synchrony than the other species, although the 95% confidence interval included the critical value in two (for tawapou) or three (for tawa) of the years.

As can be seen from Figure 5.18 and 5.19 many of the species are not significantly different from each other with regards to synchrony. Tawa is the most different with the smallest overlap values and is also different from all the species that were shown to have greater than expected synchrony values (although the critical value was included in the 95% confidence interval for several species).

Figure 5.18: A posteriori Tukey's HSD test for different fruiting synchrony variables at Wenderholm Regional Park.

Alpha=0.05

Species joined with the same bar are not significantly different.



Note that **visits with ripe** fruits pertains to occasions when ripe fruits were seen on **any** individual of a specific species, whereas **duration of ripe** fruit refers to the average length of time that trees of a particular species carried ripe fruit. **Proportion** relates to the average proportion of trees per species that had one or more ripe fruits per visit. **Synchrony within species** refers to the number of occasions that trees within a species carried ripe fruit simultaneously.

Synchrony varied between years (F=8.06, P=0.0006, df=2), with calendar year 2 being significantly different from years 3 and 4 (refer to Figure 5.19 and Appendix 5.3 Wenderholm WITHINSP). The interaction term between year and species was also significant (F=6.04, P<0.0001, df=10), indicating that some species behaved differently in different years (see Figure 5.19) and probably reflecting the biennial fruiting evident for several species.

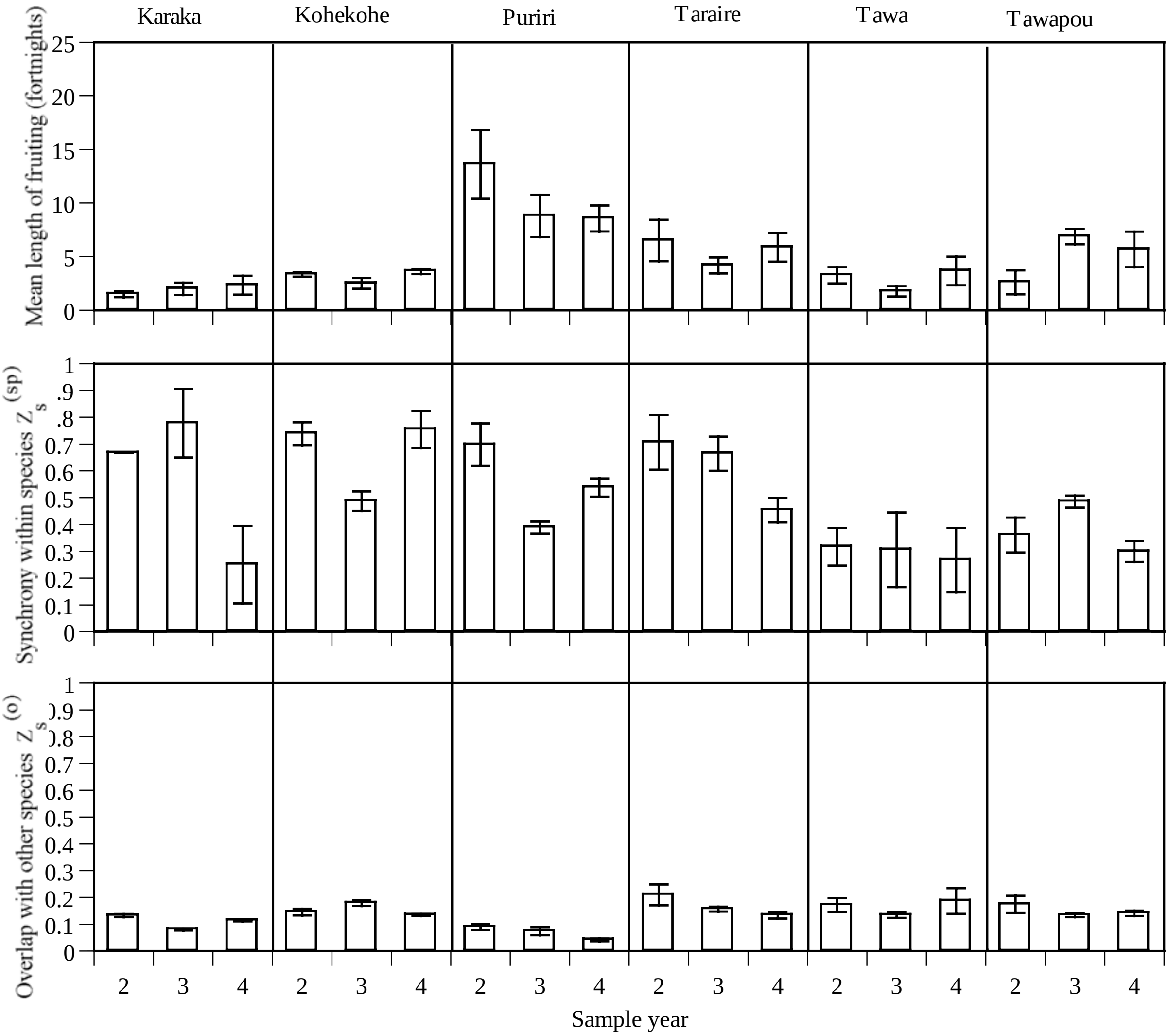
5.8.4.2 Species overlap

Various fruiting phenology population statistics (mean, median, mode, number of visits with fruit) were used in equation 3b) giving rise to species with greater or lesser degrees of overlap (with other species) according to which statistic was used. It was felt that modelling these various population statistics to determine the best fit was outside the scope of this thesis. However, rather than skew the outcomes by presenting only one type of population statistics, all five parameters are presented in the overlap results (Table 5.4) to allow more objective comparisons.

A species was considered to show less overlap than expected when three or more of the critical overlap tests ($C_s^{(o)}$ using different population statistics) were significantly larger than the population overlap value ($Z_s^{(o)}$) (refer to Table 5.4). In many instances the critical overlap values ($C_s^{(o)}$) were included within the 95% confidence limits of the mean species overlap values ($Z_s^{(o)}$). These instances are indicated by "yes?" in Table 5.4.

Figure 5.19: Mean length of fruiting (fortnights) and synchrony analysis for large fruited-species at Wenderholm Regional Park

Graphs show the means for the whole population, plus standard error for the mean, for each species for each calendar year.



Kohekohe showed significantly less overlap than expected in all years. Puriri, taraire and tawapou had less overlap than expected in two of the three years, and tended to less overlap than expected in the remaining year. Overall, these species tended to not overlap significantly with other species (refer to Figures 5.19 and 6.7).

Karaka exceeded the critical overlap values in nearly all tests and tended to overlap in fruiting phenology with puriri. Tawa tended to less overlap than expected in two of the three years, probably due the small numbers of fruiting trees seen (Table 5.3).

On average (Table 5.4), over all years, kohekohe, puriri and tawapou had significantly less overlap than expected, thus Null Hypothesis 2 can be rejected for these species. Taraire and tawa tended to have less overlap than expected, but not conclusively so. Karaka exceeded the overlap critical values, thus we fail to reject the Null Hypothesis. However, all species, including karaka, on average had less overlap with other species than synchrony within the species (Figure 5.19).

Table 5.4: Overlap and critical overlap values for sample species at Wenderholm Regional Park.
Length of fruit phenology was defined in five different ways. Mode = the most commonly occurring length of fruiting for a species in a year. Median = the mathematical middle between the shortest duration>0 and the longest. Mean all = average over all trees of a species, including non-fruiting individuals. Mean fruiting = average over all trees that had one or more fruit that year. Visits with fruit = the number of visits that a species had ripe fruit on at least one tree. (Also see explanation next page)

		$\overline{F}_s$ = **measure of length of fruiting phenology** (fortnights; except visits)							**Critical overlap values $C_s^{(o)}$**					**Overlap ($Z_s^{(o)}$) with other species**		**Critical overlap values $C_s^{(o)}$ > species overlap values $Z_s^{(o)}$?**					
Year	**Species**	Mode	Median	Mean all	Mean fruiting	Visits with fruit	**Total days overlap other species**	**# trees of co-occurring species**	Mode	Median	Mean all	Mean fruiting	Visits with fruit	**Mean**	**± 95% confidence interval**	Mode	Median	Mean all	Mean fruiting	Visits with fruit	**Overall overlap > 3× yes**
2	Karaka	1.5	1.5	1	1.5	2	26	34	0.102	0.102	0.153	0.102	0.076	0.13	0.02			yes			
3	Karaka	2	2	0.8	2	3	36	50	0.072	0.072	0.180	0.072	0.048	0.08	0			yes			
4	Karaka	2.5	2.5	0.7	2.33	5	44	50	0.070	0.070	0.251	0.075	0.035	0.11	0			yes			
2	Kohekohe	3	3.5	3.33	3.33	5	100	34	0.196	0.168	0.176	0.176	0.118	0.14	0.02	yes	yes	yes	yes		**yes**
3	Kohekohe	2.5	2.5	2	2.5	6	188	50	0.301	0.301	0.376	0.301	0.125	0.18	0.02	yes	yes	yes	yes		**yes**
4	Kohekohe	3	4	2.9	3.63	7	210	50	0.280	0.210	0.290	0.232	0.120	0.13	0	yes	yes	yes	yes		**yes**
2	Puriri	16	10	11.67	14	24	213	34	0.078	0.125	0.107	0.089	0.052	0.09	0.02		yes	yes?	yes?		yes?
3	Puriri	2	10.5	8.8	8.8	25	335	50	0.670	0.128	0.152	0.152	0.054	0.07	0.02	yes	yes	yes	yes		**yes**
4	Puriri	8.5	8.5	7.7	8.56	20	184	50	0.087	0.087	0.096	0.086	0.037	0.04	0.02	yes	yes	yes	yes	yes?	**yes**
2	Taraire	7.5	5.5	4.33	6.5	9	156	34	0.122	0.167	0.212	0.141	0.102	0.2	0.08	yes?	yes?	yes?	yes?		yes?
3	Taraire	4	4	2.5	4.17	9	212	50	0.212	0.212	0.339	0.204	0.094	0.15	0.02	yes	yes	yes	yes		**yes**
4	Taraire	4	7.5	4.1	5.86	10	265	50	0.265	0.141	0.259	0.181	0.106	0.13	0.02	yes		yes	yes		**yes**
2	Tawa	2	3.5	2.17	3.25	7	82	34	0.241	0.138	0.223	0.148	0.069	0.17	0.06	yes	yes?	yes?	yes?		yes?
3	Tawa	1	2	0.7	1.75	5	52	50	0.208	0.104	0.297	0.119	0.042	0.13	0.02	yes		yes	yes?		yes?
4	Tawa	5	3	1.1	3.67	9	95	50	0.076	0.127	0.345	0.104	0.042	0.18	0.1			yes			
2	Tawapou	1.5	4	1.3	2.6	8	86	30	0.382	0.143	0.441	0.221	0.072	0.17	0.06	yes	yes?	yes	yes?		yes?
3	Tawapou	6	7.5	5.5	6.88	16	393	50	0.262	0.210	0.286	0.229	0.098	0.13	0.02	yes	yes	yes	yes		**yes**
4	Tawapou	9	5.5	3.4	5.67	14	222	50	0.099	0.161	0.261	0.157	0.063	0.13	0.02		yes	yes	yes		**yes**
		Average total overlap per year					966.33		**Average over all years**												
All	Karaka	**Average overlap per species per year**					11.78		0.081	0.081	0.195	0.083	0.053	0.107	0.007			yes			
All	Kohekohe						55.33		0.259	0.226	0.281	0.236	0.121	0.150	0.013	yes	yes	yes	yes	yes?	**yes**
All	Puriri						81.33		0.278	0.113	0.118	0.109	0.048	0.067	0.020	yes	yes	yes	yes		**yes**
All	Taraire						70.33		0.200	0.173	0.270	0.175	0.101	0.160	0.040	yes?	yes?	yes	yes?		yes?
All	Tawa						25.44		0.175	0.123	0.288	0.124	0.051	0.160	0.060	yes?	yes?	yes	yes?		yes?
All	Tawapou						77.89		0.248	0.171	0.329	0.202	0.078	0.143	0.033	yes	yes?	yes	yes		**yes**

Further explanation for Table 5.4

The critical overlap values ($C_s^{(o)}$) were generated by using equation 3b) where $\overline{F}_s$ is in turn taken to be the mode, median, mean all, mean fruiting (all measured as number of fortnights) and visits with fruit (number of occasions).

Species overlap values ($Z_s^{(o)}$) were calculated using equations 1b) and 2b). The species overlap values ($Z_s^{(o)}$) (plus 95% confidence interval of the mean), for each statistic of fruiting duration, were compared to the appropriate critical overlap values ($C_s^{(o)}$), and a significant difference as assigned were $Z_s^{(o)} < C_s^{(o)}$. When three or more comparisons of $Z_s^{(o)} < C_s^{(o)}$ were significant, then the species was considered to have significantly less overlap than expected for that year.

5.8.5 Results for Whitford Bush

There were significant differences between fruit phenology of observed species at Whitford Bush also. Puriri and taraire had significantly longer fruiting periods than other species, both when considering the entire species population, including non-fruiting trees (F=30.08, P<0.0001, df=14; refer Table 5.5 and Appendix 5.3 Whitford DURATN), or those trees that fruited only (F=26.00, P<0.0001, df=14; refer Table 5.6 and Appendix 5.3 Whitford DAYS). The fruiting periods for puriri were also significantly longer than that of taraire (refer to Figures 5.20, 5.21 and the Tables and Appendices mentioned above)

The proportion of trees per visit producing ripe fruit also showed significant differences (F=80.16, P<0.0001, df=4; Appendix 5.3 Whitford PROP), with both puriri (57%) and taraire (21%) having significantly greater proportions of the total population producing fruit (see Table 5.5 and 5.6).

The duration of fruiting varied significantly between species and years, and year interacted significantly with species (Figures 5.20 and 5.21, Appendix 5.3 Whitford DURATN). Year 2 had significantly longer fruiting durations than year 3 and year 4. Again puriri (14.5 visits) and taraire (5.59 visits) had significantly longer periods where at least one ripe fruit could be found on a sample tree per visit (population duration, Table 5.5). Puriri had ripe fruit on at least one tree on 95% of the site visits. Tawa and taraire had at least one tree with at least one ripe fruit on about half the site visits.

Table 5.5: Occurrence of ripe fruit at Whitford Bush for the duration of the study.
Each visit is one fortnightly sampling period. Percentage (%) of trees/visit/study is the average percentage, over the entire study, of chosen trees seen fruiting per visit. These averages can be quite small for species with short fruiting seasons. Population duration is the average number of visits that individual trees within the population, including trees that did not produce fruit, had ripe fruit. This differs from **fortnights** in Table 5.6 which only considers those trees that had fruit on one or more occasion.

Species	Number of visits*	% visits*	% trees/visit/study (± 95% conf. int.#)	Population duration (± 95% conf. int.#)
Karaka	16	19.75	5.51±3.60	1.08±0.34
Kohekohe	11	14.58	5.39±3.00	1.46±0.69
Puriri	77	95.06	56.79±6.53	14.50±2.21
Taraire	38	46.91	21.06±6.08	5.59±1.53
Tawa	37	45.68	11.21±3.96	2.10±0.76

* *Number of visits when ripe fruits were seen on **any** individual of a specific species. This differs from fortnights (e.g. Table 5.3), which is the mean number of sampling days that **individual** trees had ripe fruit.*

\# *95% confidence interval of the mean*

Figure 5.20: Mean length of fruiting (fortnights) and synchrony analysis for large-fruited species at Whitford Bush

Graphs show the means for the whole population, plus standard error for the mean, for each species for each calendar year.

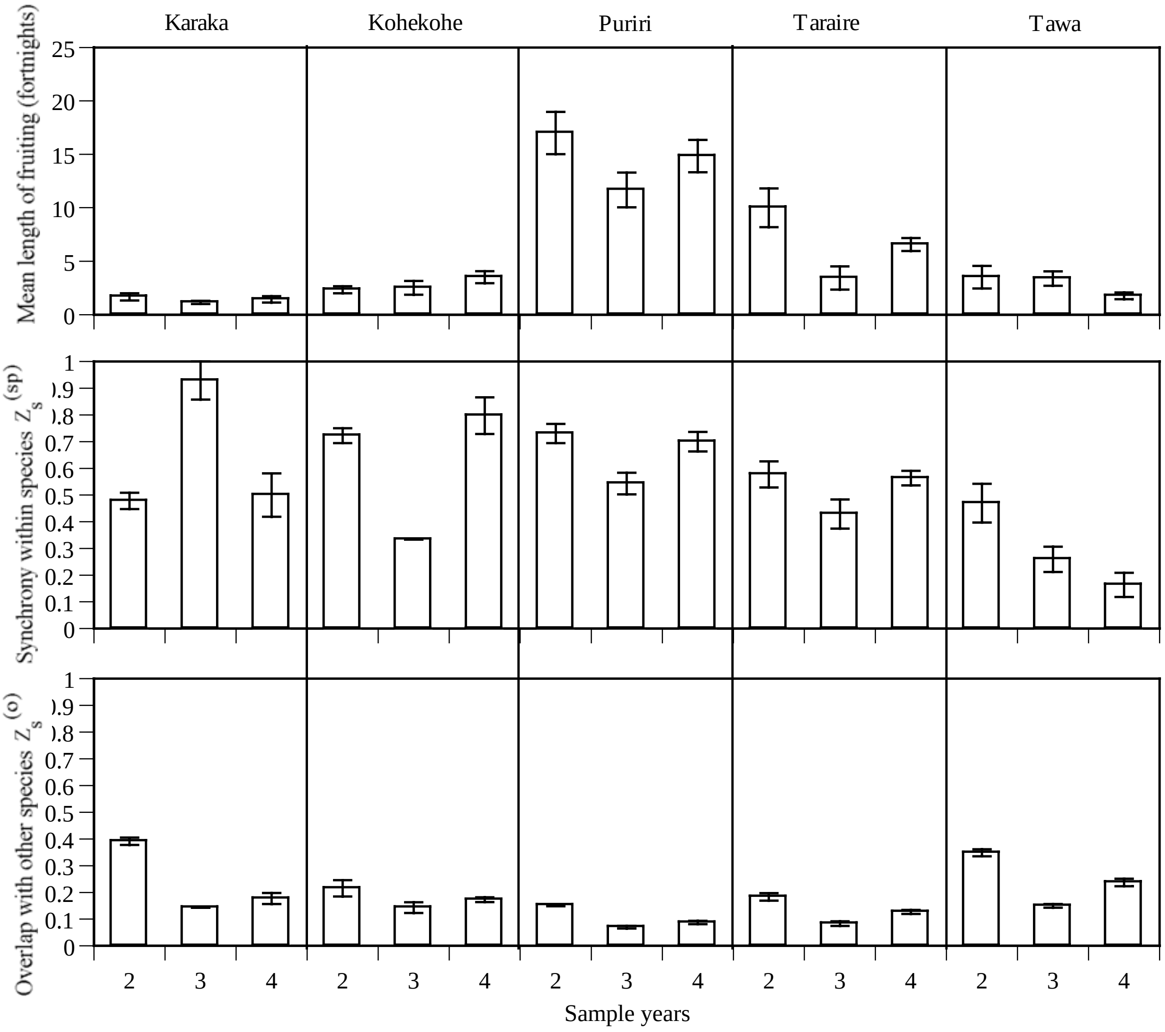
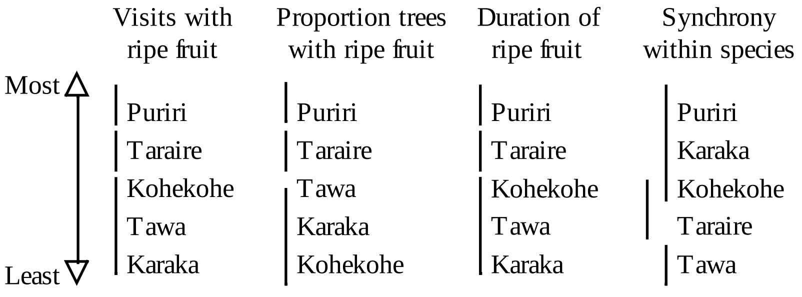


Figure 5.21: A posteriori Tukey's HSD for different fruiting synchrony variables at Whitford Bush.

Alpha=0.05

Species joined with the same bar are not significantly different.



Note that **visits with ripe** fruits pertains to occasions when ripe fruits were seen on **any** individual of a specific species, whereas **duration of ripe** fruit refers to the average length of time that trees of a particular species carried ripe fruit. **Proportion** relates to the average proportion of trees per species that had one or more ripe fruits per visit. **Synchrony within species** refers to the number of occasions that trees within a species carried ripe fruit simultaneously.

5.8.5.1 Within-species synchrony

Puriri and kohekohe had significantly greater synchrony values during two years and karaka during one year (Table 5.6). Kohekohe had one year where the population synchrony value did not exceed the critical value, but puriri and karaka exceeded synchrony values in all years, although not always significantly so. Taraire exceeded the critical value in all years and tawa in one year, but in each case the critical value was included in the 95% confidence limit around the mean.

Overall within-species synchrony was significantly greater for puriri ($Z_s^{(sp)}{}_{\text{all years}} = 0.66\pm0.06$), karaka ($Z_s^{(sp)}{}_{\text{all years}} = 0.64\pm0.13$), and kohekohe ($Z_s^{(sp)}{}_{\text{all years}} = 0.64\pm0.14$) than the critical value of 0.5 ($C_s^{(sp)} = 0.5$) (refer to Table 5.6 and Figure 5.21). So Null Hypothesis 1 can be rejected for these species. The overall within-species synchrony for taraire exceeded the critical value, but the 95% confidence intervals of the mean encompass the critical value ($Z_s^{(sp)}{}_{\text{all years}}=0.52\pm0.06$). Tawa did not have an overall population synchrony value that exceeded the critical value. We fail to conclusively reject Null Hypothesis 1 for taraire, and cannot reject it for tawa.

The low within-species synchrony for tawa was due to small numbers of ripe fruit throughout the year, although fruiting was more seasonally predictable at Whitford Bush than at Wenderholm Regional Park. The lower synchrony for kohekohe, compared to Wenderholm Regional Park, was probably in part attributable to the fact that none of the male kohekohe trees (2, 4, and 6) produced any fruit at Whitford Bush, unlike the male trees at Wenderholm Regional Park.

There were significant differences between the sampling years ($F=3.51$, $P=0.0346$, $df=2$), but it was not possible to determine which year in particular was different (refer to Figure 5.20 and Appendix 5.3 Whitford WITHINSP). The interaction term between year and species was also significant ($F=13.20$, $P<0.0001$, $df=10$), indicating that some species behaved differently in different years (see Figure 5.20) and, like for Wenderholm Regional Park, probably reflects the biennial fruiting evident for several species.

5.8.5.2 Species overlap

The overlap values for karaka and tawa were consistently (for all three years) less than the expected overlap values for at least three of the different statistical parameters (e.g. $Z_s^{(o)}{}_{\text{mean fruiting}}<C_s^{(o)}{}_{\text{mean fruiting}}$). This means that fruiting phenology for these two species shows less overlap than could be expected and they can therefore be said not to overlap with other species (refer to Table 5.7).

Taraire and puriri had two years where the overlap value ($Z_s^{(o)}$) was smaller than the overlap critical values ($C_s^{(o)}$). Moreover, the overlap critical values for both these species in the third year exceeded or nearly exceeded the overlap values, but were still within the range of the 95% confidence interval (“yes?” in Table 5.7). Kohekohe had one year where the overlap was smaller than expected and one year where it was nearly so.

On average (Table 5.7), over all years, karaka, puriri, taraire and tawa had less overlap than expected, and the Null Hypothesis of overlap can be rejected for these species. The Null Hypothesis cannot be conclusively rejected for kohekohe, possibly because of the small number of trees that fruited in some years.

Table 5.6: Duration of fruiting and synchrony of trees with one or more ripe fruits at Whitford Bush.

Data collected by observation of marked trees. Mean synchrony index within each species, and overlap of that species with other species are shown. . "Yes?" means that the 95% confidence interval includes the critical value.

					Fortnights* of ripe fruit		**Synchrony ($Z_s^{(sp)}$) within species**		**Critical value $C_s^{(sp)} = 0.5$**
Year	Species	# individs.	Not fruiting	Visits with ripe fruit	Mean ± 95% confidence interval	Range	Mean ± 95% confidence interval	Range	Species synchronous? ($Z_s^{(sp)}$)>0.5
2	Karaka	6	0	3	1.67±0.67	1-3	0.48±0.08	0.40-0.60	Yes?
3	Karaka	10	3	2	1.14±0.29	1-2	0.93±0.17	0.50-1.00	**Yes**
4	Karaka	10	3	6	1.43±0.59	1-3	0.50±0.20	0.17-0.67	Yes?
2	Kohekohe	6	3	4	2.33±0.67	2-3	0.72±0.12	0.27-0.30	**Yes**
3	Kohekohe	10	6	6	2.50±1.29	1-4	0.33±0.00	0.33-0.33	No
4	Kohekohe	10	4	6	3.50±1.13	2-6	0.80±0.18	0.50-1.00	**Yes**
2	Puriri	6	0	25	17.00±3.97	10-22	0.73±0.09	0.65-0.86	**Yes**
3	Puriri	6	0	24	11.67±3.25	8-10	0.54±0.10	0.42-0.68	Yes?
4	Puriri	6	0	26	14.83±3.03	10-20	0.70±0.09	0.62-0.86	**Yes**
2	Taraire	6	1	16	10.00±3.63	3-13	0.58±0.14	0.42-0.67	Yes?
3	Taraire	9	2	9	3.43±2.18	1-9	0.43±0.13	0.28-0.67	Yes?
4	Taraire	9	0	13	6.56±1.21	3-9	0.56±0.06	0.38-0.66	Yes?
2	Tawa	6	0	11	3.50±2.11	1-8	0.47±0.19	0.15-0.60	Yes?
3	Tawa	10	2	14	3.38±1.36	1-6	0.26±0.11	0.14-0.57	No
4	Tawa	10	2	10	1.75±0.62	1-3	0.16±0.11	0-0.29	No
			Never fruited	Average over all years					
All	Karaka		0	3.67	1.46±0.13	1-3	0.64±0.13	0.11-0.67	**Yes**
All	Kohekohe		3	5.33	2.92±0.35	1-6	0.64±0.14	0.11-0.56	**Yes**
All	Puriri		0	25.00	11.29±1.41	8-22	0.66±0.06	0.42-0.86	**Yes**
All	Taraire		0	12.67	6.33±0.80	1-13	0.52±0.06	0.21-0.66	Yes?
All	Tawa		0	11.67	2.47±0.32	1-8	0.28±0.08	0-0.60	No

* Number of days sampled on which ripe fruit was seen on **individual trees**. Each of these days is a fortnight apart. Trees that did not fruit during any one year were excluded from the averages for that year. The synchrony calculation does not include non-fruiting trees either, only trees that fruited are included in equation 1a)

Table 5.7: Overlap and critical overlap values for sample species at Whitford Bush.
Length of fruit phenology was defined in five different ways. Mode = the most commonly occurring length of fruiting for a species in a year. Median = the mathematical middle between the shortest duration>0 and the longest. Mean all = average over all trees of a species, including non-fruiting individuals. Mean fruiting = average over all trees that had one or more fruit that year. Visits with fruit = the number of visits that a species had ripe fruit on at least one tree.

		$\overline{F}_s$ **= measure of length of fruiting phenology** (fortnights; except visits)							**Critical overlap values $C_s^{(o)}$**					**Overlap ($Z_s^{(o)}$) with other species**		**Critical overlap values $C_s^{(o)}$ > species overlap values $Z_s^{(o)}$?**					
Year	**Species**	Mode	Median	Mean all	Mean fruiting	Visits with fruit	**Total days overlap other species**	**# trees of co-occurring species**	Mode	Median	Mean all	Mean fruiting	Visits with fruit	**Mean**	**± 95% confidence interval**	Mode	Median	Mean all	Mean fruiting	Visits with fruit	**Overall overlap > 3× yes**
2	Karaka	1	2	1.67	1.67	3	94	24	0.783	0.392	0.470	0.470	0.261	0.38	0.03	yes	yes?	yes	yes		**yes**
3	Karaka	1	1.5	0.8	1.14	2	40	35	0.229	0.152	0.286	0.200	0.114	0.14	0	yes	yes	yes	yes		**yes**
4	Karaka	1	2	1	1.43	6	63	35	0.360	0.180	0.360	0.252	0.060	0.17	0.04	yes	yes?	yes	yes		**yes**
2	Kohekohe	2	2.5	1.17	2.33	4	36	24	0.150	0.120	0.257	0.129	0.075	0.21	0.06	yes?		yes?			
3	Kohekohe	2.5	2.5	1	2.5	6	47	35	0.107	0.107	0.269	0.107	0.045	0.14	0.04	yes?	yes?	yes	yes?		yes?
4	Kohekohe	3	4	2.1	3.5	6	125	35	0.238	0.179	0.340	0.204	0.119	0.17	0.02	yes		yes	yes		**yes**
2	Puriri	20	16	17	17	25	371	24	0.155	0.193	0.182	0.182	0.124	0.15	0.01	yes?	yes	yes	yes		**yes**
3	Puriri	13.5	13.5	11.67	11.67	24	197	39	0.075	0.075	0.087	0.087	0.042	0.07	0.01	yes?	yes?	yes	yes		yes?
4	Puriri	14.5	15	14.83	14.83	26	310	39	0.110	0.106	0.107	0.107	0.061	0.08	0.01	yes	yes	yes	yes		**yes**
2	Taraire	12	8	8.33	10	16	209	24	0.145	0.218	0.209	0.174	0.109	0.18	0.03		yes	yes?	yes?		yes?
3	Taraire	1.5	5	2.67	3.43	9	78	36	0.289	0.087	0.163	0.126	0.048	0.08	0.02	yes	yes?	yes	yes		**yes**
4	Taraire	7	6	6.56	6.56	13	262	36	0.208	0.243	0.222	0.222	0.112	0.12	0.01	yes	yes	yes	yes	yes?	**yes**
2	Tawa	2	4.5	3.5	3.5	11	168	24	0.700	0.311	0.400	0.400	0.127	0.33	0.02	yes	yes?	yes	yes		**yes**
3	Tawa	3	3.5	2.7	3.38	14	143	35	0.272	0.233	0.303	0.242	0.058	0.15	0.01	yes	yes	yes	yes		**yes**
4	Tawa	1	2	1.4	1.75	10	116	35	0.663	0.331	0.473	0.379	0.066	0.24	0.02	yes	yes	yes	yes		**yes**
		Average total overlap per year					753		**Average over all years**												
All	Karaka	**Average overlap per species per year**					21.89		0.457	0.241	0.372	0.307	0.145	0.230	0.023	yes	yes?	yes	yes		**yes**
All	Kohekohe						23.11		0.165	0.135	0.289	0.147	0.080	0.173	0.040	yes?	yes?	yes	yes?		yes?
All	Puriri						97.56		0.113	0.125	0.125	0.125	0.076	0.100	0.010	yes	yes	yes	yes		**yes**
All	Taraire						61		0.214	0.182	0.198	0.174	0.090	0.127	0.020	yes	yes	yes	yes		**yes**
All	Tawa						47.44		0.545	0.292	0.392	0.340	0.084	0.240	0.017	yes	yes	yes	yes		**yes**

The critical overlap values ($C_s^{(o)}$) were generated by using equation 3b) where $\overline{F}_s$ is in turn taken to be the mode, median, mean all, mean fruiting (all measured as number of fortnights) and visits with fruit (number of occasions). Species overlap values ($Z_s^{(o)}$) were calculated using equations 1b) and 2b). The species overlap values ($Z_s^{(o)}$) (plus 95% confidence interval of the mean), for each statistic of fruiting duration, were compared to the appropriate critical overlap values ($C_s^{(o)}$), and a significant difference as assigned were $Z_s^{(o)} < C_s^{(o)}$. When three or more comparisons of $Z_s^{(o)} < C_s^{(o)}$ were significant, then the species was considered to have significantly less overlap than expected for that year.

5.8.6 Comparison between the sites

Whitford Bush had a higher proportion of trees fruiting than Wenderholm Regional Park (F=51.72, P<0.0001, df=10; refer Appendix 5.3 both PROP). Puriri and taraire tended to fruit proportionally more, and species 'behaviour' differed from year to year. There were significant differences in the duration of fruiting by various species between the two sites, (F=13.50, P<0.0001, df=32; refer Appendix 5.3 both DURATN). The length of fruiting for species varied significantly with puriri and taraire fruiting longer than other species. Species at Whitford Bush had significantly longer fruiting periods than at Wenderholm Regional Park, and there were also variations between years.

The significant differences between the sites are probably best explained by the somewhat different behaviour shown by various species at the two sites. For instance, tawa fruiting tended to be more common and seasonal at Whitford Bush (more consistent fruiting in January), but kohekohe fruiting was less common or of shorter duration. Karaka showed more consistent fruiting patterns at Whitford Bush, but tended to be patchier and slightly earlier at Wenderholm Regional Park. The inclusion of tawapou in the Wenderholm Regional Park data set will also have contributed to the differences found.

Only kohekohe at Wenderholm Regional Park and half the species at Whitford Bush, (puriri, kohekohe and karaka) had significantly more synchrony within species than the critical value ($Z_s^{(sp)} \pm$ 95% CI $>C_s^{(sp)} = 0.5$) and can therefore be considered synchronous. Another three species at Wenderholm Regional Park (karaka, puriri and taraire) and one additional species at Whitford Bush (taraire) had population synchrony values greater than the critical value but the results were not conclusive since the 95% confidence interval of the mean included the critical value ($C_s^{(sp)} = 0.5$). Tawa was consistently more asynchronous than synchronous at both sites, and tawapou failed to exceed the critical value at Wenderholm Regional Park. Thus the majority of species investigated at Wenderholm Regional Park and Whitford Bush had less synchrony within species than was expected. This could in part have been due to the non-fruiting of a large proportion of trees for some species (refer to Appendix 5.4).

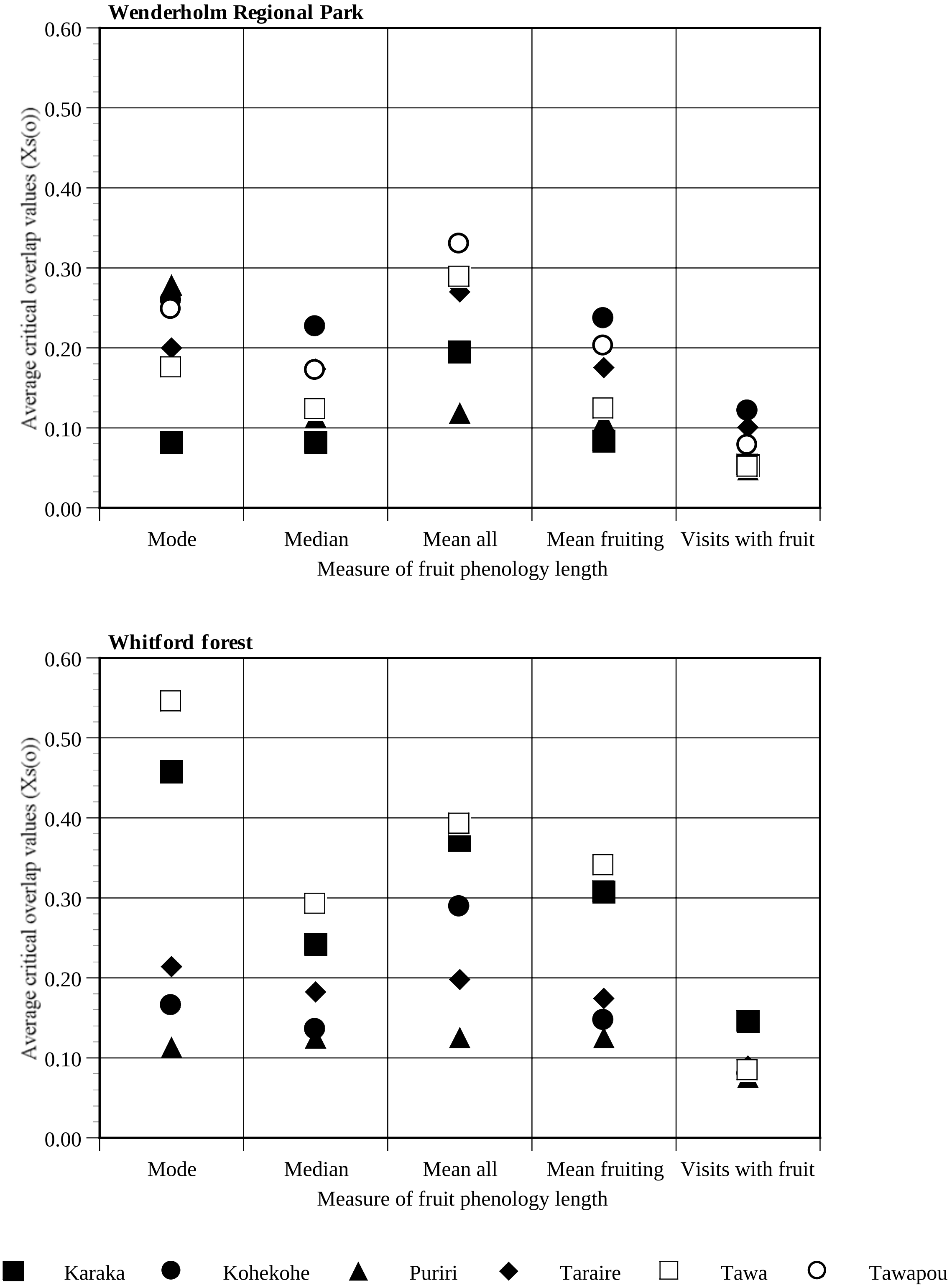
However, despite these results the majority of species at Whitford, except kohekohe, and half the species at Wenderholm (except karaka, taraire and tawa) also had less overlap with other species than expected. This result was somewhat contrary to expectations, since it was assumed that in order to have minimal overlap with other species a species should be synchronised within itself (overlap with itself on at least half the fruiting occasions). The overlap results appear to be in accordance with the visual images of fruiting phenology seen for the various species in Figures 5.16, 5.17 and Figures in Chapter 7.

More work needs to be undertaken to define which population statistics are best used to measure the length of fruiting ($\overline{F}_s$) in equation 3b). The five different statistics used in this thesis (refer to Figure 5.22) appear to have variable behaviours according to which statistics are used. Median, 'mean all' and 'mean fruiting' tended to be in accordance on most occasions, although, 'mean all' was often somewhat greater than the other two measures at Wenderholm Regional Park. Perhaps this is due to shorter fruiting phenology or fewer trees producing fruit at Wenderholm Regional Park.

Mode tended to produce relatively large critical overlap values ($X_s^{(o)}$) with the result that the expected overlap was less than expected in most instances. 'Visits with ripe fruit' tended to produce small critical overlap values, resulting in a failure to reject the Null Hypothesis on nearly all occasions. The variability in the results for the various statistical measures could also be due to the relatively small sample sizes (6 to 10 trees per species) observed throughout this study. With such small sample sizes an 'outlier' has significantly more impact on the overall measure than for larger samples.

Figure 5.22 Average critical overlap values ($Xs_{(o)}$) for species at both sites using different measures of fruit phenology length ($\overline{F}_s$).

Measures used were Mode = the most commonly occurring length of fruiting for a species in a year. Median = the mathematical middle between the shortest duration>0 and the longest. Mean all = average over all trees of a species, including non-fruiting individuals. Mean fruiting = average over all trees that had one or more fruit that year. Visits with fruit = the number of visits that a species had ripe fruit on at least one tree.



