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Effects of food supply and competition on the outcome of hihi (*Notiomystis cincta*) translocated to Mokoia Island

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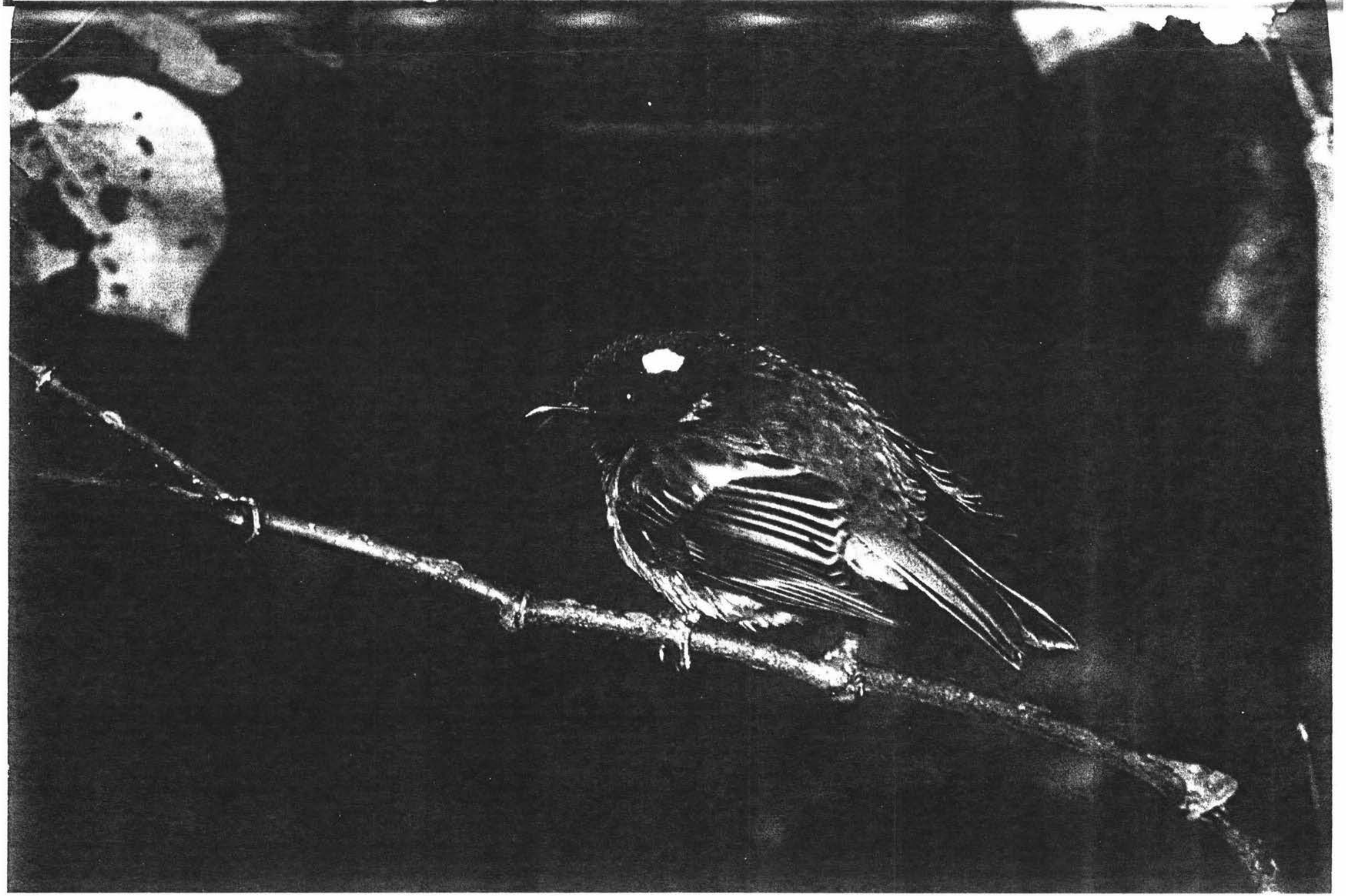

Plate:

Male hihi or stitchbird
(*Notiomystis cincta*)
Photo by Brent Stephenson

Abstract

The hihi or stitchbird (*Notiomystis cincta)* is a cavity-nesting honeyeater (family Meliphagidae) indigenous to New Zealand. Hihi were originally widespread but following European colonisation became confined to Little Barrier Island. Attempts to establish hihi on other islands appear to have been unsuccessful. The main reasons suggested for these failures are: (1) insufficient year round supply of nectar and fruit, (2) competition from the other more dominant honeyeaters (bellbirds *Anthornis melanura*, and tui *Prosthemadera novaeseelandiae*), and (3) lack of nesting cavities.

This study was conducted on Mokoia Island, situated in Lake Rotorua. 40 hihi were translocated to Mokoia in September 1994 from Little Barrier Island. Two field-trips, lasting three to four days, were made to the island every month from August 1994 through October 1995.

The primary aim of this study is to assess whether hihi suffer increased mortality, or lose weight due to seasonal shortages in their food supply, and therefore whether artificial food supplementation would be needed to sustain a population. The methods for testing this aim involved: (1) doing food supplementation experiments throughout the year (20% sugar solution), (2) measuring changes in bird's weights and mortality throughout the year, when supplementary food was available *vs* unavailable, (3) measuring nectar and fruit availability throughout the year as energy per unit area (e.g., kJ/ha), and (4) observing hihi to determine the amounts of time spent feeding on nectar, fruit, and invertebrates, and any interference from tui whilst feeding at those sources.

These data allowed me to identify periods when hihi were most limited by the naturally occurring nectar/fruit supply on Mokoia. This `limitation` is measured in terms of changes in birds body mass, survival, reproduction, and foraging effort in response to food supplementation. These data allow me to make recommendations concerning further supplementary feeding, and planting programs on Mokoia to make the habitat more suitable to hihi.

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Chapter 1
General introduction

Hihi and other nectar-feeding birds

There are 167 species of honeyeater (Meliphagidae), confined to Australia, the general Pacific region, and more recently New Guinea (Ford 1985). In Australia honeyeaters are the dominant bird family in most habitats, having about 72 different species (Ford 1985). In New Zealand the family is only represented by three species, the hihi (*Notiomystis cincta)*, tui (*Prosthemadera novaeseelandiae*) and bellbird (*Anthornis melanura*).

While the name 'honeyeater' comes from the floral nectar component of their diet, there is great dietary variation among species, some species being highly insectivorous (Pyke 1983). Other bird families also specialise on nectar. They are found in the Tropics and in all temperate regions apart from Europe: hummingbirds (Trochilidae) in North and South America and the West Indies; sunbirds (Nectariniidae) in South Africa, Middle East, eastern Australia and Asia; Hawaiian honeycreepers (Drepanididae), and sugarbirds (Promeropidae) in South Africa.

The hihi is slender and starling sized (30-40 grams). They are sexually dimorphic and have a variable mating system, including monogamy and various types of polygamy (Castro 1995). The male hihi is more colourful and on average weighs several grams more than the cryptic female (see Chapter 4). Both sexes bear a prominent white bar on each wing and have features typical of nectar and insect feeding birds (Rasch et al. 1996. DOC recovery plan).

Hihi feed on flowers, fruits and invertebrates in differing proportions from season to season (Gravatt 1970,1971; Angehr 1984a, 1985, 1986; Rasch 1985; Rasch & Craig 1988; Castro 1995). There is extensive overlap in the diets of the three New Zealand honeyeaters (Craig et al. 1981; Craig 1984; Angehr 1985, 1986; Rasch 1985). Rasch and Craig (1988) commented that flower use by honeyeaters is based on a relationship between net energy returns of the resources and the interspecific status of the birds.

Proportionally, hihi take more invertebrates than tui and bellbirds (Rasch & Craig 1988; Wilson 1997), and fruits (Wilson 1997). Tui and bellbirds have greater access to nectar sources (Angehr 1984a, 1985; Rasch 1985; Wilson 1997), and species providing the highest energy returns (Rasch 1985; Angehr 1984a). Disregarding bellbirds, this translates into two basic 'facts': (1) tui are more likely to chase hihi than *vice versa*, and (2) hihi are more likely to fed on low-grade nectar sources compared to tui. The reasons why a bird selects one type of flower over another is easily demonstrated and understood. However, its not so easy to determine whether aggressive encounters between hihi and tui regulates the type of flowers hihi visit, or the proportion of invertebrates they consume. This is because to determine this one would have to either study hihi in the absence of tui, or exclude tui from food sources while allowing hihi access.

The hihi from New Zealand and the O'o (*Moho spp.)* of Hawaii are the only honeyeaters to build their nests in tree cavities. As in New Zealand, the native lowland forest in Hawaii has been almost completely cleared and its avifauna devastated by introduced predators (the avifauna has evolved in isolation free from ground predators in both places (King 1984). Among bird species, cavity nesters and ground nesters have been the most strongly affected by introduced predators (Nice 1957; Lack 1968). Since European colonisation the hihi and O'o have both suffered dramatic declines. Hihi became confined to a small offshore island (Little Barrier Island), and two of the four O'o species became extinct the other two are extremely rare.

In pre-European times (prior to the 1800s) hihi were found throughout the North Island of New Zealand, Great and Little Barrier Islands and Kapiti Island (Oliver 1955). Like the huia, the hihi may never have reached the South. In contrast, tui and bellbirds were widespread, and found on all the main islands. Hihi were rare in the north of the North Island by 1873, but were still relatively common in the south (Buller 1888). About this time hihi seem to have vanished from Great Barrier and Kapiti Island, and there were varied population estimates for Little Barrier Island (Oliver 1955). By the 1880s hihi were found only on Little Barrier Island (Buller 1888).

Over 90 exotic bird species were introduced into New Zealand between 1860 and 1880 (King 1984). Angehr (1985) has suggested the new arrivals bought a new avian disease with them, decimating native birdlife. This implies the hihi population restricted to Little Barrier Island may have been saved by its isolation, or because of some immunity to the disease. The contraction of the hihi's range was probably caused by a combination of factors such as loss of habitat, the introduction of competitors and predators, and maybe even enthusiastic museum collectors (Fulton 1908). Atkinson (1973) suggested that the only reason hihi didn't finally go extinct on Little Barrier was because the ship rat (*Rattus rattus*) never reached the island.

Hihi recovery efforts to date

As mentioned above, hihi were confined to the Hauraki Gulf's Little Barrier Island (3076ha) by the 1880s. This is still a risky position for the hihi, as chance events such as storms, volcanic eruptions and disease could possibly wipe out such a confined population.

Since 1980 there have been 12 translocations of hihi from Little Barrier Island to other islands (Fig 1.1). There were translocations to Hen Island in 1980 and 1981, Cuvier Island in 1982 and 1985, and Kapiti Island in 1983, 1984, 1990, 1991 and 1992. The most recent have been to Mokoia Island in 1994 and Tiritiri Matangi in 1995 and 1996. While there is a small captive population at the National Wildlife Centre (Mt. Bruce) the number of birds is too small to be self-sustaining or to be considered insurance against loss in the wild.

The suitability of islands for hihi has been tentatively assessed by comparing features such as the likely impact of predators, seasonal availability of fruiting and flowering species, and the overall habitat quality with Little Barrier Island (Angehr 1984a). Mokoia differs from the other islands where translocations have been attempted in most of these respects (Table 1.1). It is the smallest (but does not have the smallest forested area), has no bellbirds, and no birds larger than the tui as fruit or flower competitors. Kereru visit Mokoia infrequently but are not resident. Mokoia and Tiri are the only islands that were free of rats at the time the hihi were delivered.

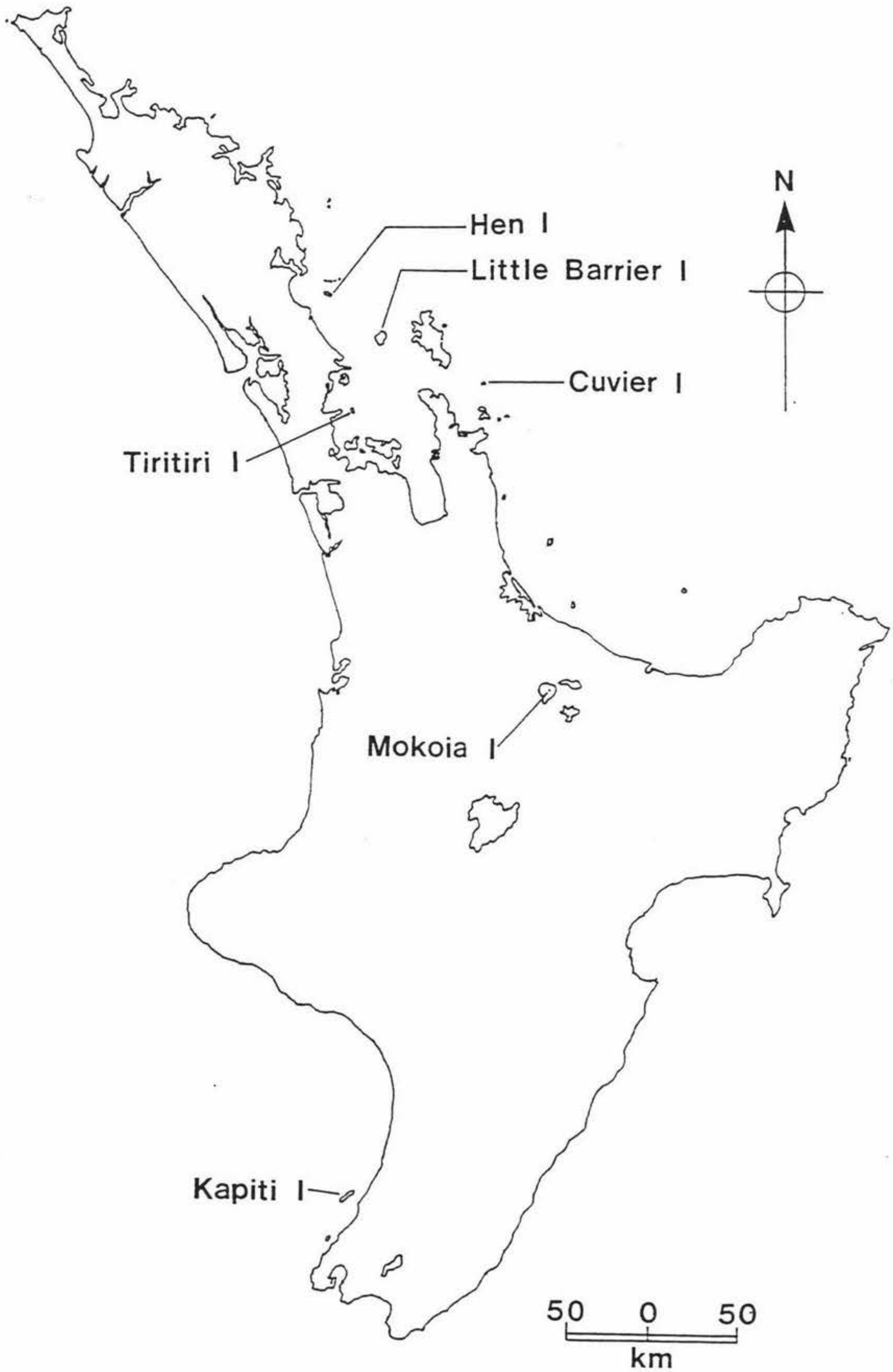

Fig 1.1. Map of the North Island of New Zealand showing the location of the islands (Hen, Cuvier, Kapiti, Mokoia, and Tiritiri Matangi) to which hihi have been transfered from Little Barrier Island since 1980.

Island	Total area (ha)	Forest area (ha)	Source	Height (m)	Minimun number of spp. in fl/fr in any month	Forest age (years)	predators	Food competitors
L B Island	3076			720	15	mature	3	6
Kapiti	1968	740	Angehr 1985	580	9	80-100.	5	5
Cuvier	181	87	Angehr 1985		8	40-60	1	2
Hen	718	320	Angehr 1985	244	12		1	3
Tiritiri	222	20		80		40 (remnant)	2	4
Mokoia	135	130		156	7	40-50	3	2

Table 1.1. General features of all islands hihi have been translocated to since 1980, in chronological order. Predators include weka, harrier, ruru, Polynesian rat and the Norwegian rat. Although Cuvier and Hen islands receive one predator each, there were three at the time of translocation. Food competitors include tui, bellbird, saddleback, kakariki, kaka, and kokako.

Hen Island is free of European rats, but has kiore (*Rattus exulans)*, bellbirds and tui. A total of 46 hihi were released on Hen Island from two translocations. In 1983 the population was estimated at between 100 to 200 hihi, from a base sample of 21 birds (Angehr 1984b). A bird count in 1994 found two hihi left.

Cuvier Island also had kiore when hihi were translocated (the kiore were eradicated in 1993). It also has bellbirds but no tui. A total of 66 hihi were released on Cuvier between 1982 and 1985. By 1984 the hihi population was estimated at 20 individuals from an original population of 29 (Veitch 1983). A further 37 hihi were added in 1985, but a search in 1987 only found 1 female and 18 males, and they were mainly survivors from the second transfer. Only 6 males were sighted in 1989, and none at all were found in 1991 (Rasch, DOC recovery plan 1991).

Kapiti Island has Norway rats *(Rattus norvegicus)*, Polynesian rats *(Rattus exulans)*, bellbirds and tui (although the rats may have been eradicated in poison drops done in September-October 1996). Kapiti also has large areas of mature forest. Over seven years a total of 167 hihi were transferred to Kapiti. Their population is now estimated to be about 50 to 60 individuals. Reproductive success appeared to be good for all translocations (Lovegrove 1986; Castro 1995), however the mortality rate still exceeded the recruitment of juveniles, and the population has continued to declined.

