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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