5.9 Concluding discussions

5.9.1 Description of fruit phenology

The species investigated all have distinctive, but not necessarily consistent annual, fruiting patterns. Puriri and taraire both have extended fruiting seasons. Individual puriri trees can produce ripe fruit continuously for about half a year and sporadically for up to 70% of the year. Taraire can have ripe fruit for about 3 months of the year. The fruiting seasons of puriri and taraire did not overlap greatly, since puriri had most fruit in the summer (December to May) while taraire fruited in the winter (May to October).

Tawapou was present only at the coastal site (Wenderholm Regional Park) and had fruiting patterns that tended more towards asynchronous. The timing of tawapou fruiting overlapped with puriri, kohekohe, taraire, and to a certain extent, with tawa. However, pigeon behaviour noted in the field revealed that three kereru (presumably two adults and a juvenile) vigorously defended the most heavily fruiting tawapou while the fruit was red, rather than the fully ‘ripe’ purple-black. They were no longer interested in the fruit once the fruit was ‘fully ripe’, which coincided with when kohekohe, and later taraire, fruit became available. Thus part of this perceived overlap could be due to misinterpreting what constitutes ripe tawapou fruit. The bird defence of the tree was most vigorous in calendar year 3 when the kohekohe crop was smaller.

Karaka and kohekohe had very short periods of ripe fruit presentation, and tended to be amongst the most synchronous of the species. However, a large proportion of individual trees for these species failed to fruit in several years (Appendix 5.4) possibly in part contributing to the large biennial fluctuations in fruit production. Karaka had ripe fruit for a fortnight to six weeks, while generally ripe kohekohe fruit disappeared over about 4 weeks.

Tawa was generally very asynchronous, with ripe fruit available sporadically throughout the year. Tawa at Whitford Bush was more predictable than tawa at Wenderholm Regional Park. The period over which tawa at Whitford Bush presented and dropped ripe fruit was about 2 months, which is similar to what West (1986) found (2 to 4 months) and to other Lauraceous species described by Snow (1962), McKey (1975) and Hyland (1989).

Howe and Estabrook (1977) predicted that tropical trees competing for a limited assemblage of dispersers should have extended fruiting seasons, while those competing for a wide variety of opportunistic frugivores should have sharply peaked fruiting seasons. This prediction is not totally supported for the species investigated here. Taraire, puriri, tawapou and perhaps tawa all had extended fruiting seasons and can be successfully dispersed only by kereru, since the fruits are too large to be swallowed by other arboreal bird species. However, karaka is also too large to be swallowed by any other species than kereru, but has a very short fruiting season, and thus contradicts the above prediction. The other species with a short fruiting season, kohekohe, has fruits that are taken by other bird species such as tui (*Prosthemadera novaeseelandiae*), and might therefore conform to the Howe and Estabrook (1977) prediction.

5.9.2 Fruiting sequence

The order of peak fruiting for the large-fruited species was not entirely consistent between years and sites, but the general sequence was tawa in January followed by karaka, puriri, kohekohe and taraire. Where tawapou was present it tended to have ripe fruit before kohekohe.

Information on the fruiting of two other large-fruited species (miro and pigeonwood) can be interpolated from other sampling localities and inserted into the fruiting sequence described in this chapter.

Ripe miro fruit could be found sporadically from late February to early May at Val's Bush and during April at various fruit collection localities (refer Chapter 6). Thus it falls between and partially overlaps with karaka and puriri fruiting.

There were significant quantities of pigeonwood fruit during the last year of this study, but much smaller quantities in other years. Pigeonwood fruit was available from September to November at Remiger's and Val's Bush and from October to December at Whitford Bush. It therefore filled the gap between taraire and tawa fruiting. However, fruit ripening of pigeonwood requires about 18-20 months from flowering (Leathwick 1984). Large quantities of pigeonwood fruit therefore probably only occur every second year, as for kohekohe (but also see Brockie, 1992, p.48). The heavy fruiting year was preceded by a heavy flowering period (especially for male trees) and followed by a low flowering season.

Other studies have reported similar fruiting sequence and timing of species as those reported in this study. Earliest times of ripe fruit presentation on Little Barrier Island (lat. 36° 12', long. 175° 05) were similar, with tawa fruiting in February, followed by miro (March), kohekohe (April) taraire (October) and pigeonwood (October) (Lee *et al.* 1997).

The timing of tawa noted by West (1986) in Pureora Forest (lat. 38° 31', long. 175° 33') differed somewhat from that in this study. At Pureora most tawa fruit fell during late March to April, but it could begin falling as soon as February and continued as late as June. However, at Pureoa the end of the fruiting season of tawa usually coincided with the beginning of the miro season (Leathwick 1984), which was similar to this study.

Both the order and the timing on Tiritiri Matangi Island (lat. 36° 36', long 174° 53'), in the Hauraki Gulf, differed from this study since karaka (January to April) was followed by tawa (April to May) and taraire (May and June), but the seasons did not overlap significantly (West 1986). Kohekohe on Tiritiri Matangi was described as fruiting from late April to early August, with the peak generally about May or June (Court 1985; Court and Mitchell 1988).

Some of the above differences could be attributable to climatic factors and the effect of latitude and altitude (Pureora is further south, inland and at higher altitude; island habitats can be warmer and drier than equivalent mainland locations). Even apparently small distances can affect the timing of fruit production for some species. Whitford Bush is more inland about 50-km south of Wenderholm Regional Park, yet taraire, karaka and nikau tended to have ripe fruit a month later than at Wenderholm Regional Park.

5.9.3 Randomness

Monte Carlo analyses, using the Simpson diversity index, demonstrated that all species had distinct non-random peaks that were greater than could be expected if fruit was produced evenly or randomly throughout the year.

However, these non-random peaks did not occur every year, or at both sites, for some species. The inconsistent results were sometimes due to the fruiting pattern of the species (e.g. kohekohe tends to have large fruit crops every second year), to the proportion of trees producing fruit in any one year (e.g. few tawa trees produced fruit at Wenderholm Regional Park) or to extended fruiting patterns (e.g. puriri has some ripe fruit most of the year).

5.9.4 Synchrony

Only kohekohe at Wenderholm Regional Park and karaka, kohekohe and puriri at Whitford Bush had significantly greater population synchrony values ($Z_s^{(sp)}$) than the postulated critical value ($C_s^{(sp)} = 0.5$) (Figure 5.20 and 5.21, Tables 5.3 and 5.6). Karaka, puriri and taraire at Wenderholm Regional Park, and taraire at Whitford Bush also had population synchrony values greater than the critical value but not significantly so ($Z_s^{(sp)}$ ± 95% confidence interval of the mean included $C_s^{(sp)}=0.5$). The synchrony values for tawa and tawapou failed to exceed the critical value at either site. Thus is was not possible to completely reject Null Hypothesis 1 “There is no synchrony of fruiting within a species” for all species at all sites. However, none of the species was totally asynchronous ($Z_s^{(sp)}=0$).

The lack of synchrony for species could in part be attributable to the number of individual trees that failed to produce ripe fruit during survey years; 70% of trees for some species failed to fruit in some years. Including only the fruiting trees for each species, as was done in this thesis, results in greater population synchrony values then when considering the entire sample population, but this also significantly increased the 95% confidence intervals associated with the mean due to smaller sample sizes (Appendix 5.4). The large proportion of non-fruiting trees, for some species, is interesting in itself and will need to be taken into account when estimating fruit production or fruit availability per year. The occurrence of such large numbers of not fruiting trees within species needs further investigation.

Primack (1980), using slightly different formulae, obtained synchrony values for two consecutive years of 0.68 and 0.74 for *Leptospermum scoparium*, 0.42 and 0.74 for *Discaria toumatou*, and 0.34 and 0.41 for *Dracophyllum* spp. He noted that flower phenology changed from year to year due to annual differences in the duration of flowering both for individual plants and the populations as a whole. Primack did not attempt to ascertain whether the various species had significantly synchronous populations (e.g. $C_s^{(sp)}=0.5$).

Augspurger (1983) obtained generally greater synchrony values than either this study or the study by Primack (1980) (refer Table 5.8). These data appear to be from one year’s study of flowering shrubs (20 individuals for most species). The paper did not report a continuation of the study, using the same tagged shrubs, for a subsequent year thus it is not possible to gauge whether all shrubs produced flowers every year, giving rise to consistently high synchrony scores, or whether some of the shrubs failed to flower the next year with subsequent lower synchrony scores as noted in this thesis.

Table 5.8: Synchrony results obtained by Augspurger (1983) for flowering phenology of six shrub species

Species	Synchrony of flowering period	Spatial density
Hybanthus prunifolius	0.89	High
Turnera panamensis	0.77	Medium-High
Rinorea sylvatica	0.95	High
Psychortria horizontalis	0.82	Medium-High
Erythrina coastaricensis var. *panamensis*	0.50	Low
Pentagonia macrophylla	0.48	Low

Interestingly the synchrony values in Augspurger’s study (1983) closely paralleled the distribution patterns of the shrubs within the forest. Shrubs of the four higher-density species were selected from within a hectare, while the lower density species required several hectares to obtain sufficient individuals (Augspurger 1983). Perhaps the high degree of synchrony for higher density species also reflected smaller climatic, soil, topography or habitat differences compared with the possibly more variable conditions for low-density species. The plants in Primack’s (1980) study were also very close spatially (*Discaria* and *Leptospermum* in a 10m by 10m block and a block of *Dracophyllum* spp. 100m away).

A similar trend appears to apply to this study. The species with the highest synchrony values in this study were all spatially closer than the species with lower values; kohekohe at Wenderholm Regional Park was restricted to one knoll behind the rangers house and karaka, kohekohe and puriri at Whitford Bush all occurred in the upper half of Whitford Bush. Most of the other species at Wenderholm Regional Park were scattered through about 15 hectares whilst taraire and tawa occurred both in the top and lower half of Whitford bush. This could indicate that micro-climatic or soil factors play a role in the timing of fruiting.

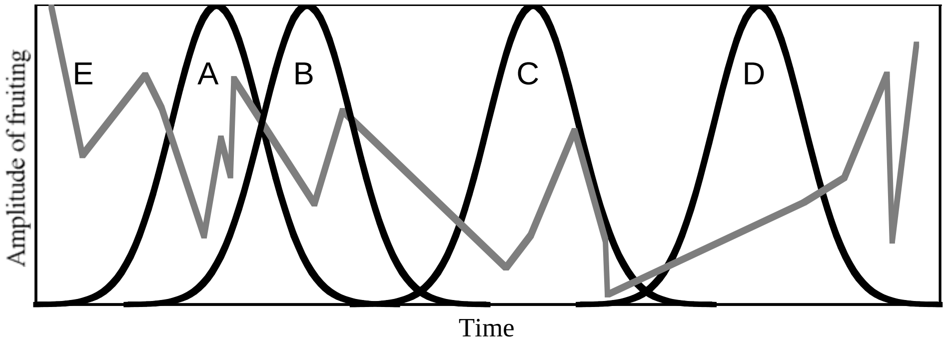
Augspurger (1983) also notes that none of the species are totally asynchronous ($Z_s^{(sp)}$=0) but that they do vary in their degree of synchrony. The same holds true for this study, no species were completely asynchronous, tawa had the lowest synchrony values, and kohekohe generally the greatest.

5.9.5 Overlap between species

All species had years and/or sites where the overlap between species was less than expected. At Wenderholm Regional Park kohekohe, puriri and tawapou had overall less overlap with other species than expected, while at Whitford Bush karaka, puriri, tawa and taraire had less overlap than expected. Taraire and tawa at Wenderholm Regional Park, and kohekohe at Whitford Bush came close to having less overlap than expected, missing out only because the critical overlap value was included within the 95% confidence intervals around the mean. The only species to show greater overlap than expected was karaka at Wenderholm Regional Park.

It was rather surprising, given the lack of significant synchrony within many species (refer 5.9.4) that the degree of overlap between species was generally less than expected. One might expect that species with asynchronous fruiting phenologies could have considerable overlap with other species, since fruiting individuals could occur during any season and thus overlap with several other fruiting species (refer to Figure 5.23). If each species is synchronous, and presumably confined to a particular season, then the chance of overlap with other species should be reduced, unless the species fruit during the same season.

Figure 5.23: Overlap between hypothetically synchronously and asynchronously fruiting species. Species A through D have synchronous fruiting patterns that overlap with other species to greater or lesser degree according to which season the species fruits (e.g. A and B overlap greatly since they fruit in same season, but A and D do not overlap at all). Species E is asynchronous and overlaps to some extent with all other species, regardless of season, therefore we would expect greater overlap values for this species.



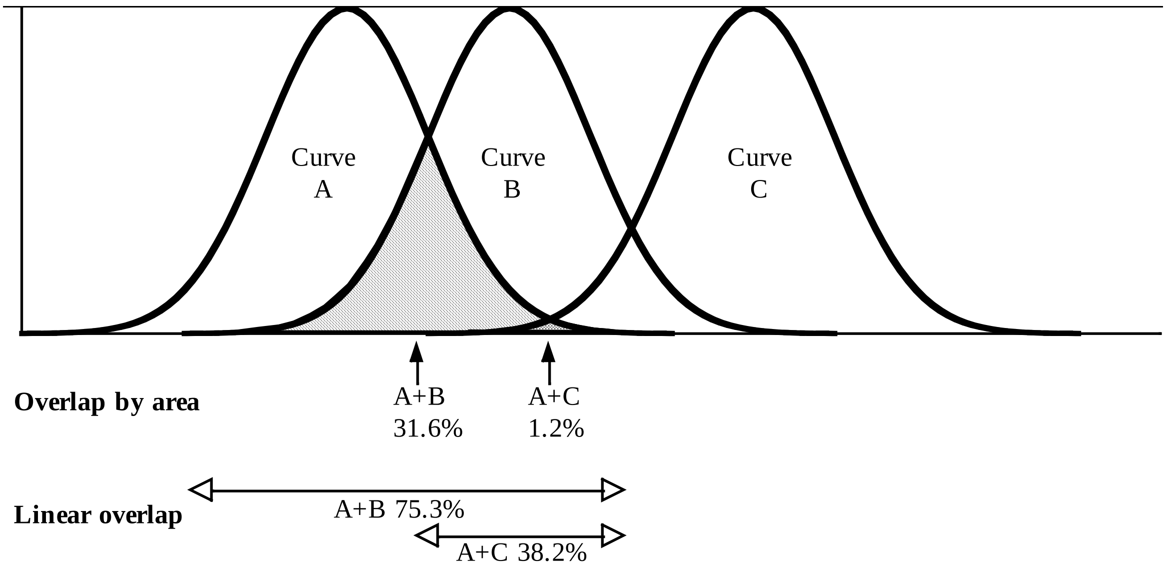
The overlap calculations used in this thesis do not take account of a number of biological attributes, which could either further reduce the perceived overlap, or increase the perceived overlap. The method does not consider the amplitude (number of fruits produced) per species. It merely notes whether a ripe fruit was present (or absent) on a particular day for individuals of the species. It is more likely to find fruit on a tree on occasions X-1 and X+1 when occasion X has fruit, and the amount of fruit produced on occasions X-1 and X+1 is likely to be more similar to X than occasions further removed in time. Thus fruiting phenology is more accurately represented as the area under a curve rather than a line.

The overlap of fruiting curves is considerably smaller than the linear distance that species overlap (refer Figure 5.24). Presence of fruit is more akin to a linear measure than a curve comparison, although this might have been alleviated to some extent by the investigation the overlap of each tree within a species, rather than presence or absence of fruit for the species as a whole.

Given that linear measures are more likely to produce higher overlap values, it seems noteworthy that all species (for at least one site) had generally small overlap values and less overlap than expected. The current method of calculating overlap also does not consider whether the overlap between species occurs in one continuous sequence (e.g. week X, X+1, X+2, X+3 … etc) or as a fragmented sequence (e.g. week X, X+1, X+5, X+8). This is probably a strength, rather than a weakness, when dealing with variable natural phenomena rather than mathematically precise models.

This innovative method of calculating overlap for a species, in relation to all sympatric species at the site, shows promise in that the results reflect the observed phenology (refer to Figures 5.16, 5.17, and 6.7). However, the critical overlap calculation still needs further refinement. In particular, the best statistic to use for fruit duration for each species (e.g. mean, mode, median etc) requires further work. "Visits with fruit" is probably not an appropriate statistic since it does not take account of the number of trees in the population that have ripe fruit, which is what the calculations are based on. This could explain why this parameter tended to produce critical overlap values ($C_s^{(o)}$) that were so small that the population overlap values ($Z_s^{(o)}$) consistently exceeded them. "Mean all", the mean that includes all trees within a species whether they fruit or not, might also not be appropriate, since this parameter appears to be unable to distinguish between species, that is, the overlap critical values are nearly always larger than the population critical values. The calculations for overlap and synchrony values might also further benefit from including some measure of fruiting phenology amplitude.

Figure 5.24: Comparison of amplitude overlap versus linear overlap.
The hypothetical fruiting phenologies of B and C overlap with A to different degrees. The area of overlap for the curves (which includes the amplitude of fruiting) are considerably smaller then the linear overlaps (only considers how far the bases of the curves overlap, akin to the formula used in this thesis.)



5.9.6 Character displacement

This study has illustrated that there are indications that character displacement attributes, as proposed at the beginning of this Chapter, may play a part for some of the species and/or time. The attributes are listed below, but species did not consistently achieve these attributes annually;

- The sequence of species fruiting did not change significantly from year to year (for some species at some sites).
- The peak quantity of ripe fruit (regardless of its magnitude) was proportionally greater than could be expected by chance (for at least one year for most species).
- No species was totally asynchronous ($Z_s^{(sp)}=0$). Kohekohe at both sites and karaka and puriri at Whitford Bush were more synchronous than the postulated critical value ($C_s^{(sp)}=0.5$) and several other species came close to exceeding the synchrony critical value. The lack of apparent

synchrony could be consequence of the large proportions of non-fruiting trees within most species.

- The overlap between species was generally lower for most species than the postulated critical values, indicating less overlap than expected. Only one species (karaka at Wenderholm Regional Park) had overlap values consistently exceeding the overlap critical values. It was not possible to conclusively establish significant overlap for some other species because the critical overlap value was included within the 95% confidence interval of the mean population overlap value. However, overall there was less overlap between species than expected.

Although the attributes of character displacement have been illustrated, it cannot be concluded that character displacement between large-fruited tree species is due solely to the interactions of these species with kereru, since the possible past contribution to fruit dispersal by ground-dwelling frugivores such as moa cannot be excluded. Janzen and Martin (1982) note that species with fruits that are predominantly dispersed by ground-dwelling frugivore often drop the fruits upon ripening or even well before they are ripe. For the species in this study a small proportion of the fruits do fall to the ground after ripening, and before the pericarp either rots or dries up. It is unclear whether this phenomenon occurred in pre-human-colonisation days to attract ground-dwelling bird dispersers. It could also be a recent change attributable to the severe reduction in kereru , with current populations unable to deal with numbers of fruit available (e.g. Burrows 1996).

The loss of possible historical, and the reduction of present day, fruit dispersers has not obviously affected the regeneration potential of, or resulted in the extinction of, any large-fruit bearing species (Clout and Tilley 1992). It could be that the loss of large dispersers has been too recent for there to have been any noticeable impact on apparent regeneration of long lived tree species. For instance, the loss of large mammalian fruit dispersers from Central America since Pleistocene times has not resulted in a noticeably large extinction of Pleistocene megaflora (Janzen and Martin 1982). However, several species could have experienced a contraction in their range, which in some species apparently has been partially remedied by the introduction of horses and cattle (Janzen and Martin 1982). The seedlings of some large-fruited New Zealand species, such as karaka, are rarely found away from parent trees, possibly signalling a contraction of its range as postulated by Janzen and Martin (1982) for Central American species. Does this indicate that New Zealand has lost a, as yet unidentified, frugivore of large fruited species capable of handling karaka fruits, or where moa gizzards gentler on fruits than currently thought?

The apparent lack of change in plant species regeneration potential could also be an illustration of the points made by Herrera (1985b) that, just because plants have animal dispersers that seem admirably suited for the job does not imply co-evolution on the part of both the plants and the animals. In most cases the frugivore assemblage has probably changed several times while the plant species, with their considerably slower rates of evolution, might not have evolved much at all. Thus in many cases ‘co-evolution’ is likely to have been due to adaptation on the part of the frugivores and not the plant species. Witness the present day example of introduced bird species consuming and dispersing native seeds (Herrera 1985b), and acting as both pollinators and dispersers for native species, though not as efficiently, in New Zealand (Anderson 1997). Other factors such as long-term changes in climate, seasonal triggers or method of pollination could have had as much influence on modifying fruiting phenologies as disperser assemblages (Howe and Smallwood 1982). Current and future analysis of co-evolution between plants and animals, specifically birds and lizards, in New Zealand is further complicated by the range of new herbivores, and frugivores, that have been introduced with the arrival of humans. This issue will be further discussed in Chapter 7.

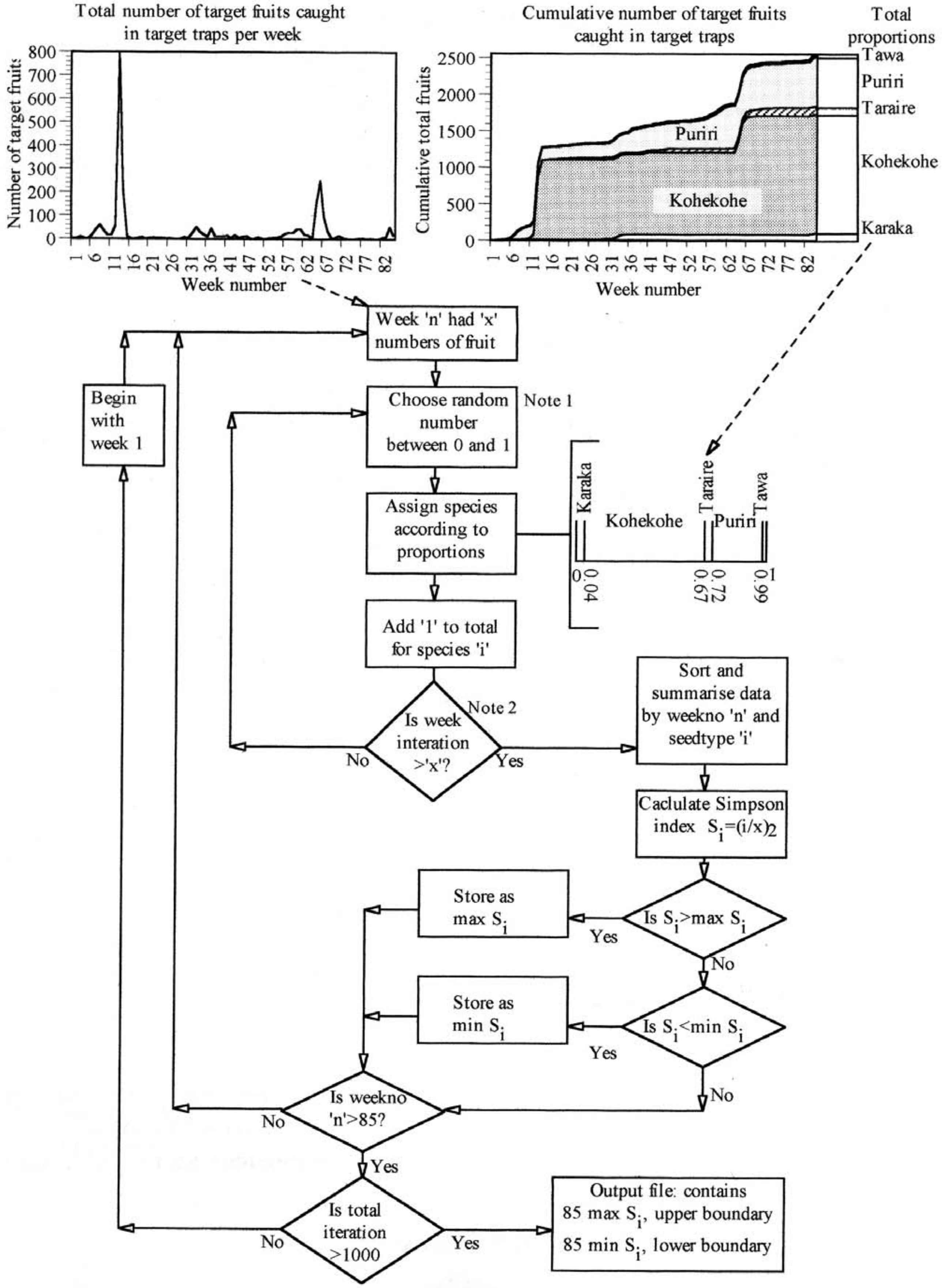
One aspect in favour of proposing co-evolution on the part of both plants and frugivores is the long isolation of New Zealand. The frugivore assemblage is unlikely to have changed as frequently (before the colonisation by humans) as the continental sites discussed by Herrera (1985b), although it might have become impoverished through various cycles of extinction. Thus it is not improbable that co-evolution of plants with their frugivores has resulted in character displacement in the form of timing of ripe fruit presentation.

5.10 Conclusions

The fruiting pattern of large-fruited species, in northern New Zealand, was more akin to tropical forests, with year round fruit supply, than temperate forest with more seasonal fruiting. The order of fruiting was occasionally consistent between years and was somewhat similar for the two sites studied. The order of fruiting for large-fruited species throughout the year from January tended to be (tawa), karaka, (miro), puriri, (tawapou), kohekohe, taraire, (pigeonwood). Species enclosed in brackets did not fruit consistently every year (tawa, pigeonwood), or were not present or did not fruit at all sites (tawapou, miro). Fruit was not produced continuously throughout the year by individual large-fruited species, but tended to occur in defined peaks for karaka, kohekohe, puriri, taraire, tawa and tawapou (insufficient data to test miro and pigeonwood). No species was completely asynchronous and individuals within most species tended to be more synchronous than asynchronous in the presentation of ripe fruits, but were often less synchronous than expected. Despite lower than expected synchrony, species tended not to overlap significantly with other species in some or all years.

The above characteristics are components that comprise character displacement. Thus character displacement, in the form of timing of ripe fruit presentation, has been indicated for some species at either or both sites, though it is not possible to conclude that this has come about solely through co-evolution with the frugivorous kereru.

Figure 5.9: Flow diagram of Monte Carlo procedure for estimating parameters for target species fruits to fall in to target traps



Note 1: Akin to choosing a random fruit, e.g. if the number falls between 0.67 and 0.72 then the fruit is assigned as taraire.
Note 2: 'x' is the number of fruit to fall into seedfall traps during that sampling period.

[1]

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[1] Pair of kereru (Photo courtesy Len Doel from lensman@writeme.com)

6. Nutritional characteristics, utilisation by kereru and success in attracting dispersers for various fruiting species.

6.1 Introduction

Fruit-eating vertebrates and fleshy-fruited plants engage in a mutualism that dates from at least Permian times, and possibly earlier, in most habitats around the world (Willson 1991). It is unclear during which geological epoch birds began to interact with fruiting species, but given the ancient avian lineages containing major frugivores it seems likely that frugivory was an important component of early avian behaviour. Jordano (1995) found that more than 50% of the variation in fruit characteristics (structural and nutritional) could be explained by phylogeny. This interaction between birds and plants has generally been regarded as mutualism; the plants potentially obtain dispersal of propagules and the birds obtain nutrition and water (Jordano 1995; Willson 1991).

It is assumed that for avian consumers the principle benefit lies in gaining nutrition. However, it is generally not known, in any qualitative or quantitative sense, how important fruits are nutritionally. It is unknown how fast birds gain weight on fruit ‘a’ versus fruit ‘b’, which fruits are important during the breeding season, and what is the minimum quantity and quality of fruit required to stave off starvation (Willson 1991). It is known that the breeding of kereru (*Hemiphaga novaeseelandiae*) and the sub-species parea (*H. n. chathamensis*) can be irregular and is correlated with fruit availability (Clout 1990; Lee *et al.* 1991; Powlesland *et al.* 1997). Powlesland *et al.* (1997) postulated that the fruit of hoho (*Pseudopanax chathamicus*), rich in lipids and carbohydrates compared to other foods, was important in the breeding success of parea.

Moreover, the mixing of fruit species within a diet could also produce ‘resource complementary’ diets, where the combination of items improve performance more than single item diets, or ‘antagonistic’ diets, where consumption of particular items reduces the benefit of other food items (Whelan *et al.* 1998). It has been suggested that foragers can enhance their diet by selecting food items that contain complementary nutritional resources, such as sugar-rich fruits, lipid-rich fruits, protein-rich fruits or fruits rich in particular vitamins or minerals. Furthermore, a mixed diet could dilute the effect of any secondary toxic or deterrent compounds (Whelan *et al.* 1998). It has also been suggested that the bird’s ability to digest the fruit plays a role in fruit selection, and that the rates of nutritional assimilation can vary seasonally (Karasov 1993).

Thus plant species could compete with each other in a nutritional sense as well as varying the timing of ripe fruit presentation that was discussed in Chapter 5. There are various ways in which fruits could demonstrate nutritional divergences.

1. Species could produce fruits with high nutritional value in order to attract specific high quality dispersers (McKey 1975).

2. Species could provide nutritional attributes that complement fruit from other species that are available at the same time (Whelan *et al.* 1998).

3. Species could provide fruits with nutritional attributes that are important for specific parts of the dispersers’ life cycle, such as breeding, moulting, or migration (e.g. Lepczyk *et al.* 2000).

4. Fruiting species could present somewhat lower-quality fruits for longer periods or small numbers of fruits for longer periods.

Thompson and Willson (1979) noted different fruiting strategies to attract resident and migratory birds, suggesting that resident birds had time to search out successive crops of ripening fruits, but migratory birds had to be enticed by large displays of fruit. A similar mechanism might work in a flora reliant on non-migratory avifauna. If most species are highly seasonal in fruit ripening and need to be sought out when ripe then providing a constant supply of ripe fruit might prove advantageous because birds would always know where to find it. However, such a constant supply of fruit may have to be offset energetically by either smaller numbers of fruit, or lower quality fruits.

This chapter investigates whether any or all of the above strategies apply for large fruits of northern New Zealand forest species. Firstly, the nutritional characteristics are presented and compared between fruiting species and with other studies. The diet of kereru (*Hemiphaga novaeseelandiae*), the only disperser for large fruited species and an important disperser for other species, is then investigated to ascertain whether certain fruits are preferred over other species. Lastly, the success of dispersal, as measured by the proportion of fruits consumed by dispersers and the rate of fruit removal, is presented for each species for which nutritional data are available. The focus remains on the large-fruited species, but a number of other plant species have been included, since they are known to be important food sources for kereru.

6.2 Nutritional analysis

The main question of interest was whether the large-fruited species, for which kereru is the sole or main disperser, had nutritional characteristics that might indicate nutritional character displacement of these species within forests of the Auckland region. Hence the majority of species that were collected for nutritional analysis had fruits that had diameters greater than 10 mm, but some fruit species with diameters of 6 mm to 10 mm were also collected. Kahikatea (*Darcycarpus dacrydioides*) fruit is considerably smaller (4 mm in diameter) but was collected because it was known to be an important component of kereru diet.

6.2.1 Method

A minimum of 5 grams of wet fruit-flesh per species was required for nutritional analysis. This sometimes meant that the fruit-flesh from several trees, often at different sites, had to be combined to obtain the requisite amount of material. Most species are therefore only represented by a single sample, and no measure of variance can be calculated (Table 6.1). However, kahikatea fruit was very abundant during 1997 and was one of the easier fruits to process. Hence five kahikatea trees were sampled and analysed separately to obtain some indication of the degree of variation present within that species (Table 6.1a).

Fruit were picked from trees or gathered from beneath trees when it was ripe. The fruit-flesh was separated from the seed as soon as possible and stored frozen at –20°C until there were several samples ready for processing (could be up to half a year). The wet pulp was delivered to SGS Food and Environment laboratories who were contracted to analyse the nutritional components. The numbers of fruit processed, dates and location of collection are provided in Appendix 6.1.

SGS Food and Environment laboratories used the following methods:

Moisture (%)	Difference between dry and wet weight after 16 hours at 70°C at 2kPa vacuum pressure.
Lipids (%)	Soxhlet extraction using mixed ether solvent
Protein (%)	Dumas combustion method, using a Leco FP-2000 analyser, to determine the nitrogen content, which is multiplied by 6.25 to obtain the % protein
Ash (%)	600°C combustion in muffle furnace
Carbohydrate (%)	calculated by difference from the above results i.e. 100% -moisture - ash - lipids – protein

Energy kJ/100g	By calculation from the nutritional data i.e. protein g/100g × 17 = kJ/100g plus lipids g/100g × 37 = kJ/100g plus carbohydrate g/100g × 17 = kJ/100g
Minerals mg/kg	Calcium, lead, cadmium, and zinc by atomic absorption spectroscopy
Sugars (%)	HPLC analysis of an ethanol extract
Dietary fibre (%)	enzymatic gravimetric method i.e. samples are digested with protease and amylogucosidase, alcohol is used to precipitate the soluble fibre. After drying one half is analysed for protein and the other incinerated to determine ash content. Total dietary fibre = weight residue - weight (protein + ash)

The raw data are presented in Tables 6.1, 6.2 and 6.2a. The nutrition and physical data (excluding pH) were normalised for the cluster analysis by subtracting the mean value for each characteristic from the value obtained for the species and dividing by the standard deviation of the characteristic. For instance, for puriri (*Vitex lucens*);

$$\text{Standardised lipids for puriri} = \frac{\text{Lipids puriri - mean lipids all species}}{\text{Standard deviation lipids all species}}$$

The nutritional data alone, and the combined nutritional and physical data, were analysed using PROC CLUSTER with average linkage in SAS (SAS Institute Inc. 1990a). The cluster method was used to elucidate similarities and differences between fruit species, but also between fruit nutritional characteristics. Where nutritional aspects of the fruits were below the level of detection ‘dummy’ values were used that were smaller than limits of detection (Appendix 6.2). This allowed all nutritional characteristics to be included in the cluster analysis. The cluster linkage data were then entered into TREEVIEW 1.6.0 (Page 1996) to produce cladograms (Figures 6.1 and 6.2).

The grouping of variables by cluster analysis was checked using discriminant analysis in SPSS (Lead technologies Inc 2001). Prior to the discriminant analysis, variables or fruit species were assigned to groups according to the results of the cluster analyses and then analysed using the direct method. Results of the discriminant analyses are provided in Appendix 6.3.

6.2.2 Results

Tables 6.1 and 6.1a contains the results of the nutritional analysis. Tables 6.2 and 6.2a contain data on the physical parameters of simple fruits and complex fruits respectively. The pH of fruit-flesh (Table 6.1) was only measured on the second batch of fruits to be processed, hence not all species have pH values.

The standard error for nutritional attributes of kahikatea ranges from 1% to about 20% of the mean (with one anomalous high lipid content sample increasing the standard deviation to 37% of the mean for lipids). Thus, for some nutritional characteristics the concentrations can vary considerably between trees of the same species. Work on feeding preferences of takahe (*Porphyrio mantelli*) has shown that they were selective for particular plants and that these plants were better sources for particular nutrients (R. Powlesland pers. comm.). Some of the error could also be due to measurement error or to slight differences in processing or analysis of fruits from different trees. These data illustrate that considerably more research is required on nutritional characteristics within species.

Table 6.1: Fruit-flesh nutritional composition for a range of larger-fruited species. Data are not transformed.

							Dietary Fibre		Sugars					Elements				
Species	Moisture %	Lipid %	Protein %	Ash %	Carbo-hydrate Total %	Energy kJ/100g	Insoluble %	Soluble %	Fructose %	Glucose %	Maltose %	Lactose %	Sucrose %	Calcium mg/kg	Cadmium mg/kg	Lead mg/kg	Zinc mg/kg	pH 10% slurry
Hinau	55	0.61	1	0.8	42.6	763.8	17.8	<0.01	<0.5	<0.5	<0.5	<0.5	0.8	264	0.01	0.5	1.5	
Kahikatea 1	88	0.7	1	0.5	9.8	209.5	3.3	1	2.9	2.3	<0.5	<0.5	<0.5	195	0.06	0.6	1.6	4.13
Kahikatea 2	88.5	0.2	1	0.5	9.8	191	2.8	0.6	2.9	2.3	<0.5	<0.5	<0.5	132	0.1	0.8	1.1	3.62
Kahikatea 3	88	0.2	1.1	0.4	10.3	201.2	3.2	0.4	3.9	3	<0.5	<0.5	<0.5	118	0.01	0.3	1.1	3.47
Kahikatea 4	85.5	0.2	1	0.5	12.8	242	3.6	0.7	3.9	3.6	<0.5	<0.5	<0.5	298	0.04	0.5	1.3	4.12
Kahikatea 5	83.2	0.2	2	0.5	14.1	281.1	5.9	1.2	4	2.9	<0.5	<0.5	<0.5	125	0.1	0.4	1.8	3.58
Karaka	86.1	0.07	1.16	1.78	10.89	208	3.6	1.4	2.2	1.9	<0.3	<0.3	<0.3	725	0.02	0.26	2.22	
Kohekohe	76.3	4.38	2.3	2.09	14.93	455	7	2.5	0.48	0.77	0.87	<0.3	<0.3	480	0.02	0.22	4.11	
Miro	70.1	1.2	2.4	2.9	23.4	483	6.6	1.8	3.7	4.4	0.9	<0.5	<0.5	529	0.09	0.6	11.4	5.57
Nikau	69.9	3.04	2.05	1.36	23.65	549	19.1	0.4	0.23	0.35	<0.3	<0.3	<0.3	995	0.02	0.33	5.76	
Pigeonwood	79.9	2.3	1.6	1.8	14.4	357.1	7.3	0.7	<0.5	0.5	<0.5	<0.5	<0.5	480	0.1	1.3	3.4	5.44
Puriri	85.2	0.08	1.11	1.34	12.27	231	6.5	0.7	1.8	1.6	<0.3	<0.3	<0.3	450	<0.01	0.26	3.95	
Supplejack	86.1	0.3	0.9	1.6	11.1	215.1	10	0.6	1.3	2.2	<0.5	<0.5	<0.5	1259	0.08	0.5	2.5	4.43
Taraire	66.6	2.14	2.36	1.58	27.32	583	15.8	3	1.9	1.8	<0.3	<0.3	<0.3	250	0.02	0.3	2.38	
Tawa	82.6	0.4	1.16	0.62	15.22	294	3.4	1.1	3.4	4.7	<0.3	<0.3	<0.3	124	0.01	0.1	1.18	
Tawapou	75	5	0.76	1.98	17.26	491	11.2	3	0.55	1.6	<0.3	<0.3	1	1080	0.02	0.29	1.5	
Titoki	82.1	0.14	2	0.93	14.8	290.8	6.8	<0.01	1.4	<0.5	<0.5	<0.5	<0.5	71	0.02	0.4	2.5	

Latin names of species are provided in Appendix 4.1.

Table 6.1a: Variability in nutritional characteristics for five kahikatea trees. Data are not transformed.

							Dietary Fibre		Sugars					Elements			
	Moisture %	Lipids %	Protein %	Ash %	Carbohydrate Total %	Energy kJ/100 g	Insoluble %	Soluble %	Fructose %	Glucose %	Maltose %	Lactose %	Sucrose %	Calcium mg/kg	Cadmium mg/kg	Lead mg/kg	Zinc mg/kg
Kahikatea average	86.64	0.3	1.22	0.48	11.36	224.96	3.76	0.78	3.52	2.82	No data	No data	No data	173.60	0.06	0.52	1.38
Kahikatea standard error	1.13	0.11	0.22	0.02	0.99	18.37	0.62	0.16	0.28	0.27	No data	No data	No data	38.01	0.02	0.10	0.16
% of mean*	1%	37%	18%	5%	9%	8%	16%	20%	8%	10%				22%	31%	18%	11%

* Illustrates how large the standard error is compared to the mean

Table 6.2: Physical measurements of simple fruits for a range of larger-fruited species.