Mokoia, Cuvier and Tiritiri Matangi (Tiri) are the smallest islands to receive hihi (Table 1.1). Tiri is the biggest of the three islands, but has only about 20 ha of forest, and has bellbirds as well as tui. Mokoia and Tiri make an interesting comparison because Tiri has successfully undergone extensive replanting of native trees and shrubs (Mitchell 1995; Cashmore 1995). Mokoia on the other hand had a lot of plantings in the 1960s, but with little effect on the present vegetation. However, Mokoia has been regenerating for about 40-50 years, and is more mature than most of Tiri. The Australian Crested wattle tree (*Albizia lophanta)* dominates a 5 ha valley on Tiri. There are several isolated individuals and small patches of *Albizia* on Mokoia, but they are not abundant.

The reasons previous hihi translocations failed are not yet clear, but Angehr (1984a,b), Lovegrove (1986), Rasch (1991), and Castro (1995) all suggested nectar availability. There is very little information on the hihi translocations to Hen and Cuvier islands. Castro (1995) attempted to find the reasons for the failures by studying Kapiti hihi. Other than her work on translocation techniques (Castro et al. 1995), this was mainly general observational research, focusing on feeding and breeding. From her observations Castro (1995) suggested the hihi on Kapiti were limited by seasonal nectar/fruit availability and competition from other honeyeaters.

With this in mind I focused on the food supply as the key habitat factor on Mokoia. Tui are abundant all year-round on Mokoia, which suggests that food is plentiful. The Mokoia habitat is predominantly secondary scrub and has few natural cavities. On Kapiti Island birds do not use Mokoia-type habitat, possibly because these areas lack natural tree cavities. It is possible the provision of nestboxes on Mokoia may be allowing hihi to reside in an otherwise unsuitable habitat. In addition, habitat use does not equate with habitat requirements (Gray & Craig 1991). The fact that hihi don't use Mokoia-type habitat on Kapiti doesn't necessarily imply that it is less suitable. Tieke, or saddlebacks (*Philesturnus carunculatus*), are another cavity nester thought to specialise in old growth forests. However, they have done extremely well on Tiri and Mokoia with nestboxes provided (Craig 1994; Armstrong & Craig 1995).

Past studies have inferred that the behaviour and ecology of New Zealand honeyeaters can be related to the distribution and abundance of nectar, and that they are also limited by it (Angehr 1984a,b; Lovegrove 1986; Castro 1995). Limitation is meant in a reproductive or survival sense, i.e. hihi who obtained greater access to nectar would have higher reproductive and survival rates. This raises several basic questions: (1) What are the environmental parameters that influence the number of hihi a habitat can hold? i.e., do birds actually lose condition and/or starve to death when nectar/fruit is scarce? (2) if true does aggression from other honeyeaters influence the abundance of nectar and/or fruit available to hihi? and (3) in turn does this effect birds reproductive and mortality rates, or one more than the other?

If hihi in the wild are primarily limited by nectar/fruit availability, one might expected hihi to be sensitive to factors which contribute to nectar crunch periods. However, these factors may be unpredictable in nature, such as asynchronous flowering from year to year, or beyond their control such as island biogeographic factors. Nectar crunch periods may become more predictable or less extreme on large islands such as Little Barrier. Also, the predictability of nectar crunch periods may vary with succession as trees mature and species change. Therefore, these areas require further investigation before we can formulate underlying theory gauging island suitability for future hihi populations. Managing hihi populations on different islands provides the opportunity to investigate these issues, and the chance to try novel solutions to persistent problems (Craig 1994).

The dependency of honeyeaters upon nectar as an energy source has often been stressed by previous authors. I therefore aimed to determine whether hihi survival is limited by natural carbohydrate availability, and if so, by how much. In doing so, I also aim to contribute to the study of energy limitation in New Zealand honeyeaters, and more practical issues about managing hihi populations in the wild.

Food limitation in honeyeaters

Most species of Australian honeyeaters differ in their dependence on nectar and invertebrates (Recher & Abbott 1970; Ford & Paton 1977). However, they all feed on the same type of flowers in the same habitat (Recher 1971, 1977; Ford & Paton 1977; Paton & Ford 1977), which can result in strong inter-specific competition when nectar is in short supply (Ford 1979). New Zealand honeyeaters also show this overlap in the use of nectar resources, and like the Australian species show little specialisation with regard to their sources of food (Terborgh & Diamond 1970; Paton and Ford 1977; Ford and Paton 1977; Recher 1977).

As a general rule New Zealand honeyeaters eat more fruits than their Australian counterparts (Craig et al. 1981; Craig 1985). A likely explanation is the differing abundance of fruit and flower species between Australia and New Zealand. Australia has far more ornithophilous flowering families and species than New Zealand (Craig et al. 1981). The 50 fruiting and 30 flowering families described by Godley (1979) as being ornithophilous flowers are not abundant and are skewed in their distribution (Godley 1979), being found predominantly in the lowland areas of the North Island (Allan 1961).

`Ornithophilous` species have large, showy flowers, and with lots of nectar. However birds may use flowers that are not considered `ornithophilous`. Many of New Zealand species used by honeyeaters, especially hihi, have small flowers with small amounts of nectar (Castro 1995). Many condense their flowers into inflorescences. In doing so the tiny flowers collectively become a more rewarding prospect as the inflorescence can be presented as a single floral unit. Hihi are commonly observed licking flowers such as five-finger (at more than one flower per second). Many other New Zealand flowering species also condense their flowers to some degree for example cabbage trees, kohekohe, and pohutukawa (see Table 2.1 for scientific names of plants used by hihi).

Energy acquisition has always played a prominent role in theories concerning breeding systems and territorial behaviour. Nectar feeding birds make good candidates for studies concerning energy acquisition. Unlike most animals, the diet of nectar-feeding birds can be split into energy and protein components, which can then be treated independently (Ford and Paton 1977). Honeyeaters may obtain practically all their energy requirements from nectar (Pyke 1980), whereas arthropods are considered their primary source of protein (Baker and Baker 1975, Baker 1977; Paton 1982). Paton (1982) argued that the Australian New Holland honeyeater's *(Phylidonyris novaehollandiae)* dependence on nectar and other carbohydrate sources depends on the size of the insects taken and the amount of energy they can extract from them. Small insects are of comparably low energetic value, especially those hawked by honeyeaters (Paton 1982).

Ford and Paton (1976) estimated that New Holland honeyeaters have a net energy loss when hawking insects, but achieve a net energetic gain when feeding on nectar. In contrast, large insects like cicadas may serve a dual purpose, as a protein and energy source comparable to some nectar sources visited by hihi. However, its likely this would depend on foraging costs i.e., hihi would probably get a net energy gain from small insects when gleaning.

Over the last 20 years a lot of research on honeyeaters has been undertaken in Australia, most dealing with the relation of their abundance and behaviour to the availability of carbohydrate food sources. The carbohydrate sources are almost always flower sources. Fruits are mentioned, but only rarely are the energetic values of fruits considered. This probably reflects the minor involvement that fruit species have in the Australian honeyeater systems.

The protein requirements of many Australian honeyeaters have been calculated under laboratory conditions, and some seem to be particularly low. Paton (1982) in a study of New Holland honeyeaters (*Phyidonyris novaehollandiae*) showed that non-breeding birds collected their daily protein requirements in about 10 minutes of insect feeding, but can spend up to 90% of the day collecting nectar to meet their energy requirements. New Holland honeyeaters were observed collecting an average of 92 kJ of nectar and 31 mg of protein per day. These both meet their calculated daily energy (75 kJ) and protein requirements (20 mg). Paton (1982) found breeding birds collected more nectar and insects than non-breeding birds, but in proportion to their increased demand for energy and protein during the breeding period. Recher (1977) reported that honeyeaters increased the insect component in their diet when nectar sources were abundant. Although these data may be unreliable, it is interesting that honeyeaters may increase the insect component in their diet when nectar sources are both superabundant (Recher 1977) and scarce (Paton 1982).

As energy sources, nectar and fruit are easily manipulated and quantified in comparison to most foods. By manipulating carbohydrate availability (i.e., periodically supplementing their diet) and quantifying the honeyeater's response in reproductive and/or survival terms one can test directly whether honeyeaters are limited by energy availability (Armstrong and Pyke 1991).

There have been many experimental studies looking at behavioural responses to energy availability, mostly in hummingbirds, (e.g., Ewald & Carpenter 1978; Ewald & Orians 1983; Ewald & Bransfield 1987). Hummingbirds become more insectivorous when they are sedentary and when nectar is scarce (Pitelka 1942; Young 1971), or when they are breeding (Gass and Montgomerie 1981). However, there have been no experiments testing directly whether the condition, and/or survival and reproduction of nectar-feeding birds is limited by energy availability, except for Armstrong and Pyke (1991). There seems to be general agreement in the literature that they are, but the majority of these studies have tested the idea indirectly, comparing either changes in bird abundance and nectar availability, and/or by quantitatively comparing a bird's energy requirements with energy production by flowers.

There are several reasons why correlation studies may be misleading. Correlations between bird abundance and nectar availability may occur for no other reason than birds moving into locations where they can obtain energy most quickly. This does not necessarily mean the honeyeaters are dependent on this source or that nectar availability influences their survival or reproduction. The only clear evidence that nectar-feeding birds are limited by energy will come from observations of the survival and reproduction rates of birds responding to experimental energy supplementation.

Plan of this thesis

The primary aim of this study is to determine whether hihi are limited by carbohydrate food, and to what degree competition from tui influences this. All data were collected in the first 15 months after hihi were released on Mokoia, from September 1994 to October 1995. Energy limitation is tested experimentally by recording changes in hihi behaviour and condition (weight) when they are 'fed' (*ad libitum* supplementary food) vs 'unfed (natural foods only). This information tells us whether or not hihi are energy limited, but does not explain why. This information comes from: (1) observing hihi when they are 'fed' vs 'unfed', noting their behaviour and interactions with tui, and (2) measuring energy availability of naturally occurring energy sources and the energy acquisition rates hihi obtain from them.

My results are reported in Chapters 2 through 5. Chapter 2 describes the abundance and distribution of plant species likely to be taken by hihi, and the fruit and/or flowering phenologies of those species on Mokoia. Chapter 3 describes temporal changes in energy availability (kJ/ha) from nectar and fruit, describes changes in amounts of time hihi spend foraging, and describes hihi interactions with tui at feeding sites. Chapter 4 describes experiments testing whether food is limiting hihi survival on Mokoia, and whether feeders affected the amount of time hihi spent foraging on natural carbohydrate sources. Chapter 5 is concerned with management recommendations to make Mokoia more suitable to hihi.

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Chapter 2

The composition and phenologies of hihi food-plant species on Mokoia Island

Introduction

Mokoia island is situated in Lake Rotorua, in the North Island. With an area of 135ha, it is the largest inland island in New Zealand. The shortest distance from the mainland is about 2.1 km. Mokoia has a long history of human occupation, with several Maori tribes occupying the island for various periods over hundreds of years. The island's name comes from the battle which led to the Te Arawa ownership of the island.

Most of the island's original forest has been succeeded by secondary forest after clearing and terracing (Wallace 1993). For hundreds of years crops grew well in the fertile soil along the narrow flat on the eastern side of the island (Andrews 1992). Formerly grassland, this flat has now been mostly covered by blackberry (*Rubus fruticosus*). Over its human history, many native plant species such as karaka, whau, totara, puriri, kowhai and southern beech have been deliberately introduced. Exotic tree species like pine, poplar and a variety of fruit trees were introduced by European missionaries. Europeans arrived on Mokoia not long after the 1823 Nga-Puhi invasion led by Hongi Hika. By 1840 Norway rats were reportedly abundant on Mokoia (King 1984). Cattle, goats, sheep, horses, pigs, and cats were also later introduced. The horses, cattle and goats were first released onto the fenced off flat area, but were eventually allowed to roam feral over the island. The goats were introduced in 1985 to control the blackberry, and by 1989 the understory was open with no further regeneration of canopy species taking place. This encouraged the blackberry. In 1989-90 the Department Of Conservation (DOC) successfully eradicated rats and goats from Mokoia. There are no reports of possums or mustelids ever being present on Mokoia.

In the 1950s weka were translocated to Mokoia, and from 1952 to 1956 pheasants were farmed as a commercial venture which probably led to the high rat and mice densities reported in the 1960s (Beveridge and Daniel 1965). The first restoration attempts, in the mid 1960s, involved planting thousands of native tree and fern saplings, most of which were probably destroyed by the already abundant rat population. These plantings seem to have had negligible effect on the present vegetation (Wallace 1993).

Since the rats and goats were eradicated, toutouwai (North Island robin, *Petroica australis*), tieke (saddleback) and hihi have also been translocated to Mokoia. Skinks, first thought to be absent from the island, have recently been discovered. A mouse eradication was attempted in September 1996, which should have left Mokoia mammal free, unfortunately this was unsuccessful. The island's vegetation is now composed largely of understory species such as five-finger, kawakawa, mahoe and rangiora. The canopy species are largest in gullies and bush edges, where mahoe, kohuhu and treefern dominate. On the south facing-slopes mamaku is the dominant canopy species. Amongst the fragments of bracken and scant blackberry on the north-facing slopes the dominant species are cabbage tree and five-finger (for scientific names see Table 2.1). Tui are the only other honeyeater species on Mokoia and are found at high densities, especially during the breeding season.

This chapter reports the results of intensive vegetation sampling conducted on Mokoia over the duration of this study (from September 1994 through October 1995). With respect to species fruit and/or flower phenologies, these data describe the abundance and distribution of plants likely to be used by hihi on Mokoia. I address the following questions: (1) how many known hihi food-plant species are on Mokoia?, (2) how does the availability of these food-plant species vary with time?, (3) how are the food-plant species distributed over the island?, (4) are there periods when food sources are scarce or confined?, and (5) how do these data relate to long-term predictions regarding natural food availability on Mokoia. This information allows for recommendations to be made concerning further planting attempts to make the island more suitable to the resident hihi population.

Methods

Vegetation Surveys

The island was divided into 28 grid squares, each 200 X 200m, using a compass and measuring tape. The 28 central grid points were measured and marked with flagging tape (Fig 2.1). Some grids were partially in the lake. If the central point was in the lake the flagging tape was placed on the nearest point on the shoreline. Each month I selected a random sample point within each grid. The sample point in each grid was determined by measuring a specific distance from the central grid point at a specific compass bearing. If the random point was in the lake, I disregarded that sample. Therefore, there was no bias for or against lake-edge habitat.

Once the sample point was established, a sample area of 3 m radius was measured out using measuring tape and a telescopic pointer. During this study 157 grid points were made, each 28.3 m squared in area, giving a total sampled area of 4443 m^2. In each sample area I counted the number of individuals per plant species likely to be used by hihi. The target list initially included all species found on Mokoia that were known to be used by hihi, or other nectar-feeding birds in other locations. When I saw hihi using other species, I added them to the list and incorporated them in the sampling design (Table 2.1, for a complete plant list see Beadle & Ecroyed 1990).

If a tree trunk fell within the sample area but the canopy of that tree fell outside it was still counted. A tree rooted outside the sample area was not counted. A ramet was adopted to define one individual plant i.e., I counted the number of trunks not joined above the ground. I only counted trees large enough to be flowering. For most trees this was about 2 m.

I recorded approximate height and canopy width of each individual plant. These data were used to calculate surface area, and to compare plant dimensions between different localities.

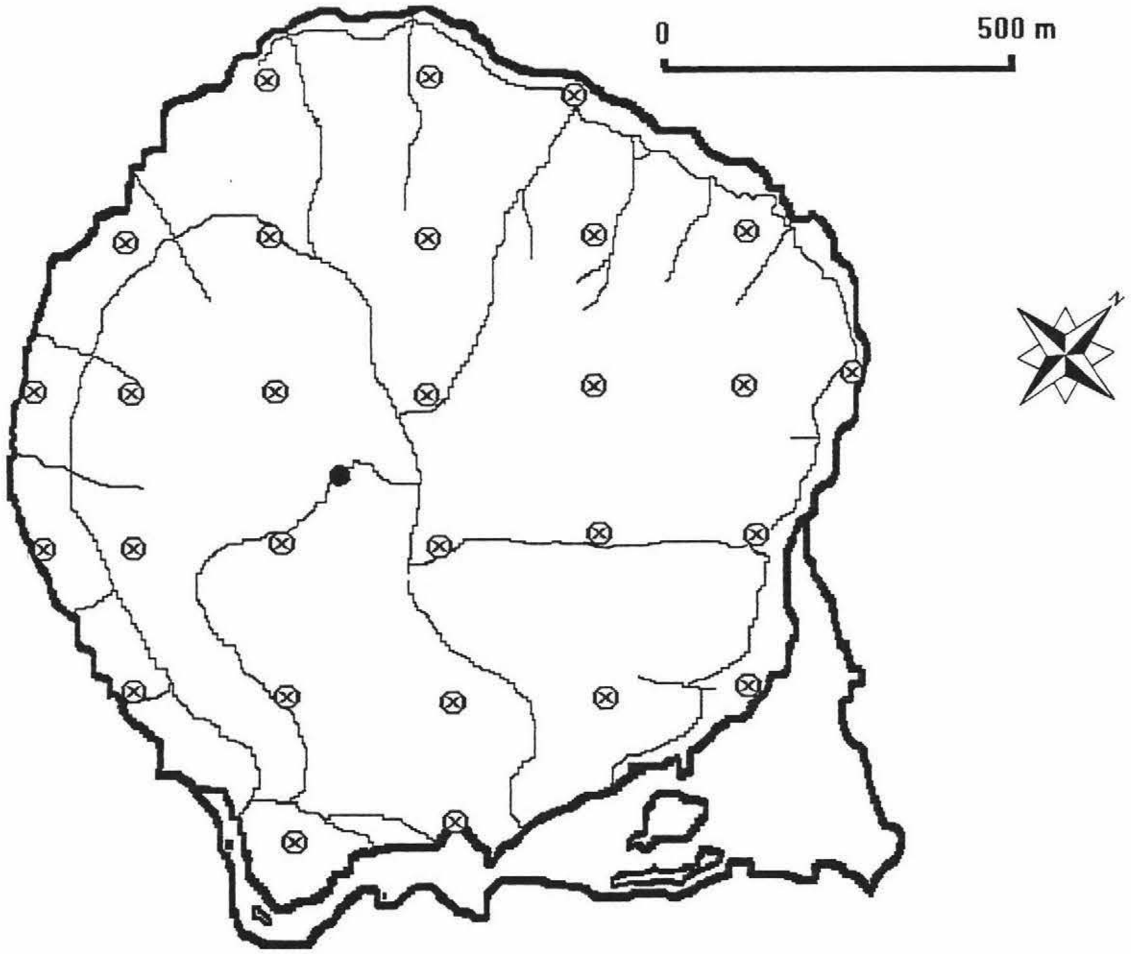


Fig. 2.1. Map of Mokoia Island showing the location of the 28 central grid points (⊗).

Sample area was classified into one of 5 topographical categories.

Habitat	**% of island**
1) Gully (bottom).	4
2) Slope	32
3) Ridge top	58
4) Within 5m of track.	2
5) Within 12m of shore.	4

This allows me to compare data on abundance, species composition and density between these habitats. This in turn allowed me to determine whether flower and fruit densities fluctuate between these habitats due to differences in the species diversity and abundance.

Measuring plant species fruit and/or flower phenologies

For each plant in the sample area, I estimated the number of fruits or flowers. Different estimation methods were used, depending on the species and situation. These were recorded for each species as long as the flower and/or fruit period lasted.

a) If the plant had less than about 300 flowers or fruits, then all flowers and/or fruits were counted.

b) If the plant had abundant flowers and/or fruits distributed around the periphery (of the canopy), a 16 cm X 16 cm sampling quadrat was used. All fruits or flowers were counted within one quadrat, and the surface area of the plant estimated from its height and width. To estimate the total number of fruit and/or flowers, I multiplied my count by the plant's surface area divided by the surface area of the quadrats sampled. Species in this category included *Muehlenbeckia* and white rata (see Table 2.1 for scientific names).

c) If fruits and flowers were not confined to the periphery, the plant was divided into branches of equivalent area, and five branches selected at random. The fruits or flowers were counted for each selected branch unit or estimated with the quadrat. The average per branch was calculated, and multiplied by the total number of branches. Species in this category included mahoe, *Coprosma spp*., and wineberry.

d) If the species had fruits or flowers in inflorescences (e.g., pohutukawa, five-finger and pate), the flowers or fruits from five randomly chosen inflorescences were counted. The number of flowers/fruits per inflorescence was then multiplied by the total inflorescence count to estimate the number of flowers/fruits on the plant.

Only open flowers were counted, and not buds. Old flowers not producing nectar were not counted, and were removed by shaking the branch. All fruits were recorded, ripe fruit being given as a proportion of the total count.

When possible, I recorded the sex of the all individuals counted for dioecious species such as mahoe, and five-finger. Sexing wasn't possible when plants didn't have flowers or fruit.

As mentioned the vegetation surveys were done monthly. On alternate fortnights I did additional flower/fruit counts, one per grid square. These data along with the counts conducted during the vegetation surveys were pooled monthly to calculate the average standing-crop of fruits and flowers per plant, for each species in the survey.

Results

Abundance of plant species used by hihi

In addition to the plant species on my initial target list, I added the following species after seeing hihi using them: kawakawa (fruits), deadly knightshade (fruits), and akeake (flowers). In total, I counted fruits from 13 species and flowers from 21 species (27 species in total). Of these, sub-canopy species such as mahoe, kawakawa, five-finger, pate, and *Coprosma spp.* are clearly the most abundant plants on Mokoia (Fig. 2.2). In most localities, normally sub-canopy tree species like mahoe make up the canopy.

Table 2.1. List of plant species known or likely to be used by hihi (From Godley 1979; Angehr 1984; Castro 1995). Those species found on Mokoia (●), and those used by hihi on Mokoia(◆) are highlighted .

(a) Nectar taken			Name used
Albizia lophantha	●	◆	*Albizia*
Alectryon excelsus			Titoki
Alseuosmia macrophylla			Toropapa
Aristotelia serrata	●	◆	wine berry
Astelia spp.	●		*Astelia*
Beilschmiedia tawa			Tawa
Carpodetus serratus			Putaputaweta
Chamaecytisus palmensis			
Clematis vitalba	●		*Clematis*
Clianthus spp.			Kakabeak
Cordyline australis	●	◆	Cabbage tree
Coriaria arborea	●		Tutu
Corynocarpus laevigatus	●	◆	Karaka
Cyathodes spp.			
Dodonaea vicosa	●	◆	Akeake
Dracophyllum spp.			
Dysoxylum spectabile	●	◆	kohekohe
Earina autumnalis	●	◆	*Earina*
Elaeocarpus dentatus			Hinau
Entelea arborescens	●		Whau
Fuchsia excorticata	●	◆	*Fuchsia*
Geniostoma rupestre	●	◆	Hangehange
Griselinea littoralis			Broadleaf
Hebe spp.	●		*Hebe*
Hedycarya arborea			Pigeonwood
Hoheria populnea			Lacebark
Knightia excelsa	●	◆	Rewarewa
Kunzea ericoides	●		Kanuka
Laurelia novaezelandiae			Pukatea
Melicytus ramiflorus	●	◆	Mahoe
Metrosideros excelsa	●	◆	Pohutukawa
Metrosideros fulgens			
Metrosideros perforata			
Metrosideros robusta	●		Northern rata
Metrosideros tetaranda	●		White rata
Metrosideros umbellata			Southern rata
Mida salicifolia			Maire

Myoporum laetum			Ngaio
Myrsine australis	●		Mapou
Myrsine salicina			Toro
Nestegis lanceolata			White maire
Pseudopanax arboreus	●	◆	five-finger
Passiflora tetranda			
Peraxilia spp.			*Peraxilia*
Personia toru			Toru
Phormium tenax	●	◆	Flax
Pittosporum crassifolium			Karo
Pittosporum eugenioides			Tarata
Pittosporum tenuifolium	●	◆	Kohuhu
Pittosporum umbellatum			Haekaro
Prumnopiys ferruginea			Miro
Pseudopanax crassifolius			Lancewood
Rhabdothamus solandri			Taurepo
Rhopalostylis sapida			Nikau
Ripogonum scandens	●		Supplejack
Rubus cissoides	●		Bushlawyer
Schefflera digitata	●	◆	Pate
Sophora spp.			Kowhai
Syzgium maire			Maire tawaki
Vitex lucens			Puriri
Weinmannia racemosa	●		Kamahi
Lupinus luteus	●		Tree lucern

(b) Fruits taken			**Name used**
Alseuosmia macrophylla			Toropapa
Aristotelia serrata	●	◆	Wine berry
Ascarina lucida			
Astelia spp.	●		*Astelia*
Coprosma dodonaeifolia			*Coprosma spp.*
Coprosma grandifolia	●	◆	*Coprosma spp.*
Coprosma lucida.			*Coprosma spp.*
Coprosma macrocarper			*Coprosma spp.*
Coprosma repens			*Coprosma spp.*
Coprosma rhamnoides			*Coprosma spp.*
Coprosma robusta	●	◆	*Coprosma spp.*
Coriaria arborea	●	◆	Tutu
Cyathodes fasciculata			
Cyathoes juniperina			
Freycinetia baueriana			

Fuchsia excoticata	●		*Fuchsia*
Gahnia setifolia			Sedge
Geniostoma rupestre	●	◆	Hangehange
Griselinea littoralis	●		Broadleaf
Ixerba brexiodes			
Macropiper excelsum	●	◆	Kawakawa
Melicytus ramiflorus	●	◆	Mahoe
Muehlenbeckia australis	●	◆	*Muehlenbeckia*
Myoporum laetum			Ngaio
Myrsine australis	●	◆	Mapou
Myrsine salicina			Toro
Nestegis lanceolata			
Passiflora tetranda			
Pennantia corymbosa			Kaikomako
Phytolacca octandra			
Pseudopanax arboreus	●	◆	Five-finger
Pseudopanax crassifolius			
Pseudopanax discolor			
Pseudopanax edgerleyi			Raukawa
Pseudopanax lessonii			
Pseudowintera axillaris			
Ripogonum scandens			
Rubus cissoides	●		Bushlawyer
Rubus fruticosus	●		Blackberry
Schefflera digitata	●	◆	Pate
	●	◆	Deadly knightshade

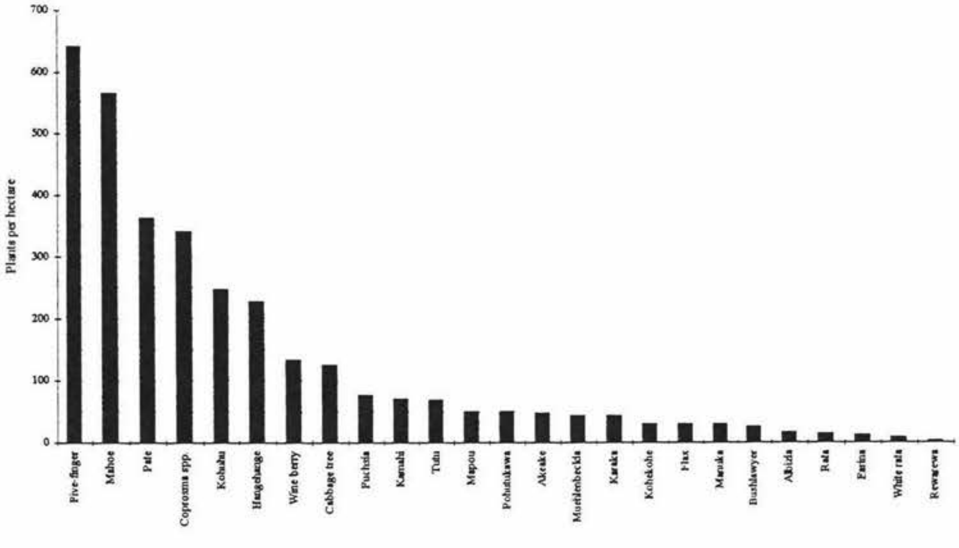


Fig. 2.2. Number of individuals per hectare, of plants likely to be used by hihi on Mokoia Island.

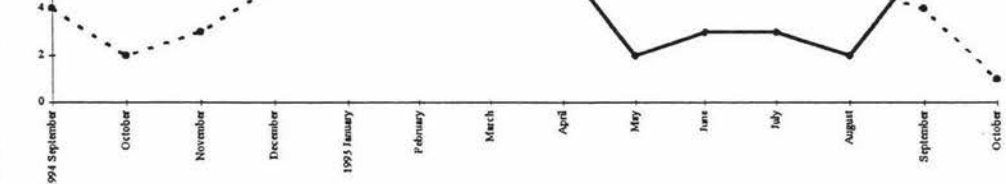


Fig. 2.3. The number of hihi food-species in fruit and flower each month on Mokoia Island

Fruit and flower phenology

Peak flowering, measured as the period with the greatest number of species carrying flowers, was between October and the end of February (Fig 2.3, 2.4). This coincides with the hihi breeding season (September-January, Castro 1995). The peak number of species in fruit is from March to May. August and September are the months with the fewest species in fruit or flower. Overall, there were 16 species that flowered over the hihi breeding season, and 5 main species that flowered outside the breeding period (February-August).

Pohutukawa flowered during summer (November-December 1994). These are the largest flowering trees on Mokoia, most being 10-12m in height. They also rival five-finger in average flower counts per tree, with counts reaching the low 100,000s. While the diversity of flowering species peaks during the pohutukawa flowering period, it's likely nectar availability (kJ/ha) also peaks for the year during this time (December-January). However, during September/October both flower and fruit counts are relatively low (Fig. 2.5).

After summer (i.e., after February) flower counts drop dramatically as flowers become scattered and relatively rare. During this time species providing fruits reach peak abundance (Fig 2.3), with twice as many species providing fruits than flowers in March and April. During March/April most flowering species are concluding their flowering period. By May there are five times as many fruiting species as flowering species, with most species providing fruits all over Mokoia. The diversity of species in fruit is greater than flowering species for most of the non-breeding season (March to August). However during June and July both fruit and flower counts are relatively low (Fig. 2.5).

While the number of species flowering peaks in December-January (Fig 2.3), the number of flowers doesn't peak until February (Fig.2.5). This is due to two factors. Firstly, during summer most flowering species are canopy species such as karaka, pohutukawa, kamahi and rewarewa. These provide many flowers per tree, but occur in low density and/or are confined to particular habitats such as gullies or the lakeshore (Fig 2.2, 2.6). Secondly, widely distributed sub-canopy species such as mahoe and pate reached peak

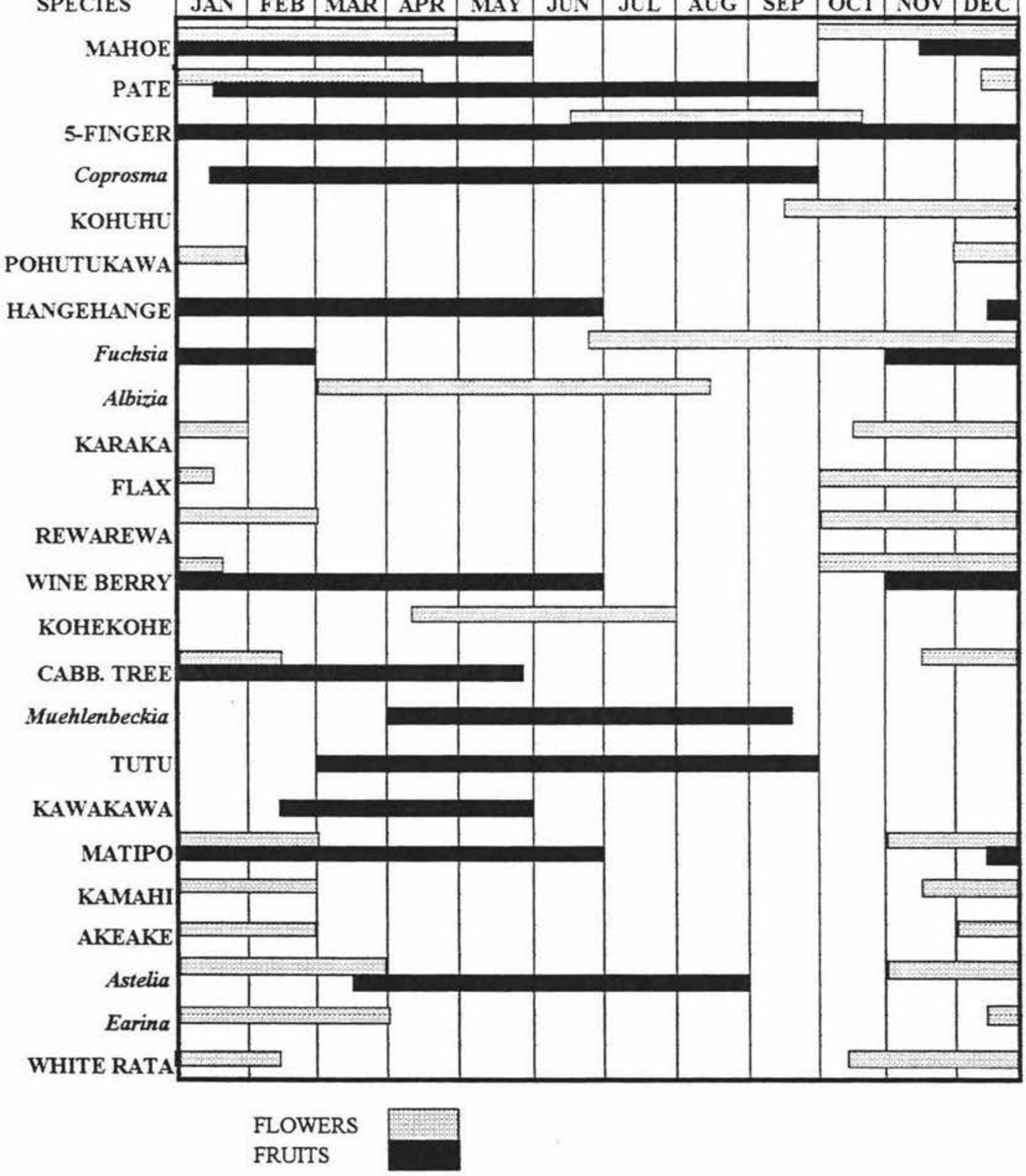


Fig. 2.4. Fruit and flower phenologies on Mokoia island.