	Number of fruits	Weight fruit (g) ± stdev	Weight seed (g) ± stdev	% fruit-flesh ±stdev	Width (mm) ± stdev	Length (mm) ± stdev
Puriri	31	3.62 ± 1.32	0.65 ± 0.18	81.44 ± 3.35	20.37 ± 2.69	19.78 ± 1.19
Nikau	1076	0.44 ± 0.07	0.31 ± 0.06	29.69 ± 5.60	8.54 ± 0.31	11.25 ± 1.01
Taraire	49	6.71 ± 1.53	4.05 ± 1.34	40.93 ± 10.55	18.91 ± 1.51	33.45 ± 3.60
Tawa	107	5.84 ± 0.66	3.02 ± 0.41	48.30 ± 2.92	18.81 ± 0.75	28.14 ± 1.50
Karaka	36	4.42 ± 1.15	1.91 ± 0.41	56.17 ± 4.74	17.23 ± 1.64	27.46 ± 3.31
Miro	83	1.37 ± 0.30	0.58 ± 0.10	57.13 ± 4.87	12.60 ± 1.10	16.53 ± 1.48
Pigeonwood	78	0.90 ± 0.14	0.48 ± 0.07	46.48 ± 3.53	11.13 ± 0.64	14.11 ± 1.04
Titoki	145	1.00 ± 0.27	0.26 ± 0.02	71.57 ± 8.12	12.48 ± 1.38	13.66 ± 1.88
Hinau	146	1.03 ± 0.28	0.44 ± 0.11	56.55 ± 5.37	10.97 ± 0.93	13.91 ± 1.40
Kahikatea 1	568	0.20 ± 0.07	0.04 ± 0.01	78.26 ± 8.75	4.00*	8.00*
Kahikatea 2	730	0.25 ± 0.07	0.05 ± 0.01	77.21 ± 7.28	4.00*	8.00*
Kahikatea 3	733	0.31 ± 0.05	0.07 ± 0.01	77.76 ± 4.66	4.00*	8.00*
Kahikatea 4	970	0.28 ± 0.05	0.05 ± 0.01	81.57 ± 5.06	4.00*	8.00*
Kahikatea 5	450	0.15 ± 0.03	0.05 ± 0.01	67.94 ± 7.94	4.00*	8.00*

* - Estimated

Table 6.2a: Physical measurements of complex fruits for a range of larger-fruited species.

Kohekohe	**Physical dimensions**	**Number of fruits per capsule or seeds per fruit**		**Range**
Number fruits	192	Numb. locules(1)/capsule±stdev	3.15 ± 0.54	2-4
Weight fruit (g) ± stdev	1.14 ± 0.28	Numb. seed(2)/ capsule±stdev	5.21 ± 1.44	3-8
Weight seed (g) ± stdev	0.44 ± 0.08	Numb. seed/ locule±stdev	1.65 ± 0.31	1-3
% Fruit-flesh ± stdev	60.06 ± 9.10			
Width (mm) ± stdev	8.35 ± 0.64			
Length (mm) ± stdev	12.13 ± 0.03			
Weight capsule(3) (g) ± stdev	8.30 ± 2.50			
Width capsule (mm) ± stdev	28.36 ± 2.67			

Supplejack fruit	**Physical dimensions**	**Number of seed/fruit**		**Range**
Number fruits	189	Numb. seed/ fruit ± stdev	1.23±0.45	1-3
Weight fruit (g) ± stdev	0.50 ± 0.17			
Weight seed (g) ± stdev	0.23 ± 0.10			
% Fruit-flesh ± stdev	54.28 ± 8.26			
Width (mm) ± stdev	9.61 ± 1.47			
Length (mm) ± stdev	10.08 ± 1.31			

Tawapou fruit	**Physical dimensions**	**Number of seed/fruit**		**Range**
Number fruits	38	Numb. seed/ fruit ± stdev	1.56 ± 0.75	1-4
Weight fruit (g) ± stdev	5.11 ± 1.89			
Weight seed (g) ± stdev	1.71 ± 0.89			
% Fruit-flesh ± stdev	67.80 ± 6.32			
Width (mm) ± stdev	19.09 ± 3.63			
Length (mm) ± stdev	25.89 ± 2.52			

(1) Full locules
(2) Each locule could contain up to 3 seeds.
(3) Weight includes fruits encased in capsule.

Figure 6.1: Cluster analysis of fruit nutritional characteristics, grouped by fruit traits.

6.2.2.1 Fruit nutritional characteristics

The fruit nutritional characteristic clusters (Figures 6.1 A and B) are broadly split into two groups, a sugar-rich fruit cluster, and a cluster containing sugar-poor fruit, which is generally rich in other nutrients. Each major cluster is further subdivided.

The sugar-rich cluster contains two sub-clusters. One cluster contains elements that had reasonably high scores (percents fructose, glucose, moisture and fruit-flesh. Refer to Tables 6.1 and 6.3.). The other cluster contains those elements that were generally below the level of detection in the tests (refer Tables 6.1 and 6.3). It seems reasonable to assume that these characteristics would generally also be below the level of detection by avifauna.

The sugar-poor cluster (Figure 6.1) is divided into 4 sub-clusters according to the presence of carbohydrate, lipids, protein or calcium. This pattern of clustering is stable, since the cluster groupings change little between the analyses with, or without, the physical characteristics (Figure 6.1 B), although the ordering within and between clusters does change somewhat.

When physical characteristics are included, percent fruit-flesh is associated with the cluster containing the higher sugar scores. The other physical characteristics all cluster together in the sugar-poor cluster.

Discriminant analysis supports the grouping of the nutritional components into the clusters derived from cluster analysis (refer to cluster analysis of fruit nutritional characteristics in Appendix 6.3) regardless of whether the physical data are included or excluded from the analysis.

6.2.2.2 Fruit 'types'.

The fruit species were also clustered together based on the nutritional characteristics. It was found that hinau (*Elaeocarpus dentatus*) and miro (*Prumnopitys ferruginea*) are consistently different from other species and from each other (Figures 6.2 A and B). The remaining fruits divide into four main groups;

- the tawapou (*Pouteria costata*), kohekohe (*Dysoxylum spectabile*), nikau (*Rhopalostylis sapida*) and taraire (*Beilschmiedia tarairi*) cluster;
- the supplejack (*Ripogonum scandens*) and pigeonwood (*Hedycarya arborea*) cluster;
- the puriri (*Vitex lucens*), karaka (*Corynocarpus laevigatus*) and tawa (*Beilschmiedia tawa*) cluster; and
- the kahikatea-rich (*Darcycarpus dacrydioides*) cluster, which includes titoki (*Alectryon excelsus*).

This clustering pattern is consistent even when physical characteristics are included (Figure 6.2 B). Discriminant analysis does not really support the grouping of the species into the clusters shown in Figure 6.2. This may be due to the fact that the analyses are based on very small sample sizes (in some cases a "group" comprises only a single sample of a single species), that the nutritional components vary along a continuum across the fruit species and are therefore difficult to categorise and distinguish between, and that percent carbohydrate will be correlated with sugar content and energy.

However the groupings of species shown in Figure 6.2 can probably be best explained by the nutritional cladograms (Figure 6.1) discussed above. These groupings are in general also supported by looking at the raw data in Tables 6.1 and Appendix 6.2, and Figures 6.3 and 6.4. Therefore, and for ease of reference throughout the rest of this thesis, the labels assigned to the clusters shown in Figure 6.2 will be used.

Hinau, which separates out by itself in Figure 6.2, is a dry, carbohydrate-rich fruit that provides a lot of energy but also contains a large amount of insoluble fibre (Figure 6.3 and Type VI Figure 6.4, Appendix 6.2).

Miro, which also separates out by itself in Figure 6.2, is a protein and sugar-rich fruit with high zinc levels and a high proportion of ash (Figure 6.3 and Type V Figure 6.4 Appendix 6.2).

Tawapou, kohekohe, nikau and taraire cluster together in Figure 6.2. These fruits have been designated as Type IV, and are all lipid-rich fruits, with a large proportion of soluble fibre, and moderate to high levels of calcium (Figure 6.3 and Type IV Figure 6.4, Appendix 6.2).

Pigeonwood and supplejack cluster closer to the sugar rich species than the lipid rich species in Figure 6.2. These two species are reasonable rich in the sugars but also have moderate amounts of lipids, soluble fibre and calcium (Figure 6.3 and Type II Figure 6.4, Appendix 6.2).

The kahikatea cluster in Figure 6.2 also includes titoki. These fruits are generally small, fructose and glucose-rich, lipid-poor with moderate to low levels of most other nutritional elements (Figure 6.3 and Type I Figure 6.4, Appendix 6.2).

The puriri, karaka and tawa cluster differs from the kahikatea group (Figure 6.2) by being somewhat lower in sugar quantities and larger in fruit size (Figure 6.3and Type III Figure 6.4, Appendix 6.2).

For the purposes of further analysis each species of fruit has been assigned to a ‘fruit type’ according to the clustering results (as in Figure 6.2).

Type I fruits:	Small sugar-rich fruits (kahikatea and titoki).
Type II fruits:	Moderately lipid-rich, moderately energy-rich (pigeonwood and supplejack).
Type III fruits:	Large, sugar-rich fruits (puriri, karaka, and tawa).
Type IV fruits:	Lipid-rich, high energy fruits (tawapou, taraire, nikau, kohekohe).
Type V fruits:	High protein fruits (miro).
Type VI fruits:	Dry, high carbohydrate fruits (hinau).

Figure 6.2: Cluster analysis of fruit species, grouped by nutritional characteristics.

Figure 6.3: Nutritional characteristics of fruits, grouped according to cluster results.

Figure 6.3 cont: Nutritional characteristics of fruits, grouped according to cluster results (page 2).

Figure 6.3 cont: Physical characteristics of fruits, grouped according to cluster results.

Figure 6.4: Mean fruit characteristics for fruit 'types' presented as averages for cluster 'categories'.

6.3 Comparison with other New Zealand studies

The fruit nutritional data from 3 other studies will be briefly compared with the values obtained in this study.

6.3.1 Data used

Powlesland *et al.* (Powlesland *et al.* 1995; Powlesland *et al.* 1997) studied aspects of parea (*Hemiphaga novaeseelandiae chathamensis*) ecology and breeding on southern Chatham Island. The study included nutritional analysis of parea preferred dietary items. Three of the fruit species are in common with this study. Kopi is the Chatham Island name for karaka (*Corynocarpus laevigatus*). The values for nutrients in the Powlesland *et al.* (Powlesland *et al.* 1995; Powlesland *et al.* 1997) study were converted to be comparable to those in this study.

Conversions of Powlesland, Grant *et al.* (Powlesland *et al.* 1995) data;
Nitrogen g/kg → multiply by 6.25 to obtain % protein
Lipids, carbohydrates, fibre, ash g/kg → divide by 100 to get g/100g = % lipids, %carbohydrates, % fibre, % ash
Micro-elements - no change

Williams (1982) compiled data from various sources to quantify the nutrients of fruits eaten by possum (*Trichosurus vulpecula*) in Orongorongo Valley. These data appear directly comparable, although it is not possible to compute the percentage of carbohydrate, as was done for this study, since the sum of moisture + ash + lipids + protein is greater than 100%.

Clout (unpublished data) analysed fruits and foliage eaten by kereru at Pelorus Bridge (41 °18’S, 173 °35”E). Results for species in common with this study are presented in Table 6.3, along with the nutritional value for young kowhai (*Sophora microphylla*) leaves, since that will be relevant later in this chapter.

6.3.2 Results

Different methods of nutritional analysis make it more difficult to undertake direct comparisons between studies. However, the general trends for different species can be compared between studies. In each case, rather than comparing absolute values, the values are taken in context relative to other species analysed in the same study, before they are compared between studies.

Hinau was analysed in two of the other studies (Table 6.3), and also found to be a dry fruit, with low levels of lipids and moderate to low levels of protein. No further data were available on levels of carbohydrate to confirm the finding of this study that hinau is rich in that nutritional component.

Karaka also occurred in two other studies (Powlesland *et al.* 1997; Williams 1982). In both cases, lipid levels appear more elevated than found in this study. Moisture, protein, carbohydrate and percent fibre appear to be comparable between the studies, but calcium levels are much lower, and zinc much higher in the Powlesland *et al.* (1997) data.

Miro only occurred in the Pelorus Bridge data (Clout unpublished data.). Most values appear comparable with those of this study, other than the % sucrose found in miro at Pelorus Bridge, which is at least an order of magnitude greater than that found in this study.

Nikau was present in the data from the Chatham Islands (Powlesland *et al.* 1997). Most nutritional attributes measured were comparable to this study, except for the calcium (much lower) and zinc levels (much higher).

Pigeonwood was analysed in two other studies (Table 6.3). Lipids were relatively high in all studies, but protein was generally higher in the other studies. Dietary fibre and some of the sugars were higher in the data of Williams (1982) and Clout (unpublished data) respectively.

Table 6.3: Comparison of fruit nutritional characteristics with some other studies

Study	This study	Williams (2)	Clout (3)	This study	Williams	Powlesland (1)	This study	Clout	This study	Powlesland	This study	Williams	Clout	This study	Powlesland	Williams	Clout	This study	Clout	Clout
Species	Hinau	Hinau	Hinau	Karaka	Karaka	Karaka (Kopi)	Miro	Miro	Nikau	Nikau	Pigeon-wood	Pigeon-wood	Pigeon-wood	Supple-jack	Supple-jack	Supple-jack	Supple-jack	Tawa	Tawa	Young kowhai leaves
Moisture %	55	56	44	86.1	87		70.1	67.1	69.9		79.9	76	80	86.1		87	85.9	82.6	89.78	70.6
Lipids %	0.61	1.7	0.34	0.07	4	1.36	1.2	2.7	3.04	7.13	2.3	9.9	5.78	0.3	5.44	6.8	0.55	0.4	0.48	18
Protein %	1	3.4	2.2	1.16	8.1	7.75	2.4	2.8	2.05	9.3	1.6	21.4	2.2	0.9	2	5.7	1.5	1.16	1.75	29.8
Ash %	0.8	3.2		1.78	8.9	13.23	2.9		1.36	7.77	1.8	8.2		1.6	5.45	9.1		0.62		
Carbohydrate Total %	42.6			10.89		38.01	23.4		23.65	21.38	14.4			11.1	35.22			15.22		
Dietary Fibre		21.8			14.3							23.7				29.4				
Insoluble %	17.8			3.6		9.62	6.6		19.1	20.74	7.3			10	4.59			3.4		
Soluble %	<0.01			1.4		8.82	1.8		0.4	11	0.7			0.6	11.63			1.1		
Sugars		12.9	1.08		55.8			15.94				7.1	0.31			36.8	3.11		7.78	2.26
Fructose %	<0.5		0.21	2.2			3.7	5.11	0.23		<0.5		<0.10	1.3			1.27	3.4	2.12	0.9
Glucose %	<0.5		0.78	1.9			4.4	5.24	0.35		0.5		0.17	2.2			0.94	4.7	2.77	0.65
Maltose %	<0.5			<0.3			0.9		<0.3		<0.5			<0.5				<0.3		
Lactose %	<0.5			<0.3			<0.5		<0.3		<0.5			<0.5				<0.3		
Sucrose %	0.8		<0.10	<0.3			<0.5	5.59	<0.3		<0.5		0.14	<0.5			0.9	<0.3	2.89	0.71
Calcium mg/kg	264			725		6.8	529		995	5.2	480			1259	4.6			124		
Cadmium mg/kg	0.01			0.02			0.09		0.02		0.1			0.08				0.01		
Lead mg/kg	0.5			0.26			0.6		0.33		1.3			0.5				0.1		
Zinc mg/kg	1.5			2.22		37.9	11.4		5.76	21	3.4			2.5	6.5			1.18		
Energy kJ/100 g	763.8	180		208	165		483		549		357.1	238		215.1		175		294		
% fruit-flesh	56	56		56	52		57		30		46	42		54		51		48		

ADDITIONAL FRUIT NUTRITIONAL INFORMATION CAME FROM (1) POWLESLAND *ET AL* (1995; 1997), (2) WILLIAMS (1982), AND (3) CLOUT (UNPUBLISHED DATA), AS WELL AS THIS CURRENT STUDY.

The values for lipids obtained for supplejack in the studies by Williams (1982) and Powlesland *et al.* (1997) are higher than found in this study, but the Clout (unpublished data) values are comparable for most nutritional attributes except some of the sugars. Powlesland *et al.* (1997) found two orders of magnitude less calcium than this study, and dietary fibre appears higher in the other studies.

Tawa was only analysed in the study by Clout (unpublished data) study, and was similar to this study with low levels of lipids, moderate levels of protein and high levels of sugars.

6.4 Comparison with overseas species

The fruit nutritional characteristics from this study tended to be generally in agreement with analysis from other New Zealand studies although, as noted a number of nutritional attributes from this study seemed to have lower values than the other studies. How do New Zealand fruit characteristics compare with those of equivalent species or genera in other parts of the world?

Jordano (1995) compiled a large database of fruit characteristics (both structural and nutritional) to test whether phylogenetic aspects might have more influence on fruit characteristics than adaptation to seed dispersers. These data, from a range of different studies (refer to Jordano 1995, for source references), were made available by P. Jordano to allow comparison of New Zealand species with their relatives worldwide.

6.4.1 Method

Most comparisons between New Zealand species and their equivalents were made at the genus level, since most genera are currently only represented by a small number of individual records in the database. Moreover, Jordano (1995) found that phylogenetic effects down to genus level explained 61% of the total variance. Fruits were classified into three disperser types in the Jordano study; bird dispersed, mammal dispersed or mixed (dispersed by both birds and mammals). The data sourced from Jordano (1995) in Table 6.4 were not converted or adjusted, so some of the observed differences could be attributable to differences in methodology for nutritional analysis.

6.4.2 Results

All *Beilschmiedia* species are bird dispersed (Table 6.4 part 1). Tawa and taraire have somewhat smaller diameters than the other *Beilschmiedia* reported on. Tawa appears to have significantly less fruit pulp than taraire and other *Beilschmiedia* species, and the energy contents, lipids, protein, and fibre contents are also lower. The New Zealand *Beilschmiedia* species appear to have greater quantities of carbohydrates, especially taraire. Tawa is a more moisture-rich fruit than other *Beilschmiedia* species.

The single overseas *Vitex* species included in the Jordano database is a drupe dispersed by both birds and mammals (Table 6.4 part 1), whereas the New Zealand puriri is only bird dispersed. Puriri has greater water content, but is generally less nutritional value than *Vitex doniana* (Appendix 6.4, Jordano ref #35).

The aril fruits of *Dysoxylum* species are all bird dispersed (Table 6.4 part 1). The New Zealand species, kohekohe, appears to be smaller in size, but provides relatively greater quantities of fruit pulp. Lipid content was only recorded for one overseas species, *Dysoxylum* aff. *Klanderi* (Appendix 6.4, Jordano ref #4) and is an order of magnitude greater than in kohekohe. The New Zealand fruit is also more moist and contains less carbohydrates.

No other *Pouteria* species were included in the database, however, tawapou is a member of the Sapotaceae family, and was therefore compared to members of that family. The Sapotaceae have a variety of dispersal mechanisms, but tawapou is bird dispersed. Tawapou has, on average, less energy, protein and carbohydrates but more fibre than other Sapotaceae (Table 6.4).

Table 6.4: Average fruit nutritional and structural characteristics from other studies as compiled by Jordano (1995).
Data are averages per genus ± standard deviation. Not all fruits within a genus had complete data, hence not all standard deviations could be calculated.

Source[2]	Jordano 35,45	This study	This study	Jordano 35	This study	Jordano 3,4	This study	Jordano 2,4,8,9,15,31,41,43,49	This study
Genus	***Beilschmiedia***	**Tawa**	**Taraire**	***Vitex***	**Puriri**	***Dysoxylum***	**Kohekohe**	**Family Sapotaceae[3]**	**Tawapou**
Disperser type[4]	3 bird, 1 mixed	bird	bird	mixed	bird	bird	bird	2 bird, 3 mammals, 11 mixed	bird
Area[5]	NTAmerica	New Zealand	New Zealand	Africa	New Zealand	Australasia	New Zealand	10 Africa, 2 Australasia, 4 NTAmerica	New Zealand
Fruit type	4 drupes	Drupe	Drupe	1 drupe	Drupe	4 aril-types	aril	10 berries, 6 drupes	Berry
Fruit length (mm)		28.14±1.50	33.45±3.60		19.78±1.19	16.78±8.10		20.22±8.54	25.93±2.50
Fruit diameter (mm)	23.33±1.52	18.81±0.75	18.91±1.51		20.37±2.96	10.93±6.31		17.44±11.73	19.06±3.59
Fruit fresh mass (g)	13.50±1.48				3.62±1.31	4.25±4.60	1.14±0.28[6]	2.10±2.65	5.10±1.86
Number of seeds per fruit	1	1	1		1		1.65±0.31[7]	1.66±1.42	1.56±0.75
Relative yield of pulp [8] (%)	14.10±4.54	8.17±0.46	19.73±3.52		12.05±0.50	9.95±5.58	14.23±2.16	21.13±7.28	19.99±1.58
Specific energy content of pulp (kJ/g)	5.90±0.89	2.94	5.83		2.31		4.55	16.32±3.56	4.91
Percent water content of fruit	71.05±5.65	82.65	66.60	61.90	85.20	47.50±13.44	76.30	74.08±8.79	75.00
Proportion of lipids (% per g dry pulp)	8.33±5.32	0.40	2.14	0.30	0.08	60.20	4.38	7.31±4.95	5.00
Proportion of protein (% per g dry pulp)	4.30±5.54	1.16	2.36	1.70	1.11	4.70±1.78	2.30	6.34±3.81	0.76
Proportion of non-structural carbohydrates (% per g dry pulp)	9.43±5.69	15.22	27.32	61.20	12.27		14.93	74.24±18.67	17.26
Proportion of minerals (% per g dry pulp) (Ash)		0.62	1.58		1.34		2.09	4.50±2.85	1.98
Proportion of fibre (% per g dry pulp)	34.30	4.50	18.80	30.10	7.20		9.50	5.28±0.84	14.20

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[2] A list of references used to collate the Jordano, P. (1995). "Angiosperm fleshy fruits and seed dispersers: A comparative analysis of adaptation and constraints in plant-animal interactions." The American Naturalist **145**(2): 163-191. data is provided in Appendix 6.2. The numbers refer to the numbered references

[3] Includes the following genera: *Aningeria, Bequaertiodendron, Chrysophyllum, Manilkara, Mastichodendron, Microphilis, Mimusops, Planchonella, Richardella, Sideroxylon, Synsepalum*

[4] Fruits were classified in to three disperser types; bird dispersed, mammal dispersed or mixed (dispersed by both birds and mammals).

[5] Geographic area - Major geographic areas of the data sources.

MEurope: Mediterranean Europe (also includes Israel and Morocco.	**NEurope**: Temperate and Northern Europe.
NAmerica: North America, excl. Southern Mexico.	**NTAmerica**: Neotropical America, incl. Southern Mexico.Africa:
Africa, south of Sahara.	**Australasia**: Australia, Malaysia, New Guinea, and whole SouthEast Asia.

[6] Individual fruits, not entire capsule, each fruit can have multiple seeds, and there can be multiple fruits within each capsule

[7] As for above

[8] For Jordano study Dry mass of pulp per fruit (g)/ Fruit fresh mass (g) × 100. For this study Calculated relative yield of pulp =average((weight fruit – weight seed)/weight fruit)*(1-proportion moisture)

Table 6.4 Continued: Average fruit nutritional and structural characteristics from other studies as compiled by Jordano (1995).

Source	Jordano 4,47	This study	Jordano 33, 70	This study	Jordano 1,2,4,9,17, 18,35,38,39,46,49	This study	Jordano 4,8,9,31,35,43,46	This study	Jordano 9,7,22,46	This study
Genus	***Elaeocarpus***	**Hinau**	***Hedycarya***	**Pigeonwood**	**Family Palmae**[9]	**Nikau**	**Familiy Sapindaceae**[10]	**Titoki**	**Family Smilacaceae**[11]	**Supplejack**
Disperser type	5 mixed	bird	2 bird	bird	1 bird, 9 mixed, 11 mammal	bird	7 mixed, 3 bird	bird	5 bird	bird
Area	Australasia	New Zealand	Australasia	New Zealand	1 Africa, 1 Australasia, 1 Meurope, 2 Namerica, 18 NTAmerica	New Zealand	6 Africa, 2 NTAmerica, 2 Australasia	New Zealand	1 Meurope, 3 Namerica, 1 NTAmerica	New Zealand
Fruit type	5 drupe	Drupe	2 drupes	Drupe	23 drupes	Drupe	2 drupes, 3 berry,1 aril	Aril	5 berries	Drupe
Fruit length (mm)	13.35±5.67	13.91±1.40		14.11±1.04	27.61±18.04	11.25±1.01	15.7±4.59	13.66±1.88	7.15±0.21	10.08±1.31
Fruit diameter (mm)	11.48±5.25	10.97±0.93		11.13±0.64	19.31±9.53	8.54±0.31	9.57±3.09	12.48±1.38	7.33±0.29	9.61±1.47
Fruit fresh mass (g)	1.89±2.61	1.03±0.28	0.59±0.11	0.90±0.14	4.08±6.38	0.44±0.07	3.49±3.87	1.00±0.27	0.29±0.10	0.50±0.17
Number of seeds per fruit		1	22.3	1	1	1	1	1	1.97±1.17	1.17±0.39
Relative yield of pulp [16] (%)	26.93±1.45	25.45±2.42	10.75	9.34±0.71	8.93±2.05	8.93±1.68		12.81±1.45	12.55±1.24	7.54±1.15
Specific energy content of pulp (kJ/g)	17.91	7.63	23.69	3.57	20.28±5.44	5.49	16.30±1.27	2.91	17.64±1.79	2.15
Percent water content of fruit	56.98±5.03	55	79.65±5.16	79.9	47.71±30.89	69.9	71.83±12.36	82.1	77.45±7.35	86.1
Proportion of lipids (% per g dry pulp)	17.68±28.24	0.61	40.95±27.65	2.3	28.53±17.10	3.04	0.09±0.15	0.14	1.05±0.70	0.3
Proportion of protein (% per g dry pulp)	4.40±1.14	1	7.40±3.54	1.6	7.01±5.61	2.05	0.07±0.02	2	5.03±1.26	0.9
Proportion of non-structural carbohydrates (% per g dry pulp)	69.9	42.6	36.7	14.4	50.98±23.91	23.65	0.58±0.32	14.8	44.85±39.28	11.1
Proportion of minerals (% per g dry pulp) (Ash)	3.2	0.8	8.2	1.8	12.43±2.28	1.36	0.04±0.01	0.93	6.85±2.62	1.6
Proportion of fibre (% per g dry pulp)	21.8	17.8	23.7	8		0.195	0.20±0.15	6.8	0.16	10.6

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[9] Includes the following genera: *Archontophoenix, Astrocaryum, Attalea, Bactris, Chamaedorea, Chamaerops, Elaeis, Jessenia, Oenocarpus, Pinanga, Roystonea, Sabal, Scheelea, Serenoa*

[10] Familiy Sapindaceae included the genera *Blighia, Gambeya, Gonophyllum, Pancovia, Paullinia, Tristiropsis, Talisia, Zanha*

[11] Family Smilacaceae included only one genus *Smilax*

Overseas *Elaeocarpus* species have a mix of birds and mammals as disperser (Table 6.4 part 2). The New Zealand *Elaeocarpus* included in this study, hinau, is bird dispersed and has less energy, lipids, protein and carbohydrates. Other parameters are similar.

Pigeonwood (Table 6.4 part 2) has lower levels of all nutritional elements, except moisture, than the *Hedycarya* included in the Jordano (1995) database.

The fruit of the New Zealand representative of the Palmae family, nikau, is at the smaller end of the size range (Table 6.4 part 2). Most nutritional components, except moisture, are lower in nikau than other members of the Palmae.

No other *Alectryon* species were included in the database, thus titoki was compared to other species in the same family, Sapindaceae (Table 6.4 part 2). Titoki fruits were comparable in size to other fruits found in the Sapindaceae family, but most nutritional elements, except energy, were greater for titoki than family members.

Supplejack was compared to other species in the Smilacaceae since no other *Ripogonum* species were reported in the database (Table 6.4 part 2). The fruits of supplejack were of comparable size, but they had on average less fruit-flesh, energy, protein but more fibre than *Smilax* fruits.

Most of the genera, or families, with which the New Zealand species were compared contain fruits with several dispersal modes and fruits of a range of sizes. Table 6.5 compares bird, mixed and mammal dispersed fruits with diameters larger than 10mm with the average for the New Zealand large-fruited bird-dispersed species.

Table 6.5: Comparison of large (>10mm) bird dispersed New Zealand fruit with large overseas bird, mixed (mammal and bird), and mammal-dispersed fruit.

Averages for each characteristic ± standard deviation. Overseas data from Jordano (1995), New Zealand data this study.

Location	Over seas	Over seas	Over seas	New Zealand
Disperser type	**Bird**	**Mixed**	**Mammal**	**Bird**
Fruit size	Diameter >10mm	Diameter >10mm	Diameter >10mm	Diameter >10mm
Fruit type	135 various	131 various	42 various	8 various
Fruit length (mm)	18.70±7.43	18.79±7.64	34.38±24.06	17.70±7.72
Fruit diameter (mm)	15.10±5.37	16.97±7.16	27.41±19.64	13.64±3.67
Fruit fresh mass (g)	3.06±3.54	2.87±3.62	9.10±21.42	2.31±2.44
Number of seeds per fruit	6.5±23.89	192.305±713.95	2.61±2.09	1.91±0.31
Relative yield of pulp[12]	12.53±5.44	16.66±7.58	23.09±14.22	13.31±2.94
Specific energy content of pulp (kJ/g)	15.39±7.02	13.32±6.39	15.21±4.17	4.03±1.79
Percent water content of fruit (%)	70.07±15.63	73.70±10.08	63.45±13.36	76.80±9.72
Proportion of lipids (% per g dry pulp)	19.94±0.17	5.51±0.10	7.37±0.12	1.67±1.81
Proportion of protein (% per g dry pulp)	5.71±0.05	5.09±0.04	5.03±0.04	1.49±0.59
Proportion of non-structural carbohydrates (% per g dry pulp)	33.60±0.29	54.98±0.26	59.04±0.24	18.59±9.44
Proportion of minerals (% per g dry pulp) (ash)	5.71±0.04	4.41±0.02	3.57±0.02	1.44±0.49
Proportion of fibre (% per g dry pulp)	12.81±0.05	14.89±0.08	18.39±0.16	11.35±5.49

The variation in fruit parameters is large and would probably not result in any statistically significant differences between fruit types. New Zealand fruits appear to have more structural similarity (length, diameter etc) to bird dispersed fruits, and to some extent, mixed disperser fruits than to mammal fruits. However, nutritionally the New Zealand fruits all seem to have considerably lower values than overseas counterparts. The only parameters that New Zealand fruits seem to score more highly in are water content and occasionally fibre content.

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[12] For Jordano study Dry mass of pulp per fruit (g)/ Fruit fresh mass (g) × 100. For this study Calculated relative yield of pulp =average((weight fruit – weight seed)/weight fruit)*(1-proportion moisture)

6.4.3 Conclusions

In broad terms the nutritional values obtained for fruits in this study tend to agree with those from other studies and overseas studies. However, there are also several differences. Some of these differences could have been brought about by different methods of nutritional analysis, or expressing the results slightly differently (e.g. the sum of moisture + ash + lipids + protein was greater than 100% in Williams, 1982).

A generalist description of New Zealand fruits could be “relatively small, moist, fibrous but nutritionally poor fruits”. Perhaps the sizes of the New Zealand fruits are constrained by only having one key frugivore, whilst the relatively poor nutrition is either admirably suited to the diet of kereru, or a consequence of reduced competition amongst plant species to attract the best (and possibly, only) frugivore, which never the less was very numerous (Clout 1990; McEwen 1978).

However it is surprising that the nutritional results from the analysis by SGS Food and Environment laboratories are consistently lower than the results for the same species reported in other New Zealand studies. For instance, lipids for karaka are 19 times greater in Powlesland *et al.* (Powlesland *et al.* 1997) and 57 times greater in the Williams (Williams 1982) study. Those same studies have about 7 times more protein and 5 to 7 times more ash. Nutritional values for pigeonwood are two to four times greater for other studies than the results obtained in this study. This implies that there are some fundamental differences in the nutritional results, or nutritional analysis of the fruits, which appears to have lowered the nutritional values of the fruits as reported in this study. However, the nutritional values are internally consistent in this study, since the same laboratory undertook all the analysis.

6.5 Nutritional availability and utilisation

This section describes the generalised annual fruiting patterns and fruit availability for a range of fleshy-fruited species. These patterns are then translated into the ‘types’ of nutrients that the fruit species provide, to illustrate what nutritional elements are available throughout the year. The utilisation of these fruit types by kereru is then investigated. Throughout this section only native plant species will be considered, although kereru also feed on some exotic species.

6.5.1 Relative abundance of fleshy-fruited species

The focus of this chapter is on availability of fruit throughout the Auckland region. The Auckland region, rather than analysis by site, was chosen since the main disperser of interest, the kereru, can travel considerable distances in search of seasonally available foods (Clout *et al.* 1991) and the forests of the Auckland region were contiguous prior to human occupation. Most of the sites used in this study would have been within kereru travelling range. The data collected throughout this study were therefore combined for this analysis, regardless of site of origin (but see Chapter 7 for the equivalent seedfall trap data for individual sites).

6.5.1.1 Data used

Only those species for which nutritional data were available were included. Observations of the number of ripe fruits per cubic metre for each tree (refer section 3.5.4 for more details) were used for most species, except for kahikatea and nikau. Fruits per cubic metre were not counted for either of these species, but ripeness as measured by the maturity scale (refer section 3.5.3) was known for kahikatea, and the proportion of palms with ripe fruit along the transect was noted for nikau.

For all species the scores were summed over each of the 26 sampling fortnights in a year, including data from all years, all sites and all trees. These total sums per sampling period were then expressed as a proportion of the total sum for that species (Figure 6.5). The data were further reduced to periods where no, less than 5%, or more than 5% of the ripe fruit was available (Figure 6.6). The nutritional fruit ‘type’ was then superimposed on the fruit availability pattern to elucidate what food types were available throughout the year.

Figure 6.5: Observations of relative abundance for each fruit species throughout a generalised year.

Figure 6.6: Availability of fruits throughout a generalised year by nutritional fruit 'types'.

6.5.1.2 Results

All species have periods of peak ripe fruit production within the year, though the amplitude and duration of these peaks varies between species (Figure 6.5). Fruit is available throughout the year. There are no periods within the year when no ripe fruit is available.

Reasonable quantities of high-lipid fruits are available throughout most of the year, except for summer, and there is little overlap between these species (Figure 6.6). The smaller moderate-lipid fruits are found most commonly during spring (pigeonwood) and summer (supplejack). Thus lipids are available throughout the year.

The high-sugar fruits are most common during summer and autumn. The large fruits predominate during the summer months while kahikatea is most common in autumn. Karaka differs from the other large-fruits in that it is available for only a short period over summer; both tawa and puriri are available in small quantities throughout the year.

Miro, a protein-rich fruit, was available in late summer and early autumn.

6.5.2 Fruit utilisation by kereru, with particular reference to fruit nutrition.

Three studies that include kereru feeding observations will be compared with the generalised yearly pattern of fruit and nutritional availability.

6.5.2.1 Data used

Throughout this study, observations were made of bird species consuming fruits. These observations have been pooled over all years and over all sites. The results are presented in Table 6.6. The majority of observations were of kereru eating fruits, possibly because kereru are less easily disturbed when feeding than other species. Only the kereru feeding observations will be compared to fruit availability.

This study also recorded the number of fruits falling into seedfall traps after having passed through a digestive system (fruits without pericarp surrounding the seed, refer to section 3.5.5 and Appendix 3.3). These consumed fruits were not necessarily all eaten by kereru, but the great majority of the larger fruits were, because most other bird species are incapable of swallowing them (refer Section 1.2.4). Thus seedfall deposition can be used as a general indicator of fruit utilisation by kereru.

A large number of kereru feeding observations were recorded by Clout *et al.* (1995b) by following radio-tagged birds, and noting other kereru feeding behaviour, at Wenderholm Regional Park during 1988 and 1989, these data were analysed by Bell (1996). These data have been grouped into ‘sampling fortnights’ to allow comparison between the generalised fruiting year and kereru feeding observations.

James (1995) noted kereru feeding observations during 6 months of the nest building and breeding period, for tagged and untagged birds. These data, as well as the deposition of consumed items below a kereru nest over a period of 3 months, will be compared to illustrate the food choices of kereru during the breeding season.

The upper-most graph in the Figures comparing each of the above studies (Figures 6.7, 6.8, and 6.9) is the same as Figure 6.6. In each case the graph has been adjusted to suit the observation period of the data set being compared.

Table 6.6: Observations of fruit consumption by bird species.
Percent of total number of observations per species. Note that observations for some species are small.

	Large fruits						Medium fruits		Small fruits								
Species	Karaka	Pigeonwood	Puriri	Taraire	Tawa	Tawapou	Kohekohe	Nikau	Astelia	Cabbage tree	Coprosma	Kahikatea	Mingimingi	Puka	Putaputaweta	Kowhai leaves	Total sightings
Blackbird							20	40			40						5
Kingfisher											100						1
Myna			10							50	10	30					10
Kereru	4.04	2.02	13.13	14.14	6.06	9.09	3.03	12.12		2.02		21.21	2.02		1.01	10.10	99
Rosella												100					5
Silvereyes[13]	50										35.71	14.29					14
Starling												100					2
Thrush								50	50								2
Tui			10.71				32.14			7.14	7.14	35.71		7.14			28
Warbler												100					1

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[13] Pecking at the fruit-flesh rather than swallowing the fruit

Table 6.7: Feeding observations and consumption of fruit by kereru in three different studies.

Site(s)/ study	Six sites/ This study		Six sites/ This study			Wenderholm/ Clout (unpublished)		Wenderholm/ James (1995)		Wenderholm/ James (1995)	
Period	1994 - 1998		1994 - 1998			1988 - 1989		1993 - 1994		1993 - 1994	
Type	Feeding observations		Consumed fruit, seedfall			Feeding observations		Feeding observations (6 months)		Consumed fruit, seedfall* (3 months)	
Species	Number of observations	% of total	Number of fruit	% of total	% minus kahikatea	Number of observations	% of total	Number of observations	% of total	Number of fruit	% of total
Kohekohe	3	3.03	1370	10.77	21.01	6	0.53				
Nikau	12	12.12	2791	21.95	42.80	180	15.79	142	22.29	114	19
Taraire	14	14.14	243	1.91	3.73	324	28.42	136	21.35	381	63.5
Tawapou	9	9.09				15	1.32				
Pigeonwood	2	2.02	54	0.42	0.83						
Supplejack			52	0.41	0.80	2	0.18				
Tawa	6	6.06	51	0.40	0.78	32	2.81				
Karaka	4	4.04	94	0.74	1.44	8	0.70				
Puriri	13	13.13	1206	9.48	18.49	341	29.91	188	29.51	57	9.5
Kahikatea	21	21.21	6196	48.72	95.02	120	10.53				
Titoki			6	0.05	0.09						
Miro						1	0.09				
Other	5	5.05	654	5.14	10.03	26	2.28	81	12.72	13	2.17
Leaf and flowers	10	10.1				85	7.46	90	14.13	35	5.83
Total sightings	99		12717		6521.00	1140		637		600	
Data summarised by fruit 'types"											
Lipid-rich		40.4		35.46	69.16		46.23		43.64		82.5
Large sugar-rich		23.23		10.62	20.72		33.42		29.51		9.5
All sugar-rich		44.44		59.39	20.81		43.95		As above		As above

* Eaten fruits to fall below the nest of one kereru pair with chick.

Figure 6.7: Observed availability and nutritional fruit 'type' throughout the year compared with kereru behaviour and seed deposition over all sites during this study.

6.5.2.2 Results from this study.

Only a relatively small number of kereru feeding observations (n=99) were made in this study (Figure 6.7b, Tables 6.6 and 6.7). The data show that kereru consumed 40% lipid-rich fruits, 45% sugar-rich fruits (21% kahikatea), 10% foliage and flowers, and 5% other fruit species. Fruits were eaten when they were available, and often observations of kereru feeding on a particular species predate the peak fruiting period for that species. Puriri was eaten throughout the year. Foliage, mainly kowhai (*Sophora microphylla*), was consumed mainly in spring, about the period of bud break.

The analysis of seedfall trap data show that the majority of consumed fruits were kahikatea (48%) with other sugar rich-fruits comprising a further 10% of fruit eaten (Figure 6.7c and Table 6.7). Lipid-rich fruits accounted for 35% of the consumed fruits and the remaining 5% were other fruit species.

However, kahikatea is a small fruit that is popular with a whole range of bird species (refer to Table 6.6) whereas most other species produce considerably larger fruits that are mainly, or solely, dispersed by kereru. Thus, though kereru will have accounted for a proportion of the kahikatea fruit consumed, a clearer picture of probable kereru diet emerges when kahikatea is left off the graph (Figure 6.7d).

With kahikatea removed, 69% of the diet comprised lipid-rich fruits (Table 6.7), mainly nikau (43%) and kohekohe (21%), with lesser quantities of taraire (4%) and less than 1% each of pigeonwood and supplejack. Consumed sugar-rich fruits accounted for 21% of the seedfall trap content, 18% of that being puriri fruit. The remaining 10% includes all other fruit species, which generally were small-fruited species such as *Coprosma* species and *Cordyline* or *Astelia* species.

6.5.2.3 Results from Wenderholm Regional Park 1988-1989 data

Systematic possum control had not yet begun at Wenderholm Regional Park in 1988/89 (refer Figure 7.2)

During the 13-month period illustrated in Figure 6.8b, 46% of feeding observations were of kereru eating lipid-rich fruits, the largest portion of that was taraire (28%) and nikau (16%). Sugar-rich fruits comprised 43% of feeding observations, with puriri (30%) and kahikatea (11%) the two single most important species. Foliage and flowers, and other fruits accounted for 7% and 2% respectively.

The species that appear seasonally most important are nikau and puriri through spring and summer, followed by kahikatea in late summer to early autumn. Taraire becomes increasingly important from mid-autumn to winter. Clout *et al.* (1995b) reported more than 300 kereru congregating at Wenderholm Regional Park during the autumn of 1989 to feed on taraire. Puriri, and foliage and flowers were mostly consumed from mid-winter to spring. Observations of feeding behaviour tend to predate peak fruiting periods of the generalised fruiting year.

The kereru breeding season, as indicated by number of new nests found in Figure 6.8c, was eight months long from September 1988 to April 1989. During the breeding season 93% of the total number of nikau feeding observations were made and 65% of the puriri observations. Nikau has its peak fruiting period during the breeding season, but puriri had relatively small numbers of fruit (less than 5% of the total yearly production) during this period. Together, nikau and puriri account for 60% of the feeding observations during the breeding season. Taraire was important at the beginning of the breeding season (7%) and kahikatea at the end (18%). During the breeding season kereru were also seen to feed on ‘other fruits’ (4%), leaves and flowers (4%), tawa fruits (4%), karaka fruits (1%) and kohekohe fruits (1%).

Figure 6.8: Availability and nutritional value of fruits throughout the year compared with observed kereru feeding and nesting in 1988/89.

Figure 6.9: Availability and nutritional value fruits throughout the year compared with observed kereru feeding and nesting in 1993/94.

6.5.2.4 Results from Wenderholm Regional Park 1993-1994 data

James (1995) focused on the behaviour of kereru during the breeding season. The first nest was found at the beginning of winter in June 1993, however, the peak breeding season was mid spring to early summer (Figure 6.9d). The breeding season included 9 months (months were new nests were found) and a loss of nests during early October was apparently caused by a period of cold weather (James 1995).

Bird feeding observations were made for 6 months from August to January. During this period adult birds were seen taking taraire, nikau and puriri in roughly equal amounts (refer Figure 6.9b and Table 6.7) but taraire was more important at the beginning of the breeding season, while the other two species were more important towards the end. This pattern reflects the peak abundance of taraire and nikau in the generalised year, but puriri was not producing peak numbers of fruit. Leaves and flowers were eaten during spring (14% of sightings) and other fruits (12%) became important diet components from spring to summer (data from James 1995).

Interestingly, the proportions of fruits deposited below the nest (Figure 6.9c), and presumably an important component of the diet of the growing chick, were quite different from the feeding pattern of the adult birds. Three times as many taraire fruits were found below the single nest monitored for 3 month during the nesting season than the proportions of taraire feeding observations made for adult birds during the 6 months breeding season (data from James 1995). Sixty-three percent of the fruits dropped below the nest were taraire, and lipid-rich fruits accounted for 82.5% of the total number of food items. A smaller number of puriri (9.5%) fruits, leaf and flower fragments (6%) and ‘other fruits’ (2%) were found below the nest.

Lipid-rich food items tend to be energy-rich and this is probably an important attribute for a rapidly growing kereru chick. The other major food item found below the nest, nikau (19%), not only has high lipid levels, but also high levels of calcium, which is important for the growth and development of bones.

6.5.2.5 Comparison of all three studies

Kereru have been shown to use fruit species as they become seasonally available. However, they do show a preference for large lipid-rich fruits, which usually amount to 40% or more of the diet. Taraire and nikau are the most commonly eaten lipid-rich fruits, but the smaller usage of kohekohe could reflect this species biennial fruiting pattern and/or the lack of fruit in areas with possums (refer Chapter 7). Tawapou is a rare coastal species and will therefore never feature large in the diet of kereru in the Auckland region, except where tawapou is locally present or common.

Puriri, a large sugar-rich fruit, is another dietary item that is common in reasonable quantities (13% to 30%) in all three studies. This species is eaten throughout the year, even when the fruit is relatively scarce. Kahikatea tends to dominate feeding observation data at the end of summer and the beginning of autumn when large quantities of ripe fruit can be available. All other species of fruit are eaten in lesser quantities. During late winter and early spring kereru feed on the nitrogen-rich foliage of kowhai (refer Table 6.3), however, fruits are still available and consumed by kereru during this period.

During the kereru breeding season large quantities of nikau, a lipid and calcium-rich fruit, are available and sought out by kereru, supplemented by puriri fruit. The end of the taraire fruit season extends into the kereru breeding season and is used according to availability. It seems likely that kereru chicks are fed a high lipid, and possibly high calcium, diet on the basis of consumed fruits caught below a kereru nest.

6.5.3 Fruit consumption as a measure of attractiveness of fruit species to dispersers.

There are fewer frugivorous birds on the mainland than was the case historically (Holdaway 1989; Towns *et al.* 1997b). It has been suggested that there now are insufficient frugivores to consume and disperse entire fruit crops resulting in drawn out fruiting phonologies (Burrows 1996). It would be reasonable to assume that, if this is indeed the case, the frugivores target the more preferred fruit species in preference to the less preferred fruit species, and this would result in variable rates of consumption and rates of fruit disappearance from trees of different species.

Therefore, the proportion of the total fruit crop that was consumed could indicate how preferred that species was to dispersers. If a large proportion of the crop was consumed, it can be assumed that the fruit was attractive. Similarly, a mostly uneaten crop indicates that the species was not favoured. Since seedfall traps caught both consumed and uneaten fruits these data can be used to illustrate what proportion of the crop was eaten (Figure 6.10).

However, not all species were equally represented in seedfall traps. The large-fruited target species, karaka, kohekohe, puriri, pigeonwood, taraire and tawa, all had trees beneath which seedfall traps were deliberately placed. Some of the other species present in the traps did overhang these seedfall traps but were not sampled as systematically as the target species. It is possible that the data for these non-target species has a bias towards consumed fruits, since the only way for seed of a non-target tree, that does not overhang a seedfall trap, to fall into a trap is to be consumed and dispersed.

Another way of gauging the attractiveness of a species' fruit crop is the speed with which a ripening crop attracts dispersers. A species whose fruits are consumed quickly after ripening can be assumed to be more attractive than one whose fruit remains on the tree for a long time and only gradually disappears. The data from this study offers two ways to illustrate this.

One is to compare the annual proportion of ripe fruit available against the annual proportion of consumed fruit caught in the seedfall traps (Figures 6.10 and 6.11). If the proportion of consumed fruit in seedfall traps exceeds the proportion of observed ripe fruit for the same period then the fruit is probably taken from the trees as soon as it ripens, and was not available to be recorded in the observational data. If the proportion of fruit caught in seedfall traps is considerably lower than the observed ripe fruit crop, then the fruit was not actively sought out by dispersers, and is probably not favoured.

There is sufficient data on kereru feeding patterns, for some species, to be able to compare the timing of ripe fruit availability with the timing of kereru feeding on those species. The annual proportions of kereru feeding behaviour, for two studies, have been overlaid on the proportion of ripe fruit available (Figure 6.11).

6.5.3.1 Data used

The total number of mature fruits and the total number of consumed fruits caught in seedfall traps were summed for each sampling fortnight (1 to 26) and pooled over all sites and all years. The number of uneaten fruits was assumed to be the difference between number of mature fruits and number of consumed fruits for the same period. These data are graphically presented in Figure 6.10. A Chi-square test was used to compare the number of consumed versus uneaten fruit for each sampling fortnight that had fruit (Table 6.8)

Figure 6.11 is a composite of annual proportion of trees observed to have ripe fruit, annual proportion of consumed fruit to fall into seedfall traps and proportion of kereru feeding behaviour

The 'ripe fruit available' data, showing the proportion of ripe fruit observed, is identical to that presented in section 6.5.1, Figure 6.5.

‘Fruits consumed’ includes all those seeds that were consumed, that is had the fruit-flesh removed by passing through a digestive system, and is based on the number of consumed ripe fruits presented in Figure 6.10.

The ‘1994/98 kereru data’ refers to the feeding observations of kereru noted during this study and are based on the data presented in Figure 6.7. The observations have been separated into individual fruit species and expressed as a proportion of the total feeding observations for that species.

The 1988/89 kereru data includes all the feeding observations for kereru collected by Clout (unpublished data) from September 1988 to September 1989. These data had a previous incarnation in Figure 6.8.

The consumed fruits data and the two kereru feeding observation data sets have been treated in the same manner as the ripe fruit observation data. That is, the observations have been summed in fortnightly sampling periods and these periods are expressed as a proportion of the total number of observations for that species (refer to section 6.5.1 for more details).

The 1988/89 kereru data set contains considerably more observations than the 1994/98 data set and is therefore more robust and less prone to large peaks in proportions. However, the 1994/98 data set was collected while both the ripe fruit observations and the seed deposition observations were made and could perhaps be more relevant than the earlier data.

6.5.3.2 Results

Table 6.8: Chi-square comparison of number of consumed and uneaten fruits per fortnightly sampling period.

d.f. are for the number of weeks that fruit was found in seedfall traps (d.f.=number of weeks fruits found in seedfall trap minus1)

	df	Chi-calculated	Chi-critical	Signif	Number consumed fruits	Number not consumed	Total fruits
Kahikatea	19	1051.15	30.14	Yes	6196	1182	7378
Kohekohe	12	90.07	21.03	Yes	1370	1349	2719
Nikau	25	252.77	37.65	Yes	2791	1281	4072
Karaka	23	51.00	35.17	Yes	94	779	873
Pigeonwood	16	58.91	26.30	Yes	54	42	96
Puriri	25	544.50	37.65	Yes	1206	2686	3892
Supplejack	19	31.49	30.14	Yes	52	34	86
Taraire	25	126.96	37.65	Yes	243	429	672
Tawa	24	36.33	36.42	No	51	101	152

Nikau

Nikau fruits can be eaten by kereru, tui and blackbirds.

As Figures 6.10 and Table 6.8 indicate this species had significantly greater numbers of consumed than uneaten fruits. Nikau palms were not targeted by seedfall traps and they produce fruit on spadices that are held close to the trunk. This would have reduced the chance of trees with fruit overhanging the seedfall traps. Thus to a certain extent, the high number of consumed seeds, in proportion to uneaten seeds, could be because fruit was mostly deposited in the trap after passage through the gut of a disperser.

However, rate of fruit take also indicated that for certain periods nikau was more preferred (Figure 6.11). The fruit was eaten mostly in proportion to the amount of fruit available, but through spring (September to November) and summer (December to February) nikau was eaten in greater quantities (fruit consumed) than the presence of ripe fruit indicated. This is shown by the greater proportion for fruits consumed than the proportion of ripe fruits available. During winter (June to August) nikau fruit was eaten in lesser quantities (Figure 6.11).

Kereru generally were seen eating the fruit in proportion to its abundance (Figure 6.11). The 1988/89 kereru observation line (180 observations) follows the columns, showing proportion of ripe fruit available, reasonably well. The smaller data set for the 1994/98 period (12 observations) noted a few kereru feeding observations at the end of winter.

Tawa

Tawa is a large fruit that can only be consumed entire by kereru.

There was no significant difference between the numbers of tawa fruits that were consumed or that fell into seedfall traps uneaten (Table 6.8). About twice as many fruits were uneaten than consumed. The fruit appears to be generally consumed in proportion to its availability (Figure 6.10).

Only a relatively small number of observations were made of kereru eating tawa, 32 for the 1988/89 data and 6 for the 1994/98 data (Figure 6.11). Tawa is anomalous, compared to other plant species, in that the peak number of kereru feeding observations did not coincide with the peak number of fruits available during summer, but with a smaller secondary peak in autumn.

However the columns showing the proportion of fruits consumed indicate that kereru were taking tawa fruit in the peak fruiting season, even though they were not seen to be taking fruit during that period.

Karaka

Karaka is a large fruit than can be swallowed whole only by kereru.

Significantly fewer karaka were consumed than the numbers that remained uneaten, indicating that karaka was not a favoured food (Figure 6.10 and Table 6.8).

Some karaka were eaten while the fruit was available as indicated on Figure 6.11, but the kereru data again illustrate that this was not a preferred species. Karaka was seen to be eaten by kereru on 8 and 4 occasions during the 1988/89 and 1994/98 observation periods respectively.

Puriri

Puriri is mostly consumed by kereru; although occasionally a few smaller fruits can be taken by tui.

A significantly greater number of puriri fruit fell into the seedfall traps uneaten than consumed (Table 6.8). Interestingly the number of puriri fruits eaten throughout the year appeared to be reasonably constant (70-80 fruits per fortnight) when the fruit was available in moderate to high numbers (Figure 6.10).

The rate of take for puriri fruit appears to vary seasonally (comparing columns for consumed versus uneaten fruits in Figure 6.11). During summer, when puriri has its peak fruiting season, proportionally less fruit are consumed than the number available. But, during autumn and spring puriri is eaten more, and at a relatively constant proportion, than its apparent availability.

Three hundred and forty-one feeding observations were made of kereru feeding on puriri during the 1988/89 period and 13 for the smaller 1994/98 data set. The numbers of kereru feeding observations are generally also reasonably constant throughout the year, and do not follow fruit availability trends as closely as, for instance, nikau (Figure 6.11).

Figure 6.10: Number of consumed and uneaten fruits to fall into seedfall traps, summed over all sites by sampling fortnight

Figure 6.11: Relative abundance of fruits (observation and seed deposition) and kereru feeding observations.

Miro

No miro fruits fell into any seedfall traps, and there was only one observation of kereru feeding on miro fruits. The lack of data is probably a reflection of the lack of fruiting miro at the sites, rather than a lack of preference for the fruit. Miro is known to be a favoured fruit from other studies (Clout *et al.* 1986; Clout *et al.* 1991; Clout and Tilley 1992).

Kahikatea

Kahikatea is a small fruit that is eaten by a variety of bird species.

Kahikatea appears much preferred since the majority of the fruit to fall into seedfall traps was consumed (Figure 6.10). However, this could in part reflect that kahikatea was not one of the target species and that one way for fruit to fall into seedfall traps was being dropped there by dispersers.

All indices of fruit take (fruit consumed, and the two kereru data sets) indicate that the fruit was most commonly eaten early in the fruiting season rather than when peak numbers of kahikatea fruit were observed (Figure 6.11). Kahikatea is a small fleshy fruit with high levels of moisture and sugar. Other nutrition data (not shown) indicate that late season fruits tend to be less moist and have a smaller percentage of fruit-flesh to seed ratio. Thus perhaps desiccation makes these small fruits less attractive to dispersers later in the season.

Tawapou

Tawapou is a large fruit that can only be consumed by kereru. It is also a rare coastal species.

No seedfall data are available.

Kereru were seen feeding on tawapou when it was available. Although only a few observations were made of kereru eating tawapou (15 for 1988/89 and 9 for 1994/98) this is probably a reflection of its scarcity rather than a measure of the extent to which it is preferred by kereru. Fruiting tawapou trees were vigorously defended by several kereru, who chased away all other kereru.

Kohekohe

Kohekohe is eaten by kereru, tui and blackbirds.

Significantly more kohekohe were consumed than left to fall uneaten into seedfall traps (Figure 6.10 and Table 6.8.) Kohekohe had a biennial pattern of fruit availability with alternate years of large and small fruit crops (refer to Chapter 5). During years with small fruit crops it was difficult to collect any uneaten ripe fruit to process for nutrition analysis. The impression was that fruits were taken as soon as the capsules opened.

The proportion of fruits consumed peaks before the proportion of ripe fruits observed peaks (Figure 6.11). This is partially an artefact of the designation of the degree of ripeness, which in the case of kohekohe was open capsules. An open capsule was scored as ripe, regardless of whether the fruits had already been removed or not. In most cases the capsules were empty when scored.

On the other hand, it also indicates that kohekohe is a preferred fruit since, not only the proportion of fruit consumed, but also the proportions of kereru feeding observations (though number of observations were small; 6 for 1988/98 and 3 for 1994/98) peak prior to the observation of ripe fruit peak (Figure 6.11).

Taraire

Taraire is a large fruit that can be eaten only by kereru.

Significantly less of the taraire fruits were consumed than uneaten (Table 6.8). The bulk of these uneaten fruits occurred during the last summer of the study when taraire at several sites appeared to have two flowering periods followed by two fruiting peaks within one year (Figure 6.10). This unusual occurrence of taraire fruit in summer apparently did not attract as many kereru as the more usual winter fruiting period. Perhaps, taraire is less attractive than some of the other species that are available during the summer months, e.g. nikau.

Most taraire fruit is eaten during the winter months, and fruit is especially preferred at the beginning of the taraire fruiting season (Figure 6.11) as indicated by the peaks of consumed fruit and the kereru feeding observations (324 for 1988/89 and 14 for 1994/98).

Pigeonwood

Pigeonwood is a medium to large fruit that is eaten by kereru and possibly by tui.

The number of observations for pigeonwood is small, since most sites had only a few trees, and only one site had seedfall traps placed beneath pigeonwood trees. Unfortunately, most of the selected trees were male and only one heavy crop occurred during this study, thus few fruits were caught. Still, significantly more fruits were eaten than left untouched (Figure 6.10 and Table 6.8).

There is a tendency for more fruits to be consumed early in the season (Figure 6.11) but with such low numbers and only 2 feeding observations for kereru this is by no means conclusive.

Supplejack

Supplejack is a medium-sized fruit that can be eaten by kereru, and possibly tui and blackbirds.

As for pigeonwood, the number of observations is small, but more fruits were consumed than left uneaten (Table 6.8). Supplejack is a scrambling vine that reaches for the canopy and could be found throughout most forests. Fruiting vines were not noted often, possibly because the canopy obscured the fruit. The majority of consumed fruits fell into seedfall traps during late spring and through summer, and the only kereru feeding observation occurs in early spring. Supplejack fruit in late summer and early autumn did not seem to be favoured.

6.6 Concluding discussions

6.6.1 Fruit nutrition

All fruiting species investigated in this study had unique combinations of nutritional and physical characteristics. Cluster analysis assigned species to one of six fruit ‘types’ based mainly on; sugar, lipid, carbohydrate, protein and calcium content, and fruit size.

These results are in general agreement with the major nutritional groupings that Jordano (1995) reported in a paper analysing the evolutionary association between the phenotypic traits of 910 fleshy-fruited angiosperm species and the type of seed disperser known to disperse the fruit (birds, mammals or both). Size differentiation was the most significant attribute in the principle component analysis, followed by lipid and fibre-rich fruits versus non-structural carbohydrate-rich fruits. The third component differentiated between relative yield of pulp, energy content per fruit and fibre, versus water content. The fourth component addressed levels of protein and the last component depicted a trade-off between individual seed mass and seed number per fruit (Jordano 1995).

Size differentiation was not significant in this study since most of the fruits analysed were large-fruited species. Cluster analysis showed the greatest differentiation between nutritionally rich and high moisture sugar-rich (non-structural carbohydrates) fruits. The nutritional fruits in this study could be further differentiated on lipid-rich, carbohydrate rich, protein rich and physical attributes of the fruit. However, in general the fruits analysed in this study had less nutritional value than did the fruits from overseas. The New Zealand fruit are smaller, nutritionally poor and fibre- and moisture-rich. This could be a consequence of plant species competing for the services of a single frugivore, which might have constrained the size of the fruits able to be dispersed and may have reduced nutritional competition amongst plant species for a single key (and possibly only) frugivore that was numerous.

The availability of these fruit types within a general fruiting year tended to be complementary during late summer and autumn as proposed by Whelan *et al.* (1998), that is fruits with different characteristics were more often available simultaneously than fruits with similar nutritional values. The lipid-rich species, preferred by kereru, were spread throughout the year and complemented by other fruit types during summer and autumn. However, fruit-complementarity for large-fruited species was not clear for the rest of the year, but this does not consider the food choices of the main disperser, kereru, which may be eating smaller sugar-rich fruits that were not included in this study.

Witmer (1998; Witmer and Van Soest 1998) noted that frugivorous thrushes preferred lipid-rich fruits to sugar-rich fruits and appeared to have a digestive system more suited to the digestion of lipid-rich fruits compared to cedar waxwings (*Bombycilla cedrorum*). Whereas, cedar waxwings preferred sugar-rich fruits and appeared to have reduced capability to digest lipids. There is no indication from the data presented here that kereru have become quite so specialized, since they eat both fruit types throughout the year depending on availability.

American robins (*Turdus migratorius*) also generally preferred sugar-rich fruits to lipid rich fruits, but the energy assimilation rates for the two types of fruit differed seasonally, with lipids becoming nearly as efficiently assimilated in autumn as the sugar-rich fruits (Lepczyk *et al.* 2000). These changes in assimilation rate of nutrients were postulated to be related to extrinsic cues, such as photoperiod or temperature, that signal the need to accumulate fat in preparation for migration. Kereru do not undertake long migrations as robins might, but they do perhaps require increased lipid intake while feeding chicks on crop milk.

6.6.2 Seasonality of fruit nutrition

The fruiting seasons of the tree species studies were asynchronous (also refer chapter 5), this resulted in fruit being available throughout the year and also resulted in the diet of kereru changing according to fruit-species availability. Similar patterns have been noted elsewhere, for instance, for the fruit pigeons of Northern Queensland (Crome 1975b), the Torres Strait pigeon (Crome 1975a).

The large-fruited sugar-rich species were all clumped in late summer, when lipid-rich fruits were relatively scarce. Analysis of fruit consumption patterns of kereru indicated that some sugar-rich species were more preferred than others. Karaka is not particularly favoured as a food source and its fruits remained mostly uneaten. This could possibly also be attributed to the size of the fruits, which appears to exceed even the gape of kereru on occasion. The only occasion that significant quantities of karaka fruit were seen to be taken was after a particularly dry summer, when large fruit crops appeared to have smaller than usual fruits.

Tawa, in the Auckland region, has a more diverse fruiting pattern than regions further south (refer to discussion in Chapter 5) but it is unclear whether this is the result of underlying genetic diversity or differences in climate (e.g. warmer winters in Auckland). The proportion of fruit eaten during the peak fruiting season (summer), relative to its abundance, was possibly less than the proportion of fruit eaten during the smaller secondary autumn peak. The number of tawa fruits eaten was generally greater than for karaka but less than for puriri, possibly indicating that tawa is of intermediate nutritional value, or preference. However, this could also be related to the relatively small number of tawa fruits produced compared to the number of puriri and karaka fruits.

Puriri is eaten throughout the year, with roughly equal numbers of fruit eaten during each sampling fortnight that had moderate to high numbers of fruit. The impression is that this species is a “bread and butter” type of fruit, it is not nutritionally spectacular, but nearly always available and therefore a

basal component of kereru diet. It is the species most commonly eaten in conjunction with the kereru preferred lipid-rich fruits.
Kahikatea, a small sugar-rich fruit, is greatly preferred by a whole range of bird species when it first ripens, but there are indications that late-season fruit might not be quite so attractive.

Hinau, a carbohydrate-rich fruit, was present from April to September (mid autumn through to early spring) in Waimana Valley (38°17' S lat, 177°07' E long), Otamatuna, Urewera National Park (R. Barraclough pers. comm.) and over the same period in the Orongorongo Valley (Brockie 1992). Hinau has been observed with ripe fruit during April in Auckland (Anonymous 1995) and the fruiting period in Auckland will probably be similar to that observed in other areas, but this study was unable to verify that with observations.

6.6.3 Utilisation by kereru

Kereru, as indicated previously, prefer the lipid-rich fruits supplemented by puriri and other fruits as they become seasonably available. It appears that kereru chicks could be fed on a diet of 80% lipid rich fruits. Other fruit pigeons, such as the Torres Strait pigeon (Crome 1975a), and Northern Queensland pigeons (Crome 1975b), also show a preference for lipid-rich fruits.

It is also interesting to note that nikau, which is both lipid and calcium-rich, has its peak of ripe fruit production during the breeding season, when calcium is most needed for egg production and bone growth. It can not be ascertained if the fruiting of nikau during the breeding season is a co-evolutionary response to the requirements of the kereru breeding cycle, or whether kereru have chosen to breed when this species is maximally available. Nikau has the lowest ratio of fruit-flesh to seed. Just 30% of the fruit is flesh, whereas most other species have at least 50% fruit-flesh. This means that more nikau fruits need to be eaten to get equivalent levels of nutrients. Perhaps the supply of an essential element (calcium) has allowed an evolutionary trade-off in the reduction of amount of fruit-flesh required to attract dispersers.

It seems likely that the high lipid fruit diet postulated for kereru chicks is related to the fact that increases in body mass changes are related to rates of nitrogen intake and not sugar assimilation (Witmer and Van Soest 1998). Sugary fruits can be high-energy, but tend to be low in nitrogen.

A lack of fruit availability has been postulated as the reason for the switch in kereru diet from fruit to leaves in late winter and early spring (e.g. Baker 1999; Clout *et al.* 1986). Such a lack of fruit certainly appears pertinent at sites further south than Auckland such as Pelorus Bridge (Clout *et al.* 1986; Clout *et al.* 1991), but this study has shown that key fruit species are available and eaten throughout the period that foliage is eaten. Fruit pulp is considered nutritionally inadequate for frugivorous birds because of its low protein content (Bosque and Pacheco 2000). Perhaps the switch to foliage is more an issue of nutrient complementarity, during the periods of egg development and nesting, in the Auckland region than lack of food.

Lipid rich foods tend to be taken whenever they are available, and probably maintain the condition of kereru so that they can breed. It has been shown previously that bad fruiting years reduce or prevent kereru breeding at Pelorus Bridge (Clout 1990) and the same for parea on the Chatham Islands (Powlesland *et al.* 1995; Powlesland *et al.* 1997). But egg production and chick rearing would also require considerable quantities of nitrogen or protein, which are not supplied in sufficient quantities by the lipid-rich foods (generally about 2%). However foliage, such as, young kowhai and new willow leaves can contain around 30% protein (M. Clout unpublished data) and would therefore be a crucial supplement during egg-production and chick rearing. The same was seen for the parea on the Chatham Islands, they acquired supplementary protein by foraging on herb foliage and flower buds during nesting season (Powlesland *et al.* 1997).

Observational data indicate that kereru generally prefer larger fruits to smaller ones. The greatest numbers of feeding observations are for fruits that are too large to be taken by other bird species.

6.6.4 Success of plant species in attracting dispersers

Some plant species appear more successful in attracting dispersers than other species. The lipid-rich fruits all appear to be successful in attracting dispersers, and miro, which has both high protein and reasonably high sugar content, has also been reported as much favoured (Clout 1990). Kahikatea, a small seasonal sugar-rich fruit successfully attracts a whole range of bird dispersers, but larger sugar-rich fruits, that rely solely on the kereru, have a proportionally smaller part of the crop dispersed. This might not always have been so, kereru numbers are reportedly considerably smaller than they have been (Clout 1990; Pierce *et al.* 1993), and perhaps the numbers of kereru available now are too small to consume and disperse the number of fruits produced by large-fruited species.

Within the large sugar-rich fruiting species puriri appears to have the best fruiting strategy by presenting moderate quality fruit in moderate numbers throughout the entire year. In this way it appears to ensure a reasonably consistent rate of fruit consumption and probably dispersal. Tawa and especially karaka are perhaps somewhat more seasonal and thus have to rely more on being ‘discovered’(as postulated by Thompson and Willson 1979) by the frugivores during the peak fruiting season. Dispersal of these species appears to be less consistent.

Not enough information is available from this current study to judge the dispersal success of some of the medium-sized and moderately nutritious fruits such as pigeonwood and supplejack. A greater proportion of the fruits caught in seedfall traps was consumed, and probably dispersed, but the number of fruits involved was small, as were the number of feeding observations on the fruit. It is even possible that another species of disperser, which is now locally extinct such as the kokako, was more attracted to these species than kereru appeared to be.

6.7 Conclusions

The fruit species tested here all had different nutritional characteristics but could be broadly grouped into nutritional fruit types based on key characteristics (lipids, sugars, protein, carbohydrates, calcium and size). These groupings are in concordance with a study done by Jordano **(1995)**. Fruit is available throughout the year because the periods of ripe fruit presentation for different species closely abut in time. Lipid-rich fruits are available throughout the year but sugar rich fruits are more common in summer and autumn.

The diet of kereru comprises mostly of lipid-rich and sugar-rich fruits and the lipid-rich fruits appear especially important during the breeding season. Calcium- and lipid-rich nikau fruits are especially preferred during the nesting period.

Fruits eaten solely by kereru are nutritionally superior to fruits that can be taken by several species. The presentation of fruit types (e.g. lipid-rich or sugar-rich) is complementary, with generally more than one type available at any point in the year, and kereru utilising fruits with different nutritional characteristics.

Nikau, a high calcium food, was available and heavily utilised during the kereru breeding season, but it is not possible to determine whether nikau has evolved to provide high calcium levels during this period, or whether kereru time breeding to coincide with nikau fruit production.

Puriri (a sugar-rich species) has a somewhat different fruiting strategy, presenting moderately attractive fruits nearly continuously. This could enhance its’ dispersal overall since kereru utilise this species throughout the year. The tree species studied have different strategies for attracting bird dispersers; some are more successful than others.

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[1] Brush-tail possum (Photo courtesy New Zealand Geographic)

7. Impacts of possums and rodents

7.1 General background

The impact on the New Zealand forest ecosystem of the arrival of humans and introduced mammals has been briefly described in Chapter 1. This chapter will provide more details of the effects on native forests by two groups of introduced mammals, the Australian marsupial brushtail possum (*Trichosurus vulpecula* Kerr) and the introduced European rodents (ship rat *Rattus rattus* Linnaeus, Norway rat, *R. norvegicus* Berkenhout, and house mouse, *Mus musculus* Linnaeus).

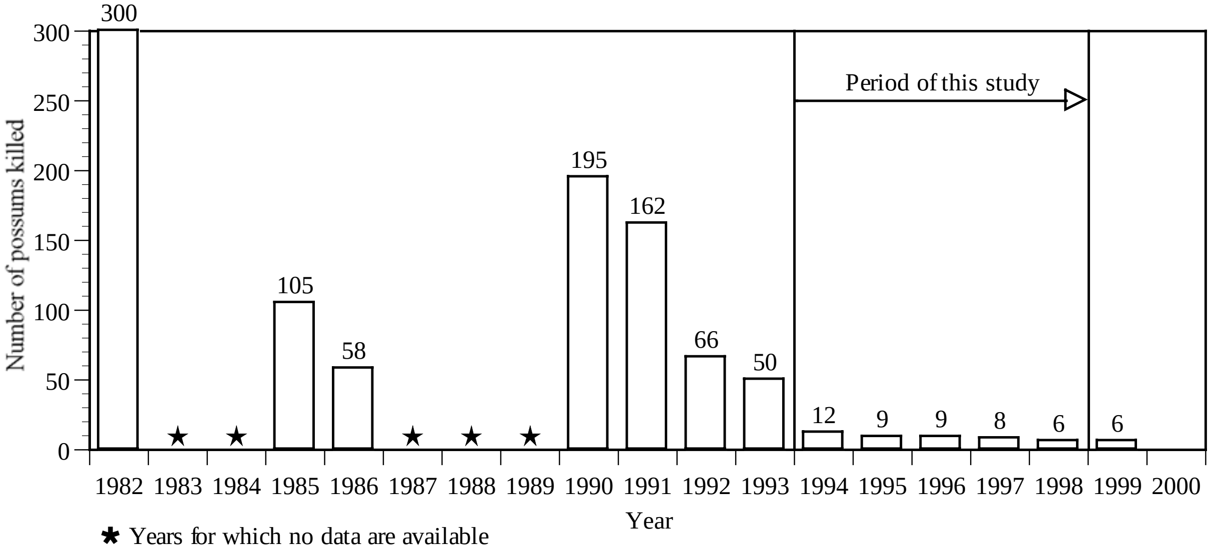
All of the mammalian species mentioned above have had significant impacts on the native flora and fauna of New Zealand (Chapter 2). Even the kiore (*R. exulans*), which preceded the arrival of the European commensal rodents, was considered a harmless vegetarian by many but probably significantly affected small native animals and some plant species in New Zealand (King 1998). The impacts of introduced mammals in New Zealand have been especially severe because the native flora has evolved in the absence of browsing and grazing mammal and were therefore especially vulnerable to them. Mammals were introduced without their full complement of natural predators, parasites or diseases. The lack of natural controls, mild climates and abundant food resulted in explosive population increases of introduced mammals with consequent damage to, and changes in, flora and fauna (Allen *et al.* 1997; Campbell 1984, 1990; Coleman *et al.* 1985; Green 1984; Nugent 1994; Poole 1969; but also see Velben and Stewart 1982). Descriptions of possums, rats and mice, their known habits and food preferences, are provided in Chapter 2.

7.2 Suppression of mammals. The history of each site

Wenderholm Regional Park

Possum control in the forested areas of Wenderholm Regional Park (Figure 7.3) was begun in 1982 and became more systematic from 1986 onwards (Wotherspoon 1994). Staff at Wenderholm Regional Park arrange for annual cyanide poisoning, or trapping, of possums during winter or late spring. Figure 7.1 illustrates that initial possum densities were higher than under sustained possum control. From 1994 onwards the number of possums at Wenderholm Regional Park have been consistently low (Figure 7.1), as surrounding private land has become incorporated into the possum suppression programme. This slowed the immigration of possums from adjoining land into the park. The study described here commenced in November 1994.

Figure 7.1: Number of possums killed per annum at Wenderholm Regional Park in relation to the duration of this study



Clout *et al.* (1995a) conducted snap trap indices at Wenderholm Regional Park, from 1990 to 1993 (Table 7.1 and Figure 7.2), while determining if high rodent numbers were adversely affecting the breeding success of kereru. Rodent control was carried out, from October 1992 until the beginning of February 1993, using poisoned baits placed in Novacoil tunnels in a 50 x 100-m grid on the forest headland. The timing of rodent control was chosen to protect kereru nests during peak breeding. Tunnels were pinned to the ground with hoops of heavy gauge wire. Each bait-station was baited with six Talon WB 50 wax pellets and was checked fortnightly and rebaited as necessary. During the first year of rodent control pigeon breeding success improved significantly (Clout *et al.* 1995a)

The systematic rodent control begun in 1992/93 has continued to the present day (Table 7.1 and Figure 7.2). Rodent bait type is changed biennially to reduce bait-shyness, and varies between Shell Agricultural ‘Storm Rodenticide’ one year and Talon 50WB the following. Bait take generally peaked in the second week of poisoning and remained high for about a month, declining sharply thereafter, but some bait continued to be taken until the beginning of February, especially around the perimeter (Clout *et al.* 1995a). Re-invasion of rats was greatest nearest road edges (especially near the bridge over the Waiwera River), picnic areas and areas bounding non treated blocks (eg Schiska's Farm Lovegrove 1996a). Possums and mice were suspected of consuming much of the late season bait take in view of evidence such as the removal of wire hoops and movement of baitstations (attributed to possums) and partially eaten baits with small tooth marks (attributed to mice) (Clout *et al.* 1995a). Green rat droppings in seedfall traps indicated that arboreal rodents accessed the bait (A. Dijkgraaf pers. obs.), and recently dead possums indicated that rat poison also contributed to reducing their numbers (Clout *et al.* 1995a; Lovegrove 1996a).

Table 7.1: Rats and mice captured per 100 trap nights at Wenderholm Regional Park

Method as per Cunningham and Moors (1993) with corrections as per Nelson and Clark. (1973)

	Ship rats	Mice	Source
November 1990	10.8	0	(Clout *et al.* 1995a)
November 1991	15.2	0	(Clout *et al.* 1995a)
November 1992	0	0	(Clout *et al.* 1995a)
July 1993	0.74	9.23	(Clout *et al.* 1995a)
November 1993	0	1.49	(Greene 1994)
March 1994	0	1.48	(Greene 1994)
November 1994	0	1.08	B. Sinclair, pers. comm.
May 1995	2.38	6.10	Dijkgraaf, pers. obs.
September 1995	0.45	5.84	(Lovegrove 1996b)
March 1996	0	21.47	(Lovegrove 1996b)

These indices were calculated from pairs of traps set at 36 stations over 3 nights. Up to, and including, March 1994 only rattraps were used, so mice numbers could have been underestimated (Greene 1994). From November 1994 both mouse and rattraps were used, at the same 36 sites but with 2 rattraps and 2 mice traps at each position (Dijkgraaf pers. obs. 1995). These data are also illustrated in Figure 7.3.

Possum and rodent suppression was carried out throughout the study by ARC staff or contractors. They undertook possum trapping or cyanide poisoning during winter or early spring and put out rodent baits for about 3 months (spring to summer) during the peak of the kereru breeding season.

Loch Amber Bush

Loch Amber Bush, about 2km from Wenderholm Regional Park (Figure 7.3), did not have any systematic pest control and the owner was willing to forgo pest control for the duration of the study. Prior to this study, the owner or hunters conducted occasional nocturnal shooting of possums, but none had occurred in the two years prior to this study. The proximity and similar forest type to Wenderholm Regional Park allows comparison between these two sites (refer to Chapters 3and 4 for more details).