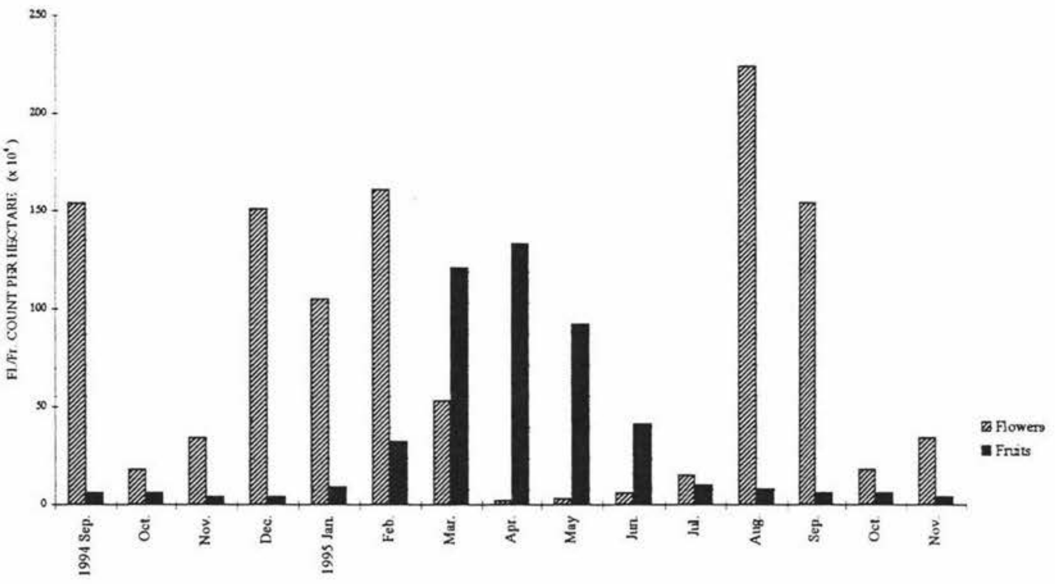


Fig. 2.5. Monthly variation in total number of flowers and fruits per hectare for species used by hihi on Mokoia Island.

flowering in February. Whether or not these periods represent significant changes in food availability to a hihi will be the focus Chapters 3 & 4.

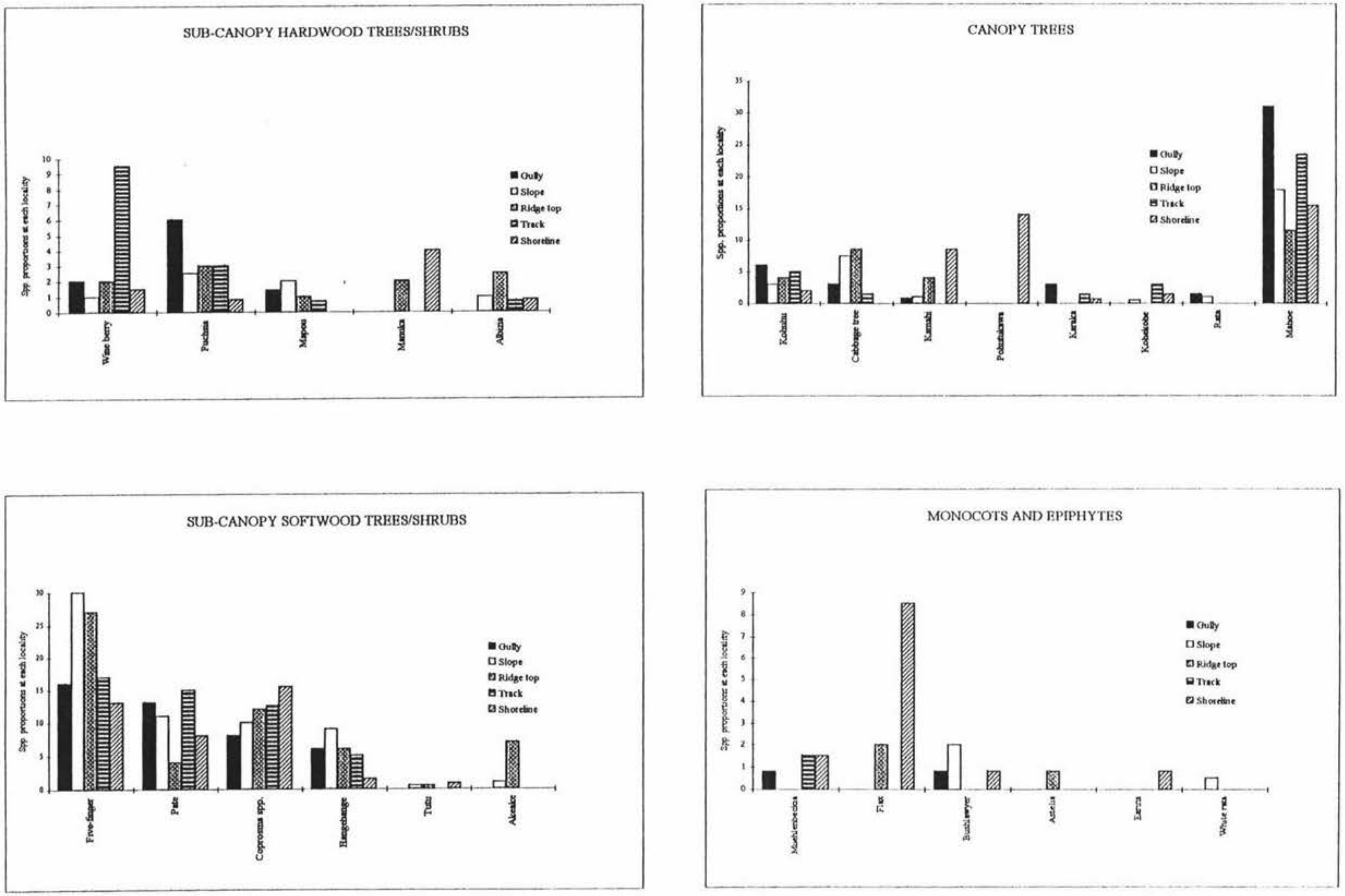
The Winter months begin with relatively low fruit and flower densities on Mokoia (Fig 2.5). Only kohekohe and *Albizia* are providing flowers at any significant level during this time (Fig 2.4), and neither is abundant on Mokoia (Fig 2.2). By July, *Fuchsia* and male five-finger have commenced their flowering periods with female five-finger following shortly after. During July and August birds have little nectar available other than five-finger, *Albizia* and *Fuchsia*, and fruit counts decline. The flower counts outside the hihi breeding period peak in August. Five-finger is responsible for this, as its flowers reach very high densities all over Mokoia during August-September.

With Spring comes the conclusion of the *Albizia*/five-finger flowering period. *Fuchsia* and kohuhu provide most of the available nectar, but these are less abundant than five-finger (Fig 2.2). While October and November sees an increasing number of species coming into flower, there is a large drop in mean fruit and flower densities (Fig 2.5). During October five-finger is the only remaining fruiting species, while the number of flowering species increase to 11. October is also a cross-over period, most species either commencing flowering (e.g., karaka, kohuhu, rewarewa, hangehange) or concluding fruiting (e.g., pate, *Coprosma*, tutu, *Muehlenbeckia*) (Fig 2.4). After October the flower count per hectare increases sharply.

In the 1994-95 Summer period, mahoe had two peak flowering periods. These were in November and February, and were confined mostly to edge areas and gullies. During Spring/Summer all canopy tree species were in flower except kohekohe. While flowering species were declining during late summer, and early Autumn, fruiting species were increasing and becoming widely available over Mokoia. Wineberry, pate, kawakawa, five-finger, cabbage tree, hangehange, *Muelenbeckia*, tutu, and a high proportion of *Coprosma* fruit ripen over Autumn. A small number of *Coprosma* appeared to be infected with mites, and all fruits produced by these plants were green and fibrous.

Table 2.2. Plant species used by hihi on Mokoia, divided into successional and size categories. The percentage scores represent the proportion abundance of each plant species shown in Figure 2.2.

Category	Species	Name	%	Part used
Canopy trees	*Melicytus ramiflorus*	Mahoe	13	Fr
	Pittosporum tenuifolium	Kohuhu	5.8	Fl
	Cordyline australis	Cabbage tree	3.6	Fl
	Weinmannia racemosa	Kamahi	1.3	Fl
	Meterosideros excelsa	Pohutukawa	1.1	Fl
	Corynocarpus laevigatus	Karaka	1	Fl
	Dysoxylum spectabile	Kohekohe	0.5	Fl
	Meterosideros robusta	Rata	0.2	Fl
	Knightia excelsa	Rewarewa	0.1	Fl
		Total	26.6	
Sub-canopy hardwood trees/shrubs	*Aristotelia serrata*	Wine berry	3	Fl, Fr
	Fuchsia excorticata	*Fuchsia*	1.8	Fl
	Myrsine australis	Mapou	0.9	Fl, Fr
	Albizia lophantha	*Albizia*	0.4	Fl
	Leptospermum ericoides	Manuka	0.1	Fl
		Total	6.2	
Sub-canopy softwood trees/shrubs	*Macropiper excelsum*	Kawakawa	27.4	Fr
	Pseudopanax arboreus	Five-finger	15	Fl, Fr
	Schefflera digitata	Pate	8.1	Fr
	Coprosma spp.	*Coprosma spp.*	8	Fr
	Geniostoma rupestre	Hangahange	5	Fl, Fr
	Dodonaea viscosa	Akeake	1	Fl
	Coriaria arborea	Tutu	0.9	Fr
		Total	65.4	
Monocots and epiphytes	*Muehlenbeckia australis*	Puka	1	Fr
	Phormium tenax	Flax	0.4	Fl
	Rubus cissoides	Bushlawyer	0.2	Fl, Fr
	Astelia spp.	*Astelia*	0.2	Fr, Fl
	Earina autumnalis	*Earina*	0.1	Fl
	Meterosideros tetraranda	White rata	0.1	Fl
		Total	1.8	


SUB-CANOPY HARDWOOD TREES/SHRUBS

CANOPY TREES

SUB-CANOPY SOFTWOOD TREES/SHRUBS

MONOCOTS AND EPIPHYTES

Fig. 2.6. Distribution of 27 plant species used by hihi between five topographical categories on Mokoia Island.

Albizia, Fuchsia should be important nectar sources to hihi on Mokoia. They are in flower when most species are out of flower, and between them flower for 11 months of the year (November to September). Kohekohe is also important, although it has a much shorter flowering period. It is not an abundant species on Mokoia, representing 0.5% of all individuals sampled. However, it's important because it flowers when mean flowering is at its lowest (Fig 2.5). Kohekohe flowers are produced from late March to late July with peak flowering around May and June. Some counts reached into the 10,000s of flowers per tree, though most were in the high thousands.

Cabbage tree flowers during Summer when the number of species in flower peaks for the year, and fruits during Autumn when the number of species in fruit peaks. In contrast, Female five-finger provides fruits all year, and is the only fruiting species available during October (Fig 2.4). Male and female flowers are available during August-September when *Fuchsia* is the only other species in flower.

Plant species distribution and successional composition

The species are divided into four categories: canopy trees, sub-canopy hardwood trees/shrubs, sub-canopy softwood trees/shrubs, and monocots/epiphytes (Table 2.2). The contributions from these categories are important for predicting likely successional dynamics. The more important species to hihi are singled out, and their distribution described.

As mentioned in the introduction, much of the island is dominated by secondary scrub and forest (about 40 years old), rats, grazing mammals and fires having all heavily influenced successional changes over much of the island until recently. At present the trees are highest in gullies, and around lower shoreline areas (6-12 m). For most of the island the trees/shrubs are only 2-4 m. Compared to other islands such as Kapiti and Little Barrier the canopy itself is not far removed from the sub-canopy, and this affects how far away hihi can forage from the ground and from tui.

Canopy trees

Mahoe represents 13% of all vegetation sampled, and 49% of all canopy species (Table 2.2). Without mahoe in this category, the canopy species make up only 13.6% of all plants counted (Fig 2.6).

Canopy trees will tend to be less abundant than sub-canopy trees/shrubs because they are bigger. However, at present canopy species are mostly confined to gullies and shoreline, and may with time spread further into areas dominated by scrub. This is already occurring around gully, track and peripheral areas where the oldest trees are located on Mokoia. Although the canopy tree species are well represented in terms of their diversity, there are only a few mature trees.

Saplings from many of these species are a common sight around the hut and summit tracks. Kohekohe and karaka are the predominant saplings in this category. Rewarewa saplings are also common in some areas, while pohutukawa saplings are confined to the shoreline.

Pohutukawa is one of the most spatially confined species on Mokoia. They are confined to a narrow strip around the lake edge, particularly in the northwest, west and southwest where the shore is rocky and steep. Because pohutukawa are low in number and confined in space, the total monthly mean flower counts for December and January are still low when compared to February. When mahoe and pate flowers reach their peak densities (Fig 2.5).

Kohekohe is confined to the hut area along the southern end of the island and above Hinemoa's Pool. This stand of forest is considered to be the most mature vegetation type on the island (Wallace 1993). Wallace (1993) remarked that this stand of forest may reflect the island's original forest type. Kohekohe juveniles of moderate size (2-4m) are almost totally absent, and over 90% of the kohekohe trees are 8-10 m tall.

Mahoe is the second most abundant food plant on Mokoia, after five-finger (Fig 2.1). The largest individuals are found in gullies, track areas and bush edges. However, most of the mahoe outside of the gullies and bush edges are stunted and produce few flowers and fruits. Trees get smaller further away from the shoreline and tracks.

Kohuhu is found in all localities, but especially near gullies. Kohuhu is particularly common in the west and northwest areas. Kohuhu is the second most abundant canopy tree species on Mokoia, representing 5.8% of all plants counted. As an interesting sideline, Wallace (1993) comments on the number of large trees that have died and fallen over on the west side of the island, and mentions disease as a possible cause. This still occurs in the area, with high winds claiming the largest trees. Other plant species within the same area, such as *Fuchsia, Albizia*, and karaka, have also partially or completely fallen over. It's possible that disease has little to do with this as soil depth in these areas may be partially contributing to this.

Cabbage tree is distributed mainly on the north facing slopes. Wallace (1993) mentions that perhaps 10-12% of the cabbage trees were showing obvious signs of sudden decline syndrome. However, the recruitment of cabbage tree juveniles appears reasonably high with many trees of intermediate dimensions spread over the north-facing slopes. The larger cabbage tree specimens are found away from the north facing slopes, around the lower gully areas.

Only one rewarewa was found during the vegetation sampling. Other trees were located around the upper slopes and the south side of the island. These were easily found when in flower as tui congregated at these trees.

Sub-canopy hardwood trees/shrubs

This category contains the lowest number of species (Table 2.2). If mahoe were included in this category it would comprise 19.2% of the, with the canopy species reducing to 13.6%. Wineberry is the most abundant. Its population is composed mainly of spindly juveniles found over much of the island. However, there are a few very large trees. Fruit counts varied between trees, with some in the 100s and others in the high 1,000s.

Fuchsia is a widespread species on Mokoia, found in all localities. Most are small trees or shrubs. In some gullies mature trees exceed 12 m in height, but these are usually elongated individuals producing relatively few flowers. *Fuchsia* is spread across all five habitats but are most common in gullies and least common on the shoreline (Fig 2.6). Trees found along tracks, bush edges and slopes are usually younger than the gully individuals and appear to be flourishing in the absence of mahoe. *Fuchsia* is possibly dying off in some locations along with kohuhu (Wallace 1993).

Albizia and *Fuchsia* are the only species in this category that flower during Winter (Fig 2.4). *Albizia* is scattered in small patches around the island from lake edge to ridge top but is not particularly abundant (Fig 2.1, 2.6). *Albizia* comes in all sizes with the largest individuals found on the west side and in the southeastern areas (6-9m).

Sub-canopy softwood trees/shrubs

These are early successional plants, and clearly are the most widespread and abundant category of plants on Mokoia. As mentioned, five-finger is the most widespread and abundant species used by hihi on Mokoia. This species is particularly dense around the midline, especially on northern slopes and ridge areas.

Except for akeake, all of the species in this category provide fruits that hihi eat. Five-finger and pate also provide flowers, but compared to the other flowering species are of relatively low sugar content (Chapter 3). However, they compensate through abundance and high flower densities. *Coprosma* is also well represented in this category, making up 8.0% of all plants counted. Like wineberry, the *Coprosma* population is largely composed of young individuals that have responded favourably since the goat eradication (1989-90). Most of the *Coprosma* sampled were under 1.5m tall and/or spindly, but one individual in the kohekohe-karaka forest was 4m tall by 4m wide. *Coprosma spp.* (*C. robusta and C. grandifolia*) are evenly distributed throughout all localities (Fig 2.6), but are most dense outside of gullies.

Pate is an abundant food source on Mokoia (Table 2.2). It is most commonly found as an understorey plant in gullies and southern slopes dominated by mamaku. It is least abundant in open areas like ridge tops (Fig 2.6). Some large individuals (6-7m) are found in the lower regions of the island where the canopy is highest, such as the kohekohe-karaka forest of the hut area.

Epiphytes and monocots

This is a poorly represented category on Mokoia (Fig 2.2). *Muehlenbeckia* and flax are the most abundant in this category. Cabbage tree is not included in this category because it is a large canopy species on Mokoia. *Muehlenbeckia* is least common under the mamaku canopy of the southern slopes and most commonly found among mahoe. Those flax producing flowers during the summer of 1994/95 were widely scattered over a few locations, mostly on ridge tops and along the shoreline. *Earina* and white rata are localised in small areas. Most of the white rata are found growing on ponga trunks while *Earina* and *Astelia* are found mainly on pohutukawa trees and rocky outcrops.