Figure 7.2: Number of rats and mice per 100 trap nights at Wenderholm Regional Park in relation to the rodent bait station programme and the duration of this study

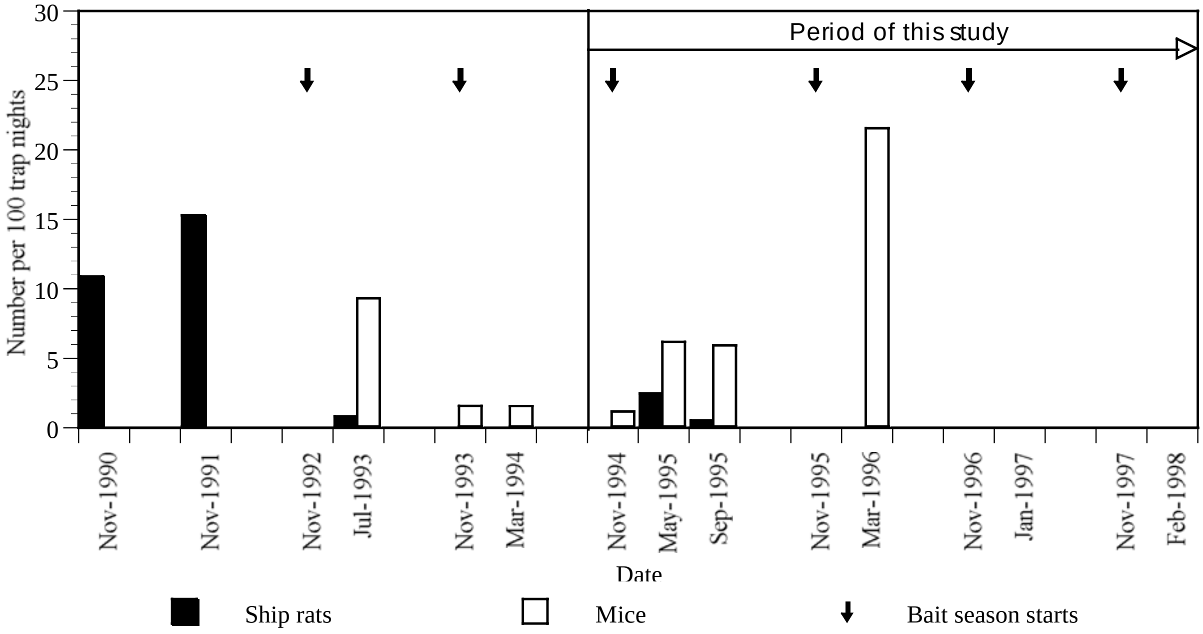
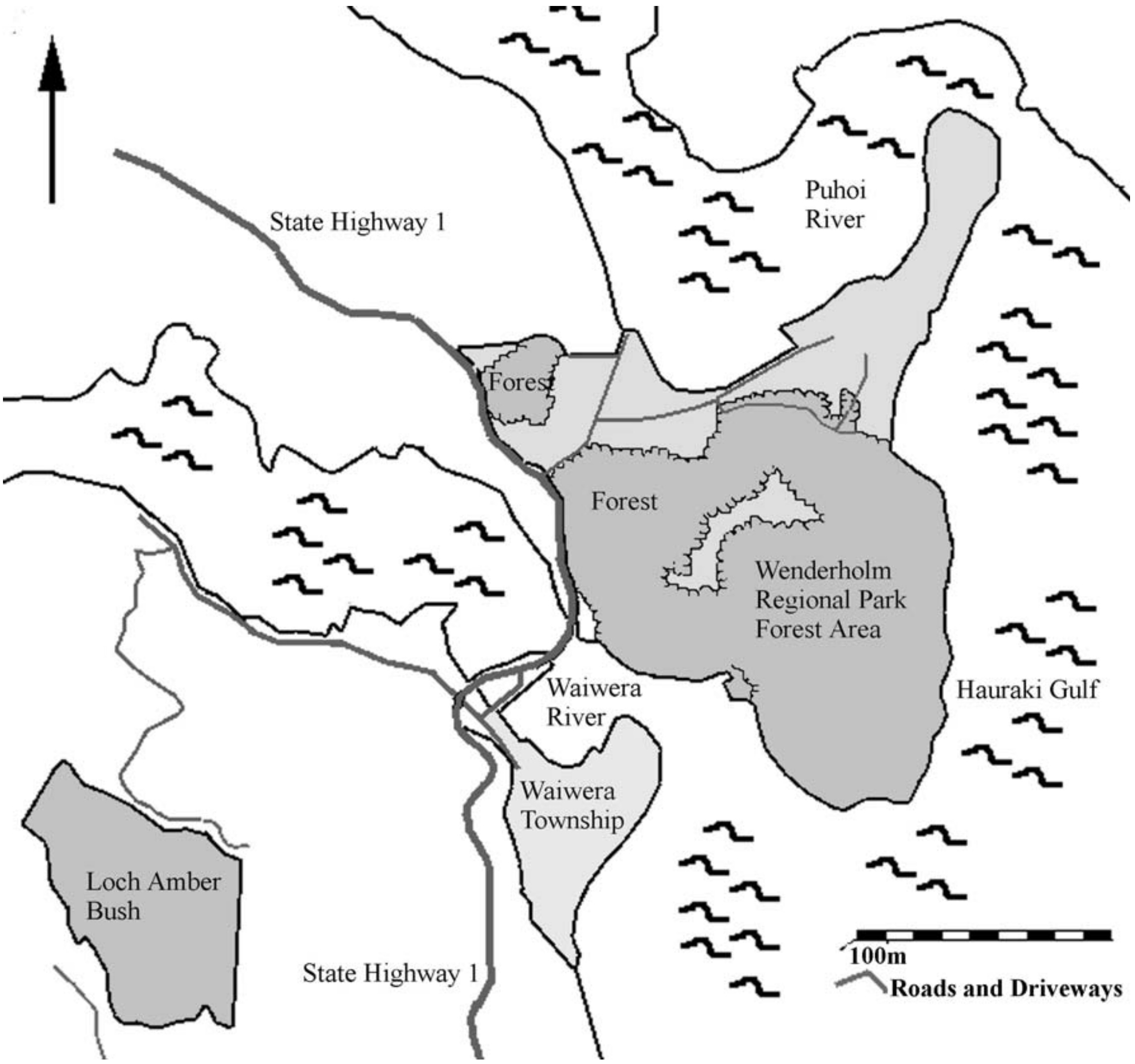


Figure 7.3: Locality map of Wenderholm Regional Park and Loch Amber Bush
(For more details refer to photos in Chapter 3)



Whitford Bush

Possum control at Whitford Bush (refer to Figure 7.4) began in late 1993, a year before the start of this study. The owners had placed bait-stations in trees throughout the patch and had been filling these stations with Talon® cereal pellets as possum sign was noted. The owners were committed to continuing with possum control and were happy for rodent control to be initiated (refer to Chapter 3 for more site details).

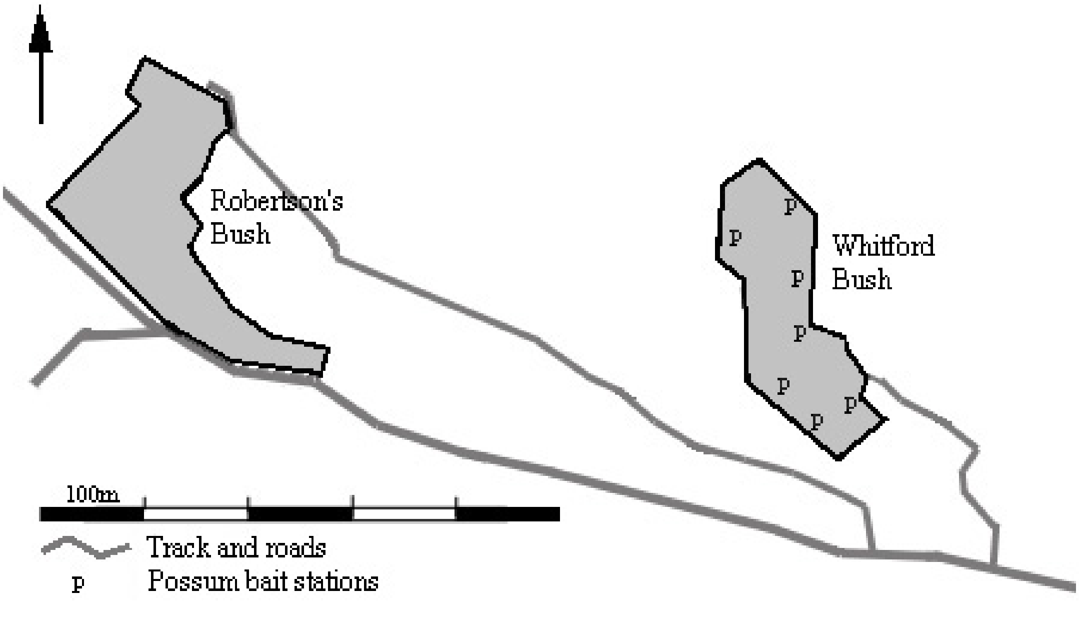
At the beginning of the study, the bait supply was increased to ensure that all possums were eradicated from the forest. Subsequent to that, bait-stations were filled when possum sign was noted. This method of control was continued throughout this study and baits were alternated between Talon and Pindone to reduce the chance of bait-shyness in possums.

Ground-based rodent bait-tunnels, spaced at 50-m intervals, were installed along two lines within the site. These tunnels were 600 mm lengths of Novacoil, staked to the ground by wire, in which 4 Talon 50WB baits were placed once a month. To minimize toxins entering the environment, the tunnels were restocked less frequently as bait take reduced. Baits were only replaced when rat droppings were once again found in seedfall traps. Towards the end of the study rodent sign (e.g. droppings in seedfall traps) was infrequent and the tunnels were not stocked often. Moreover, a poisoned rat was found, indicating that the possum bait was not only controlling possum numbers.

Robertson's Bush

This small privately owned forest remnant is less than 1-km from the Whitford patch (refer Figure 7.4), and did not have regular mammal control. The owners were willing to forgo pest control for the duration of the study, provided that pests were eradicated at the end of the study.

Figure 7.4: Locality map of Whitford Bush and Robertson's Bush
(For more details refer to photos in Chapter 3)



Remiger's Bush

This forest was comprised of two patches (Figure 7.5): a larger lower section on a steep slope, and the smaller part on the flat at the top of the hill. The smaller patch at the top of the hill (Upper Remiger's) was used for this study.

Remiger's Bush was selected as a site with no previous pest suppression, which was small enough to control mammals with poisoning on a limited budget. It was hoped to be able to switch from a non-poisoning site, to a 'possum suppressed' site and then to introduce rodent control also, whilst monitoring the changes. However, once work started the healthy appearance of the forest and lower than expected levels of possum browse (compared to other sites) pointed to the fact that possums at the site were already controlled to some extent.

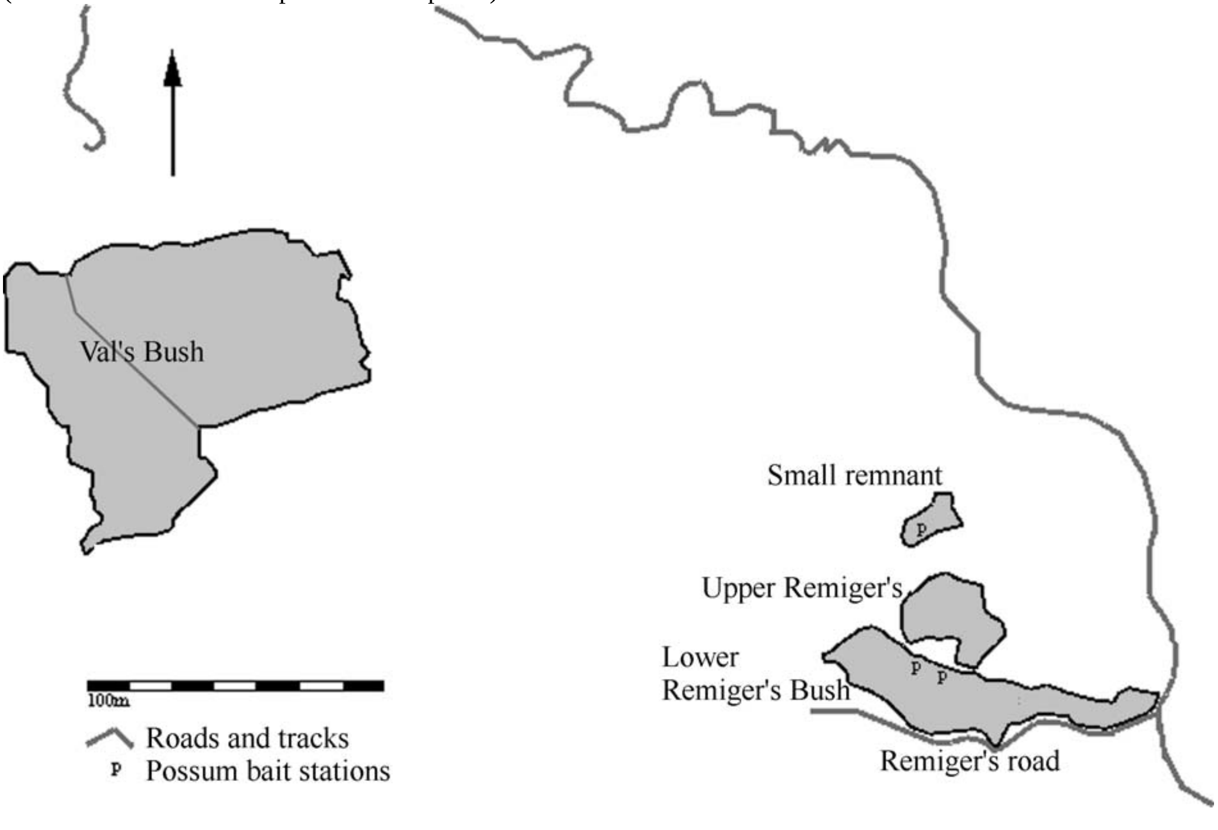
It was discovered that the previous owner of the forest patch was intermittently filling bait-stations along the lower boundary (Remiger's Road) of lower Remiger's Bush (Figure 7.5). These bait-stations would be well within the home-ranges of possums, but beyond the home-ranges of rodents, in the upper section of Remiger's. Thus possums were suppressed to some extent.

It was therefore decided to use this site instead to elucidate the effect of rodent predation compared with the damage caused by possums. Three Philproof bait station were affixed to fence-lines of adjoining forest patches, c. 100-m away, which would be included in possum home-ranges but probably not in rodent home-ranges. The forest patches were separated from each other by pasture of moderately tall grass. The bait-stations were filled once a month with either Talon or Pindone cereal baits.

Val's Bush

This forest (Figure 7.5) had no systematic possum or rodent control, although during July and August 1997 spotlight hunting by commercial hunters on the perimeter of adjacent forest (Photo 3.5) netted more than 400 possums, including 44 in one night (J. Tolhopf pers.comm.).

Figure 7.5: Locality map of Remiger's Bush and Val's Bush
(For more details refer to photos in Chapter 3)



7.3 Effect on mammal presence

7.3.1 Possum and rodent numbers.

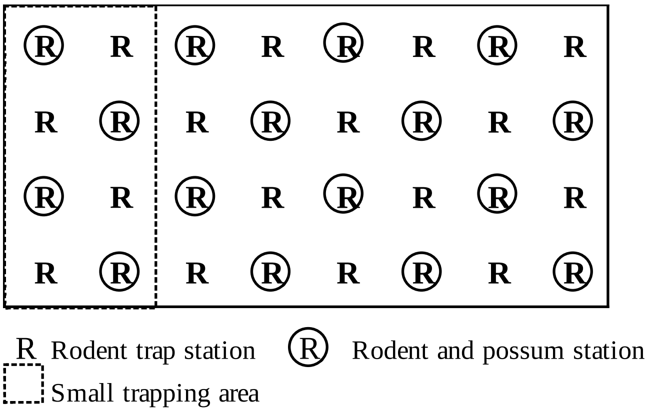
At the end of the phenology study, in February 1998, all forest patches were kill-trapped simultaneously to determine the densities of possums, rats and mice.

The usual spacing for rat snap traps is about 25-50 m between traps (Cunningham and Moors 1993). The spacing for the rodent index trap lines at Wenderholm Regional Park was roughly 50-m between stations (refer to Wenderholm Regional Park under section 7.2). James (1995) noted that the 100 x 50-m poisoning grid for rats at Wenderholm Regional Park substantially reduced rodent numbers. Thus, it was decided to place rodent trapping stations at 50-m intervals.

The smallest bush areas (Whitford, Robertson’s and Remiger’s Bush) were each about 2 ha in area. A maximum of 8 stations could be located in these sites. There seemed to be a high likelihood that all the rodents would be captured in these small bush patches. In other words, these sites would be trapped to extinction. Two lines, 50-m apart with four trap-stations each, were located in these smaller areas, using a hip-chain to locate the positions, with 50-m intervals between stations (Figure 7.6).

It was deemed impossible to achieve extinction trapping in the larger bush areas (Wenderholm Regional Park, Loch Amber and Val's Bush) due to their size, amount of equipment required, accessibility and the need to service the traps on a daily basis. Instead, a larger area, comprising of 4 lines, 50-m apart, with 8 trap-stations per line were laid out in these forests, in the same general locality that most of the phenology studies took place. The aim was to trap to extinction within the trapping area. Extinction was defined as 3 consecutive nights without catching a rat or mouse, or 14 days of continuous trapping, whichever occurred first.

Figure 7.6: Trapping grid layout for small and larger sites.
Each rodent station ‘R’ had two rattraps, and two mousetraps. Every other station also had a Timm’s possum trap.



At each trap station two ‘Ezeset’ rat traps and two ‘Ezeset’ mousetraps were located on a flat surface below natural cover, when this was available. Every second station was also a possum station, at which a Timm’s neck-break possum trap was placed. Possum stations were staggered along the lines so that they were not adjacent to each other (Figure 7.6). The layout for the larger sites can be seen in Figure 7.6. The layout for one of the smaller sites was essentially one quarter the size but the traps were in the same density.

Rodent traps were baited with peanut butter, and the possum kill traps (Timm’s traps) with 1/8 sections of apple coated in cinnamon. Trapping began on 15 February 1998 and continued for up to 14 nights (refer Table 7.2). Animals caught were weighed, rats and mice with a 500-g Pesola balance, and possums with a 2.5-kg or 12-kg Pesola scale. Animals were sexed, and judged on sexual maturity.

Results

No possums or rodents were caught at the two sites with systematic possum and rodent suppression (Wenderholm Regional Park and Whitford Bush). However, Moors (1986) notes that the detection of the last few rodents at low density can prove difficult, and other sign indicated that rodents and possums were occasionally present at these sites. Rodent numbers at the other four sites were variable (refer Tables 7.3 and 7.4), with generally low catches.

Possum numbers at these four sites were more or less as expected. The density of 2.8 to 7.7 possums/ha (Table 7.3), recorded by this study, is low for podocarp-broadleaf forest (where density averages 10-12 possums/ha) but higher than that for scrubby farmland (averages 1-3 possums/ha) (Cowan 1998 , and reference therein). A commercial trapper, who was asked to finish trapping at Loch Amber Bush, estimated that more than half the possums had been caught in the area of the trapping grid. The density of possums at Remiger's Bush (2.8 possums/ha) was the lowest for sites with possums, indicating that the local poisoning regime for possums was having an effect.

Trap indices (possums per trap night) do not differ greatly among sites. Robertson's Bush had the highest index, the result of a relatively large number of possums caught over a short period, with no reinvasion of the trapping grid from other forest patches (or parts of the forest). The nearest forest patch to Robertson's Bush (Whitford Bush) had no possums and other patches were several kilometres away (refer to photo in Chapter 3). Thirty-seven percent of the possums caught were juveniles (Table 7.2 and Appendix 7.1), probably reflecting the seasonal influx of newly independent young.

Table 7.2 Average weight and number of possums caught.

Average		Juvenile female	Mature female	Juvenile male	Mature male
Robertson's	Number	2	3	2	3
Robertson's	Average weight	1250.00	2533.33	1500.00	2400.00
Remiger's	Number	2	1	2	2
Remiger's	Average weight	1975.00	2700.00	1725.00	2275.00
Val's	Number	4	11	2	10
Val's	Average weight	1962.50	2100.00	2100.00	2415.50
Loch Amber	Number	4	12	9	4
Loch Amber	Average weight	1560.00	2308.33	1372.22	2750.00
Total all sites	Number	12	27	15	17
Total all sites	Average weight ±std error of mean	1711.67 ±111.46	2262.96 ±65.70	1533.33 ±95.25	2512.06 ±76.10

A total of 73 possums were caught over the four sites that had possums. The numbers at the smaller sites were equally divided between the sexes and maturity (also refer to Figure 7.7). The larger sites had a non-significant tendency towards more female possums. The average body weights are comparable to those of other North Island studies (Cowan 1998, and references therein). The data from this study are included in Appendix 7.1

Three large dependent juvenile possums were recorded during this study, two at Robertson's Bush and one at Remiger's Bush. Possums give birth mostly in the autumn, although births are recorded for every month of the year in New Zealand. The spring birth season is usually associated with early breeding in the previous autumn, and both are related to food supply (Cowan 1998; Fletcher and Selwood 2000). Females in colonising populations, and in exotic forest or pasture/scrub mosaic habitat breed more often than those in established populations in mature native forest (Cowan 1998).

All sites in this study can be counted among the forest-pasture mosaic, however, the small size of Remiger's and Robertson's Bush might produce more transient possum populations, especially in view of possum suppression at Remiger's Bush with other untreated forest patches adjacent (refer to photo in Chapter 3). Trees in both these small forests tended to be better condition than the larger forests.

Table 7.3: Summary of index trapping at all sites

		Wenderholm			Loch Amber			Whitford			Robertson’s			Remiger's			Val's		
		Possum	Rat	Mouse	Possum	Rat	Mouse	Possum	Rat	Mouse	Possum	Rat	Mouse	Possum	Rat	Mouse	Possum	Rat	Mouse
Site information	Control of pest	Yes	Yes	?	No	No	No	Yes	Yes	?	No	No	No	Part	No	No	No	No	No
	No. traps/site	24	24	24	24	24	24	8	8	8	8	8	8	8	8	8	24	24	24
	Trap area -ha	3.75	3.75	3.75	3.75	3.75	3.75	2	2	2	2	2	2	2.4	2.4	2.4	3.75	3.75	3.75
	Tot. trap nights	4	4	4	14	6+2*	6	4	4	4	8	8	8	11	11	11	14	14	14
Number of animals caught	First 4 nights	0	0	0	10	1	0	0	0	0	7	0	0	4	0	1	12	4	0
	Sum (all nights)	0	0	0	29	5	0	0	0	0	10	0	2	7	3	3	25	17	1
	Per hectare	0	0	0	7.73	1.33	0	0	0	0	5	0	1	2.8	1.2	1.2	6.67	4.53	0.27
Number of traps sprung	Total 4 nights	4	17	21	13	20	24	7	3	7	15	9	9	4	8	9	15	30	33
	Total all nights	4	17	21	46	29	30	7	3	7	15	13	17	7	23	30	32	121	125
Catch /100 trap nights #	First 4 nights	0	0	0	11.17	1.16	0	0	0	0	28.57	0	0	13.33	3.64	3.64	13.56	4.94	0
	All nights	0	0	0	9.27	3.86	0	0	0	0	17.7	0	3.6	8.28	3.92	4.11	7.81	6.17	0.37

? = incidental control through mice taking rat and possum baits
* = caught rats in possum traps on 2 days after rat trap removal
# = number of animals corrected for sprung traps as per Nelson and Clark(1973) using the equation

$$CE = \frac{A \times 100}{(TU - IS/2)}$$

Where CE = Catch effort (expressed in percentage trapping success or animals caught per 100 trapping units),
A = number of animals captured of the desired species,
TU = P × I × N number of trapping units,
where P = number of trapping intervals,
I = length of trapping interval, and
N = number of traps, and
S = total traps sprung by all causes.

Figure 7.7: Number of possums trapped per site.
The data are separated into male and female, and mature and juvenile animals

Table 7.4: Number of rodents caught during the extinction trapping session. No rodents were caught at Wenderholm Regional Park or Whitford Bush. Where no trap is indicated the animal was caught in the trap appropriate for the species (e.g. mouse caught in mouse trap).

Site	Species	Weight	Sex (M/F)	Maturity	Trap
Remiger's	Mouse	16	F	Juvenile	
Val's	Mouse	8	F	Juvenile	Rat
Remiger's	Mouse	15	M	Juvenile	Rat
Robertson's	Mouse	12	M	Juvenile	
Remiger's	Mouse	25	M	Mature	
Robertson's	Mouse		M	Mature	
Loch Amber	Norway rat	212	M	Mature	Possum
Loch Amber	Norway rat	202	M	Mature	Possum
Loch Amber	Norway rat	200	M	Mature	Possum
Val's	Ship rat	75	F	Mature	
Loch Amber	Ship rat	140	M	Juvenile	
Remiger's	Ship rat	35	M	Juvenile	
Remiger's	Ship rat	115	M	Juvenile	
Remiger's	Ship rat	65	M	Juvenile	
Val's	Ship rat	47	M	Juvenile	
Val's	Ship rat	74	M	Juvenile	
Val's	Ship rat	60	M	Juvenile	
Val's	Ship rat	73	M	Juvenile	
Val's	Ship rat	110	M	Juvenile	
Val's	Ship rat	65	M	Juvenile	
Val's	Ship rat	100	M	Juvenile	
Val's	Ship rat	80	M	Juvenile	
Loch Amber	Ship rat	185	M	Mature	
Val's	Ship rat	160	M	Mature	
Val's	Ship rat	80	M	Mature	
Val's	Ship rat	172	M	Mature	
Val's	Ship rat	167	M	Mature	
Val's	Ship rat	172	M	Mature	
Val's	Ship rat	70	M	Mature	
Val's	Ship rat	195	M	Mature	

Only six mice were caught, half of these at Remiger's Bush where possums were suppressed to a certain extent. Three Norway rats were caught (in Timm's traps) at Loch Amber Bush. The remaining 21 rodents caught were all ship rats, with the majority caught in the large untreated Val's Bush. Most animals caught were juvenile males (14) or mature males (13), with only 3 females caught.

Discussion

The two sites with long-term mammal suppression, Wenderholm Regional Park and Whitford Bush, did not have any trappable possums, rats or mice. Possum numbers per hectare were lower for Remiger's Bush (possums suppressed to some extent) than the sites with no possum suppression. Possum trapping indices (numbers caught per 100 trap nights) are probably influenced by invasion of the trapping grid from other parts of the forest, or from other forest patches. Rodent numbers were generally too low to make valid comparisons. Mouse numbers appeared somewhat elevated at Remiger's Bush and Norway rats were only caught at Loch Amber Bush.

The overall catch rate of rodents was lower than expected, but information from other forests in the upper North Island showed that rodent numbers were equally low or erratic there during February 1998 (M. Clout and C. Gillies pers. comm.). Rodent populations can fluctuate quite widely (e.g. King *et al.* 1996a; King *et al.* 1996b). Mouse numbers were low during February for most of the years that King *et al.* (1996a) were monitoring rodent numbers in Pureora Forest. Trap catch indices for mice vary greatly (range 0 to 130.2 mice/100 trap nights) depending on season, habitat and food availability (Murphy and Pickard 1998 and references therein).

There was no obvious increase in mouse numbers associated with control of rats, as found in some other studies (Clout *et al.* 1995a; Craddock 1997; Innes *et al.* 1995). Rodent numbers at Remiger's Bush appear comparable with numbers caught in forest with no mammal suppression, although mouse numbers are somewhat elevated. However, the low numbers of animals caught make such comparisons tentative at best.

The density of Norway rats at Loch Amber Bush (0.8 rats/ha) was lower than recorded for other studies. Moors (1985) recorded a density of 2.6 to 4.2 rats/ha on Motuhoropapa and Bettesworth and Anderson (1972) caught 5 to 10 rats/ha on Whale Island. However, there were indications of greater rat presence at Loch Amber Bush in toppled Timm's traps with rodent chews on the apple, and the occasional trap with a limb or tail caught, thus numbers of Norway rats were likely to be higher than trapping has shown.

Non-commensal ship rats are most abundant in mature, diverse, lowland podocarp-broadleaved forests, with density indices up to 22 rats per 100 trap nights (Innes 1998; King *et al.* 1996b). Trapping rates in this study were considerably lower, 1.16 to 4.94 rats/100 nights for the first 4 nights to a maximum of 6.17 rats/100 trap nights over the two weeks. The population density of ship rats for this study was similar to other studies in New Zealand at 1-3 per hectare (Innes 1998) although Val's Bush exceeds that with 4.53 rats/ha.

Possum and rodent control was reflected in the number of possums and/or rodents caught in a forest patch.

7.3.2 Mammal droppings

Possum, rodent and other identifiable droppings found in the seedfall traps were recorded as present or absent per trap. Droppings were identified to species when possible. This study made no distinction between ship (*Rattus rattus*) or Norway rat (*R. norvegicus*) droppings and mouse droppings were incorporated into the broader category of rodent droppings. These data are presented in Figures 7.8a to 7.9c for the duration that all sites were active.

Data used

The data consisted of the number of seedfall traps per site (therefore a maximum of 30 seedfall traps per site) that contained one or more droppings of each of the fruit predatory species (rats, mice or possums). These data were collected fortnightly for the period where all sites were active (fortnights starting 14 October 1996 to 2 February 1998). Note that it is not the number of droppings per trap per site that were analysed, but the number of traps in which any of these droppings were found.

Method

The faecal presence/absence data were analysed using the GLM procedure in SAS. The model defined the level of pest suppression as a random variable, since other sites could have been substituted to represent the same levels of pest suppression. Site was nested within the level of suppression, since sites were essentially sub-samples of the different levels of control. A simpler model, using site and fortnight sampled, was used to elucidate significant differences between those variables. The syntax used for the analysis is presented in Appendix 7.2.

The parameters of most interest are possum and rodent droppings. Rodent droppings can be any of the three rodents found on the mainland. The smaller and less robust data set containing rat droppings only (less robust since it proved difficult to positively identify two week old rodent droppings as either mouse or rat) has been included to help explain the effect of rodent levels at one site in the models.

Figures 7.8 a to c: Number of seedfall traps at each site containing one or more possum droppings.

Figures 7.9 a to c: Number of seedfall traps at each site containing one or more rodent droppings.

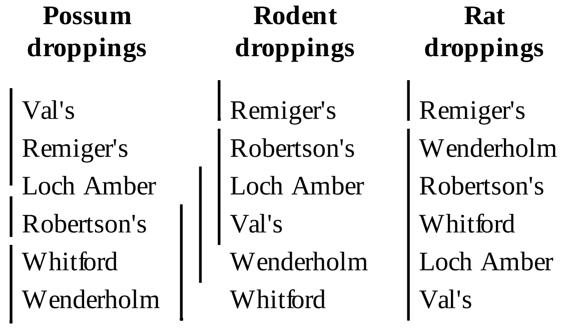
Results

The full SAS output for each of the pest species for droppings per trap are presented in Appendix 7.3.

Figure 7.10: A posteriori Tukey's Studentized Range (HSD) test for mammalian droppings in seedfall traps by site.

Alpha= 0.05 df= 42;

Sites joined with the same bar are not significantly different.



Possum droppings

The level of possum suppression had a significant effect on the number of droppings encountered in seedfall traps (Appendix 7.3; Site nested within suppression F=40.41, P<0.0001, df=4). In areas with good possum suppression, such as Whitford Bush and Wenderholm Regional Park, few droppings were encountered. Areas with no poisoning regime (Val's, Loch Amber and Robertson's Bush) tended to have significantly more traps containing possum droppings. Remiger's Bush was the exception. Although possum numbers were lower here than in the non-suppressed areas (refer Section 7.3.1), possums were still present and were evidently feeding in preferred tree species (e.g. taraire and kohekohe) that had seedfall traps placed beneath them.

Another factor that affected the results was the intermittent beginning of systematic possum control at Remiger's Bush. The possum control regime can be divided into three periods (refer to Figure 7.8c and Table 7.5). In the first period, possums were periodically suppressed by the use of poison bait-stations in the lower part of Remiger's Bush (A. Dunn pers. comm.), but no systematic control took place in the smaller, upper patch used for the phenology study. Then followed a period when possums were killed in the phenology patch using Timm's traps, (indicated on the graph as Remiger's Bush Timm's traps). These caught 6 possums over a month, but proved too time consuming to continue indefinitely. During the third period the three bait-stations (within possum ranging distance, but presumed to be outside of rodent home-range distance) were filled every month. However, there was a lag between the trapping and initiation of possum poisoning using bait-stations.

The effects of this lag can be seen in Figure 7.8c. A reduction in the number of seedfall traps containing possum faeces occurred whilst using Timm's traps, followed by a gradual increase during the lag between the trapping and the start of the bait-station poisoning. A gradual reduction of possum droppings appears to have been the result of the bait-station programme (also see Table 7.5). No such patterns were evident in number of traps with rodent droppings at Remiger's Bush (Figure 7.9c and Table 7.5). However, the number of rat droppings captured by seedfall traps at Remiger's Bush was significantly higher than at other sites, and resulted in both a significant site difference and a significant difference in the level of pest suppression (Figure 7.10, Appendix 7.3; site nested within suppression, F=31.46, P<0.0001, df=5, and difference between sites, site F=49.71, P<0.001, df=5).

At Whitford Bush, possum droppings in seedfall traps increased in number every 2 to 3 months (refer to Figure 7.8b). Appearance of possum sign (whether droppings, fruit chews, vocalisation or sighting) was the trigger to refill bait-stations. The relationship between filling bait-stations at Whitford Bush and number of possum droppings found in the traps was not as clear as demonstrated for Remiger's Bush, although, in general possum droppings did decrease after bait-stations were filled (Figure 7.8b).

Table 7.5: Average number of seedfall traps at Remiger's Bush containing possum or rodent droppings during the three periods with different levels of possum control.

		Possum		Rodent	
Period	Dates	Average	Standard deviation	Average	Standard deviation
Before systematic poisoning	16 Sep 1996 to 17 Feb 1997	9.83	4.22	4.75	2.80
Between traps and bait-stations	3 Mar 1997 to 9 Jun 1997	7.00	2.67	9.63	2.39
During bait-station period	23 Jun 1997 to 2 Feb 1998	4.35	2.33	5.94	2.99

For most of the site pairs (pest suppression versus no poisoning) the difference between levels of control is reflected clearly in the number of traps with possum droppings (Figures 7.8a to c). Val's and Remiger's Bush are the exception. Part of the probable reason has been explained above, but it is possible that shooting of possums by hunters in surrounding forest during July and August 1997, could have affected possum numbers in Val's Bush. The number of seedfall traps containing possum droppings decreased after the shooting (Figure 7.8c). The average number of seedfall traps with possum droppings before the shooting was 8.58 ± 3.25 (±1 standard deviation) while after shooting it had dropped significantly (t-test assuming equal variances $t = -2.31$ $P<0.05$, 31df) to 6.14 ± 2.57.

Rodent Droppings

The patterns for number of seedfall traps containing rodent droppings are much less clear. In general there appears to be no significant difference between levels of pest suppression (Appendix 7.3; site nested within suppression, rodent F=0.13, P=0.7200, df=1), although differences do appear at the site level (Appendix 7.3; site nested within suppression, F=29.34, P<0.0001, df=4, and difference between sites F=22.67, P<0.001, df=5). Specifically, Remiger's Bush had significantly higher numbers of rodent droppings (mostly rats, refer to Rat dropping analysis Appendix 7.3) than the other sites.

Discussion

The data for number of droppings in seedfall traps generally support the mammal trapping data presented earlier. Possum droppings were more frequent in seedfall traps at sites with no systematic possum suppression. Numbers of possum droppings were significantly lower at Wenderholm Regional Park and Whitford Bush (both sites with long-term systematic mammal suppression), but higher than expected at Remiger's Bush, and lower than expected at Robertson's Bush.

Rodent droppings had less clearly defined patterns and showed more seasonal variability than possum droppings. Wenderholm Regional Park and Whitford Bush tended to have less rodent droppings, but Remiger's Bush had significantly more rat droppings than any other site. This was not unexpected since rodent numbers can increase when possum numbers are suppressed.

The lack of significance difference in number of rodent droppings for different levels of pest suppression could be due to the inclusion of both rat and mouse data in the same data-set. It appears from other studies that when rat numbers are reduced mouse numbers increase (e.g. Clout *et al.* 1995a; Craddock 1997; Greene 1994; Innes *et al.* 1995; Lovegrove 1996b). Thus, a decrease in number of rat droppings could have been offset by an increase in mouse droppings.

Alternatively, the high number of rodent droppings (mainly higher numbers of rat droppings) seen at Remiger's Bush (a possum suppressed site) may have obscured any differences that might have been observed between levels of rodent suppression. Whitford Bush and Wenderholm Regional Park tended to have fewer seedfall traps with rodent droppings, as would be expected with successful pest suppression.

7.4 Effect on fruit availability

Various methods were used (see Chapter 3) to measure and describe fruit production of key species at each site. Only one of these methods, seedfall collection, lent itself to the analysis of the impacts of pest species and distribution by avian species, since it was possible to examine each propagule for such evidence. In this section overall fruit production, the degree of predation by various pest species, and the consumption (and thus likely dispersal) of seeds by birds will be compared between sites and between pest suppression levels.

Throughout the study note was made of the number of propagules that were animal-damaged and the numbers that had been consumed and passed by birds. Animal-damaged fruits were considered to be fruits that were no longer available or attractive for dispersal, regardless of whether the embryos were still viable or not. These fruits might have had the pericarp partially removed without damage to the seed, or the embryo could have been damaged or eaten out.

Consumed fruits were those seeds that had been cleaned of fruit-flesh, without harming the propagules, by passage through a gut. These seeds were intact and lacked any evidence of mammal teeth marks, or insect bore holes. Presumably most of the consumed fruits, especially the larger species (diameter greater than 14 mm, see Chapter 1), were eaten and dispersed by kereru. However, since these data did not directly measure the number of propagules in pigeon faeces we cannot attribute all consumed fruit (especially smaller diameter fruit) to kereru dispersal. Therefore, the term ‘bird consumed fruits’ is preferred.

7.4.1 Overall fruit production.

Data used

During the first part of the study, with only Whitford Bush and Wenderholm Regional Park as active sites, few fruits were noted as animal-damaged and predation agents were not specifically recorded. This changed with the inclusion of Loch Amber Bush, were copious fruits were damaged by different agents. Detailed observation, as described in section 3.5.5 and Appendix 3.3, began in the week starting 22 January 1996 and continued for the remainder of the study period. Various sets of graphs present fruit production and predation over various lengths of time in order to illustrate or emphasis a point.

Fruit was classified as either animal-damaged or bird consumed and, if damaged, was further classified according to the agent causing the damage. Seeds that had been cleaned of fruit-flesh by passage through a gut, without damage to the seed, were classified as bird consumed. Fruit was considered animal-damaged if the fruit flesh was removed or partially removed by non-dispersal agents (indicated by teeth marks or pecking marks) or if the propagule was damaged in some other way to render it non-viable or not available for dispersal (e.g. possum predation of both embryo and surrounding tissue).

The widths of the teeth-marks left on the fruits were used to assign damage fruits to various mammalian predation categories. If the bite marks were incisor-like and wider than 5 mm then the damage was assigned to possums, if teeth-marks were between 5 and 2 mm then rats were deemed the culprit, but if they were less than 2 mm wide the damage was assigned to mice (Cunningham and Moors 1993). Mice are the only rodents in New Zealand with a notch on the rear surface of their upper incisors (Craig *et al.* 1984), and close examination of bite marks could sometimes reveal this. Often it was difficult to establish whether rats or mice were the causal agent, and in that case damage was attributed to the general category of rodents. Small holes with frass protruding were assigned to insect damage.

In some cases it was not possible to establish the identity of the fruit predator. In that case the predation was assigned to the ‘unknown’ category. This category also included predation of fruits by other animals that had no specific category (e.g. predation of kahikatea fruits by rosella (*Platycercus eximius*)).

Results

Figures 7.11 to 7.16 illustrate the number of undamaged mature fruits (including bird consumed fruits) to fall into seedfall traps at each site. All fleshy-fruited species are shown, including small-fruited species. The graphs for the individual species have been drawn to scale to allow visual comparison between sites and species. The sites have been arranged in pairs (pest-suppressed followed by pests not suppressed).

In each case the fruits of the large-fruited species were less abundant in seedfall traps at sites without pest suppression. Moreover, quite often the small-fruited species were also significantly less abundant, possibly because possums and rodents ate flowers or immature fruits. Kahikatea at Robertson's appears to be an exception to this rule; however, this is more to do with the placement of the seedfall traps at this site compared to Whitford. Seedfall traps were placed beneath trees of the selected species (karaka, kohekohe, puriri, taraire, tawa) with no reference to the locality of other species. At Robertson's seven of the seedfall traps ended up in the vicinity of 3 mature female kahikatea, whereas only one seedfall trap at Whitford was directly beneath a large female kahikatea.

To illustrate this, mature fruit production at Wenderholm Regional Park and Remiger's Bush (both pest-suppressed sites) require more than one page to illustrate the number and quantity of fruits available, whereas the corresponding sites Loch Amber and Val's Bush (no pest control) require less than a page.

Fruit, large or small, is available throughout the year at sites with pest suppression. At sites without pest control fruit quantity was occasionally low to non-existent. The differences in the amount of fruit produced cannot be attributed to different species composition of the forest pairs (Chapter 4).

Discussion

These graphs (Figures 7.11 to 7.16) illustrate the adverse effects that possums and rodents were having on fruit production at sites without pest suppression. Possums and rodents caused a reduction in fruit numbers, and increased periods without, or with low availability of, fruit. It seems likely that this in turn may be having equally adverse effects on the breeding success, condition and survival of a whole range of native species, especially bird species.

Figure 7.11: Number of mature, damaged fruits found in seedfall traps at Wenderholm Regional Park

Mature fruits also include those fruits that were consumed, but excludes fruits that were animal-damaged.

Figure 7.12: Number of mature, undamaged fruits found in seedfall traps at Loch Amber Bush
Mature fruits also include those fruits that were consumed, but excludes fruits that were animal-damaged.

Figure 7.13: Number of mature, undamaged fruits found in seedfall traps at Whitford Bush
Mature fruits also include those fruits that were consumed, but excludes fruits that were animal-damaged.

Figure 7.14: Number of mature, undamaged fruits found in seedfall traps at Robertson's Bush
Mature fruits also include those fruits that were consumed, but excludes fruits that were animal-damaged.

Figure 7.15: Number of mature, undamaged fruits found in seedfall traps at Remiger's Bush
Mature fruits also include those fruits that were consumed, but excludes fruits that were animal-damaged.

Figure 7.16: Number of mature, undamaged fruits found in seedfall traps at Val's Bush
Mature fruits also include those fruits that were consumed, but excludes fruits that were animal-damaged.

7.4.2 Fruit consumption and predation by species

This section analyses the fate of fruits at sites with and without pest suppression. The emphasis will be on the large-fruited species, those with diameters greater than 10 mm, which are the focus of this study. Two smaller fruited species, nikau and kahikatea, are also included since both show marked differences between sites with and without pest suppression, although for different reasons. Rewarewa (*Knigthia excelsa*) is not a fleshy fruit, but has been included to illustrate that the effect of some pest species is wider ranging than just the fleshy-fruited species.

Data used

The data include the two-year period from the week starting 22 January 1996 up to and including the week starting 2 February 1998. The data have been categorised into four predation categories, possum, rodent or insect -damaged, or predator unknown. This last category includes those cases where it was not possible to establish what the predator was, or when predation was by other animals that had no specific category (e.g. predation of kahikatea fruits by rosella). For more detail on the mammal predation categories refer to section 7.4.1.

Analysis

Figures 7.17 to 7.25 present the predation, bird consumption and overall production pattern of the various fruiting species at all sites. Each page of graphs relates to one species, arranged in site pairs (Wenderholm Regional Park/Loch Amber Bush, Whitford Bush/Robertson's Bush and Remiger's Bush /Val's Bush).

The solid line on the graphs representing mature fruits includes fruits that were animal-damaged and bird consumed. The dashed line representing immature fruit also includes immature fruits that were animal-damaged. The dashed line representing the number of immature fruits has been stacked on top the solid line representing mature fruits. Therefore, the upper most line (whether it is a solid line for mature fruits, or a dashed line for immature fruits) indicates the total number of fruits produced per fortnight.

The predation and consumed stacked bar graphs do not exceed the upper most line. In some case the upper most line is higher than the sum of the stacked bars, this indicates that fruits fell into the seedfall trap without being animal-damaged or consumed.

Results

<u>*Kohekohe*</u>

Very few kohekohe fruits made it to maturity at sites with high possum numbers (Figure 7.17 note the difference in scales for site pairs) since kohekohe was very susceptible to possum browse. Possums not only eat the fruit of kohekohe, but the leaves and flowers also (e.g. Buddenhagen 1995; Court 1985 , A. Dijkgraaf pers.obs.; Ogden and Buddenhagen 1994). Any fruit that set was eaten by predators, generally possums (refer to relevant graphs), well before it was ripe, or available for dispersal.

The sites with possum suppression produced great quantities of kohekohe flowers every other year, followed by large numbers of fruit the following year (Chapter 5). The largest proportion of fruit produced passed through a vertebrate gut (fruit consumed). Only a few seeds were not consumed (the difference between the top of the bar and the total mature fruit line on Figures 7.17).

Thus possums were not only having a major effect on kohekohe fruit production but, since very few fruits mature, also on subsequent consumption, dispersal and regeneration of kohekohe. At Remiger's Bush, where possum numbers were partially suppressed, rodents were more noticeable as predators of kohekohe fruit (refer Figure 7.17 last graph)

Taraire

Taraire was also heavily impacted at sites without possum suppression (Figure 7.18). The comparison between Wenderholm Regional Park and Loch Amber Bush is especially striking (Figure 7.18 top pair of graphs). Possums would generally start eating the immature fruit when it was about one centimetre long, well before it was full-sized or ripe (A. Dijkgraaf pers. obser.). By the time that ripe taraire fruit should be available very little, if any, was left on the trees for bird consumption, thus very few mature fruits fell in the seedfall traps. At Wenderholm Regional Park however, taraire fruit was rarely animal-damaged and most of the mature fruit caught by seedfall traps had been through digestive tracts (fruits consumed).

The other sites without pest-suppression also produced very few if any ripe taraire, since most were animal-damaged before they were mature.

At Whitford Bush few fruits were animal-damaged, but few were dispersed either. This illustrates the lack of sufficient kereru to disperse all taraire fruit (Figure 7.18, 4th graph down), especially around July 1997 when large numbers of taraire fruits fell into seedfall traps untouched by either predators or dispersers. Whitford Bush is a small and rather isolated forest remnant with a maximum of 5 resident kereru (M. Clout pers. comm.). This number of birds did not appear to be seasonally supplemented from other localities, as happened in the more connected sites north of Auckland, and would easily be satiated given the number of taraire fruits available at the peak of the season. Kereru are the only birds capable of swallowing taraire fruits whole.

Partial suppression of possums at Remiger's Bush resulted in a considerably larger taraire fruit crop than at Val's Bush (refer Figure 7.18 last two graphs), with more fruit reaching maturity, including at least some fruit that were available to, and eaten by kereru. However, large numbers of fruits were animal-damaged, mainly by possums but rodents also had a significant impact.

Karaka

Karaka fruits were generally only animal-damaged when they were ripe (Figure 7.19), in fact, only the yellow fruit flesh was eaten. Possums and rodents avoided the green, unripe fruit flesh, nor did they eat the fresh kernel.

A few possums can do considerable damage to a fruit crop as illustrated by the summer of 1997 at Wenderholm Regional Park (Figure 7.19, 2nd graph down). One or two possums invaded the grove behind the ranger's house and were dropping many animal-damaged karaka fruits in the seedfall traps. As soon as these possums were eliminated predation levels dropped.

Puriri

Not many puriri fruit were animal-damaged, except at Val's Bush (Figure 7.20) where tooth-marks in the remainder of the fruit flesh indicated that possums were responsible. The possums were unable to penetrate the hard woody kernel (A. Dijkgraaf pers. obs.).

Consumed puriri fruits occurred virtually throughout the whole year, although at most sites these comprised only a small proportion of the fruits falling into the seedfall traps (Figure 7.20). Hence many fruits were evidently never consumed or dispersed, perhaps due to the relatively low nutritional value of puriri flesh (refer Chapter 6) compared to other fruits, or possibly because of reduced numbers of dispersers. The two sites with most kereru sighting (Wenderholm Regional Park and Remiger's Bush) also had the greatest proportions of consumed puriri fruit.

Figure 7.17: Predation and consumption of Kohekohe fruits

Figure 7.18: Predation and consumption of Taraire fruits

Figure 7.19: Predation and consumption of Karaka fruits

Figure 7.20: Predation and consumption of Puriri fruits

Figure 7.21: Predation and consumption of Tawa fruits

Figure 7.22: Predation and consumption of Pigeonwood fruits

Figure 7.23: Predation and consumption of Nikau fruits

Figure 7.24: Predation and consumption of Kahikatea fruits

Figure 7.25: Predation and consumption of Rewarewa seed capsules

Tawa

The production of tawa fruits was low (Figure 7.21) and therefore precludes much comment on the rates of consumption or predation of tawa fruits.

Loch Amber Bush (top graph) appears to have had somewhat greater predation of tawa fruits than Wenderholm Regional Park (2nd graph down), but the occasional mature fruit was still consumed at Loch Amber Bush while other mature fruits fell into the traps without passing though a digestive system. Most sites had some consumed fruits, and most sites had mature, undamaged, fruits that had not passed though a gut. The low number of tawa fruits at Remiger's Bush is due to the lack of tawa trees at the study site. Only one tawa tree was located in the small block used.

Pigeonwood

Very few pigeonwood fruits were collected in seedfall traps during this study and most fruit was produced in October 1997 (Figure 7.22). The majority of fruits captured by the seedfall traps had passed through a digestive system and only a few fruits were animal-damaged.

Nikau

Nikau fruit have been included since it proved to be a very important food species for kereru (refer Chapter 6). Most nikau fruits to fall into seedfall traps had been consumed (Figure 7.23). This is to some extent logical, since nikau palms are slender and most uneaten fruits would fall directly below the palm in a small radius. One of the reasons why nikau was not selected for seedfall study was the difficulty of placing seedfall traps below the narrow nikau crowns (the other reason being that other bird species, apart from kereru, also eat the fruit). Unless a nikau overhung a seedfall trap the only way for fruit to fall into a trap was after consumption and dispersal. The sheer number of fruits to have landed in seedfall traps is testimony to how preferred this fruit is by bird species (refer to Chapter 6).

Nikau is also much preferred by rodents, who eat not only the pericarp of mature fruits, but also the embryonic tissue, leaving only slivers of the seed coat. The number of fruits eaten had to be estimated from these remnants. Most of the fruits appeared to be damaged by rats (Figure 7.23), however, it was hard to categorise the predators of the seed-coat remains, except for a number of occasions where the tooth-marks allowed definitive identification. Thus, possum and mouse damage could comprise a proportion of the 'rodent' category.

Rodent predation, probably rat, of nikau fruits was greatest at the site with partial possum suppression (Remiger's Bush), although Robertson's Bush (no pest-suppression) also had significant nikau fruit predation. Sites without pest suppression tended to produce fewer fruits, which was probably a result of more flower spadices being destroyed by possums (Cowan 1991 , A. Dijkgraaf pers. obs.).

Kahikatea

Pest species appeared to affect the quantity of kahikatea fruits produced rather than predating the fruit directly; only one or two fruits were found with mammal teeth-marks or encased in possum faeces (Figure 7.24). Kahikatea fruit production tended to be one to several orders of magnitude greater at sites with pest suppression, than at sites without. The only exception to this, the Whitford-Robertson's Bush pair, can be explained by the placement of seedfall traps. At the small Robertson's Bush site five of the thirty seedfall traps were in the vicinity of two female kahikatea, whereas at Whitford Bush only two seedfall traps were in the vicinity of one female kahikatea, thus there was a greater chance of fruit falling into seedfall traps at Robertson's Bush than at Whitford Bush.

The fruits were small enough to be dispersed by a wide range of species, including possums (some intact seeds found in possum droppings). Most of the seeds to fall into seedfall traps no longer had the swollen fleshy receptacle attached, and were considered to have been consumed. At Robertson's Bush it was noted that rosella were predating the fruits by nipping the fleshy receptacle off, thus avoiding seed consumption (A. Dijkgraaf pers. obs.).

Rewarewa

Not only fleshy fruits were damaged by possums. The dry woody seed-capsules of rewarewa contain one or more winged seed. These seed-capsules were damaged by possums (as shown by the teeth-marks) as soon as the capsules were about half grown, which is presumably when the seeds are starting to develop (refer to Figures 7.25). Very few seed-capsules escaped predation in the tree, but the number of possum-damaged fruits to fall into seedfall traps was inconsistent between years or sites.

Around the Auckland region undamaged rewarewa seed-capsules could remain attached to the trees for at least three years and were not dislodged by strong winds (A. Dijkgraaf pers. obs.). At sites with good possum suppression (Wenderholm Regional Park and Whitford Bush) it was possible to use the presence of fallen flowers, and chewed broken infructescences as accurate indicators of possum presence.

Discussion

In general, suppression of possum and rodent numbers resulted in more fruits being produced, more fruits reaching maturity and more fruits being consumed, and probably dispersed, by animals which void the seed unharmed. Pest suppression also ensured that ripe fruits were available throughout the year, supporting resident native frugivores.

Lack of pest suppression generally saw increased levels of possum and rodent predation on fruit, with significantly less fruit available for bird consumption and dispersal. Often particular species of fruit were targeted by the pest species, causing ‘gaps in seasonal fruit availability.

One of the species that was notably preferred was kohekohe, since the trees were systematically stripped of flowers, fruits and foliage by possums (A. Dijkgraaf pers. obs.). Female trees with greatly reduced canopies did not flower; hence no fruit was produced (A. Dijkgraaf pers. obs.). It was noted on Kapiti Island that possum control allowed the kohekohe to flower again (Anonymous 1983; Atkinson 1985). Lack of flowering would also impact on the amount of fruit produced.

It seems likely that possums target taraire fruit heavily even when food is not in short supply. The proportion of possum-damaged taraire fruits at Remiger’s Bush (Figure 7.18) exceeded the proportion animal-damaged fruits for any other fruiting species. Moreover, as soon as the taraire fruits reached half-size, at any site, possums predictably damaged them, even when other fruits were in plentiful supply. This preference by possums might reflect the earlier observation that the fruit is rich in lipids (refer Chapter 6).

Possums and rodents also favoured karaka fruits. However, only the yellow ripe part of the karaka fruit-flesh was eaten, while the unripe green parts and kernel were avoided. This could be attributable to the presence of the severely toxic karakin, which is found in the kernel and possibly in unripe fruit flesh too (Brooker *et al.* 1987). Both possums and rodents ate the kernel after it had been on the ground for about 3 months after the toxin presumably had leached out (A. Dijkgraaf pers. obs.).

General observations of kereru in karaka trees showed that they did not particularly favour karaka fruit (Bell 1996, A. Dijkgraaf pers. obser.; James 1995). Silvereyes (*Zosterops lateralis*) did favour the fruit and many fruits fell into seedfall traps with the fruit flesh pecked off (part of the ‘unknown predator’ fruits in Figure 7.19). During the 1998 summer at Wenderholm Regional Park (Figure 7.19, 2nd graph) kereru were seen taking karaka fruit more often than previous summers. This was attributed to a particularly large crop of unusually small fruits following a dry warm spring.

It is unclear why kahikatea seed production was affected by the presence of the pests to the extent shown at Loch Amber and Val's Bush. The numbers of kahikatea trees were not notably less at those sites, but the amount of fruit on the trees was obviously less than at Wenderholm Regional Park and Remiger's Bush. Possums are known to favour the pollen cones of *Pinus radiata* (Clout 1977), thus perhaps they are also partial to male kahikatea strobilii or the juvenile seeds on the female trees, reducing pollination or preventing seed set respectively. Kahikatea has not been observed to be heavily browsed by possums, unlike totara (*Podocarpus totara* and *P. hallii*) or pahautea (*Libocederus bidwillii*) (Rogers 1997), but perhaps this aspect requires more investigation.

The nutritional value of rewarewa requires investigation. Possums seem to strongly favour this food source, which like taraire, is preyed on once the seed capsules reach about half size (A. Dijkgraaf pers. obs.). Rewarewa inflorescences were also much favoured by possums. Rewarewa trees in areas without pest suppression look much less dense (less foliage) than trees in areas with pest suppression. It is unclear whether possums also eat young rewarewa shoots (no mature eaten leaves were observed) or whether they damage the tree as they forage for seeds and flowers.

Possums were shown to be especially damaging to the fruit production of the species investigated. However, it can be difficult to separate the effects of possum and rodent impact on fruit production (Veltman 2000). Remiger's Bush provided some indications of the different impacts that possums and rodents might be having, but there were still too many possums in that forest patch to provide any definitive answers.

7.4.3 Overall patterns of fruit production between paired sites.

Data used

The data analysed to compare fruit production between paired sites included the two-year period from the week starting 22 January 1996 up to and including the week starting 2 February 1998. The data were categorised into four predation classes: possum, rodent, or insect damaged, or predator unknown. This last category includes those cases where it was not possible to establish what the predator was, or when predation was by other animals that had no specific category (e.g. predation of kahikatea fruits by rosella). Refer to 7.4.1 for more details.

The total numbers of fruits damaged at each site were compared between pairs of sites. These were predetermined prior to the study as pest-suppressed sites or sites without pest-control. The number of immature, mature, and bird-consumed fruits were also compared between pairs of sites, as was the total number of fruits produced.

Analysis

The data were analysed using PROC GLM in SAS (The SAS System for Windows v6.12) to elucidate which species or categories (predation, bird consumption and production) were significantly different between site pairs. Since the site pairs were chosen to be comparable to each other in tree species composition, climate and slope they were not interchangeable, thus the pest suppression level was not set to random as for the previous analysis (pest species droppings). Furthermore, because climate, slope and location could affect fruiting patterns and production levels it was considered inappropriate to compare all sites simultaneously, hence *a priori* site pairs were analysed. The syntax used is provided in Appendix 7.2 (B). The data are presented below and in Tables 7.6, 7.7 and Figures 7.26 to 6.28.

Results

<u>Fruit predation</u>

The analysis of variance between paired sites showed that fruit predation by possums was more common at sites without pest suppression, although the difference between Remiger's and Val's Bush was not significant (Tables 7.6 and 7.7). The differences in possum predation between the site pairs are also illustrated in the top-left graphs in Figures 7.26 to 7.28. Generally, the sites without pest suppression (white bars) occupy a greater portion of the columns than the sites with pest suppression (black bars) showing that more fruit was preyed on at sites without possum suppression. Different species had different levels of possum predation, as can be seen in the order of species arranged along the X-axis of these graphs (Figures 7.26 to 7.28, also Appendix 7.4 and Section 7.4.1).

The species most affected by possum predation were taraire (Loch Amber, Robertson's, Remiger's and Val's Bush) and rewarewa (Loch Amber, Whitford and Robertson's Bush). Karaka, puriri, kohekohe and nikau were damaged to a lesser extent by possums (refer to Figures 7.26 to 7.28).

Table 7.6: Differences between paired sites in fruit predation, bird consumption and fruit production.

Full SAS output is provided in Appendix 7.4. 'Suppress' relates to the level of pest control at each site (possum suppression, or no pest control). 'Species' relates to the fruiting species included in the analysis. The Type III error ANOVA F values are given for suppression level, species and the interaction between species and suppression.

	By site	Wenderholm-Loch Amber				Whitford-Robertson's				Remiger's-Val's			
Variable	Model type	d.f.	F	Pr > F	Signif	d.f.	F	Pr > F	Signif	d.f.	F	Pr > F	Signif
Possum damaged	Main model	19	6.18	0.0001	Yes	19	4.77	0.0001	Yes	19	9.12	0.0001	Yes
Possum damaged	Suppress	1	14.69	0.0001	Yes	1	10.77	0.0011	Yes	1	0.09	0.7657	-
Possum damaged	Species	9	5.7	0.0001	Yes	9	5.06	0.0001	Yes	9	13.43	0.0001	Yes
Possum damaged	Species*suppress	9	5.71	0.0001	Yes	9	3.82	0.0001	Yes	9	5.82	0.0001	Yes
Rodent damaged	Main model	19	8.89	0.0001	Yes	19	21.22	0.0001	Yes	19	68.3	0.0001	Yes
Rodent damaged	Suppress	1	5.29	0.0217	Yes	1	34.31	0.0001	Yes	1	39.63	0.0001	Yes
Rodent damaged	Species	9	10.14	0.0001	Yes	9	27.07	0.0001	Yes	9	104.95	0.0001	Yes
Rodent damaged	Species*suppress	9	8.03	0.0001	Yes	9	13.91	0.0001	Yes	9	34.83	0.0001	Yes
Insect damaged	Main model	19	6.37	0.0001	Yes	19	4.68	0.0001	Yes	19	4.14	0.0001	Yes
Insect damaged	Suppress	1	5.59	0.0182	Yes	1	0.85	0.3555	-	1	3.8	0.0518	-
Insect damaged	Species	9	7.02	0.0001	Yes	9	8.18	0.0001	Yes	9	6.72	0.0001	Yes
Insect damaged	Species*suppress	9	5.8	0.0001	Yes	9	1.6	0.1114	-	9	1.6	0.1125	-
Unknown damaged	Main model	19	2.11	0.0036	Yes	19	1.15	0.2903	-	19	1.08	0.3644	-
Unknown damaged	Suppress	1	0.66	0.4153	-	1	1.73	0.1888	-	1	0.77	0.38	-
Unknown damaged	Species	9	3.19	0.0008	Yes	9	0.93	0.5022	-	9	1.07	0.3861	-
Unknown damaged	Species*suppress	9	1.19	0.2963	-	9	1.32	0.2218	-	9	1.13	0.3363	-
Damaged total	Main model	19	7.16	0.0001	Yes	19	4.81	0.0001	Yes	19	20.71	0.0001	Yes
Damaged total	Suppress	1	15.43	0.0001	Yes	1	7.43	0.0065	Yes	1	6.14	0.0135	Yes
Damaged total	Species	9	7.03	0.0001	Yes	9	7.35	0.0001	Yes	9	32.43	0.0001	Yes
Damaged total	Species*suppress	9	6.38	0.0001	Yes	9	1.99	0.0379	Yes	9	10.6	0.0001	Yes
Immature number	Main model	19	10.22	0.0001	Yes	19	6.11	0.0001	Yes	19	16.61	0.0001	Yes
Immature number	Suppress	1	3.46	0.0632	-	1	0.97	0.3238	-	1	11.76	0.0006	Yes
Immature number	Species	9	14.66	0.0001	Yes	9	10.81	0.0001	Yes	9	27.8	0.0001	Yes
Immature number	Species*suppress	9	6.53	0.0001	Yes	9	1.98	0.0389	Yes	9	5.97	0.0001	Yes
Mature total	Main model	19	6.11	0.0001	Yes	19	4.3	0.0001	Yes	19	7.62	0.0001	Yes
Mature total	Suppress	1	11.69	0.0007	Yes	1	2.94	0.0868	-	1	11.01	0.001	Yes
Mature total	Species	9	6.43	0.0001	Yes	9	5.67	0.0001	Yes	9	11.07	0.0001	Yes
Mature total	Species*suppress	9	5.16	0.0001	Yes	9	3.09	0.0012	Yes	9	3.79	0.0001	Yes
Consumed number	Main model	19	6.43	0.0001	Yes	19	3.75	0.0001	Yes	19	4.6	0.0001	Yes
Consumed number	Suppress	1	15.08	0.0001	Yes	1	0.75	0.3862	-	1	7.01	0.0083	Yes
Consumed number	Species	9	6.74	0.0001	Yes	9	5.8	0.0001	Yes	9	6.55	0.0001	Yes
Consumed number	Species*suppress	9	5.15	0.0001	Yes	9	2.04	0.0325	Yes	9	2.38	0.0117	Yes
Total fruit	Main model	19	6.96	0.0001	Yes	19	5.58	0.0001	Yes	19	14.08	0.0001	Yes
Total fruit	Suppress	1	7.5	0.0063	Yes	1	0.02	0.8891	-	1	22.99	0.0001	Yes
Total fruit	Species	9	7.11	0.0001	Yes	9	8.54	0.0001	Yes	9	21.86	0.0001	Yes
Total fruit	Species*suppress	9	6.75	0.0001	Yes	9	3.22	0.0007	Yes	9	5.3	0.0001	Yes

Rodent predation was greater at sites without pest suppression, except for Remiger's Bush where rodent predation was significantly higher than its site pair, Val's Bush (refer to Tables7.6 and 7.7 and

Figure 7.28). Control of both possums and rodents results in a drop in damage caused by both agents, but control of possums alone could possibly enable rodent numbers to increase, with a resultant increase in damage by rodents (as seen at Remiger's Bush). At all sites nikau generally sustained the greatest amount of damage from rodents (refer Figures 7.26 to 7.28).

Table 7.7: A posteriori Tukey's HSD means for fruit predation, bird consumption and fruit production at paired sites.

The means are average number of fruits affected per sampling fortnight. More details provided in Appendix 7.4.

	Wenderholm	Loch Amber	Signif.	Whitford	Robertson's	Signif.	Remiger's	Val's	Signif.
Possum damaged	0.12	1.32	Yes	0.05	0.25	Yes	0.68	0.75	-
Rodent damaged	0.19	0.38	Yes	0.11	0.44	Yes	1.37	0.41	Yes*
Insect damaged	0.12	0.45	Yes	0.28	0.20	-	0.23	0.10	-
Unknown damaged	0.11	0.07	-	0.03	0.29	-	0.08	0.22	-
Damaged total	0.53	2.37	Yes	0.59	1.25	Yes	2.42	1.56	Yes*
Immature number	2.44	3.58	Yes	5.24	3.49	-	6.98	3.04	Yes
Mature total	11.29	3.49	Yes	2.52	4.57	-	8.85	3.27	Yes
Consumed number	8.83	1.23	Yes	1.29	1.98	-	5.28	1.47	Yes
Total fruit	13.73	7.08	Yes	7.76	8.06	-	15.83	6.31	Yes

Yes* means that the significant result was opposite the expected direction.

There were significant differences between species in the numbers of fruits (mature or immature) damaged by insects, but these were not related to the type or level of pest suppression. Rewarewa and nikau had the greatest level of insect predation, regardless of whether pests were suppressed or not.

Predation by 'unknown' predators was generally not significantly different for species or between levels of pest suppression, except at Wenderholm Regional Park (Tables 7.6 and 7.7), where significantly more karaka fruits were damaged than at Loch Amber Bush (Figure 7.26). Most of these fruits were damaged by flocks of silvereyes that pecked at the fruit flesh. This also happened, to some extent, for karaka at Val's Bush (Figure 7.28). Large, but not significant, numbers of kahikatea fruits were damaged by rosella at Robertson's (7.27). These birds ate the fleshy pedicels and discarded the seed below the trees, occasionally damaging the seed also.

The total numbers of fruits damaged was at least twice as great at Loch Amber and Robertson's Bush (sites without pest suppression) than at their paired sites Wenderholm Regional Park or Whitford Bush (refer Table 7.7 and Figures 7.26 and 7.27). This illustrates that sustained effective possum and rodent control significantly reduced the numbers of fruits damaged. Partial suppression of possums without suppression of rodents, as at Remiger's Bush, resulted in proportionally greater amounts of fruit being damaged than at the paired site without any control, Val's Bush (Table 7.7 and Figure 7.28). Balanced against that however, is the fact that the site with partial control still produced significantly more fruits than the site without pest suppression.

Fruit production

The number of immature fruits produced (regardless of whether or not these fruits were animal-damaged) showed no pattern in relation to pest suppression, but differed significantly between species. Taraire aborted a lot of juvenile fruit shortly after flowering and differs from other species in that respect (Figures 7.26 to 7.28). Nikau trees at Remiger's and Val's Bush also dropped significantly more juvenile fruits than other species.

The number of mature fruits was generally greater at sites with pest suppression than sites without (Tables 7.6 and 7.7). The large number of kahikatea fruits to fall into seedfall traps at Robertson's Bush reversed that trend for that pair of sites (Figure 7.27). When kahikatea fruits were excluded from the analysis, there was still no significant difference in number of mature fruits produced between the two sites (ANOVA F=0.02, P=0.8799, df=1). Nikau and kahikatea tended to be the most prolific fruit producers at most sites, but kohekohe and puriri also contributed large numbers of fruit to the totals (Figures 7.26 to 7.28).

Figure 7.26: Comparison between levels of predation, bird consumption and fruit production for Wenderholm Regional Park and Loch Amber Bush.

Figure 7.27: Comparison between levels of predation, bird consumption and fruit production for Whitford Bush and Robertson's Bush.

Figure 7.28: Comparison between levels of predation, bird consumption and fruit production for Remiger's Bush and Val's Bush.

Total fruit production (immature and mature fruits summed) at sites with pest suppression was significantly greater than sites without pest suppression (Table 7.6, 7.7 and Figures 7.26 to 7.28). This was not the case for the Whitford and Robertson's Bush pair (Figure 7.27). The amount of fruit at Whitford Bush was double that of Robertson's Bush when kahikatea was excluded from the analysis (mean number of fruits/fortnight for Whitford Bush 13.4, mean for Robertson's Bush 6.9), however, this difference in fruit production was still not significant (ANOVA F= 2.78, P= 0.0962, df=1).

Bird consumed fruits

The number of fruits consumed by birds was generally greater for sites with pest suppression. This was probably due to greater numbers of mature fruits being available for bird consumption, as shown by production of fruits. The numbers of fruits consumed at Whitford and Robertson's Bush were not significantly different between the two sites and the mean values were also quite low compared to other sites. This could be due to the large numbers of bird-consumed kahikatea fruits caught in seedfall traps at Robertson's. These fruits are small and can be dispersed by a large range of bird species whereas most of the other fruits can only be dispersed by kereru. It might also be possible that there were insufficient kereru to consume the number of large fruits available. The other four sites, north of Auckland, are part of a forest-pasture mosaic that supports greater numbers of kereru. Whitford and Robertson's bush are small isolated fragments that cannot support as many birds.

Discussion

Fruit predation

Predation of fruits was generally greater at sites lacking possum suppression, than at sites with possum suppression. There were some exceptions to this general observation. Partial possum control at Remiger's Bush resulted in both the production of more fruits and proportionally more possum damaged fruits. Partial pest control also saw an increase in the number of fruits damaged by rodents, probably mostly rats, illustrating that possum numbers and rodent numbers could be inversely related as has been noted elsewhere for rats and mice (Clout *et al.* 1995a; Craddock 1997; Innes *et al.* 1995).

The lack of difference between Remiger's and Val's Bush (F=0.09 Pr=0.7657), for proportions of fruits damaged by possums, was probably due to higher fruit production of key species at Remiger's Bush, coupled with possums targeting those key species as they became ripe. Fewer possums at Remiger's resulted in less damaged trees that were able to produce more flowers and fruits. For instance, kohekohe at Remiger's Bush had considerably more foliage, which resulted in more flowers and fruits than at Val's Bush. Nikau spadices at Remiger's Bush were not all broken or chewed off by possums before opening, as at Val's Bush, allowing more fruit to set. More rewarewa flowers remained on the trees at Remiger's Bush resulting in greater numbers of seed capsules. The canopies of most trees were denser and healthier at Remiger's Bush than Val's Bush and possibly contributed to higher fruit production in other species such as taraire.

Greater numbers of fruits can also result in more fruits damaged by a few possums. This was seen at Wenderholm Regional Park, when one or a few possums damaged a large number of karaka fruits in one grove. The same might have happened at Remiger's Bush for taraire and rewarewa fruits, perhaps indicating that possums prefer these fruits to others when food is not limited.

Fruit production

Total fruit production was greater at sites with pest suppression than at sites without pest suppression. This difference was attributable to production of greater numbers of mature fruits, especially for the smaller-fruited species, rather than differences in the number of immature fruits produced. Fruit production did not consider whether the fruits were animal-damaged or not, only whether the fruits were mature or immature.

The number of mature or immature fruits produced per species varies between sites. There was no consistent pattern, over all sites, as to which species produced the most fruits but nikau and kahikatea tended to produce copious fruits.

<u>Bird consumed fruits</u>

More bird consumed fruits fell into seedfall traps at sites with pest suppression than at sites without pest suppression. The four most preferred fruits were kahikatea, nikau, kohekohe and puriri. The lack of significant difference in bird consumed fruits between Whitford and Robertson's Bush is probably caused by the large number of kahikatea fruits deposited in seedfall traps at Robertson's Bush.

The mean number of bird-dispersed fruits was relatively low for the Whitford/Robertson's pair. This could be the result of insufficient bird dispersers due to the relative isolation of these two forest fragments in a mostly pastoral landscape (Photo 3.3). The four northern forests were in close association with other small or large forest remnants, which could have resulted in greater numbers and greater diversity of bird dispersers. Other studies have found that the number of bird species decreased as forest patch size decreased (Willson *et al.* 1994), or that the number of individuals of particular species could be adversely affected by further fragmentation of forests (Price *et al.* 1999).

7.5 Effect on other animal species

The aim of this study was to examine aspects of fruit production of the large fruited species and how fruit production was affected by introduced pest species. While gathering these data, other useful (but often less rigorously collected) data was obtained. Some of those data are presented here to illustrate that the impacts of introduced mammalian species are wider than just reducing the production of fruits.

7.5.1 Non-mammalian droppings

The seedfall traps did not only catch fruits and mammal droppings, but also invertebrate droppings and occasionally faeces identifiable as kereru. No attempt was made to identify invertebrate droppings to genus or species, other than the relatively easily distinguishable weta (*Hemideina*) droppings. The weta pellet is a cylinder up to about 12 mm long with blunt, neatly rounded ends, not pointed as in mammals. The pellets were also often marked by up to six length-wise striations caused by grooves within the rectum (Gibbs 1998).

Data used

The data used non-mammal droppings (weta, insect, and kereru) from 14 October 1996 up to and including the week starting 2 February 1998. This was the period where all sites were active.

Data analysis

The treatment and analysis of the data are the same as for mammalian droppings described in 7.3.2. The SAS syntax used is provided in Appendix 7.2 and the full results from the SAS analysis are presented in Appendix 7.5.

Results

The results from the SAS analysis are presented in Appendix 7.5. Both insect (F=12.24, P<0.0001, df=25) and weta (F=6.02, P<0.0001, df=25) droppings fluctuated significantly with season (Appendix 7.5; difference between sites ANOVA, weekno for insects and weta), with an increase in number of traps with droppings from December to May (Figures 7.29 and 7.30) and fewer dropping during the rest of the year. No seasonality was detected for pigeon droppings (Figure 7.31 and Appendix 7.5, difference between sites ANOVA, weekno F=0.57, Pr=0.9334).

Figure 7.29 a to c: Number of traps at each site containing one or more insect dropping.

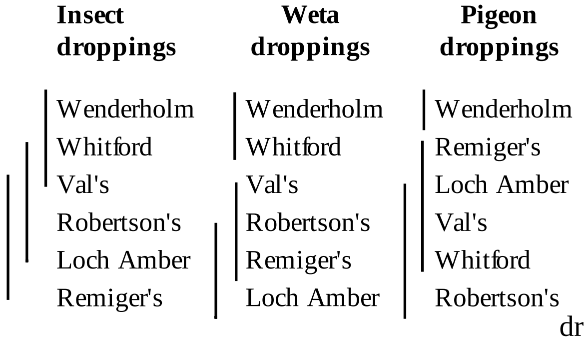
Figure 7.30 a to c: Number of traps at each site containing one or more weta dropping.

Figure 7.31 a to c: Number of traps at each site containing one or more kereru dropping.

Figure 7.32: A posteriori Tukey's Studentized Range (HSD) test for non-mammalian dropping in seedfall traps by site.

Alpha= 0.05 df= 42;

Species joined with the same bar are not significantly different.



The level of control did not significantly impact on the number of insect droppings encountered (Appendix 7.5; site nested within suppression ANOVA, suppress for insect F=2.46 P=0.1183, df=1) possibly because droppings were not identified to genera or species level, but pest suppression increased the number of weta and kereru droppings (Appendix 7.5, site nested within suppression ANOVA, suppress for weta F=34.47 P<0.0001, df=1, suppress for pigeon F=41.79 P<0.0001, df=1).

Site significantly contributed to the variation in the models for all three types of droppings (Appendix 7.5). Insect and weta droppings were generally more common (though not always significantly so, refer to Appendix 7.5) in sites with pest suppression (especially Whitford Bush and Wenderholm Regional Park). Remiger's Bush was the exception with generally lower numbers of insect and weta droppings. This is possibly due to the higher rodent (especially rat) level and the inadequate suppression of possums at that site.

Discussion

Pest suppression generally had a positive effect on the number of traps with weta or kereru droppings, but did not appear to affect insect droppings (Figures 7.29 to 7.31 and Appendix 7.5). However, it is not possible to ascertain whether the benefits to these species are solely through a reduction in possum numbers, through a combination of reduced possum and rodent numbers (also see Veltman 2000), or through greater availability of food. Increased rodent numbers, in the face of somewhat reduced possum numbers, appeared to be having an adverse effect on insect numbers at Remiger's Bush. The effect of pest suppression is likely to be variable according to how mobile a species is. Kereru can travel considerably greater distances than most insects will.

The variation between sites for kereru droppings reflects the encounter rates of bird species, discussed below. Wenderholm Regional Park and Remiger's Bush had a conspicuously rich avifauna, while Whitford Bush and Robertson's Bush had few bird encounters; possibly due to the small size and isolation of these two forest patches in a semi-rural landscape. Loch Amber and Val's Bush fall between these two categories, which could be a reflection of larger forest patches providing more diversity, or to the proximity of other forest patches with rich avifaunas.

7.5.2 Bird species abundance

Throughout the study bird presence was noted, along the transects used to empty the seedfall traps, as seen or heard. The data have been pooled per site for the period where all sites were active.

Data used

The time that birds were seen or heard was noted while traversing the forests. The data used included the period when all sites were active (fortnights starting 14 October 1996 to 2 February 1998). The data were grouped in two ways; number of individuals of each species seen or heard during each site visit, and number of birds of each species heard or seen simultaneously. If pest control is having an affect on the amount of food available this could also be reflected in the size of the flocks that a site can sustain.

Data analysis

The data were analysed using the GLM procedure in SAS (the syntax was similar to that used for the analysis of droppings per trap, refer to Appendix 7.2). The data were analysed in two ways. The number of observations (sightings or heard) for each bird species per site visit were summed and compared (Appendix 7.6). However, since several of the sites were small (about 2-ha), and the duration of the visit long (usually 2 to 4 hours), there was the likelihood of sampling the same bird several times, thus overestimating the number of birds actually found at a particular site.