Discussion

It's clear from the phenology results that five-finger could be an important flowering source from mid winter to spring. *Fuchsia* is crucial during October when most species are producing flowers at low densities, and there is only one species in fruit (5-finger). Kohekohe, which flowers from late autumn to late winter, and *Albizia* are about all that is available during early winter in terms of nectar. This leaves *Albizia*, *Fuchsia* and five-finger as almost the only naturally occurring nectar sources through August to October. For the rest of spring, kohuhu, *Fuchsia* and hangehange are the only species providing flowers at significant levels, and they become relatively scattered as they are replaced by summer flowering canopy species. Castro (1995) has shown there can be great variation in phenology from one year to the next. This leaves the possibility that crunch periods could become more pronounced in some years. The periods hihi are dependent on few species may have the greater potential in the long-term to be problem periods in terms of food scarcity.

Phenology results showed there are periods on Mokoia when nectar sources are restricted to two or three plant species at a time (e.g., Autumn, and early spring/late winter). Most of the flower species listed as being used by hihi on Mokoia flower during the hihi breeding period (16/21), and most of these are canopy tree species (9/16). It's clear that most of Mokoia is covered by regenerating forest that has succeeded scrub, bracken and fernland, and that most large canopy trees are confined.

The understorey vegetation of Mokoia is composed largely of young plants which have flourished undisturbed since 1989 (e.g., five-finger, pate, *Coprosma* and hangehange). Most of these are known hihi food-plant species on other islands, providing mostly fruits which on Mokoia are available throughout the year. The much older canopy trees (e.g., mamaku, tree-fern, pohutukawa, karaka, kohekohe, kohuhu and cabbage trees) are either not hihi food-plants, or flower during the warmer months (with the exception of kohekohe). In contrast to the understory plants, only one canopy tree species (mahoe) provides fruits which hihi can eat.

Since phenologies can vary greatly between years (Castro 1995), this makes predicting future crunch periods difficult. Large islands (e.g., Little Barrier Island, 3076 ha, holding about 102 hihi food-plant species, Angehr 1984) generally constitute a habitat of greater diversity of species than habitats found on small islands (e.g., Mokoia Island, 135 ha, about 27 hihi food-plant species). It's likely crunch periods are more common and/or pronounced on smaller islands, and this in turn may influence the abundance of honeyeaters on those islands.

Several studies have looked at the relationship between nectar availability or inflorescence density and abundance of honeyeaters in Australia. Most studies have found a positive correlation between them (e.g., Ford 1979; Collins & Briffa 1982; Ford 1983; Collins & Newland 1986; McFarland 1986), while other studies have found no significant correlation (e.g., Pyke 1983), or that the degree of correlation varied widely between species in the same community (e.g., McFarland & Sale 1985). However, Ford (1991) found that most honeyeaters either left a feeding area, or lost weight during

With this in mind, Angehr (1984) assessed the vegetation of islands proposed for hihi translocations. This was done tentatively by comparing between these islands a total of 125 plant species known, and likely to be used by hihi. Angehr (1984) suggested all broadleaf forests provided good or medium quality habitat. However, other factors are also likely to influence bird's survival and distribution (e.g., nesting sites, aggression).

Mokoia Island contrasts markedly with Little Barrier Island in most respects. As mentioned, Little Barrier Island is a large island, containing several mature forest types most of which are untouched by introduced browsing mammals. The lower third of the slopes are covered with *Leptospermum* and *Kunzea* (Rasch & Craig 1988) which are rare on Mokoia. While hihi use most forest types on Little Barrier Island, they seem to favour the mature moist forests found in the larger valleys and on ridges over 300 m above sea level (Angehr 1985). During the breeding season they are found largely in valleys, where nest sites may be most common (e.g., pohutukawa and Puriri tree cavities, Rasch 1989). In early autumn hihi, especially juveniles move to higher elevations to feed on abundant ripening fruit of five-finger, raukawa, and *Coprosma spp*. (Angehr 1985).

Of the 125 plant species likely to be used by hihi, Little Barrier has 102 of them. Of these, hihi visit 27 flower species and 34 fruit species (Angehr 1984). Kapiti Island has 75 of these species, with hihi visiting more flowering species (33 spp.) than fruiting species (17 spp.) (Castro 1995). This is more than twice the available species found on Mokoia Island (27 spp), but like Kapiti hihi, Mokoia hihi visit a wider variety of flower species (21 spp.) than fruiting species (14 spp.) (Chapter 3). Castro (1995) commented that preferred fruiting species may be rare or absent on Kapiti, forcing hihi to forage more on invertebrates and more dispersed flowers. On Little Barrier the greater diversity of fruiting species may mean hihi have sufficient food to fall back on when exclusion pressure at nectar sites increase. Compared to Kapiti, Mokoia Island has about twice the species with available fruits during the months Rasch & Craig (1988) and Angehr (1984) showed Little Barrier hihi were spending most of their time taking fruits (Autumn, March to July). In contrast, Kapiti shows a drop in fruiting species during these months, but has more fruiting species available during Spring and Summer compared to Mokoia (Table 2.3).

Table 2.3. Comparison of hihi food-plant species in flower and fruit each month on Kapiti (Castro 1995) and Mokoia (this study)

	Kapiti Island			Mokoia Island		
Month	**Flowers**	**Fruits**	**Total**	**Flowers**	**Fruits**	**Total**
January	5	15	20	15	9	24
Feburary	5	12	17	12	11	23
March	3	6	9	6	12	18
April	2	6	8	6	13	19
May	3	2	5	2	10	12
June	4	3	7	3	8	11
July	6	3	9	3	6	9
August	6	2	8	2	5	7
September	6	6	12	6	4	10
October	7	11	18	12	1	12
November	9	13	22	13	3	16
December	10	16	26	16	5	21
Total	33	17	50	21	13	34

Mokoia also differs from Kapiti in the proportional availability of the flower species used by hihi with each season (Table 2.3). The flowering periods between the islands are similar, both showing a drop between February and March. Mokoia also differs from Kapiti in having more species in flower during the hihi breeding season and less during May and August. Castro (1995) commented that on Kapiti 13 flowering species are available during the hihi breeding period, but that most were rare, confined or low quality (e.g., pohutukawa, *Fuchsia*) This leaves only hinau and five-finger providing most of the available nectar to hihi during the breeding season on Kapiti (Castro 1995). On Mokoia there are a total of 16 flowering species available during this time, while only half of them are rare, eight of them are reasonably abundant including pohutukawa and *Fuchsia*.

Secondary forest islands constitute a landscape with greater species richness than those found in landscapes dominated by climax forests (Lugo 1988). It's therefore possible Mokoia may be less suitable for hihi if it were a climax habitat. This would occur if the already existing canopy species were to succeed much of the area presently occupied by five-finger and *Albizia*. The most abundant species on Mokoia are early successional species that have responded well since the goat eradication in 1989-1990 (e.g., *Albizia* and five-finger). With the exception of kohekohe, all canopy species on Mokoia flower during summer, and only one species (mahoe) having fruits which hihi use. Without additional plantings species abundance and/or diversity on Mokoia may decrease with time as the forest matures. If the early successional species (e.g., Albizia and five-finger) are replaced by species that fruit or flower at different times then crunch periods could become more pronounced. This may be typical of climax habitats on small islands, and possibly contributed to restricting hihi populations to the mainland and larger offshore islands in the past.

Simply knowing which environments have more or fewer species does not qualify those habitats. It is possible to speculate on the significance of differences between the composition and abundance of certain plant species on different islands. However, it is difficult giving this meaning to hihi when the underlying theory qualifying one habitat as more suitable than another is lacking. This is made more difficult by the fact that the islands are different in many ways other than the composition of their vegetation. In the past this has confined speculation about what is suitable hihi habitat to mostly intuition. In this study I collected data on actual amounts of food available to hihi each month, I converted this to a monthly estimate of available energy per unit area (e.g., kJ/ha), and then related this to changes in bird's weights during those months when supplementary food (i.e., 20% sugar solution) is available *vs* unavailable.

In Chapter 3 the estimated energy rewards of the corresponding flower and fruit sources are added to the densities of these food source species. This will give a better idea of how much, and to what degree naturally occurring carbohydrate sources vary seasonally on Mokoia. This is important, as it can be better compared between islands than just relative species availability. This is done by comparing four general components of a crunch period separately. These components are: monthly species diversity; relative species abundance; monthly flower and fruit abundance; and species flower and fruit mean energetic rewards. Whether or not these components represent a crunch period to a hihi is the focus of the remainder of this thesis.

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Chapter 3

Energy value of nectar and fruit sources, hihi foraging behaviour, and competition from tui on Mokoia Island

Introduction

Nectar is a major source of energy for most Australian honeyeaters, and arthropods provide for most of their protein requirements (Ford and Paton 1976; Pyke 1980; Collins & Newland 1986; Collins et al. 1984a). High levels of interspecific aggression between Australian honeyeaters frequently result in exclusion of some species from nectar sources (Wolf 1978, Ford 1979). However, most species differ in their dependence on nectar and invertebrates (Recher & Abbott 1970; Ford & Paton 1977). While some honeyeater species are highly mobile, and show regular migrations to distant nectar sites (Ford & Paton 1985), other species are sedentary and show little indication of any relationship between their distribution and the abundance of nectar (Pyke 1983).

The assertion that honeyeaters are highly dependent on nectar assumes there is a close link between the abundance of flowering plants, and the abundance of honeyeaters, and that nectar availability is the limiting variable (Craig & MacMillen 1985). In New Zealand ornithophilous flowers are few in number (Godley 1979; Craig et al. 1981). New Zealand honeyeaters (Meliphagidae) commonly take fruits as well as nectar, while for most Australian species fruit consumption is a negligible component of their diet (Craig et al. 1981). The hihi (*Notiomystis cincta*) is a rare New Zealand honeyeater. Hihi have an omnivorous tendency, feeding on three main food types: nectar, fruits and invertebrates (Gravatt 1970; Angher 1984, Rasch 1985; Lovegrove 1986; Castro et al. 1994; Castro 1995).

The hihi is more sedentary than the tui, *Prosthemadera novaeseelandiae* (Craig et al. 1981). A consequence of birds being highly sedentary and nectarivorous is that they will deplete their nectar resources when nectar production is low. When nectar is scarce hihi may have to rely heavily on fruits and invertebrates for their energy needs. Additionally, hihi may suffer exclusion from some flowering species by the more dominant tui population on Mokoia. These two factors are interrelated, and may contribute to hihi becoming energy limited during some months. Alternatively, tui may leave the island, so that the nectar sources available can be exploited by hihi. This hypothesis is supported by evidence showing that smaller less dominant nectar feeders tend to be better able to support themselves on low-grade nectar sources (Ford 1979).

When hihi are carbohydrate limited the following may occur. First, hihi may die or lose condition. As tui are plentiful on Mokoia this may result from competition from tui. Second, hihi may spend more time feeding, and/or spend a higher proportion of time invertebrate feeding. However, the size of the insects, and the amounts of energy they extract from them will probably influence this also. The success of two recent introductions of insectivorous birds (North Island robin *Petroica australis* and saddleback *Philesturnus carunculatus*) suggests that invertebrates are abundant on Mokoia. Third, if feeding time is inversely related to energy availability then birds should give more time to meeting their energy requirements when nectar and fruit are scarce.

The purpose of this chapter is to describe the relationships between carbohydrate availability (e.g., kJ/ha), competition from tui, and hihi foraging behaviour on Mokoia. These results are then compared to previous studies involving hihi foraging behaviour on other islands. The primary question this chapter addresses is whether hihi feeding behaviour varied predictably with seasonal changes in nectar and fruit availability, and to what degree competition from tui contributes to this.

Methods

40 hihi were translocated from Little Barrier Island to Mokoia on September 5 1994. All birds were individually colour banded. After a traditional welcoming ceremony, the birds were divided into three groups which were released at the three permanent feeding stations (Fig 3.1). See Armstrong et al. (1997) for details of the translocation.

The methods for this chapter are split into three parts. First, I outline the methods and procedures concerned with nectar extraction, and the calculation of the different flower/fruit sugar values. Second, I outline the methods adopted to investigate the amounts of time hihi spent feeding on nectar and arthropods, and the extent to which they were excluded from food sources by tui. Third, I outline the methods for determining changes in abundance of tui over the duration of this study. These data were collected from, September 1994 to October 1995. There were two field-trips each month (usually 3-4 days in duration).

Quantifying the energetic value of nectar

A) Sampling nectar and fruit- Nectar and fruit samples were taken fortnightly from those species in flower/fruit at the time. Nectar sampling was done at three times of day, morning (sunup to 9:00am), midday (11:00am to 1:00pm) and afternoon (3:00pm to sundown). Samples taken during these periods come from the sample points used in vegetation surveys (Chapter 2), but also from other plants found while moving about the island. When a plant was sampled, 10 to 20 flowers were selected randomly, and their nectar extracted as outlined below. At least five plants per grid were sampled in each time period. For those species that condense their flowers into inflorescences the individual flowers were taken randomly from at least five inflorescences per plant. Fruit sampling was done the same as flower sampling, except that fruits were collected whole. I didn't equalise fruit sampling between the three periods, as the energy content of fruits is unlikely to change with time of day.

All nectar samples were from unbagged flowers (Fig 3.1). The joules per flower measurements therefore represent the mean a nectar feeder could expect if it too was foraging randomly. Gill and Wolf (1977) have demonstrated that two species of African sunbird forage non-randomly at *Leonotis nepetifolia*, selecting those flowers that have the highest nectar standing crops, and thereby increasing foraging efficiency by up to 25%. However, given that hihi foraged widely and did not defend nectar sources, their nectar intake rates may have been quite close to those measured by random sampling.

B) Nectar extraction- Nectar was collected from flowers by absorbing it onto filter paper "wicks" either by placing the filter paper into the flower or by extracting the nectar with a micropipette then absorbing it onto the filter paper (McKenna and Thomson 1989). For some flowering species it was necessary to redissolve dried nectar on the flower using a small volume of distilled water, which is then absorbed onto filter paper (Cresswell 1990). Prior to this, pollen bearing structures on those flowers were removed. This is because pollen contains carbohydrates and this small amount could confound the nectar results.

C) Calculating nectar carbohydrate content per flower. The sucrose content (mg) per flower were calculated using an anthrone colorimetric assay of the dried nectar redissolved from the filter paper wicks (McKenna and Thomson 1989). The corresponding energy values of the nectar samples were calculated assuming that 1 mg sucrose = 16.5 Joules. To calculate the monthly mean available nectar standing-crop for each species, the mean flower count for each species (Chapter 2) was multiplied by the mean energy content of that species per flower. This is then converted to energy per hectare and compared on a monthly basis.

No attempt was made to quantify the protein/energy value of invertebrate sources, nor was the energy value of fruit lipids measured. This is because the specific aim of this thesis is to test whether Mokoia hihi are limited by carbohydrate availability. We assume that the very low concentration of amino acids in the nectar of flowers are not energetically important nor of high nutritive importance in view of the ingestion of invertebrates by honeyeaters, (Baker & Baker 1973).

D) Calculating carbohydrate content per fruit. The sucrose content per fruit was calculated using an anthrone colorimetric assay of the fruit pulp (seeds removed). The corresponding fruit energy values were calculated in the same way as the nectar samples.

Hihi feeding behaviour

Observations of hihi feeding were made fortnightly by following hihi and recording their activities on a dictaphone. These were carried out in association with the vegetation surveys and nectar/fruit sampling. As I covered the island systematically birds were located by sight or sound. I made a conscious effort to obtain as many observations away from the feeders as possible. Observations were made for as long as the individual remained in sight. During this period its band combination and sex were recorded as well as foraging activities. I aimed to follow at least 10 individuals and to collect at least 20 minutes of observations per field trip. Feeding activities were classified as nectar feeding, fruit eating and invertebrate feeding. All plant species either foraged from or perched on were recorded. Foraging rate on each species was determined from either the number of flowers/fruits probed per time or the time spent foraging at each inflorescence. Invertebrate feeding included both gleaning (picking invertebrates from leaves and bark), and hawking (catching insects on the wing). When possible the type of insect taken was recorded.

Data on diet was combined monthly and presented as a percentage of the foraging activities. I assumed that the amount of time birds spent feeding on the different fruits and flowers represented the true contribution those species was making to the hihi diet (Castro 1995). Likewise, I assumed that if birds were observed hawking or gleaning more times in a particular month this meant that invertebrates were contributing a larger extent to their diet. These data were converted to items taken per minute and, mean energy intake per minute, and given as a measure of the monthly foraging effort.

Calculating nectar extraction rates

When calculating the energy hihi obtained from feeding on the different species of plants, I assumed (1) the birds were taking all the nectar in each flower per visit, and (2) that birds would spend more time per flower, on the flowers with the greater energetic rewards. The nectar reward gained is therefore the product of flowers visited per unit of time and the average energetic content of each flower.

As time per flower, and the energetic content per flower were collected independently, each parameter therefore had its own confidence interval which would compound the error of their product. To provide some idea of the possible range of energy obtained whilst feeding the data was treated in the following way. For each month a random sample from the range of observed feeding rates (seconds per flower) were chosen for each plant species, and an equal number of random entries was chosen from the observed array of flower energetic values. These data were then put into two columns with the highest and lowest values being paired up. For each datum set the estimated energetic value per flower was divided by its matching time per flower to give an estimated joules per second measurement. The resulting products (for all months) were then summed to give a mean profitability measurement (i.e., joules per second), and 95% confidence interval for each plant species sampled.