The observations were recorded in blocks of time, hence it was possible to analyse the number of the occasions that more than one bird of a particular species was noted simultaneously (hereafter called ‘flock’ size). Flock size is merely the number of simultaneous observations for a particular species and represents the minimum number of birds present at that location at that time. Observations were grouped by flock size and the number of occasions that flocks of a particular size were observed for each species was summed. The additional level of categorisation (flock size) imposed on the data, meant that these data could not be analysed with level of control as a random variable (i.e. other sites could have been substituted to represent the same level of pest control), as was done for number of birds per species and number of traps with droppings. Therefore, ANOVAs were used to compare the effects of level of control (pest suppressed or not poisoned), site and flock size for frugivorous species (Appendix 7.7).

Results

The bird species have been separated into frugivores and non-frugivores on currently known diet (e.g. Falla *et al.* 1979, Clout unpublished data). Most species eat some fruit, but those classified as frugivores are more reliant on fruits, or fruits comprise a large part of their diet during some seasons.

The results for number of birds per site are summarised in Tables 7.8 and 7.9 and Figures 7.33 and 7.34, and the results for flock-size of are summarised in Tables 7.10 and 7.11 and Figures 7.35 to 7.37. The data were analysed using General Linear Models in SAS, with site nested in level of pest suppression since, theoretically, the chosen sites are a subset of sites with a specified level of pest control. The SAS output for number of birds per site per visit are presented in full in Appendix 7.6 and those for flock size are given in Appendix 7.7.

Number of birds per visit

In all cases, except for harriers (*Circus approximans*) and magpies (*Gymnorphina* spp), sites with pest suppression had greater numbers of bird observations than sites without poisoning (Figures 7.33 and 7.34). These differences were generally not significant for non-frugivorous species (Table 7.9 and Figure 7.34), but there were significantly more frugivorous species at sites with pest suppression (Table 7.8 and Figure 7.33). The only exception among the frugivorous species was the thrush, due to low numbers of observations.

In most cases, the differences between frugivorous species was most extreme for Wenderholm Regional Park and Loch Amber Bush (Figure 7.33) while the difference were the least between Whitford and Robertson’s Bush. The last named pair also tended to have the smallest numbers of observations. This indicates that although pest control has a major effect on the number of frugivores present at a site, other factors such as patch size and isolation also affect the number of birds that can be supported by a forest patch. Introduced frugivores, including the self-introduced silvereye (*Zosterops lateralis*), also appear to benefit, though perhaps to a lesser degree, by pest suppression.

Table 7.8: ANOVA of number of frugivorous bird species observations per site visit
'Suppression' refers to whether pest control was undertaken at a site; either yes or no. In the analysis, 'site' was nested in suppression, since different sites could have been selected with the same level of pest control.

		Analysis of variance				
Species	**Aspect tested**	**df**	**F Value**	**Pr > F**	**Signif**	**A posteriori Tukey's HSD**
Kereru	suppression	1	46.83	0.0001	Yes	Suppressed>no poison
Kereru	site(suppression)	4	13.23	0.0001	Yes	
Tui	suppression	1	27.41	0.0001	Yes	Suppressed>no poison
Tui	site(suppression)	4	15.66	0.0001	Yes	
Rosella	suppression	1	12.09	0.0007	Yes	Suppressed>no poison
Rosella	site(suppression)	4	3.4	0.0111	Yes	
Silvereye	suppression	1	15.52	0.0001	Yes	Suppressed>no poison
Silvereye	site(suppression)	4	14.94	0.0001	Yes	
Blackbird	suppression	1	15.62	0.0001	Yes	Suppressed>no poison
Blackbird	site(suppression)	4	11.87	0.0001	Yes	
Thrush	suppression	1	0.01	0.9393	-	
Thrush	site(suppression)	4	1.09	0.352	-	
Myna	suppression	1	6.67	0.0109	Yes	Suppressed>no poison
Myna	site(suppression)	4	3.16	0.0163	Yes	

Table 7.9: ANOVA of number of non-frugivorous bird species observations per site visit
'Suppression' refers to whether pest control was undertaken at a site; either yes or no. In the analysis, 'site' was nested in suppression, since different sites could have been selected with the same level of pest control.

		Analysis of variance				
Species	**Aspect tested**	**df**	**F Value**	**Pr > F**	**Signif**	**A posteriori Tukey's HSD means**
Harrier	suppression	1	2.97	0.0888	-	
Harrier	site(suppression)	4	1.7	0.1588	-	
Pukeko	suppression	1	1.02	0.3293	-	
Pukeko	site(suppression)	4	0.64	0.5985	-	
Kingfisher	suppression	1	0.82	0.3661	-	
Kingfisher	site(suppression)	4	1.58	0.1846	-	
Fantail	suppression	1	17.31	0.0001	Yes	Suppressed>no poison
Fantail	site(suppression)	4	46.26	0.0001	Yes	
Warbler	suppression	1	1.18	0.2793	-	
Warbler	site(suppression)	4	12.47	0.0001	Yes	
Pheasant	suppression	1	0.38	0.543	-	
Pheasant	site(suppression)	4	1.63	0.181	-	
Magpie	suppression	1	6.77	0.0113	Yes	No poison>suppressed
Magpie	site(suppression)	4	7.99	0.0001	Yes	
Finches	suppression	1	3.74	0.0563	-	
Finches	site(suppression)	4	1.19	0.3186	-	
Swallow	suppression	1	1.52	0.2266	-	
Swallow	site(suppression)	4	0.76	0.5562	-	
Skylark	suppression	1	1.51	0.2499	-	
Skylark	site(suppression)	4	0.66	0.5995	-	

Much less can be said about patterns for non-frugivorous species (Figure 7.34, Table 7.9). The numbers of non-frugivorous birds were smaller than frugivorous birds. This could partially relate to the flocking behaviour of some frugivores as opposed to the more territorial behaviour for some non-frugivorous birds (e.g. warbler, *Greygone igata*). Some of the non-frugivorous birds were associated with particular habitats such as watercourses (e.g. pukeko, *Porphyrio melanotus* and kingfisher, *Halcyon sancta*) and therefore encountered less frequently. The numbers of observations for some species were very low at some sites, giving rise to large standard errors.

Figure 7.33: Average number of observations (seen or heard) of frugivorous bird species per site visit.

Figure 7.34: Average number of observations (seen or heard) of non-frugivorous bird species per site visit.

It is also possible that pest suppression affects the behaviour, and hence conspicuousness of some species. Fantails (*Rhipidura fuliginosa*), tui (*Prosthemadera novaeseelandiae*) and kereru all appeared less likely to fly off at sites with pest control, compared to sites without (A. Dijkgraaf pers. obs.).

Flock size

The data for 'flock size' are presented in Tables 7.10 and 7.11, and Figures 7.35 to 7.37. 'Flock size' does not imply that the birds were seen in close proximity to each other or moving as a flock, it is merely a convenient term to denote the number of birds noted simultaneously at the same site.

The tables and figures present somewhat different aspects of the same data. The figures show the **total numbers of birds** seen or heard, grouped by flock size that they occurred in. For instance, at Wenderholm Regional Park, multiples of three tui were noted simultaneously on 53 occasions, giving a total of 159 tui (Figure 7.35). The tables contain the analysis of the **number of occasions** that each site had flocks of a particular size. Thus in the above example, tui were noted in 'triplets' on 53 occasions. Only the data for frugivorous birds has been presented as graphs

Table 7.10: ANOVA of 'flock size' for frugivorous species at each site.
Note that 'flock size' is a convenient term to denote the number of birds noted simultaneously at a particular site, it does not imply that the species exhibit flocking behaviour.

		Analysis of variance				**A posteriori Tukey's HSD means**			
Species	**Aspect tested**	**df**	**F Value**	**Pr > F**	**Signif**	**Suppressed**	**No poison**	**Signif**	**Multiples of birds**
Kereru	suppression	1	5.53	0.0207	Yes	7.12	4.143	Yes	1>2> the rest
Kereru	site	4	2.55	0.0435	Yes				
Kereru	multiples of birds	20	34.3	0.0001	Yes				
Tui	suppression	1	3.06	0.0834	-	10.016	6.524	-	1>2,3> the rest
Tui	site	4	5.21	0.0007	Yes				
Tui	multiples of birds	20	19.22	0.0001	Yes				
Rosella	suppression	1	3.01	0.0856	-	3.3333	2.3016	-	1,2>3,4> the rest
Rosella	site	4	3.97	0.004	Yes				
Rosella	multiples of birds	20	23.33	0.0001	Yes				
Silvereye	suppression	1	3.16	0.0787	-	4.8254	3.5238	-	3>1>2 >4>5> the rest
Silvereye	site	4	7.98	0.0001	Yes				
Silvereye	multiples of birds	20	18.07	0.0001	Yes				
Blackbird	suppression	1	4.62	0.034	Yes	2.7302	0.9524	Yes	1> the rest
Blackbird	site	4	2.22	0.0725	-				
Blackbird	multiples of birds	20	9.35	0.0001	Yes				
Thrush	suppression	1	2.7	0.1033	-	0.6349	0.0476	-	1> the rest
Thrush	site	4	1.87	0.1391	-				
Thrush	multiples of birds	20	2.05	0.0107	Yes				
Myna	suppression	1	8.45	0.0045	Yes	3.6032	1.746	Yes	1>2> the rest
Myna	site	4	2.6	0.0404	Yes				
Myna	multiples of birds	20	22.44	0.0001	Yes				

The level of control (pest suppressed or not poisoned) affected the 'flock size' of less than half the species. The site or numbers of individuals in the flock were more consistently significant. Among the frugivores only the flock size of kereru (F=5.53, P=0.027, df=1), blackbirds (*Turdus merula*, F=4.62, P=0.034, df=1) and myna (*Acridotheres tristis*, F=8.45, P=0.0045,df=1) were significantly greater at sites with pest suppression, while among the non-frugivorous species only finches (F=7.38, P=0.0078, df=1) and swallows (F=4.86, P=0.0297, df=1) had greater significantly greater ‘flock sizes’. However, most other species tended to have larger flocks at sites with pest suppression than at sites without, even though the differences were not significant (Tables 7.9 and 7.10).

Generally Wenderholm Regional Park had larger flocks of birds than any of the other sites. The most common ‘flock size’ was single birds, or pairs of birds. Silvereyes, rosella (*Platycrecus eximius*) and swallows (*Hirundo neoxena*) were more common in larger flocks. The large flocks of tui coincided with the flowering of kowhai trees (*Sophora microphylla*) at Wenderholm Regional Park.

Table 7.11: ANOVA of ‘flock size’ for non-frugivorous species at each site.
Note that ‘flock size’ is a convenient term to denote the number of birds noted simultaneously at a particular site, it does not imply that the species exhibit flocking behaviour.

		Analysis of variance				**A posteriori Tukey’s HSD means**			
Species	**Aspect tested**	**df**	**F Value**	**Pr > F**	**Signif**	**Suppressed**	**No poison**	**Signif**	**Multiples of birds**
Harrier	suppression	1	1.02	0.316	-	0.8413	1.1746	-	1>2> the rest
Harrier	site	4	2.08	0.0884	-				
Harrier	multiples of birds	20	21.85	0.0001	Yes				
Pukeko	suppression	1	0.14	0.7077	-	0.19048	0.15873	-	1> the rest
Pukeko	site	4	2.79	0.0303	Yes				
Pukeko	multiples of birds	20	6.05	0.0001	Yes				
Fantail	suppression	1	1.31	0.2554	-	7.048	5.571	-	1>2> the rest
Fantail	site	4	4.24	0.0033	Yes				
Fantail	multiples of birds	20	42.92	0.0001	Yes				
Warbler	suppression	1	0.01	0.9294	-	5.381	5.492	-	1>2>the rest
Warbler	site	4	2.33	0.061	-				
Warbler	multiples of birds	20	45.45	0.0001	Yes				
Pheasant	suppression	1	0.08	0.7808	-	0.5119	0.5873	-	1> the rest
Pheasant	site	4	2.21	0.0715	-				
Pheasant	multiples of birds	20	13.36	0.0001	Yes				
Finches	suppression	1	7.38	0.0078	Yes	1.7302	1.0317	Yes	1>3,2> the rest
Finches	site	4	2.29	0.0645	-				
Finches	multiples of birds	20	43.74	0.0001	Yes				
Swallow	suppression	1	4.86	0.0297	Yes	0.7619	0.1587	Yes	2,1,3,4>the rest
Swallow	site	4	4.05	0.0043	Yes				
Swallow	multiples of birds	20	2.76	0.0005	Yes				
Skylark	suppression	1	0.2	0.6532	-	0.1429	0.1905	-	1> the rest
Skylark	site	4	0.79	0.5025	-				
Skylark	multiples of birds	20	5.88	0.0001	Yes				
Ducks	suppression	1	0.89	0.3496	-	0.07143	0.02381	-	1,3> the rest
Ducks	site	4	2.22	0.1172	-				
Ducks	multiples of birds	20	2.16	0.0117	Yes				

Figure 7.35: Number of frugivorous birds at Wenderholm Regional Park and Loch Amber Bush, grouped by flock size

Figure 7.36: Number of frugivorous birds at Whitford Bush and Robertson's Bush, grouped by flock size

Figure 7.37: Number of frugivorous birds at Remiger's Bush and Val's Bush, grouped by flock size

Discussion

Suppression of pest species, such as possums and rodents, contributes to increasing the number of birds at those sites, but other factors such as forest patch size and isolation are also important. The number of birds observed simultaneously ('flock size') was generally greater at sites with pest suppression, but only significantly so for a few species. This was probably because other factors, including forest patch size and isolation, seasonal food abundance, territorial and flocking behaviour, affected the number of occasions when multiple individuals of the same species were recorded.

7.6 Concluding discussions

7.6.1 Effect of pest suppression on mammal presence

The results presented here illustrate that systematic suppression of pest species, such as possums and rodents, reduced the number of these mammals within forest patches to very low numbers. Less systematic or effective control, such as that at Remiger's Bush, still reduced the numbers of target pest species and had some positive benefits for native forest species.

When only possum numbers were reduced, as occurred at Remiger's Bush, rodent sign (especially rat droppings) and rodent damage of fruits tended to increase. Ship rats are known to be arboreal. In fact one study at Rotoehu Forest showed that 73% of the fixes on radio-tracked ship rats occurred above 2-m (Hooker and Innes 1995), thus possums and ship rats could compete arboreally for food and nesting sites. A reduction in competition from possums could, in such a case, result in increased damage by ship rats. However, the degree to which ship rats are arboreal might be site dependent. For instance, a study in Puketi Forest (a kauri forest in Northland) found radio-tracked rats on the ground for 93% of the time (Dowding and Murphy 1994).

An increase in rodent numbers, or sign, when possum numbers are suppressed has not been previously reported in the literature. It has been noted in several studies that mouse numbers increase after rats are controlled, possibly because of reduced competition and/or predation by ship rats (Clout *et al.* 1995a; Craddock 1997; Innes *et al.* 1995). In these studies rat numbers were usually reduced after a poison operation for possums, which had a by-kill of rats (Innes 2001), so it could be difficult to separate the effects of possum and/or rodent numbers on mouse populations (Veltman 2000). However, in this study, rats at Remiger's Bush were assumed to not have access to the poison in the bait-stations, thus only possum numbers were suppressed.

Perhaps we should not be surprised at a possible increase in rat numbers after possum suppression since other studies have found that the mammals introduced to New Zealand have established an interrelated food-web (Gillies 1998; Innes and Barker 1999) and that some species become more numerous after the removal of a key competitor (Gillies 1998). The interaction between possums and rats warrants further investigation.

7.6.2 Effect on fruit availability

The positive benefits of pest control included healthier more dense canopies that were capable of producing more fruits. These results are common to many other possum control operations (e.g. Frimmel and Turner 1999; Pekelharing *et al.* 1998a). Reduction of pest numbers reduced the quantity of fruit that was animal-damaged, and resulted in increased numbers of ripe or mature fruits at those sites.

This was also true when possum numbers were not totally suppressed, as at Remiger's Bush. Nugent, *et al.* (2000) note that although foliage comprises the bulk of the possum diet it is probably the least preferred, and that possums prefer high-energy foods such as fruits, or nitrogen rich foods such as insects, eggs and nitrogen rich foliage (e.g. willow, clover). The greater proportions of animal-damaged fruits at Remiger's Bush probably reflect the preference of possums for fruits. It was notable that the canopies of kohekohe, the leaves of which are generally preferred by possums (Buddenhagen

1995; Ogden and Buddenhagen 1994), were in reasonable condition at Remiger's Bush unlike the sites without pest suppression (E. Jousellin unpublished data, A. Dijkgraaf unpublished data). Thus there was no apparent shortage of food for possums, yet they preyed on a large number of taraire fruits. The high level of predation on taraire at Remiger's Bush would indicate that it is highly nutritious or energy-rich food, which was borne out by fruit nutritional analysis in the previous chapter.

A somewhat surprising finding was that partially developed rewarewa seed capsules were also much preferred by possums, and that pest suppression has a significant positive impact on the number of kahikatea seeds produced. It would be of interest to ascertain what nutrients rewarewa seed supplies, and at which point the seeds develop. Further work is also required to discover at which point(s) mammalian pests affect the fruit production of kahikatea, and which of the mammals is the main culprit.

7.6.3 Effect on other animal species

Pest suppression also resulted in an increase in the number of frugivorous birds. Kereru, the only species to be able to swallow the largest fruits (greater than 10 mm in diameter), increased both in number of birds and flock size at sites with pest suppression.

The bird sampling method used (birds heard or seen) was essentially a measure of conspicuousness of the various species (Dawson and Bull 1975) and increased bird counts could also have occurred through behavioural changes associated with a reduction of pests. For instance, kereru at Wenderholm Regional Park seemed less inclined to fly off when disturbed than at some of the other sites. Number of birds and number of species can also vary according to patch size and degree of isolation of the forest (Willson *et al.* 1994). However, greater numbers of fruit were consumed at sites with high bird numbers and good pest suppression, indicating that apparent increased bird numbers were not solely attributable to changes in behaviour. Other data and observations support the increase of bird numbers in sites with good pest suppression.

The majority of large fruits were consumed, and presumably dispersed, at sites with good pest suppression. The numbers of large fruits produced were greater at sites with pest suppression, as were the proportions of fruits consumed (Figures 7.17 to 7.25). Many of the large fruits at sites without pest suppression were predated before reaching maturity, and were thus unavailable to be consumed and dispersed. These factors should significantly improve the regeneration potential of the forests with pest suppression over the sites without pest suppression.

However, small isolated sites in which pest suppression is undertaken may not be able to support sufficiently large populations of frugivores to effectively disperse the greatest part of the fruit crop. At Robertson's Bush and Whitford Bush a much greater proportion of the large-fruit crop was not consumed compared to other more interconnected or larger sites. Furthermore, the number of kereru sighted in these two forest patches was lower than at the other sites. Burrows (1996) has suggested that there are insufficient frugivores in present-day Canterbury to consume and disperse entire fruit crops. A study in Australia showed that some species of pigeons or doves would decline significantly if forest patches became more isolated (Price *et al.* 1999), and this could have consequences for seed dispersal, and Willson *et al.* (1994) noted that the diversity and relative abundance of south-temperate rainforest birds decreased as the size of the habitat patch decreased.

Whitford Bush had about four resident kereru (M. Clout pers. comm.) and a similar number of kereru were noted at Robertson's Bush. The impression at these two sites, and especially at Whitford Bush, was that large numbers of taraire, karaka, and puriri fruits fell from the tree over-ripe or desiccated. Thus dispersal isn't as effective at these small isolated sites, or there are inadequate numbers of birds to disperse the seeds. A lack of sufficient bird dispersers has been noted elsewhere in New Zealand. Insufficient bellbirds at Craigieburn could explain the lack of adequate mistletoe pollination (Robertson *et al.* 1999) and dispersal (Murphy and Kelly 2001), lack of karaka consumption near Christchurch was attributed to a possible of lack of kereru (Burrows 1996), and fruits of various species were eaten more often on predator-free Tiritiri Matangi Island, where several native bird species have been reintroduced, than in Wenderholm Regional Park (Anderson 1997).

The impact of possums and rodents on insect species was unclear, and was probably confounded since both possums and rodents eat invertebrates (Veltman 2000). Numbers of weta droppings increased significantly at sites with reduced possum and rodent numbers, but a reduction of possum numbers without reduction of rodent numbers resulted in reduced numbers of weta droppings. Craddock (1997) also found that Wenderholm Regional Park had a greater abundance and diversity of insects, especially beetles, weta, and cockroaches than an adjacent site without pest suppression, and rats had a greater impact on invertebrates than mice. However, it is still not possible to say that rodents, especially rats, have a greater impact on weta numbers than possums (Veltman 2000).

No difference was detected for overall numbers of insect droppings for sites with different pest suppression regimes, probably because most insect droppings were not identified to family or genus. It has been suggested that changes in fruiting, flowering and litterfall will change above- and below-ground forest processes (Cowan 2001), which would in turn have consequences for invertebrate species.

Thus systematic suppression of possums and rodents has significant benefits for native plants, animals and forest communities. Less rigorous suppression of possums, without controlling rodents, still has some benefits but these may be partially negated by increased rodent numbers.

7.7 Conclusions

Systematic suppression of possums and rodents in forest patches resulted in a reduction in the number of these pest animals. Significant positive benefits to the forest community were noted, including increased fruit production, increased availability of ripe fruits, increased number of frugivores, increased consumption of fruits and increased weta presence.

Less rigorous pest suppression had fewer benefits and was partially negated by increased damage to preferred food species and increased damage by the species not suppressed.

8. Interaction of large-fruited species, seed dispersers and seed predators

8.1 Introduction

This thesis focussed on tree species with large, fleshy fruits, the principal native consumer of these fruits, the kereru (*Hemiphaga novaeseelandiae* (Gmelin)), and the introduced arboreal predators of these fruits, possums (*Trichosurus vulpecula* Kerr) and rodents. Previous Chapters have investigated the timing of ripe fruit presentation of large-fruited species (Chapters 5 and 6), the preference by and profitability for kereru eating particular fruits (Chapter 6) and the effects of possums and rats preying on fruits and other ecosystem components (Chapter 7).

This final chapter will first briefly summarise the key points made in each chapter. I will then illustrate how all of these components interrelate and how knowledge of these relationships can have implications for managing pest-suppression and ecosystem restoration projects.

8.2 Fruit phenology of large fruited species

This thesis began with the hypothesis that;
"Given a single disperser for the largest fruits, and only a few dispersers for fruits greater than 10 mm[1], there has been inter-specific competition amongst the co-existing fleshy large-fruited species for dispersers."

This hypothesis arose partially from the knowledge of past and present frugivores within New Zealand and partially from the central hypothesis for Chapter 5, that the timing of ripe fruit presentation has been altered, through inter-specific competition amongst large-fruited tree species to maximise species dispersal, so that co-occurring species have distinct and non-overlapping annual fruiting periods. Proving such displacement in time can be difficult because displacement is a multi-facetted phenomenon and natural variation can obscure patterns (Chapter 5). Character displacement, in the form of timing of fruiting, was deemed to comprise several elements, including;

- that each species fruited at a particular time of the year,
- that magnitude of the fruiting peak was greater than could be expected by chance,
- that fruiting was synchronous within a species, and
- that fruiting of different species did not overlap.

Each of these was tested, and most tended to be verified for the majority of species, in some years or sites. Breaking fruiting phenologies into these components made statistical analysis easier and more robust, but natural variation, including supra-annual cycles, precluded definitive answers in some cases.

For instance, the fruiting of tawa (*Beilschmiedia tawa*) did not differ significantly from random fruit production, because many trees (sometimes more than 50% of the population) within the sample population did not produce any fruit, produced only small amounts of fruit throughout the year or fruited at different times to other tawa at the same site. Tawa fruited heavily just prior to the period of data collection, but had low and sporadic fruiting throughout this study. This species had previously been reported as having supra-annual cycles (Burrows 1999; Knowles and Beveridge 1982; Leathwick 1984; West 1986), including a time of low fruit production immediately following 'masting'. The fruiting pattern observed in this study supports the observations by Knowles (1982) and Burrows (1999), and resulted in tawa

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[1] Mean transverse diameter through the smallest axis of the fruit is 10 mm or more

exhibiting a lack of synchrony within the species, a significant overlap with other species and a fruiting 'peak' that appeared to be no different from random. It is likely that the synchrony of tawa will improve and overlap decrease during a masting year.

Kohekohe (*Dysoxylum spectabile*) also had supra-annual cycles, in this case biennial, with heavy flowering years alternating with heavy fruiting years. It is possible that this biannual cycle is a consequence of high resource allocation to fruit production during the heavy fruiting years (fruits take a year to mature) that precludes copious flower initiation. It also appeared that sun-exposed parts of kohekohe trees produced more fruits than the shaded parts, and canopy trees produced more fruits than subcanopy trees (A. Dijkgraaf pers. obs.).

In New Zealand it would appear that years of low and high fruit production are synchronised across large geographic areas for a range of species, this argues for climatic cues. For instance, there are indications that winter temperatures affect the size of tawa fruit crops; colder than average winters reduce fruit crops, while warmer than average winters produce good crops (West, 1986). Beech flowering mast years occur at irregular intervals averaging 3 to 5 years apart. They are often widespread but not always synchronised across all species or sites and may be triggered by hot dry summers in the preceding season (Wardle 1984). Small beech seeding events, after heavy flowering, have been attributed to floral abortion after heavy frosts and wet weather or high humidity interfering with wind pollination (Wardle 1984). Large kohekohe fruit-crops also appear to be synchronised across the country. Flowering occurs more or less simultaneously across New Zealand during June and July and is probably initiated by changes in day-length. Kohekohe fruit ripening can lag by more than a month in the more southern regions thus it is suspected that speed of fruit ripening could depend on local temperatures (A. Dijkgraaf pers. obs.).

Most years a proportion of trees within a species do not produce any fruits. Non-fruiting individuals within a species can comprise half the population monitored (as shown in this study for karaka, tawa, tawapou) and therefore lower the synchrony values for those species (Chapter 5). Such large numbers of non-fruiting trees were obtained despite deliberately choosing healthy, mature, trees and using data from sites with good pest-suppression. Thus, non-fruiting individuals are an important aspect of ecosystem functioning and need to be to taken into account when attempting to calculate fruit production in an ecosystem.

This also raises the question "at what level does within-species synchrony become biologically significant?" Primack (1980) described within-species synchrony values of 0.34 to 0.41 for *Dracophyllum* spp. as low, but did not comment on the values for *Leptospermum* (0.68 and 0.74) and *Discaria* (0.42 and 0.72), or compare the values statistically. This study investigated the chance (with 95% confidence) that synchrony values obtained for the different species exceeded a critical value of 0.5. This value indicates that 50% of the trees bear ripe fruit simultaneously, but is a ratio of 50% of a population appropriate? For species with short fruit phenologies, it could be possible that more than 50% of the trees bear fruit within the same month but do not overlap (e.g. kohekohe and karaka in this study). It could also be that those trees that do fruit produce copious amounts of fruit. It seems likely that the total amount of fruit produced per year could be more important for frugivores than the number of trees producing the fruit. The synchrony measure used took no account of the amount of fruit produced, only whether phenologies overlapped. It would be worthwhile to investigate whether there is a predictable relationship between number of trees producing fruit and total number of fruits produced per site.

It was assumed that for a tree species to minimise fruit phenology overlap with other species it would need to have tightly synchronised fruiting patterns. For instance, puriri, which has a long fruiting period, would have minimal overlap with other species only when all puriri trees produced fruits simultaneously during a season when no other species carried ripe fruits. This was not found to be the case. Some species were more asynchronous than synchronous

($Z_s^{(sp)}$<0.5 = fewer than 50% of the trees or occasions had conspecific fruit simultaneously), whilst for others the 95% confidence limits of mean species synchrony included the critical synchrony value ($C_s^{(SP)}$=0.5, $Z_s^{(sp)}$ ± 95% included $C_s^{(sp)}$). Kohekohe was the only species that significantly exceeded the synchrony critical value at both sites. Puriri and karaka had a species synchrony value significantly greater than the critical value at Whitford Bush. Yet most species were also found to not overlap significantly with other species through comparison of the overlap values with calculated overlap critical values (overlap values $Z_s^{(o)}$<critical overlap value $C_s^{(o)}$). This situation was unexpected and could have arisen because of the large number of non-fruiting individuals in the sample population (refer to Appendix 5.4), thereby suppressing synchrony values.

The modification of the synchrony formulae (Augspurger 1983) to calculate the degree of overlap has not been previously explored in the literature. The adaptation was ecologically plausible and generated values that seemed appropriate to the species. A further innovative step was to generate critical values, for both synchrony and overlap, with statistical confidence intervals. The synchrony critical values were simple to generate, although, as mentioned above, further work is required on what constitutes biologically significant synchronous fruiting. The overlap critical values were more difficult to calculate and require further work.

In particular, the best measure of fruiting length needs to be identified. Different measures were tried (e.g. mean, mode, median etc) which produced somewhat different outcomes. Both the synchrony and overlap critical values would benefit from inclusion of some measure of fruiting amplitude (amount of fruit produced). Furthermore, is what humans perceive as an available or suitable food source seen in the same way by frugivores, or as Hutto (1990) (but also see Cooper and Whitmore 1990; Wolda 1990) put it, what is the relevance of the various dietary items to the bird and how can we better quantify that? In Chapter 6, timing of fruit presentation was further explored in relation to nutritional components of fruits preferred by the primary disperser, kereru.

In the lowland forests of northern New Zealand, large fruits and other smaller, kereru-preferred fruits are available throughout the year (Chapters 6 and 7). Tree species producing lipid-rich fruits, the fruits most preferred by kereru (Chapter 6), are available throughout the year and complemented (Whelan *et al.* 1998) seasonally by species producing sugar-rich and/or carbohydrate rich-fruits. Sugar-rich fruits were more common in spring and summer. Relatively high-calcium fruits were available, and more preferred, just before and during the kereru-breeding season (spring and summer).

The timing and nutrient composition of fruits might also reflect the energy input required to construct tissues of different composition. The fruit-flesh of sugar-rich fruits (pericarp of karaka, puriri and peduncle for kahikatea) took less than 3 months to ripen, while lipid-rich fruits (taraire, kohekohe and nikau) took considerably longer (6 months to 1 year, A. Dijkgraaf pers. obs.). Perhaps sugar-rich fruits develop rapidly during high solar radiation periods, i.e. summer. Among the large fruited sugar-rich species, puriri appeared to be most preferred, karaka least preferred, with tawa intermediate. Puriri fruits appear to be a basal component of the kereru diet, that was available all year round and a reliable food source for kereru. Hence kereru ate this species in approximately equal quantities throughout the year when it was available, even though the fruit doesn't have particularly high nutritional levels.

These fruiting patterns, lack of phenological overlap between large-fruited species, the availability of particular nutrients throughout the year, and the illustrated preferences by kereru for particular fruiting species and large-fruited species, are notable and provide support for co-evolution of these species with a single principal disperser. There is a lack of phenological overlap between the species producing the most preferred lipid-rich fruits (character displacement in time through interspecific competition amongst sympatric species e.g. Fleming and Partridge 1984; McKey 1975; Rathcke and Lacey 1985) and yet lipid-rich fruits are available virtually throughout the entire year to support kereru. The relatively high-energy lipid-rich fruits tend to be the largest fruits (taraire, tawapou, kohekohe, nikau) that are solely or most often dispersed by kereru (high quality fruit to attract high-quality disperser McKey 1975). Fruit species with other characteristics (e.g. sugar-rich, protein-rich) are also available throughout the year to complement lipid-rich fruits and ensure a balanced diet for the kereru (fruit complementarity Whelan *et al.* 1998). There is a lack of significant phenological overlap in the presentation of ripe fruit for the large-fruited species studied (character displacement in time) even though they have different nutritional characteristics, illustrating that there is competition for the services of one disperser.

However, the current pattern might have evolved for a number of reasons and we cannot show causality for the reasons outlined in Chapter 5 (e.g. Fischer and Chapman 1993; French 1991; Gorchov 1990; Herrera 1982, 1985b; Janzen 1977; Rathcke and Lacey 1985). Furthermore, we cannot completely exclude the effects that flightless moa, or other bird and/or lizard species, might have had on fruiting phenology in the past.

Thus, though there are several lines of evidence to support the hypothesis made earlier, “That, given a single disperser for the largest fruits, and only a few dispersers for fruits greater than 10 mm, there has been inter-specific competition amongst the co-existing large fleshy-fruited species for dispersers;” the issue of causality remains speculative. The presence of a single effective disperser may well have caused tree species to modify the fruiting phenology or fruit nutritional characteristics so that each species obtains the maximum service from the disperser, but the ecological antecedents of this relationship are now obscure.

8.2.1 Effect on kereru populations

Kereru have a broad diet (in excess of 90 species, refer Chapter 2 and McEwen 1978) but, as this study has shown, prefer some fruits or nutritional classes to others (Chapter 6). They favour lipid-rich fruits in particular (Figures 6.9 to 6.11). This is not unexpected given the results from other studies, since pigeons in New Zealand (Powlesland *et al.* 1997) and Australia (Crome 1975a, b), and species elsewhere (e.g. Firth *et al.* 1976; Snow 1962) have been reported as favouring lipid-rich fruits or families of fruits (e.g. Lauraceae) that are known to be high in lipids.

The preference for lipid-rich fruits could be related to specializations of the digestive system, such as increased gut passage time giving more processing time for lipid-rich fruits than is required for carbohydrate or sugar-rich fruits (Fuentes 1994). Frugivorous birds might modulate digestive processing of fruits according to the time needed for efficient digestion and/or absorption of sugars and lipids and might show digestive specialization for sugar-rich or lipid-rich fruits, respectively (Witmer and Van Soest 1998). For instance Cedar Waxwings (*Bombycilla cedrorum*) appear to specialize in sugary fruits and are less efficient in digesting and absorbing nutrients from lipid-rich fruits than frugivorous American thrushes (Witmer and Van Soest 1998).

Kereru showed a greater preference for lipid-rich fruits than sugar-fruits, but also consumed other ‘fruit types’ or nutritional components (Figures 6.9 to 6.11). Kereru may not be able to meet their energetic (Wheelwright 1991) or nutritional (Whelan *et al.* 1998; Whelan and Willson 1994) demands on a pure diet of large, lipid-rich fruits because gut space is limited and it takes so long to process individual large fruits (often 2 hours or more Bell 1996) or because lipids take longer to digest than sugars (Witmer 1998, 1999; Witmer and Van Soest 1998). It has been suggested that fruit foragers can enhance their diet by selecting food items that contain complementary nutritional resources. Combining sugar-rich fruits, with lipid-rich or protein-rich fruits or selectively choosing fruits rich in particular vitamins or minerals could provide synergistic nutritional resources that outweigh consuming fruits from only a single species (Wendeln *et al.* 2000; Whelan *et al.* 1998). This could explain why puriri fruits are consumed by kereru in roughly equal proportions throughout the year, despite their relatively low nutritional benefit or relative availability.

Other nutritional components may be seasonally significant and cause kereru to switch to less nutritional or scarcer fruit. Examples are the consumption of nitrogen-rich foliage in early spring, whilst there still is plentiful fruit around, or the high preference for lipid and calcium-rich nikau fruit (*Rhopalostylis sapida*) at the beginning of the breeding season when these fruits are relatively scarce. Lipids, nitrogen and calcium are likely to be important in the formation and development of eggs, embryos and chicks. Such dietary switches can occur for other reasons, for instance, pre-migration dietary preferences of robins in America showed greater selection of lipid-rich fruits than at other times of the year (Lepczyk *et al.* 2000). However, kereru are non-migratory in New Zealand.

Powlesland, *et al.* (1997) showed that heavy fruiting of matipo (*Myrsine chathamica*) and hoho (*Pseudopanax chathamicus*) promoted early nesting of parea (*Hemiphaga novaeseelandiae chathamensis*) and prolonged nesting for 6 months, including nesting during winter. Conversely, low fruiting years adversely impacted on breeding productivity. Lack of sufficient fruit also caused breeding failure for kereru at various sites throughout New Zealand, and may even have contributed to the deaths, through starvation, of some adult kereru (Clout *et al.* 1995b). Thus kereru breeding success appears to be dependent on sufficient quantities of energy-rich fruits. Fruit are available throughout the year in the northern forests of the North Island (Chapters 5, 6, and 7), but might not be equally abundant each year (Chapters 5 and 7) resulting in different levels of breeding success.

Reduction in fruit quantity is not only caused by supra-annual fluctuations in fruit production by key species, but can also be a consequence of competition for fruit by possums and rodents. At times, for certain tree species, a hundred-fold more fruits are produced in areas where possum and rodent numbers are suppressed than in adjacent areas where these pest species are not poisoned (Chapter 7, Figures 7.11 to 7.25). Even when the differences were not of that magnitude there were still significant differences in the numbers of fruits damaged, and hence numbers of fruits that were available for consumption by kereru. Possums, and to some extent rodents, also prefer the high-lipid fruits that appear to be crucial in maintaining condition and breeding success of kereru. Thus at times of the year, when other fruits are rare (i.e. winter) and kereru rely on lipid-rich fruits to survive, or when kereru require large nutritional input for successful breeding (e.g. nikau fruits), these fruits may not be available because they have been predated as juvenile fruits by possums and/or rodents (Chapter 7).

Thus kereru are not only directly impacted by possums and rodents through predation on eggs and chicks and causing adults to abandon nests through nest disturbance (Clout *et al.* 1995a; Grant *et al.* 1997; James and Clout 1996), but probably also by a lack of food caused by those same pest species (Fitzgerald and Wardle 1979). This may be the reason why at times more than 300 kereru were recorded at Wenderholm Regional Park (e.g. Clout *et al.* 1995b) after possum suppression began. Wenderholm Regional Park became a ‘food basket’ for kereru in surrounding, more degraded, forests. Reductions in possum and rodent populations have benefited kereru breeding success (Clout *et al.* 1995a; James 1995; James and Clout 1996), but have also resulted in increased fruit production (Chapter 7) and seedling recruitment (Clout and Lowe 1994) relative to sites without pest suppression.

8.2.2 Effect on possums and rodent populations

Possums have been described as reluctant folivores (Nugent *et al.* 2000) in that they resort to foliage when other preferred food items, such as fruits, insects and eggs, are in short supply.

It is thought that possums may often be food-limited in New Zealand forests resulting in poorer physical condition and slower breeding than Australian populations (Cowan 2001; Green 1984). However, when possums invade a new area, or are reduced to low numbers and abundant food becomes available, then a higher proportion of females breed and they can often produce two young per year rather than usual one (Green and Coleman 1984; Humphreys *et al.* 1984; Ritchie 2000). Thus temporary possum suppression can actually enhance breeding success and accelerate recovery of the possum population in the area (Green and Coleman 1984).

Possum populations (whether suppressed or invading) generally undergo an initial slow but steady increase in numbers that eventually results in a relatively short-lived irruption to a peak population. At this peak possum population level severe damage to vegetation can become evident, and the population often undergoes a sharp decline in numbers to a lower density (Cowan 1998, 2001). Some recovery of vegetation is possible when possum numbers decline (Cowan 1998). However, sensitive plant species may have been removed from the habitat by this time (e.g. *Fuchsia excorticata*, mistletoes, Campbell 1984; Fitzgerald 1976; Norton 1991; Pekelharing *et al.* 1998b; Wilson 1984), or dominant canopy species may have been damaged beyond recovery (e.g. kamahi - *Weinmannia racemosa*, tawa - *Beilschmiedia tawa*, rata - *Metrosideros* spp.Batcheler 1983; Cowan and Petersen 1991; Norton 2000; Payton 1990; Pekelharing and Batcheler 1990; Rose *et al.* 1992). Sometimes this results in complete canopy collapse, especially when aided by introduced ungulates (Batcheler 1983; Payton 1990; Rogers and Leathwick 1997). Comparison of adjacent sites suggests that control before possum populations attain peak densities is critical for limiting canopy mortality (Pekelharing and Batcheler 1990). Possum suppression must therefore be ongoing or repeated (Ritchie 2000) unless they can be completely eradicated and reinvasion prevented.