This method was used because its unrealistic to just assume that the two parameters (time per flower, and flower energetic rewards) are random in respect to each other. The more realistic assumption is that birds are more likely to spend more time feeding (per flower) at the flowers with the higher energetic rewards. For this reason, and given that the datum set was sufficiently large a Montecarlo randomisation procedure was not used.

Tui estimates

The tui present on Mokoia are unbanded, and are found all over the island. Tui counts were conducted on a monthly basis in association with the vegetation sampling. At each sample point, I did a five minute tui count. During the five minutes any tui seen or heard within a 100 m radius was recorded. I therefore did 28 tui counts each month, which were pooled to give a mean monthly tui frequency count. These methods were not intended to calculate the absolute tui numbers on Mokoia, as a relative measure of abundance is suitable.

Hihi faecal samples

Hihi faecal samples were collected throughout the year at the feeding stations, and in nestboxes during the breeding season. These samples were collected daily during each fieldtrip, and grouped according to the month they were collected. All seeds were removed, identified, and counted for each plant species, all insect parts were also removed and identified. The number of seeds counted each month for each species was then divided by the known number of seeds per fruit for those species. This was done to obtain the number of represented fruits for each species. The number of fruits per month for each represented species were then summed and their proportions calculated.

RESULTS

Carbohydrate sources visited by hihi

Hihi were observed taking nectar from 14 species, and fruit from 12 species (Table 3.1). However, nectar and fruit samples were collected from more species than hihi were observed feeding from (21 species for nectar, and 14 species for fruit). Hihi on Mokoia were not observed feeding on the flowers of mapou, kamahi, akeake, *Astelia spp,* rata, or white rata, which are known to be used by hihi elsewhere (for scientific names see Table 3.1). Most of these species are rare or confined on Mokoia. Hihi may have still been using these species even though I didn't see them do so.

Those species contributing more than 45% of the available nectar (kJ/ha) on Mokoia in any one month were five-finger (July to October), mahoe (December, February, March), kohuhu (November), *Albizia* (April to June), kohekohe (May and June), and pohutukawa (January). Other species were also visited by hihi for their nectar, but their measured nectar availability

Table 3.1. CHARACTERISTICS OF HIHI FOOD-PLANT SPECIES FOUND ON MOKOIA ISLAND

SPECIES	NAME	RANK ABUNDANCE	Species used by hihi during this study	J per Fruit (95% CI)	total samples J per Flower (95% CI)	Mean time per flower (s)	PROFITABILITY OF FLOWERS (Js^{-1})
Melicytus ramiflorus	mahoe	7	Fr. Summer, Autumn	10.4 ±1.56 (n=64)	0.32 ±0.07 (n=72)		
Schefflera digitata	7-finger	6	Fr. Autumn, Winter	7.45±1.45 (n=56)	0.24 ±0.07 (n=39)	1.06 ±0.38	0.38 ±0.14
Pseudopanax arboreus	5-finger male	6	winter, Spring		3.5 ±0.73 (n=134)	1.23 ±0.47	1.83 ±0.88
P. arboreus	5-finger female	5	Fl. Spring/Fr. all year	8.1 ±1.0 (n=69)		1.61 ±0.73	
Coprosma spp	karamu/kanono	5	Fr. Autumn, Winter	15.5 ±2.26 (n=58)			
Pittosporum tenuifolium	kohuhu	4	Fl. Spring, Summer		3.2 ±0.63 (n=101)	1.84 ±0.24	2.15 ±0.5
Metrosideros excelsa	pohutukawa	2	Fl. Summer		38.5 ±9.5 (n=107)	2.1 ±0.75	
Geniostoma rupestre	hangehange	4	Fl. Winter, Spring/Fr. Summer	4.77 ±0.89 (n=20)	2.3 ±0.55 (n=42)	1.08 ±0.96	2.12 ±0.75
Fuchsia excorticata	kotukutuku	3	Fl. Winter, Spring/Fr. Summer		9.6 ±2.3 (n=158)	2.46 ±0.3	2.92 ±0.66
Albizia lophantha	Crested wattle	1	Fl. Autumn, Winter		3.3 ±0.41 (n=159)	0.9 ±0.2	3.48 ±0.67
Corynocarpus laevigatus	karaka	2	Fl. Summer		1.2 ±0.42 (n=36)	1.54 ±0.6	1.04 ±0.02
Phormium tenax	flax	1			30 ±7.1 (n=57)		
Knightia excelsa	rewarewa	1	Fl. Summer		13.5 ±2.4 (n=30)	2.3 ±1.3	7.69 ±0.41
Aristotelia serrata	wine berry	3	Fl. Spring/Fr. Summer, Autumn	71.26 ±10.82 (n=71)	0.24 ±0.09 (n=35)		
Dysoxylum spectabile	kohekohe	2	Fl. Autumn, Winter		3.5 ±0.5 (n=158)	1.45 ±0.32	2.13 ±0.24
Cordyline australis	cabbage tree	3	Fl. Summer	5.23 ±1.17 (n=31)	0.6 ±0.3 (n=36)	1.2±0.33	1.1 ±0.05
Muehlenbeckia australis	puka	2	Fr. Autumn, Winter	7.13 ±1.0 (n=46)			
Coriaria arborea	tutu	2	Fr. Autumn, Winter	10.4 ±3.41 (n=64)			
Macropiper excelsum	kawakawa	8	Fr. Autumn	>300 (n=6)			
Myrsine australis	mapou	1	Fr. Summer, Autumn	8.5 ±1.87 (n=40)			
Weinmannia racemosa	kamahi	2			0.05 ±0.04 (n=21)		
Dodonaea viscosa	akeake	1			4.9 ±0.5 (n=33)		
Astelia spp.	Astelia	1		14.1 ±3.94 (n=32)	2.8 ±1.0 (n=11)		
Earina autumnalis	Earina	1	Fl. Summer/Autumn		4 ±1.7 (n=42)		
Metrosideros tetaranda	white rata	1					
Metrosideros robusta	rata	1					
Rubus fruticosus	Black berry	3					

RANK ABUNDANCE **1=very rare, 2=rare, 3=occurs, 4=common, 5=very common, 6=abundant, 7=very abundant, 8=super abundant**

Table 3.2. % of nectar foraging per species in relation to availability

SPRING	Flower species	% available (kJHa^{-1})	% feeding time
1994 Sept	5-finger	88	75
	Fuchsia	6	22
	kohuhu	5	
	Albizia	1	3
Oct	5-finger	46	55
	kohuhu	30	30
	Fuchsia	20	13
	wine berry	< 1	2
Nov	kohuhu	60	65
	Fuchsia	18	24
	5-finger	12	17
	karaka	6	
	hangehange	6	

SUMMER	Flower species	% available (kJHa^{-1})	% feeding time
Dec	mahoe	67	1
	Fuchsia	19	38
	karaka	8	10
	pohutukawa	4	42
	kohuhu	2	9
1995 Jan	pohutukawa	98	97
	mahoe	1	1
	rewarewa	< 1	1
	cabbage tree	< 1	1
Feb	mahoe	54	
	pate	42	96

AUTUMN	Flower species	% available (kJHa^{-1})	% feeding time
Mar	mahoe	87	
	pate	11	81
	Albizia	2	
	Earina	< 1	19
Apr	*Albizia*	77	12
	kohekohe	23	88
May	*Albizia*	55	59
	kohekohe	45	41

WINTER	Flower species	% available (kJHa^{-1})	% feeding time
Jun	*Albizia*	46	60
	kohekohe	42	34
	5-finger	13	6

Jul	5-finger	90	35
	Albizia	5	
	Fuchsia	3	60
	kohekohe	2	6
Aug	5-finger	98	35
	Fuchsia	1	52
	kohekohe	< 1	5

SPRING	**Flower species**	**% available (kJHa^{-1})**	**% feeding time**
1995 Sept	5-finger	94	89
	Fuchsia	5	11
	kohuhu	1	
Oct	5-finger	76	17
	kohuhu	12	65
	Fuchsia	8	24

% of fruit foraging per species in relation to availability

SPRING	**Fruit species**	**% available (kJHa^{-1})**	**% feeding time**
1994 Sept	5-finger	86	65
	pate	5	35
	Coprosma	6	
Oct	5-finger	98	100
	Coprosma	1	
	pate	< 1	
Nov	5-finger	98	99
	mahoe	1	1
	Fuchsia	< 1	
	wine berry	< 1	

SUMMER	**Fruit species**	**% available (kJHa^{-1})**	**% feeding time**
Dec	mahoe	72	31
	5-finger	24	67
	wine berry	3	< 1
	hanehange	< 1	1
1995 Jan	mahoe	55	2
	wine berry	34	< 1
	5-finger	8	1
	pate	< 1	96
Feb	wineberry	72	61
	kawakawa	17	10
	Coprosma	6	13
	5-finger	2	2
	mahoe	2	1
	pate	1	13

AUTUMN	**Fruit species**	**% available (kJHa^{-1})**	**% feeding time**
Mar	wine berry	46	36
	kawakawa	26	9
	mahoe	15	4
	Coprosma	7	30
	5-finger	1	2
	pate	<1	19
Apr	kawakawa	32	1
	wine berry	17	< 1
	5-finger	14	5
	pate	12	61
	mahoe	9	1
	Coprosma	9	12
	mapou	5	15
	tutu	1	3
	hangehange	< 1	2
May	5-finger	31	4
	kawakawa	29	3
	pate	24	57
	Muehlenbeckia	4	11
	Coprosma	2	15
	mahoe	< 1	9
	mapou	< 1	< 1

WINTER	**Fruit species**	**% available (kJHa^{-1})**	**% feeding time**
Jun	*Muehlenbeckia*	31	12
	pate	24	54
	Coprosma	12	17
	5-finger	10	15
	hangehange	2	2
Jul	*Muehlenbeckia*	45	43
	pate	20	49
	5-finger	13	2
	Coprosma	10	5
	D. knightshade	< 1	1
Aug	5-finger	67	69
	Muehlenbeckia	20	19
	Coprosma	8	3
	pate	4	5
	D. knightshade	< 1	3

SPRING	**Fruit species**	**% available (kJHa^{-1})**	**% feeding time**
1995 Sept	5-finger	92	98
	Coprosma	5	1
	Muehlenbeckia	3	1
Oct	5-finger	99	100

was proportionally lower, or they flowered when the majority of species were also in flower (Table 3.2).

The mean energy value per flower varied 1000-fold among species (Fig 3.1, Table 3.1). The mean energy value per flower also varied within species, being greatest when flower counts for that species were highest. Therefore, the nectar content per flower was generally lower at the beginning and conclusion of each species flowering period.

Most species visited by hihi had less than 5 J per flower on average. Pohutukawa, flax, rewarewa, and Fuchsia had mean energy rewards between 10 and 40 joules per flower. Of the flowering species hihi were recorded feeding at, all but pate, five-finger, karaka, and cabbage tree had nectar extraction rates above 2 Js^{-1} (Fig 3.3). kohuhu, hangehange and kohekohe all received nectar extraction rates between 2.0-2.15 Js^{-1}. *Fuchsia* and *Albizia* had nectar extraction rates of 2.92 and 3.48 Js^{-1} respectively. Pohutukawa and rewarewa are likely to be even higher, but since its unlikely visits to these flowers resulted in total nectar extraction, calculating profitability would be unreliable. The fact that tui defend pohutukawa and rewarewa suggests they are very profitable nectar sources.

Fruit sources were available to hihi throughout the year. Five-finger was the most abundant fruit source from August through November (Table 3.2). Other species contributing more than 45% of the available fruit carbohydrates in any one month were, mahoe (December and January), wineberry (February and March), and *Muehlenbeckia* (July), however from Autumn to early Winter additional fruiting species reached peak availability, most being spread widely over the island (e.g., pate, *Coprosma spp.*, hangehange, kawakawa, tutu, and mapou (Table 3.2). Other fruiting species on Mokoia likely to be used by hihi but omitted from Table 3.2 include *Fuchsia*, *Astelia spp.*, and kohekohe. The fruits of these species were not included in Table 3.2 because their seeds were not found in hihi faeces samples (except one *Fuchsia* seed in January), and they were not observed being taken by hihi.

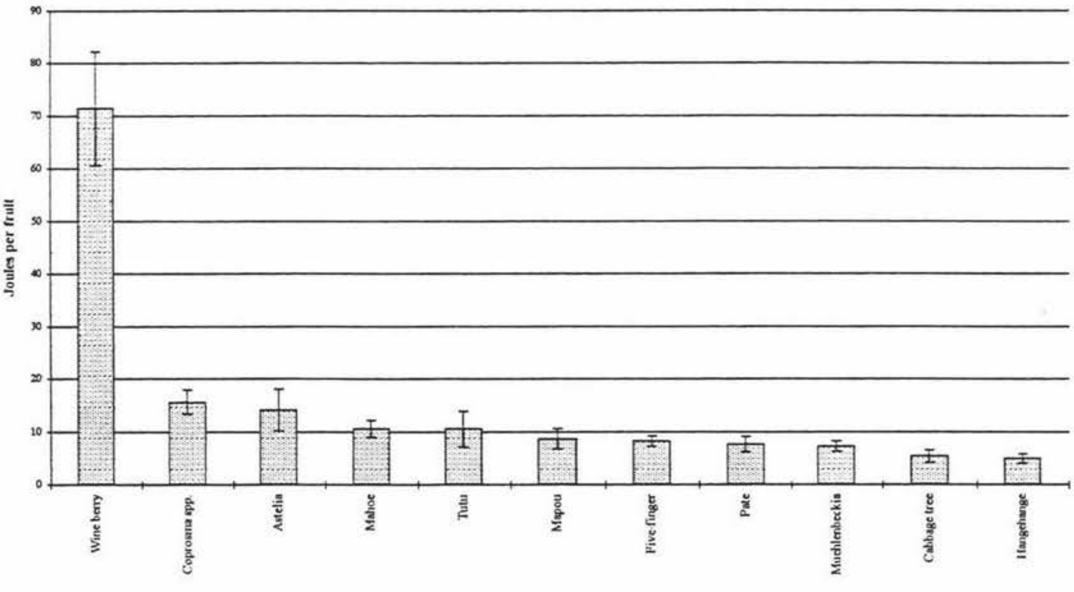

Fig 3.1. Mean energy content (joules) per flower for each species sampled on Mokoia. Error bars indicate 95% CI.

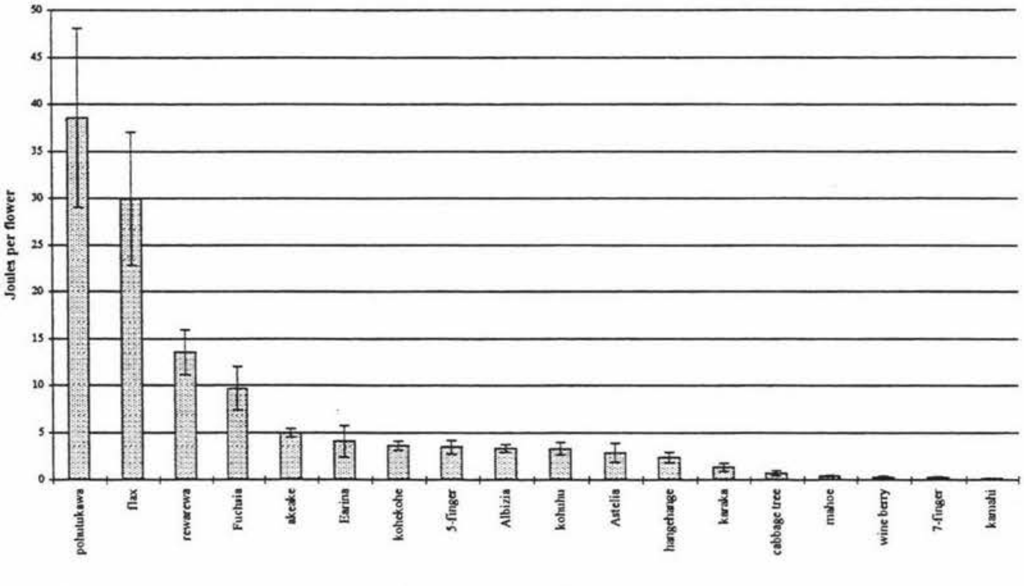

Fig 3.2. Mean energy content (joules) per fruit for each species sampled on Mokoia, except kawakawa which has a mean energy content (>300 J) per fruit. Error bar indicate 95% CI.

The mean energy content per fruit for each species shows most species offer fruits with higher concentrations of soluble carbohydrates than the majority of available flowers on Mokoia (Figs 3.1, 3.2). Wineberry fruits have concentrations of soluble sugars that exceed those of flax and pohutukawa flowers (Table 3.1).

Seasonal changes in carbohydrate availability

There were pronounced seasonal changes in nectar availability. The average nectar standing-crop of energy ranged from 36.4 $kJHa^{-1}$ in June to about 268,000 $kJHa^{-1}$ in January (Fig. 3.4). Standing-crops increased during the warmer months, corresponding to the pohutukawa and five-finger flowering periods. Fruit availability varied less seasonally than nectar sources did. Fruit availability was lowest during Spring at about 1,000 $kJHa^{-1}$ and peaked during mid Autumn at around 200,000 $kJHa^{-1}$. Seasonal changes in availability of nectar and fruit energy mainly reflected species phenologies (Chapter 2).

Nectar availability dropped from February through March (Fig 3.4). The most profuse flowering species during this time were all low grade nectar sources such as mahoe and pate (Fig 3.1), which accounted for over 95% of the available nectar energy during this time (Table 3.2). Those flower species which have more profitable flowers are either low in number, such as *Astelia spp*, rata, and *Earina*, or do not reach peak flowering till late Autumn or early Winter, such as kohekohe and *Albizia*.

During late summer and autumn fruit availability peaked for the year (Fig 3.4). Fruits comparatively high in carbohydrate energy become available all over the island, such as wineberry, kawakawa, mahoe, and *Coprosma spp.* (Fig 3.2). These fruiting species are favoured by hihi during Autumn (Table 3.2). The fruits of these species were produced at such quantities during late summer/autumn that many went unforaged and left to desiccate on their branches.

Winter peaks in nectar availability corresponded to the flowering of kohekohe and *Albizia* which together accounted for 87% to 100% of the nectar energy available from April

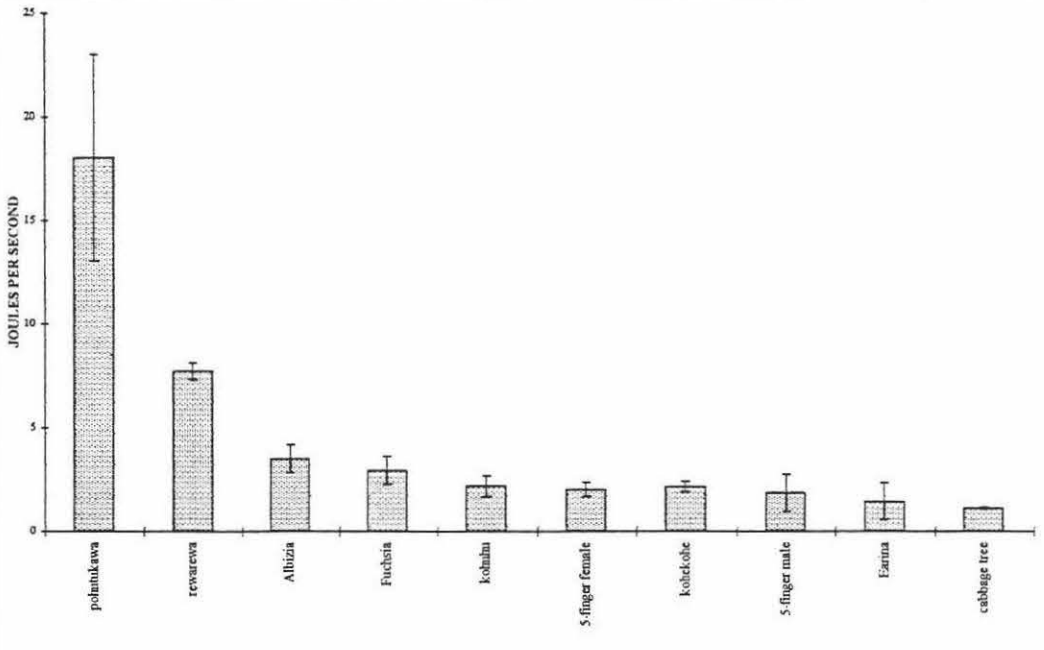

Fig 3.3. Profitability of the main nectar species used by hihi on Mokoia. Error bars are 95% CI.

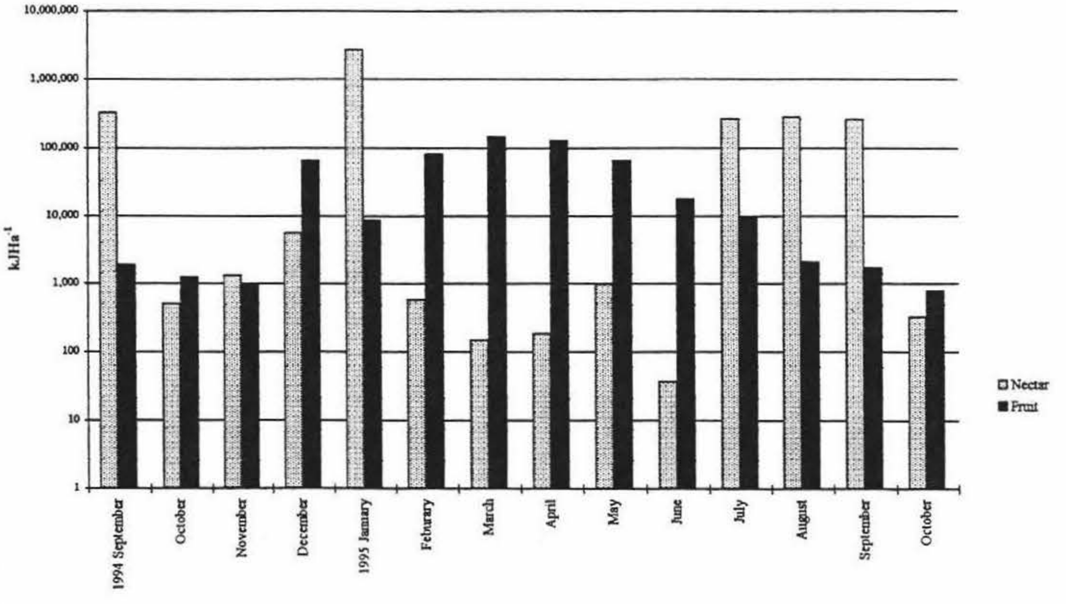

Fig 3.4. Monthly changes in carbohydrate availability per hectare for nectar and fruits likely to be used by hihi on Mokoia.

through June. During that time fruit availability still exceeded nectar availability (Fig 3.4). In July five-finger came into flower over much of the island. Although the flowers of this species are not particularly high in nectar (Fig 3.1), there are enough flowers produced to substantially raise the nectar standing-crop for late winter and early spring. From July through September five-finger accounted for 90%- 98% of the available nectar energy on Mokoia. After September, *Fuchsia* becomes increasingly important as nectar availability decreases in October. By late spring, *Fuchsia*, kohuhu, karaka, and hangehange are accounting for most of the available standing nectar crop for October (53%) and November (88%). Like nectar availability, fruit availability drops on Mokoia during spring, when 5-finger and left over *Coprosma*, pate, and hangehange fruits from the previous autumn are accounting for much of what is available.

Hihi observations at carbohydrate sources

The proportion of observation time hihi spent foraging varied seasonally. Hihi spent the highest proportion of time foraging (nectar, fruit, and invertebrates) in Spring (58% 1994, 56% 1995), and the least during autumn (39%), winter (29%), and summer (24%). As mentioned, spring is the only time carbohydrate availability nectar and fruit are both low compared to other seasons. During autumn nectar availability is also low but fruit carbohydrate availability peaks (Fig 3.4). Therefore, while birds may have increased their foraging time during spring because nectar was scarce, they decreased their feeding time in autumn and winter when nectar availability was even lower.

The proportion of time spent feeding on the three food categories (nectar, fruit, and invertebrates) varied throughout the year (Fig. 3.5). Time given to nectar feeding was highest in spring 1995 (75% of total foraging time) and winter (54%), and lowest in summer (15%) and autumn (21%). In 1995, spring and winter were the only times hihi fed predominantly on nectar. However, time given to invertebrate feeding was equally high (57%) in spring 1994, but much lower in 1995 (20%). Invertebrate feeding was highest in the first three months following the translocation (57%), in summer (73%), and autumn (51%). Apart from spring 1995, winter was the only period invertebrate feeding was lower

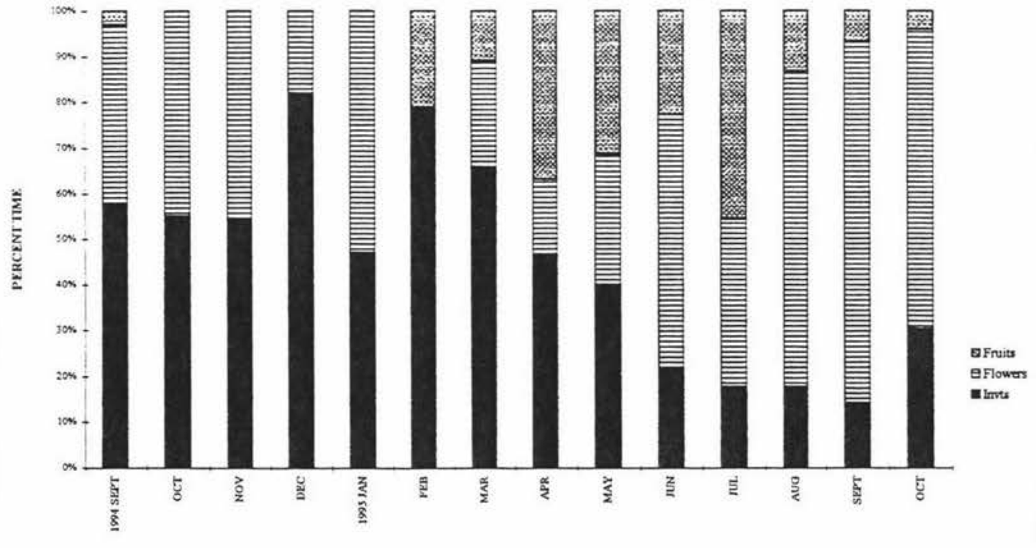

Fig 3.5. Hihi feeding behaviour (nectar, fruit and invertebrates) on Mokoia Island.

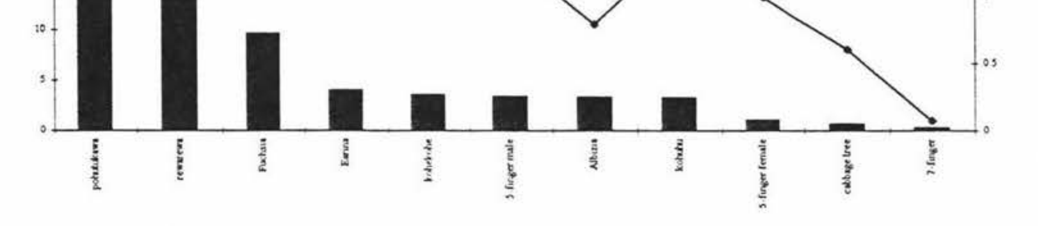

Fig 3.6. Mean time spent feeding per flower by hihi, and the mean energy rewards (joules) of those flowers.

than nectar feeding (19%, Fig 3.5). Time given to fruit feeding was highest in autumn (28%) and winter (27%). During the breeding period time given to fruit feeding is lower (spring 1994 = 3%; spring 1995 = 5% and summer 1994 = 12%). Therefore, it seems birds fed mostly only flowers and fruit in winter and spring, and mostly on invertebrates in summer and autumn (Fig 3.5).

The flower species used most by hihi were generally those that contributed the greatest proportion of the available nectar standing crop at the time (Table 3.2). Birds spent the highest proportion of foraging time collecting nectar at five-finger (late winter and spring), kohuhu (Spring), pohutukawa (summer), pate (early autumn), *Albizia* (late autumn and early winter), *Fuchsia* (late winter and spring) and kohekohe (late autumn to early winter) (Table 3.2). However, birds tended to avoid flowers comparatively low in nectar, even at times when their combined nectar availability was higher than more scattered nectar rich flowers of other species. For instance, during December abundant mahoe flowers contributed 67% of the available nectar, yet hihi spent on average only 1% of their time nectar feeding on this species. Instead, birds were more likely to be found feeding on the flowers of *Fuchsia* (38% foraging time) and pohutukawa (42% foraging time) (Table 3.2).

In every season except spring, birds used a greater variety of fruiting species than flowering species. The proportion of time birds gave to feeding on the various fruiting species seems to relate little to their proportional carbohydrate availability, but some fruit species seemed to be used in favour of others at times (Table 3.2). Mahoe fruits again, like their flowers, seemed to be avoided, as birds foraged at other fruit species with lower carbohydrate availability. However, this occurred in summer when most birds were spending little time fruit feeding (12% of foraging time), and were mostly invertebrate feeding (73%). Hihi could be spending little time feeding in mahoe over summer because tui are most active in these areas during this time, and/or hihi are predominantly foraging in sub-canopy species during summer because invertebrates are more easily found there.

When fruit feeding was contributing most (e.g., autumn and winter, Fig 3.5), birds showed a particular preference for pate fruit, even when green. From January through July birds did most of their fruit feeding at pate, except during February when wineberry fruits were more widely available. Other fruit species birds used most included five-finger (August through December), *Muehlenbeckia* (winter), and *Coprosma spp.* (March through June). During autumn, tutu, kawakawa, mapou and mahoe fruits are taken to differing degrees (Table 3.2), while deadly-knightshade fruits were also seen being taken during winter.

Seeds collected from hihi faeces taken at feeding stations in spring and early summer were almost 100% five-finger. Five-finger seeds were found in faecal samples in all months except April and May. The seeds of *Muehlenbeckia* were present in faecal samples for seven months of the year, placing it alongside five-finger, pate, and *Coprosma* as the most frequently taken fruiting species over the year. *Muehlenbeckia* seeds were most common in May (45%), but were also high in January (17%) and August (20%). Pate seeds dominated samples from April to August. It's interesting that most pate seeds were from small immature green fruits. *Coprosma* seeds peaked in faecal samples during March (30%) and April (31%), when pate and kawakawa seeds were also high. Mapou, mahoe, tutu, *Fuchsia*, and hangehange seeds were found in smaller numbers (< 5%) in the faecal samples mainly during autumn. Fruit species not represented in the faecal samples include cabbage tree, kohekohe, blackberry, bushlawyer and Astelia.

Displacement frequencies and tui estimates

Most displacements occurred at the highest grade nectar sites, such as rewarewa and pohutukawa. These species are not evenly distributed over Mokoia, and are relatively few in number.

Tui densities and hihi displacement frequencies varied seasonally on Mokoia (Fig. 3.7, 3.8). Tui counts were highest from December through May. Hihi mean displacement times (MDT) were highest in February (one displacement every 6 minutes of feeding time), and during October 1995 (MDT = 7 min. feeding time, Fig 3.8). The first two months following

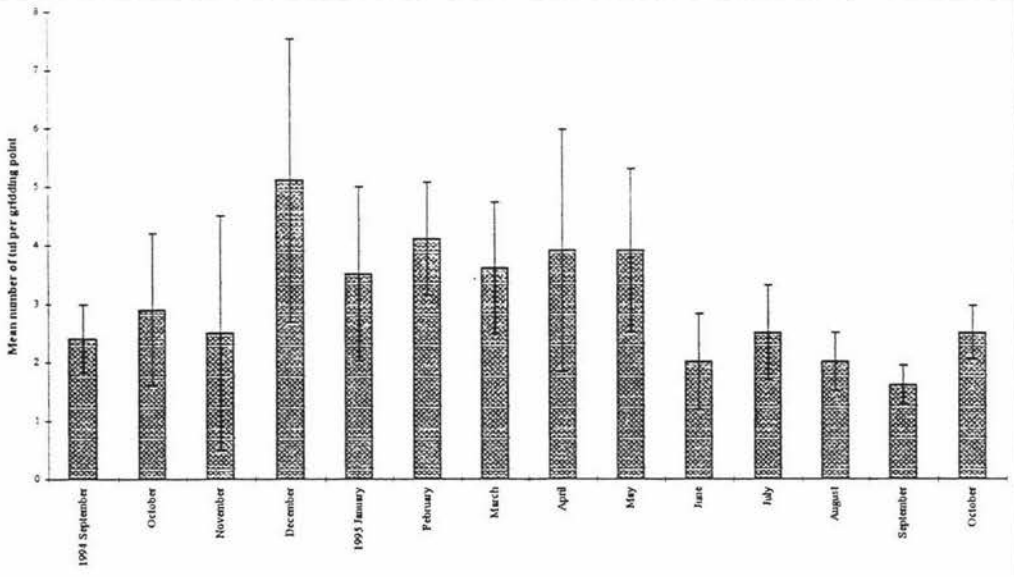

Fig 3.7. Mean monthly tui counts on Mokoia. Error bars indicate 95% confidence intervals.

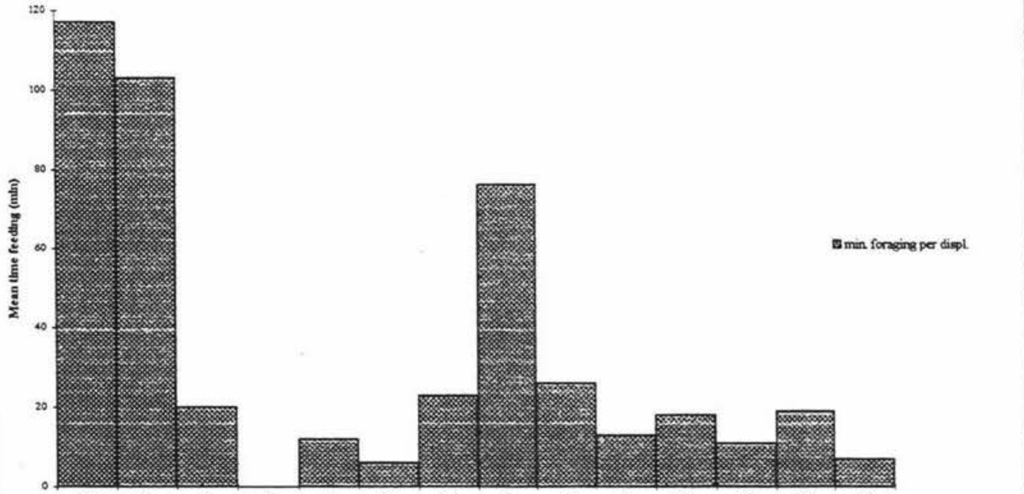

Fig 3.8. Tui displacements per amount of hihi feeding time. No displacements were recorded in December.

the translocation hihi were rarely displaced by tui (MDT 1994 = 103 to 117 mins. feeding time), which was low compared to the same time the following year (MDT 1995 = 7 to 19 min. feeding time). However, tui counts also dropped during this time. Displacement pressure increased over summer (MDT = 13 min. feeding time), peaking in February. In summer tui counts are highly variable over the island, as most birds are confined to areas dominated by canopy trees (Fig 3.7). During Autumn tui seem to forage over a wider area than they do during summer and winter. Probably, like hihi, they are predominantly fruit and insect feeding during this time. Once Winter arrives the resident or transient tui remaining confine themselves mostly to the profitable patches of *Albizia*, kohekohe and *Fuchsia*. Displacement pressure increases during this time (MDT = 14 min. feeding time). By September tui counts and their variance are relatively low, indicating those tui left are distributed uniformly across the island.