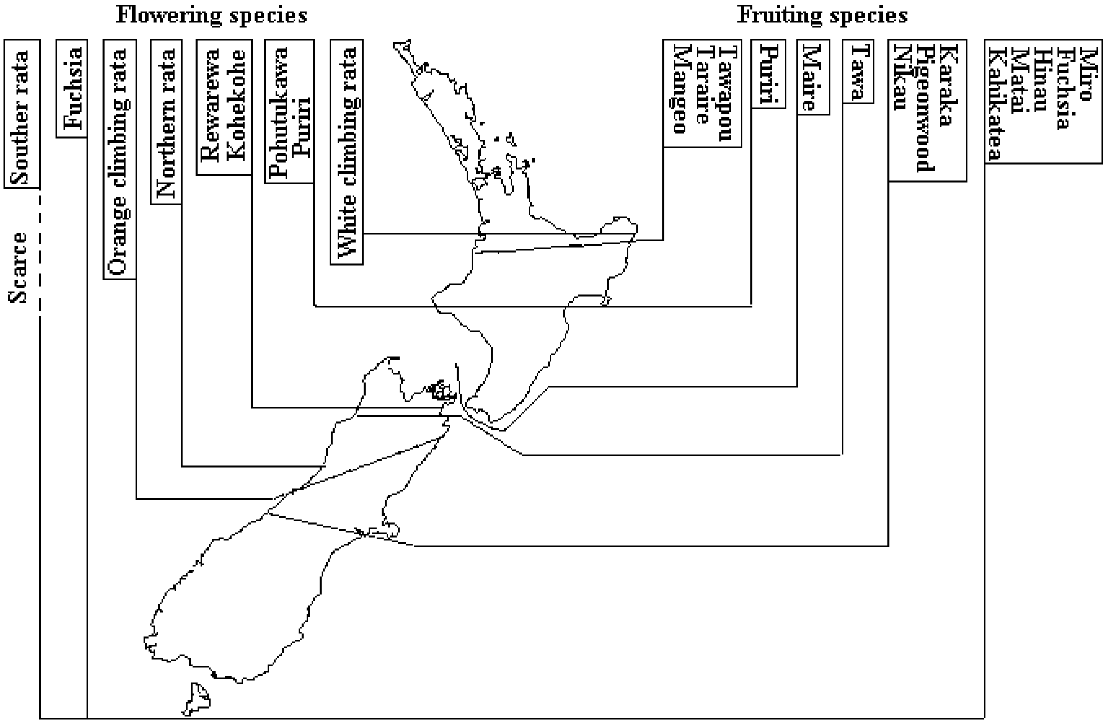
With sustained ongoing possum control it is possible to reverse the damage done to the remaining vegetation, although it can take a decade or more before trees are once again fully leaved and producing large quantities of flowers and/or fruits (Norton 2000). For example, it took at least 5 years of sustained possum control at Wenderholm Regional Park before kohekohe trees had noticeably large fruit crops (B. Green pers. comm.). The lag in tree recovery will delay the return or recovery of the native bird fauna, especially those species dependent on fruits. The impacts of peak possum numbers on the survival of native fauna are unclear, and it could be that possum suppression prior to the peak irruptive phase might reduce the impact on (or perhaps even prevent the extinction of) native fauna as well as flora.

Possum control in New Zealand is often undertaken using aerially sown poison-baits over large areas and difficult terrain, or by means of hand or bait-station delivered baits for smaller or easier to negotiate blocks of land (e.g Powlesland *et al.* 1999; Thomas *et al.* 1998; Warburton 1996). It would be preferable if baits could be presented at times when food supplies are limited and during which possums might be more attracted to alternative food sources such as toxic baits (e.g. Morgan 1982; Warburton 1996).

The year-round fruit availability in the lowland forests of the northern North Island (Chapters 5, 6 and 7) could potentially mean that there is no season in which food-shortages occur. In the case of the widely used toxin sodium monofluoroacetate (also known as 1080) ambient temperature and latitude are known to have an influence on the percentage of possums killed. Colder temperatures and more southerly latitudes resulted in greater possum mortality (Veltman and Pinder 2001). Increased kill rates at southerly latitudes could be a function of cooler temperatures, but might also reflect fewer fruiting and flowering species in those forests resulting in more seasons with food ‘shortages’. A schematic distribution of key fruiting and flowering species is presented in Figure 8.1. A study is required to investigate whether or not fruits are available year-round at more southerly latitudes, and how that impacts upon the breeding success of kereru and how that affects pest control operations.

In areas where rats have access to bait laid for possums or are specifically targeted with baits, it has been noted that mice increase in numbers or in conspicuousness (Clout *et al.* 1995a; Craddock 1997; Innes *et al.* 1995). This occurred at some sites (e.g. Wenderholm Regional Park Greene 1994; Lovegrove 1996b) in this study. Interestingly enough, when only possums were suppressed (as at Remiger's Bush) there was an increase in rat droppings (Figure 7.9c) and rat-chewed fruits (Figures 7.17 to 7.25). This suggests top-down control of rodent populations by possums but the mechanism (predation, competition, behaviour) is unclear. This will be further investigated in Section 8.2.3.

Figure 8.1 Approximate latitudinal limits for species with large fruits and large flowers. Tree species towards the limits of their distribution are often patchy and generally found more often along, or confined to, the coast.



The availability of year-round fruit in northern North Island lowland forests might also make it more difficult to deliver toxic baits to rodents as there will be few times when other food sources are in short supply. A study is currently underway to investigate whether rats have a seasonal preference for aerially delivered 1080 baits (C. Gillies pers. comm.). This study was implemented because aerial 1080 applications for possum suppression during autumn did not result in a significant reduction in rat numbers in the target areas, whereas winter drops were more successful (N. Marsh and J. Campbell pers. comm.).

The catch rate of rats in this study was lower than expected, but was similar to other trap catch rates reported elsewhere over the same period. Rodent populations are known to fluctuate widely (e.g. King *et al.* 1996a; King *et al.* 1996b). For instance where beech trees (*Nothofagus*) occur mouse and rat numbers can increase rapidly in mast seed years (e.g. Alterio *et al.* 1999; King and Moller 1997; O'Donnell *et al.* 1992; O'Donnell and Phillipson 1996) yet be considerably lower during other years (Innes 2001). Fluctuations in rat numbers might also correlate with years of abundant fruit production, large invertebrate populations or particular climatic factors. The low catch rate at the end of this study may have been due to insufficient food resources at that time. The only index that could be correlated with fruit abundance throughout this study was number of seedfall traps containing rodent droppings. However, it is currently not clear what the numerical relationship is between rodents caught in ground-set snap traps and number of seedfall traps containing droppings from arboreal rats, thus it is not yet possible to relate fruit abundance to rat abundance.

The ecological implications of increased rat numbers following possum removal include more predation of eggs and chicks, and possibly higher stoats numbers since rats tend to be a large component of stoat diets (Innes and Barker 1999). A subsequent reduction in rat numbers can lead to stoats switching to prey other than rats such as native birds (Murphy and Bradfield 1993). Changing the abundance of one small mammal is likely to have effects on the abundance of other introduced mammals within that forest, sometimes with unforeseen impacts on native fauna (Innes and Barker 1999; Murphy and Bradfield 1993; Murphy *et al.* 1998)

8.2.3 Interaction between species

The detrimental impacts of introduced possums and rodents on native plants and animals are now well recognised, but we are only just beginning to appreciate the complex interactions of factors influencing the type, degree and consequences of damage by these mammalian pests (Cowan 2001; Norton 2000; Payton 2000; Sadleir 2000). Moreover, it is often not possible to predict all the outcomes of the removal, or reduction, of a single pest species and managers can be faced with unexpected additional problems. For instance removal of Norway rats (*R. norvegicus*) from Breaksea Island not only resulted in increased seedling numbers but a notable increase in herbivorous invertebrates, such as weta (*Stenopelmatidae* and *Rhapidophoridae*) and a large herbivorous slug *Pseudaneitea* sp. which probably adversely affected seedling recruitment or seedling survival of some species (Allen *et al.* 1994).

Similarly, an herbivorous brown chafer beetle (*Odontria* sp.) increased in numbers at Wenderholm Regional Park after possum and rat control. This resulted in the defoliation of some karaka and lemonwood (*Pittosporum tenuifolia*) trees. The apex of each branch on a karaka tree either produces new leaves or flowers. Defoliated karaka trees tended to produce foliage rather than flowers and consequently failed to produce fruits (A. Dijkgraaf pers. obs.). Defoliated lemonwood trees also failed to flower or fruit (A. Dijkgraaf pers. obs.). A similar event occurred on Tiritiri Matangi Island in the Hauraki Gulf. Here the removal of kiore allowed a beetle to increase in numbers to such an extent that pohutukawa trees (*Metrosideros excelsa*) were visibly impacted (M. Clout pers. comm.). There is the potential, if herbivorous insects became numerous enough and inflict sufficient damage on trees, for reduced fruit production within a forest, which in the short term could reduce food availability for birds.

Removal or reduction of mammalian pest species can also have unexpected consequences for predation. For instance, there was concern that the illegal introduction of rabbit haemorrhagic disease (RHD) to New Zealand in 1997 would significantly reduce rabbit (*Oryctolagus cuniculus)* populations causing the main predators, stoats and ferrets, to switch to other, possibly native, prey (Norbury and Murphy 1996). One study documented increased predation of pukeko (*Porphyrio porphyrio*) nests, coinciding with strong anecdotal evidence that rabbit abundance had decreased (Haselmayer and Jamieson 2001). However, in this case the predators thought to be responsible were not stoats or ferrets but Australasian harriers (*Circus approximans*) . This result was not predicted since the focus of concern had been prey switching of small predatory mammals such as stoats and ferrets (Haselmayer and Jamieson 2001).

Similarly, predation by possums or rodents on native bird populations is not the only element that affects successful breeding and raising of chicks. During the 1995-1996 season, only one kereru was fledged from 13 nests at Wenderholm Regional Park. Possums and rats were implicated in two cases of nest failure. There were six other cases where the predators could have been possums or rats, however, those eggs and chicks could also have been taken by stoats, harriers (*Circus approximans*), moreporks (*Ninox novaeseelandiae*) or kookaburras (*Dacelo novaeguineae*) (Lovegrove 1996a). Stoat numbers were high at Wenderholm Regional Park during the 1995-1996 kereru breeding season (B. Green, pers. comm., A. Dijkgraaf, pers. obs.), and other studies have shown that successful reduction of possum and rodent numbers can cause stoats to switch to predating bird species (Murphy and Bradfield 1993). Perhaps the combination of low rat numbers and high stoat numbers resulted a high predation rate by stoats on kereru eggs and chicks for the 1995-1996 season. Alternatively, the low rat numbers may have forced harriers, moreporks and/or kookaburras to switch to other prey such as kereru eggs and chicks.

Conservation managers are becoming more aware that introduced species must be managed collectively. Aerial 1080 operations no longer solely target possums, but are generally timed to ensure the largest ‘by-kill’ of other pests such as rodents, and secondary poisoning of species such as stoats and cats (Gillies 1998; Innes 2001; King *et al.* 2001) to ensure more positive outcomes for endangered species such as kereru, kokako (*Callaeas cinerea*) and kiwi (*Apteryx* spp.). Reductions in the numbers of those species can in turn increase the number of mice (Gillies 1998; Innes *et al.* 1995), rabbits (Gillies 1998), and pigs (*Sus scrofa*, A. Dijkgraaf pers. obs.) through lack of predation or increased food supplies.

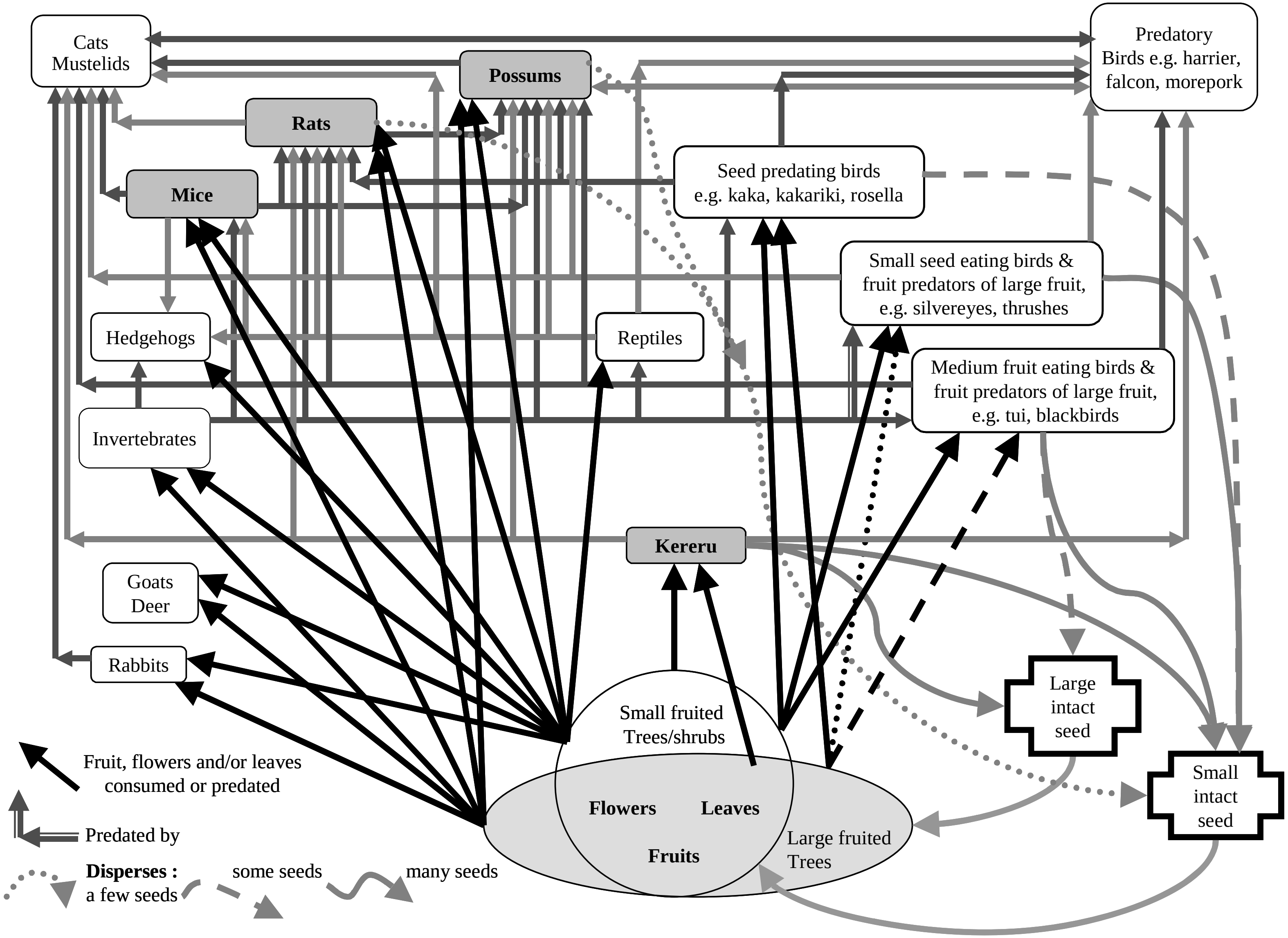
Stoats and rats can quickly re-colonise and re-establish at high population numbers (a few months for rats (Innes 2001), two months for stoats (Gillies 1998)). If mouse or rat numbers are high this can result in subsequent higher than expected stoat numbers (e.g. during a beech masting year Fitzgerald *et al.* 1996; O'Donnell *et al.* 1992; Studholme 2000), which can in turn have adverse effects on native species (e.g. yellowhead - Mohoua ochrocephala O'Donnell *et al.* 1992; O'Donnell and Phillipson 1996). Reduction of mustelids in an area can result in increased numbers of rabbits, which can in turn impact on the regeneration of native species and the productivity of adjoining rural farms (Gillies 1998). Possum control operations often result in increased fruit production, which in turn can increase pig numbers in a forest. High pig numbers can adversely impact on invertebrate populations, soil processes (including nutrient cycling and increased erosion), plant species composition and kiwi populations through predation of eggs, chicks and adults or through competition for invertebrates (McIlroy 2001). Often these linkages were not identified until after pest control operations were undertaken.

8.2.4 Food webs

Past conservation efforts in New Zealand have tended to focus on species conservation or eradication rather than ecosystem conservation and management. Globally, awareness is growing that in order to conserve or manage particular species in the longer term the processes and biota that sustain these species within an ecosystem must also be conserved (Baskin 1994; Simberloff 1998; Westman 1990). Often the consequences of eliminating or reducing particular pest species are not immediately evident. The consequences can be quite complex, may involve many inter-species linkages, and also depend on other native and exotic species found in the habitat (Towns *et al.* 1997a; Zavaleta *et al.* 2001, and references therein).

Westman (1990) notes that the impact of introduced and/or invasive species can be both harmful (e.g. rate of spread, degree of threat to other species, degree of damage) and beneficial (e.g. sustaining other processes, providing social or biotic opportunities that can not be quickly replaced), and these impacts should be carefully considered in setting management priorities. The traditional view of totally interdependent communities, in which a change to any species’ abundance is a threat to the entire community is no longer thought accurate. Natural communities are continually subjected to new arrivals and usually the adjustments among the resident populations do not result in a net loss of species (Westman 1990).

Figure 8.2 Simplified food web for functional groups in forest remnants in the Auckland area (northern New Zealand). This food web emphasises elements explored in this thesis, that is, native fruits, kereru, possums and rodents. Diagonal black arrows relate to components of the vegetation being consumed, be they flowers, fruits or foliage. Horizontal and vertical arrows indicate which animals are preyed by other animals. Curved arrows show which animal species are thought to contribute to seed deposition.



Generally however, the introduced mammal species in New Zealand adversely impact native flora and fauna. Moreover, these introduced species interact with each other so that the removal of one or more species from the system can have unexpected deleterious consequences through the increase of remaining mammalian species or prey-switching (Gillies 1998; Norbury and Murphy 1996).

The many interactions at a location are probably best illustrated by use of a food web depicting trophic cascades and predator-prey interactions (Innes and Barker 1999; Zavaleta *et al.* 2001). A food web can be defined as network of consumer resource interactions amongst a group of organisms, populations, or aggregate trophic units (Winemiller and Polis 1996). They are often presented as a diagram depicting which species in a community interact (Pimm 1982), or depicting interactions between community members and their linkages with ecosystem processes (Bengtsson and Martinez 1996). Presenting communities as food webs allows the inclusion of various non-trophic interactions such as pollination, seed dispersal and competition for nesting or den sites (Innes and Barker 1999). To enable accurate prediction of the consequences of a management action, such food webs should be specific to the locality and include all resident species. However, inclusion of all species will generally be a major undertaking and result in a very complex food web.

One way to simplify food webs is to use functional groups rather than species. Functional groups are groups of organisms that have equivalent functions or roles (Stone 1995). For instance in Figure 8.2, ‘Seed predating birds’ includes parrots (kaka, kakariki and rosella) that damage the embryo of large seeds but can swallow smaller seeds intact (Chapter 1). Some species are the sole occupiers of a particular functional group. Kereru are the only vertebrate dispersers of large canopy borne fruits and totally vegetarian. Other bird species cannot swallow the large fruits and disperse them intact, and most birds (other than kereru) are partially insectivorous (Chapter 1).

The food web in Figure 8.2 is a simplification of currently known or suspected interactions between functional groups in terrestrial hardwood-podocarp forest remnants of the Auckland area. The data for this food web come from a wide range of New Zealand literature (key references provided in Appendix 8.1) and personal observation. This food web does not necessarily indicate the importance of any of these species, or functional groups, in maintaining or disrupting functioning ecosystems. It merely illustrates the trophic linkages and other non-trophic interactions (seed dispersal) relevant to this study.

At times it can be difficult to separate species into functional groups. Possums and rats are known to impact on a similar range of species, including invertebrates, reptiles, birds, seeds, fruits and vegetation (refer Chapters 2 and 7). Thus they could be classified in to one omnivorous functional group that has impacts on both canopy and terrestrial species. However, the impact of possums appears to be much greater than that of rodents, in that only possums have been implicated in forest canopy collapse (Rogers and Leathwick 1997), complete defoliation of trees (Payton *et al.* 1997b) and disappearance of large invertebrate species such as *Powelliphanta* snails (Veltman 2000). Thus the separation of possums from rats is based on the degree of damage more than differences in functional groups impacted.

The diagonal black arrows in Figure 8.2 indicate which species (or functional groups) are known to consume foliage, flowers and leaves of large-fruited and/or small-fruited species. Some species can consume all of the vegetation components. For instance, kereru eat large and small fruits and are known to eat foliage and flowers (McEwen 1978, M. Clout unpublished data). Possums prefer eating fruits and flowers but also eat prodigious quantities of foliage (Allen *et al.* 1997; Cowan 1998; Mason 1958; Nugent *et al.* 2000). Including more detailed dietary preferences in this generalised food web would result in excessive clutter and make the food webs hard to interpret.

Furthermore, some species are more preferred than other species. For instance kereru prefer taraire fruit to supplejack fruits (Chapter 6), and possums prefer kohekohe leaves to pigeonwood leaves (Payton *et al.* 1999). It would also be useful to be able to quantify the degree to which a species (or functional group) impacts on the vegetation. Kereru can defoliate trees (e.g. kowhai *Sophora* spp.) but generally do not cause their death, whereas possums are known to kill trees (e.g. tree rata, kohekohe or kamahi) by defoliation. This more detailed information is probably best presented as summaries or in tabulated form. It will not be easy to illustrate all those aspects using a single food web. However, a food web is a useful tool for managers to identify which species are likely to have greatest impacts or current gaps in information.

For example, the horizontal and vertical grey lines in Figure 8.2 illustrate which species (or functional groups) are preyed on by other species (or functional groups). By simply counting the arrows that end at a particular species it is possible to gain some understanding of how a particular species might be affecting the ecosystem. Possums prey on, or impact on, eight other functional groups, as well as all aspects of the vegetation. Rats have an effect on vegetation and one less animal functional group, whereas the top predators (cats and mustelids) prey on nine other functional groups but do not impact directly on vegetation processes. Combining these trophic interactions from the food web with information on the degree of impact from the literature should allow predictions to be made regarding the possible impacts that a species (or functional group) is having within a habitat.

Such an approach would also identify those species that are thought to be having an impact, but for which little current information is available. Hedgehogs (*Erinaceus europaeus occidentalis*) were thought to be rural and urban species, they were known from forested habitats (Brockie 1990) but little information existed on their impacts within native forests. Recent studies (Berry 1999; Hendra 1999; King *et al.* 1996b) have shown that some hedgehogs reside solely in forests, consume significant numbers of invertebrates and lizards, and may impact on ground-nesting birds such as kiwi by preying on eggs and by utilising the same food-sources or nesting sites (Moss and Sanders 2001). Hedgehogs are now recognised as potentially serious threats to invertebrates, lizards and ground-nesting birds, but further study is required to quantify the impacts on native fauna and the level of hedgehog reduction required to produce a positive outcome for native fauna (Moss and Sanders 2001). Inclusion of hedgehogs within food webs may allow the identification and remediation of potentially adverse outcomes within a habitat.

Construction of food webs will also allow some prediction of the likely perturbations when one (or several) species is removed from the habitat. Possum suppression alone was not sufficient to reduce the incidence of predation on kereru nests because other introduced predators (feral cats, stoats, rats, or kookaburra) and native predators (falcon and harrier) were still preying of eggs and chicks (Lovegrove 1996a; Wotherspoon 1994). Reduction of both possum and rodent numbers reduced kereru nest predation in some years (Clout *et al.* 1995a) but there were still several predation events, possibly by other predators, which impacted on kereru recruitment (Lovegrove 1996a) and mouse numbers also increased (Clout *et al.* 1995a). Managers can be surprised when suppression of a pest does not result in a desired outcome, or sometimes even worsens a situation, because the impact of other (pest) species increases.

Conservation managers are often interested in the impacts of management actions on particular species or functional groups. However, at times they might find it difficult to construct a food web for the habitat of interest because little information is available. Moreover, in most cases, resources also preclude monitoring the effect of the management regime on all species or functional groups. In terms of practical management and realistic research goals it is often more useful to focus on one or a few interactions and quantify those.

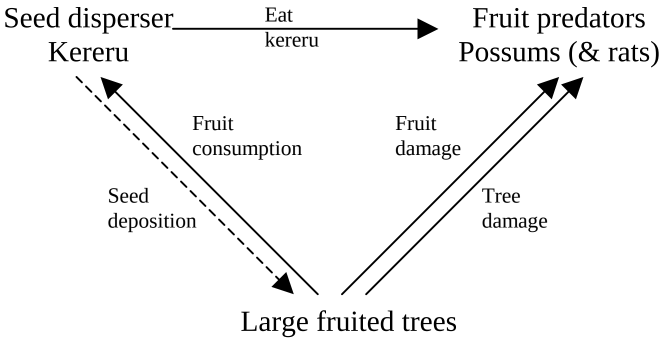
There is sufficient empirical evidence, as well as deductive logic, to support the idea that the dynamics of a particular population in a defined ecosystem are determined by a limited number of interactions. Furthermore, these interactions can be explored using simple models and simple experimental manipulations which tend to have greater predictive capabilities (Berryman 1993). Berryman (1993) proposed the idea that in a particular habitat one species is having the greatest impact on the parameter of interest (e.g. productivity of large-fruited species). If this dominant species is removed the next most ‘important’ species will take control of the parameter. As more and more of these key species are removed other control mechanisms are revealed (Berryman 1993; Navarrete and Menge 1996). An example of this is discovering, after possum suppression, that rodents are also impacting on breeding success of kereru (Clout 1995a).

These nested control mechanisms essentially mean that good predictions and management decisions can be made without knowing all the details of the food web in which the species of interest are embedded (Berryman 1993), provided that only one perturbation is applied (e.g. removal of a predator) and the consequences closely monitored and documented quantitatively. This was essentially the approach in this study, with pest suppression at some sites while paired sites had no pest control. A simplified interaction model for the key species is discussed in the next section.

8.2.5 Implications for management of the large-fruited species-frugivore system

This study examined the implications of fruit production by large-fruited species for seed dispersers and predators, and the utilization of these large-fruits by seed-dispersers and seed-predators. The species investigated, large-fruited trees, kereru, possum and rodents, are part of the food web explored in Figure 8.2, but the interactions between these species can be expressed much more succinctly (Figure 8.3).

Figure 8.3 Interaction web for large-fruited species and frugivores



Large-fruited trees produce fruits that can be consumed by a number of species, the most important of which are kereru and possums. Kereru are seed dispersers and enhance future regeneration of large-fruited trees. Possums are seed predators and may therefore reduce future regeneration of some tree species. Possums also impact on the continued survival of some species (e.g. kohekohe) by killing mature individuals. Rats are also detrimental to fruit production, albeit to a lesser degree than possums, and probably also reduce seedling survival.

Possums affect kereru survival directly, by preying on eggs and nestlings, and indirectly, by reducing food availability, which may reduce kereru fecundity. Rats also impact on kereru directly, by preying on eggs and nestlings, and indirectly, to a lesser extent, by predating some fruits. Kereru appear not to have any impacts on the survival of possums or rats.

Thus far, the greatest potential impact on the interactions depicted in Figure 8.3 would be the removal or addition of possums to the system. However, there is a potentially larger perturbation for this system and that is the removal of the large-fruited trees. This could cause the extinction of kereru, since they rely on large quantities of high-energy fruits to reach breeding condition and to rear chicks (this study and Powlesland *et al.* 1997). Absence of the tree species would also cause a reduction in possum and rodent numbers. Physically removing large-fruited trees to test this theory, while monitoring the population dynamics and breeding success of all three species, is not good conservation management. However, it may be possible to estimate the impacts of large-fruited tree removal by modelling the distribution of kereru, possums and rodents against the New Zealand distribution of large-fruited tree species (Figure 8.1).

Kereru are currently most common in northern and lowland forests of New Zealand (Clout *et al.* 1995a; Heather and Robertson 1996). These are also the forests that have the greatest range of large-fruited trees or podocarps. Forests further south or at higher altitudes lack many large-fruited species

(Figure 8.1) and can have seasonal gaps in fruit availability (Clout 1990). The predictions for kereru would be that population density and breeding success (including repeated clutching) would;

- decrease at more southerly latitude since there are fewer large-fruited species
- decrease at higher altitudes since large-fruited species tend to be lowland species
- decrease in forests with greater proportions of beech (*Nothofagus*) trees since there would be fewer large-fruited species in those forests.

Some of these effects could be offset by the presence of smaller-fruited podocarp species (e.g. rimu *Dacrydium cupressinum*, kahikatea *Dacrycarpus dacrydioides*, matai *Prumnopitys taxifolia*) or the larger-fruited miro, *Prumnopitys ferruginea*, at more southerly latitudes and higher altitudes. However, unless fruit is available throughout the year kereru breeding is likely to be reduced. Both kahikatea and rimu produce large crops irregularly, which would not maintain kereru in breeding condition every year. The competitive displacement theory examined in Chapter 5 would hold that large-fruited species at southerly latitudes have extended fruiting seasons, compared to more northerly latitudes, since there is less competition amongst the large-fruited species for the ‘key’ disperser. Such a result would in itself be interesting.

Possums are more abundant in mixed hardwood forests (which generally contain greater numbers of large-fruited species) than in beech or plantation pine forests (Cowan 1998). When more fruits are available, e.g. after possum suppression, Chapter 7), or a large hinau (*Elaeocarpus dentatus*) crops (Nugent *et al.* 2000) then possums are usually in better condition, have greater birth rates and improved survival of young (Cowan 1998, 2000; Green and Coleman 1984). Possums are known to prefer fruits, flowers and high protein foods to foliage (Nugent *et al.* 2000). Furthermore, possum populations are known to reduce sharply after an irruptive phase, which usually also involves loss of possum-preferred species (often fruiting species) from the forest (Brockie 1992; Campbell 1990; Nugent *et al.* 2000; Thomas *et al.* 1993). The predictions made for possum densities and breeding rates throughout the country are therefore similar to those expressed for the kereru above.

It will be more difficult to model rat abundance and reproductive rates against distribution of large-fruited trees since the interaction between large fruits and rats is weaker and probably involves fewer species (Chapter 7). Rats are more predatory than they are frugivorous (Innes 2001; Innes 1998) weakening the link between large-fruited species distribution and rat density and breeding success. Furthermore, rat populations fluctuate considerably, more so than possum and kereru populations, making it more difficult to detect any trends.

The distribution of large-fruited species is relevant for pest management since there is a potential for higher densities of mammalian pests where species with large fruits are abundant. More frequent or consistent pest suppression may be necessary in forests with abundant large-fruited species to maintain possum numbers below a certain residual trap catch, maintain the health of forest canopies, or increase the breeding success of kereru or kokako. In northern North Island forests there may be no season when pest species such as possums and rats are food-limited (Chapter 5, 6 and 7) and more likely to eat baits, making pest control more difficult. Other factors such as temperature (Veltman and Pinder 2001) might be more important in achieving pest control success. However, seasonal food-limitation might be more important in more southerly latitudes.

There are also management implications for kereru. Kereru need to be in good condition if they are to breed successfully (Clout *et al.* 1991; Clout *et al.* 1995b; Powlesland *et al.* 1997) and they breed more frequently when copious food is available (Clout 1990). Depending on the management outcomes required, it might be cost effective to suspend suppression of possums and rodents in years where fruit production is predicted to be very low. Kereru are less likely to breed in such years, thus providing less opportunity for possums, rats and other predators to prey on nests. However, it could be crucially important to ensure maximum fruit availability in years where large-fruit production is predicted to be higher. Pest control during years when fruit supplies are marginal for breeding might make the difference between sufficient fruit availability, and therefore successful breeding, or insufficient food resulting in lack of breeding or abandonment of nests.

Low intensity possum control (such as at Remiger's Bush) could boost the breeding condition of kereru by increasing fruit abundance. However, the rate of nest predation could also be quite high and might not result in a net gain to the kereru population. This kind of situation may lend itself to intermittent intensive pest control in years with predicted abundant fruit production, resulting in sufficiently large pulses of juveniles recruited into the kereru population to ensure its continued survival.

The problem with these proposed management options are that there currently are no models to predict which species will fruit abundantly or fail to fruit in any given year. Considerably more work needs to be undertaken to establish the causal links between climate and environmental conditions and the rates and timing of fruit production.

In the interim, the best strategy to ensure the survival and reproductive success of kereru, in the absence of hunting by man, could be to have intensively managed (excellent pest control) substantial pockets of forest that act as 'food baskets' for the surrounding landscape. Wenderholm Regional Park and Remiger's Bush certainly seem to act in that capacity. Both sites were seen to attract large numbers of kereru from surrounding native and pine forests (Clout 1990, and A. Dunn pers. comm.). Small isolated sites such as Robertson's and Whitford Bush appear too small to maintain large numbers of kereru.

Maintaining substantial 'pest free' forest pockets would enable the local kereru to breed successfully without predation and perhaps produce several clutches throughout the year. Eventually the kereru population inside the 'pest suppression area' would exceed the carrying capacity of the forest and birds would spill over into adjacent areas. Kereru in adjoining forests would be maintained in breeding condition since they can feed occasionally in the 'pest suppressed area' and perhaps successfully raise some chicks.

8.3 Conclusions and further research opportunities

This study has demonstrated that the large-fruited/frugivore system in New Zealand is uniquely simple, with a sole frugivore, kereru, and a few fruiting species that rely on dispersal by kereru. These large-fruited species compete with each other for the services of the kereru through providing fruit in different non-overlapping seasons or providing fruit of different nutritional qualities. The timing of fruit production and the nutrient content of fruits results in some species of fruit being more attractive to frugivores. This results in these fruits being consumed more often by both seed dispersers (kereru) and seed predators (possums and rodents).

Such a simple system has great potential to further investigate indigenous fruit/frugivore interactions. Some research questions that warrant further investigation include:

- *What are the minimum nutritional requirements for successful breeding by kereru?* This could be partially answered by compiling and cross correlating studies that monitored both kereru breeding attempts and fruit phenology, or through a long-term study monitoring those aspects.
- *What is the kereru foraging strategy, are they faithful to a particular tree or species or do they search for food more opportunistically?* Radio-tracking and following individually marked birds should provide more data.
- *Do they select trees with fruits that are more nutritious than con-specific trees, and if so what are the mechanisms by which they choose such trees?* Observe kereru feeding behaviour and collect and analyse any fruits that were deliberately discarded. Also analyse fruit from trees in which they spend a great deal of time foraging and from trees in which they spend little time.
- *Do particular trees within a species always produce above (or below) average quality fruits or do they vary from one year to the next?* Analyse fruit from selected individuals for a number of years to ascertain if fruit quality varies greatly. If nutritional factors do not vary annually for individual trees (e.g. a particular tree tends to have above average fruits each year) then determine whether site soil factors contribute to variable nutritional levels within the species. If soil factors do not correlate with differing nutritional levels then there might be

a genetic component that determines nutritional values. This will need to be ascertained either through propagating seed from trees of known nutritional values or through genetic analysis.

Further study is also warranted on the phenology of the large-fruited trees, such as:

- *Does the fruiting period of a species change when it co-occurs with more or fewer large-fruited species?* Compile data on fruit phenology length and fruiting season from different latitudes and altitudes. Relate this to which species are present. Or it might be possible to conduct a simultaneous nation-wide study of phenology for selected species.
- *What are the environmental parameters that result in good fruit crops, and which environmental cues signal reduced fruit productivity?* Compare fruit phenologies from studies with climatic data, or conduct a long-term study that monitors fruit production and environmental conditions.
- *Do synchrony and overlap values improve during years with large fruit crops?* Computer modelling might be able to answer this question, but it probably will need further field data to confirm or deny the hypothesis.
- *Is there a predictable relationship between the number of trees fruiting in any given year and the total amount of fruit produced in that forest?* The answer to this question would greatly benefit managers of native forests as it might lead to some simple predictable indices that trigger additional management (e.g. supplementary feeding or initiation of pest control). Conduct phenological censuses within a number of habitats.

The introduction of mammalian frugivores has altered the fruit/frugivore system in New Zealand. Possums and rats consume and destroy copious quantities of fruit, of large- and smaller-fruited species, and especially prefer the lipid and nutrient rich fruit species. Predation of fruits has negative consequences for the survival and fecundity of kereru. Fruit predation can results in ‘gaps’ in the fruit availability that can reduce the condition and breeding success of kereru. These ‘gaps’ often occur during critical seasons for kereru, such as breeding or during winter. Possums and rodents target fruiting species that are most preferred and/or required by kereru, such as the lipid and/or calcium rich fruits (taraire, nikau, kohekohe). Possums and rodent also have a direct impact on kereru through predation of eggs and chicks, or through reduced breeding success due to nest disturbance by possums and rats.

Predation of fruits has long-term implications for the survival of the large-fruited tree species. Mammalian predation reduces the potential number of seedlings recruited into the population, since the embryos of the fruits are usually damaged and are often preferentially eaten by possums and rats. The reproductive potential of these large fruited species is also reduced because the seed-disperser (kereru) has fewer opportunities to consume fruits and deposit seeds in suitable sites. Some large-fruited tree species might produce sufficient numbers of fruits that a few seeds escape predation, ensuring the survival of a local population, but over time we could witness a contraction in range of large-fruited species due to lack of dispersal.

The interlinking of these aspects, and the reduced number of large-fruited species at southern latitudes and higher altitudes, has implications for managing both pest and kereru populations. At northern latitudes pest suppression through toxic bait application might have lower success than more southerly areas. Fruit is available virtually throughout the year at northern latitudes, which could result in possums and rats being less interested in novel food sources, such as baits, with consequent lower kill rates. This could make kereru and other threatened species populations in these forests more susceptible to collapse because it is more difficult to reduce possums and rat predation on fauna and fruits. In the absence of mammalian predators these forests should have a higher carrying capacity of native fauna than forests further south.

The full range of large-fruited species is generally not found at more southerly or higher altitude locations and might result in ‘windows’ of food shortage that can be utilised for delivering toxic baits. Thus poisoned bait application might be more effective and result in greater kill rates because novel foods are more readily accepted. This will in turn have implications for populations of kereru and other species that are vulnerable to predation by introduced mammals. It could be easier to reduce predation on kereru and kereru preferred fruits at these locations, but balanced against that is the reduced availability of large-fruited species, which, even without mammalian predation, will likely result in smaller kereru populations than at northern latitudes.

A further facet is that fruit production is variable between years, which results in variable reproductive success for kereru and mammalian predators. In good fruiting years kereru are likely to have increased breeding success, but could also experience increased predation from greater than usual pest mammal populations. During years of high fruit production it could prove beneficial to implement additional pest suppression to bolster kereru breeding success. In poor fruiting years kereru might not attempt to breed at all, and would not benefit greatly from pest suppression. Being able to predict unusually large or small fruiting events would therefore be very useful for the management of both kereru and pest species. More research is required to link environmental and climatic conditions with fruit timing and abundance so that native fauna and flora and introduced mammal predators can be managed most effectively.

This study has shown that the large-fruited/frugivore system in New Zealand is a relatively simple model with great potential for understanding fruit/frugivore interactions. It is highly important to further explore the relationships between large-fruited species, kereru and mammalian predators at different latitudes and altitudes and through years of low and high fruit production, as this will provide conservation benefits for a range of species and ensure the most effective management of these systems.

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