Hihi displacement frequencies dropped between March and May, which may be because tui are leaving Mokoia or fruiting species and insects are so abundant and widespread that tui and hihi can forage successfully away from each other. Tui counts decrease after May reaching their lowest in September. This gives evidence to tui not being able to economically forage five-finger flowers, as this species is responsible for over 90% of the available nectar during September (Table 3.2). June is the month of lowest nectar availability for the year (Fig. 3.4) and it's likely most of the tui have left to nectar feed elsewhere. By July *Albizia*, kohekohe and *Fuchsia* are in flower. These are not widespread, and were associated with 75% of displacement observations during July (with mostly five-finger making up the rest).

As mentioned earlier, hihi spent the least amount of time feeding during summer and winter, with feeding time only accounting for 24% to 29% of total observation time. During this time hihi are predominantly nectivorous and it's likely tui are also. This may explain why hihi displacement frequencies increase over winter compared with autumn. Fruiting species taken by hihi and tui are more widespread than the flowering species during Autumn. Therefore hihi displacement frequencies may be lowest during Autumn because they can forage away from tui, and higher in Winter because they are forced to forage closer together

Discussion

There were interrelated seasonal changes in availability of nectar and fruits, hihi time-budgets, displacements by tui, and tui counts. While seasonal changes in availability of nectar and fruit carbohydrates on Mokoia primarily reflected species flower and fruit phenologies, it's important to note these can be highly variable between years even within the same community (Castro 1995).

The proportion of time hihi were seen foraging was greatest during those months carbohydrate availability was relatively scarce (October/November) (Fig 3.4). Nectar availability varied between seasons, and was lowest in late spring and autumn. Fruit carbohydrates were available all year (i.e., > 1000 kJ/ha) and were at their highest in autumn (March and April).

Relating carbohydrate availability to hihi foraging behaviour on Mokoia

When nectar availability is low hihi may elevate their foraging time, and/or rely heavily on invertebrates and/or fruits for their energy needs (Castro 1995). Additionally, hihi may suffer exclusion from some flowering species by other honeyeaters (Craig et al. 1981), which on Mokoia is the more abundant tui population. These factors are interrelated, and may contribute to hihi becoming energy limited during some months. When faced with a situation in which nectar distribution is patchy, many honeyeaters forage preferentially at those species that offer the greatest nectar rewards (Collins & Briffa 1982; Ford & Paton 1982; Paton & Ford 1983; Collins & Newland 1986). While hihi are considered subordinate to tui, they generally foraged most at the species with the highest gross energy rewards (Table 3.3). However, displacement pressure was higher at pohutukawa and rewarewa flowers, so the mean time birds spent per flower tended to be lower at these flowers compared to other flower species (Fig 3.6).

While it's possible hihi elevated their foraging time in spring 1994 and 1995 in response to low carbohydrate availability, an increase in activity by birds could also produce the same result without a change in carbohydrate availability. Additionally, increasing time spent carbohydrate feeding in response to low carbohydrate availability assumes carbohydrate availability is high enough to supplement this increase in demand. Therefore, when carbohydrate availability is limiting (to bird's condition and/or survival) birds may not necessarily elevate their time carbohydrate feeding if extra nectar and fruit is not available. However, its likely they would spend a greater proportion of their feeding time on alternative energy sources (e.g., invertebrates).

The proportion of time hihi spent invertebrate feeding was higher in spring 1994 (57%) compared to spring 1995 (20%). While this in part could be explained by birds responding to being released into an unfamiliar area, it's more likely to be related to the higher proportion of birds making use of the feeding stations in spring 1994 (Chapter 4). Also, compared to spring 1994 the proportion of time birds gave to invertebrate feeding was higher in summer (73%), and similar in autumn (51%). Therefore, while birds were feeding more in spring, their energy needs were being met mostly from feeding on nectar, especially in spring 1995. This suggests that in spring birds were probably not elevating their foraging time in response to low carbohydrate availability, but probably because demand for carbohydrates had increased during this time. This is important because spring was the period overall carbohydrate availability was at its lowest, and birds their most active.

Winter and summer both recorded low foraging times. Winter was the only period the proportion of time given to nectar feeding was greater than time spent invertebrate feeding. During summer hihi were a lot more active compared to winter. Feeders were up all day, and birds were mostly invertebrate feeding (73%) (Fig 3.5). Day hours are longer in summer, but there is also an increase in activities performed other than foraging (e.g., aggression, courting, nest building). During summer birds may minimise foraging time by collecting food at higher rates i.e., collecting nectar preferentially at the most profitable nectar sites. This is because the foraging rate (Js^{-1}) is very species specific, and would need to be increased if time given to foraging were reduced. This may especially be true for hihi feeding chicks, because collected food has to be unloaded on returning to the nest. In winter hihi may be minimising energy expenditure instead of maximising nectar intake, and this again may relate more to long-term behavioural adjustments by birds than short-term responses to food availability. Time spent feeding may drop because of additional activities such as aggression, nest building and courting, or increase because of added demand as when feeding chicks. Therefore, time spent meeting their own energy requirements may time-limit hihi, and predispose them to the flowers and inflorescences where they can obtain the greatest energy in the shortest time..

Between the months February to July fruit availability ($kJHa^{-1}$) far exceeded nectar availability, which was at its lowest for the year (Fig 3.4). During those months birds were spending most of their time feeding on invertebrates (51%) and fruit (28%). While fruit feeding progressively increased, peaking in April (Fig 3.5), invertebrate feeding progressively decreased reaching its lowest in July. Invertebrate feeding during winter may be low because invertebrates are harder to find, and/or because hihi energy needs are low enough to be met by nectar/fruit availability. Invertebrate feeding during summer and autumn is not so easily related to carbohydrate availability, as demand for protein vs nectar/fruit may primarily influence this.

During winter its likely that the colder conditions incur additional thermoregulatory costs. Over-wintering hihi may adopt a form of inactivity to reduce their energetic costs. If true, this would partly explain the low activity in winter compared to spring. Invertebrate levels are possibly lower in winter. If nectar sources are also low hihi will not have the invertebrates to fall back on as a supplementary energy source. Alternatively hihi may be able to extract greater amounts of energy from invertebrates during these periods. It's interesting that although fruit availability exceeds nectar availability for most of winter, birds are mostly nectivorous.

It's likely nectar is a more readily digestible form of carbohydrate energy compared with fruits. Fruits probably incur a load greater than nectar, as they have seeds and get increasingly bulky with greater energy rewards (Levey 1987). However, its possible seeds and fruit pulp pass through hihi in a matter of minutes. Just squeezing out the juice alone leaves a wineberry fruit some 223 times higher in soluble sugars than a single mahoe flower, or 5.5 times higher than an average rewarewa flower (nectar sources which are available around the same time).

With flower feeding, the foraging rate is principally constrained by nectar renewal rates, the probabilities of visits by competitors, travel costs and energy rewards, and these should relate to how much time is given per flower (Gill & Wolf 1975, 1977; Wolf et al. 1975). With fruits, the foraging rate may be more constrained by crop size and digestion time. This load incurred while processing fruits may be to the hihi's advantage providing the energetic rewards are sufficiently high compared to continuous nectar feeding. A hihi feeding on *Fuchsia* at a mean foraging rate of 2.92 Js^{-1} given a 60% feeding time for three minutes could expect to obtain, 316 J of energy. A hihi feeding on wineberry with 71.26 joules on average per fruit, would only need to eat one or two wineberry fruits per minute to equal this. It's likely that not all soluble sugars locked up in all fruits are assimilated by hihi, as some fruits are passed through with little more than the shine taken from their skins.

Rasch (1985) suggested that hihi preferred nectar to fruit, as foraging in her study area followed patterns of flower availability more closely than the availability of fruit. Pyke (1980), Stewart & Craig (1985), and Craig (1985) pointed out that many studies in different areas and different times have shown that the diet and behaviour of many honeyeater species varies markedly. Therefore models based on the assumption that nectar is the major component of diet may not hold for other areas, times or individuals.

Rasch and Craig (1988) on a study of honeyeaters on Little Barrier Island wrote that "hihi appeared to avoid flowers that were used by bellbirds. It is possible tui did not consider hihi as much a rival as bellbirds hence hihi may reduce the level that they are harassed by moving into flowers used by the more dominant tui rather than those used by bellbirds". Although this is likely, it could be explained to some extent by the type of flowers hihi and bellbirds feed on compared to tui on the same tree rather than the flowers taken from different species. Craig et al (1981) in a discussion on factors that affect honeyeater diet and foraging wrote under the subheading `Importance of body size', `larger birds such as the tui are excluded from feeding within confined areas such as small divaricating shrubs (eg *Coprosma rhamnoides*) and from perching on less robust plant parts (eg flower stems of *Dysoxylum*) or species (Stewart 1980)'. Hihi and bellbirds can also forage flowers while hanging upside down which tui seem not to do. Possibly hihi are more likely to forage around tui than bellbirds because they deplete similar flowers, and ones which tui don't. It's also possible tui are more inclined to displace bellbirds for reasons related to which flowers they visit on the same tree and how long they stay. Maybe bellbirds are more inclined to flock at these sites than hihi, or less inclined to move quickly between flowers, or take the most peripheral ones. This view favours the idea of co-utilization and exploitation to explain resource competition between tui and hihi, and pure exploitation between hihi and bellbirds. When tui and hihi are present but bellbirds absent, those flowers hihi can feed from in the same tree as tui may become less predictably distributed (to a hihi) on that tree when bellbirds are also present.

Relating flower profitability to hihi foraging and tui displacements

The flowering species with the highest nectar energy per flower, such as pohutukawa, rewarewa, and flax are also the sites most vigilantly defended by the tui. This means hihi visitations to these flowers were generally always of short duration, but with the majority ending before displacement by tui (Fig 3.6). Assuming birds depleted all the nectar per flower per visit, the calculated energy extraction rates at pohutukawa and rewarewa would be 15-24 Js^{-1} and 6-10 Js^{-1} respectively. In contrast, bird's energy extraction rates calculated at Fuchsia (2-4 Js^{-1}) and kohekohe (2-2.4 Js^{-1}) are comparatively less profitable. However, its unlikely hihi are depleting all the nectar per flower at pohutukawa or rewarewa. Birds on average spent more time per flower at the lower grade flowers not so heavily defended by tui (e.g., *Fuchsia* and *Earina*, Fig 3.6). This may place more importance on relative profitability, because the profitability of the heavily defended sites are only beneficial to hihi relative to the background nectar availability of the other, undefended flowering species. For example, if hihi can obtain more energy in two seconds of feeding per pohutukawa flower than three seconds or more on alternative lower grade flowers, then foraging at pohutukawa is still relatively profitable. If tui don't displace the intruder within the minimum time for profitability, then hihi would be expected to continue visiting these sites. In addition, hihi may opt to vary their foraging behaviour at these sites to minimise the chance of displacement within the time of profitability. I believe I have observed this, as hihi clearly opt for a fleeting foraging style at these sites, foraging almost always from the lower peripheral flowers while moving quickly from tree to tree. Tui, when in the same tree tend to occupy the crown or top half of the pohutukawa tree, away from these flowers. In contrast, hihi feeding on lower grade undefended flower species generally spend more time per flower, more time per tree and visit flowers all over undefended trees.

Flower profitability is also likely to depend on a number of other factors apart from floral structure, nectar concentration and the positioning of flowers on plants (Wolf et al. 1976; Montgomerie 1984; Montgomerie et al. 1984; Collins & Paton 1989). These probably relate to the mechanics of nectar extraction. Many flowers visited by hihi, such as five-finger, have so little nectar that hihi literally have to lick the sides of the flowers. The nectar extraction rates may differ for flowers which hihi dip their tongues into (Hainsworth 1973; Kingsolver & Daniel 1983). Licking probably relies most on tongue surface area, whereas dipping probably relies on both tongue surface area as well as capillary pressure as a result of the brush tipped tongue (Weymouth et al 1964; Kingsolver & Daniel 1983). Because of this, the viscosity, as well as the volume of nectar may also contribute to nectar extraction rates (Baker 1975; Kingsolver & Daniel 1983). *Fuchsia* has very fluid nectar so is quite dilute. The nectar energy per flower is greater in *Fuchsia* compared to *Albizia* (Fig. 3.1). *Albizia*, however, receives a higher profitability score (Fig 3.3) than *Fuchsia* because *Fuchsia* has flowers further apart, so flower visitation rates are lower at *Fuchsia* compared to *Albizia*. *Albizia* has sufficient floral nectar packed into dense enough inflorescences to make this species a more profitable alternative. Also, tui seemed more inclined to displace hihi at *Albizia* than *Fuchsia*. During the *Fuchsia*-kohekohe-*Albizia* flowering period tui were more often observed in *Albizia* than *Fuchsia*. *Albizia* though is more easily located when in flower, so it is possible I was more inclined to note tui in *Albizia* compared with *Fuchsia* when moving between locations.

Tui usually only displaced hihi that came near their centres of activity. Tui numbers were highest during the months November to February (Fig 3.7). Taking these two factors into account there tended to be strong seasonal changes in displacement frequencies (Fig 3.8). Tui were most aggressive towards hihi when carbohydrate sites were confined (i.e., summer and winter). Hihi were displaced most at the most profitable flower species such as flax, pohutukawa and rewarewa. Tui also regularly displaced hihi in some wineberry trees. Although hihi were displaced most at these sites, hihi were never totally excluded. They were probably not depleting all nectar per flower visit but possibly taking nectar at maximal rates to minimise time per flower and so the chance of displacement. During autumn, displacements and tui counts drop. This is because in February tui have moved out of the pohutukawa and into the areas hihi are more commonly found. During early autumn wineberry, kawakawa, *Coprosma spp.* and pate fruit become abundant all over Mokoia. Many tui and their fledglings are seen feeding on these species. Cicadas were also very abundant in 1994/95, and both tui and hihi were regularly seen hawking them.

Tui were often seen in Autumn flying towards Mokoia, sometimes at great height above Lake Rotorua. It's clear that many tui breed on Mokoia as a good number of nests and recently fledged juveniles have been seen. Some tui may bring their young to Mokoia from surrounding districts to feed on the abundant wineberry fruits and cicadas during February. During summer, feeders were up everyday, yet during late summer hihi visitations to feeders were at their lowest even though tui counts peaked for the year during that time (Chapter 4). This may be explained, in part, by the way hihi forage around tui, as mentioned earlier, and may possibly indicate nectar sources are so high that tui can't or don't have to defend them at all costs. Once pohutukawa has finished flowering hihi displacements peak (e.g., February), possibly because tui numbers are still high. During this time hihi were also observed displacing tui fledglings which were still being fed by their parents. So the tui counts during this period may reflect more that seasons reproductive success than any standing adult population. Juvenile tui may be forced to remain on the island till strong enough to leave. It may be that some adult tui vacate Mokoia for brief periods after the pohutukawa flowering period, leaving their young. The tui drop after May might, therefore, be the juveniles leaving the island after feeding on wineberry and insects.

Comparing foraging data from this study with previous studies

Figure 3.9 compares foraging data of hihi on Little Barrier (white bars), Kapiti (grey bars) and Mokoia (black bar) islands. Castro (1995), in a study of Kapiti hihi, pointed out that although there are variations in the seasonal use of different food items from year to year, there is a consistent difference in autumn between Kapiti and Little Barrier island. On Little Barrier island hihi fed mostly on fruits in autumn, while on Kapiti they predominantly take invertebrates. Mokoia hihi also, during autumn, feed mostly on invertebrates, and take a similar proportion of fruits to Kapiti hihi. Little Barrier hihi seem to take proportionally more fruits in every season except winter than both Kapiti and Mokoia hihi. In winter, both Little Barrier and Mokoia hihi feed predominantly on nectar, while Kapiti hihi are still mostly invertebrate feeding.

Castro (1995) explained the high consumption of invertebrates on Kapiti in three ways. First, as a shift in diet due to a shortage of fruit and/or flowers. Second, as a result of exclusion from the available flower and/or fruit sources, and third as a shift in diet due to an increase in access to artificial nectar sources. Castro`s data supported the first explanation as fruit and nectar sources were probably scarce. This would have had the added effect of elevating exclusion pressure forcing hihi to the artificial feeders. Therefore, its likely these three explanations are related to why hihi visitation rates at the artificial feeders should increase, but not explain why hihi who have access to feeders should predominantly feed on insects. Unless, even though nectar feeders are up, hihi are still forced to take insects as an additional energy source. It may be that hihi are primarily protein limited not energy limited during autumn and winter. If nectar is sufficiently scarce hihi may be forced to take more fruits and/or frequently return to the artificial feeders. If invertebrates themselves are scarce

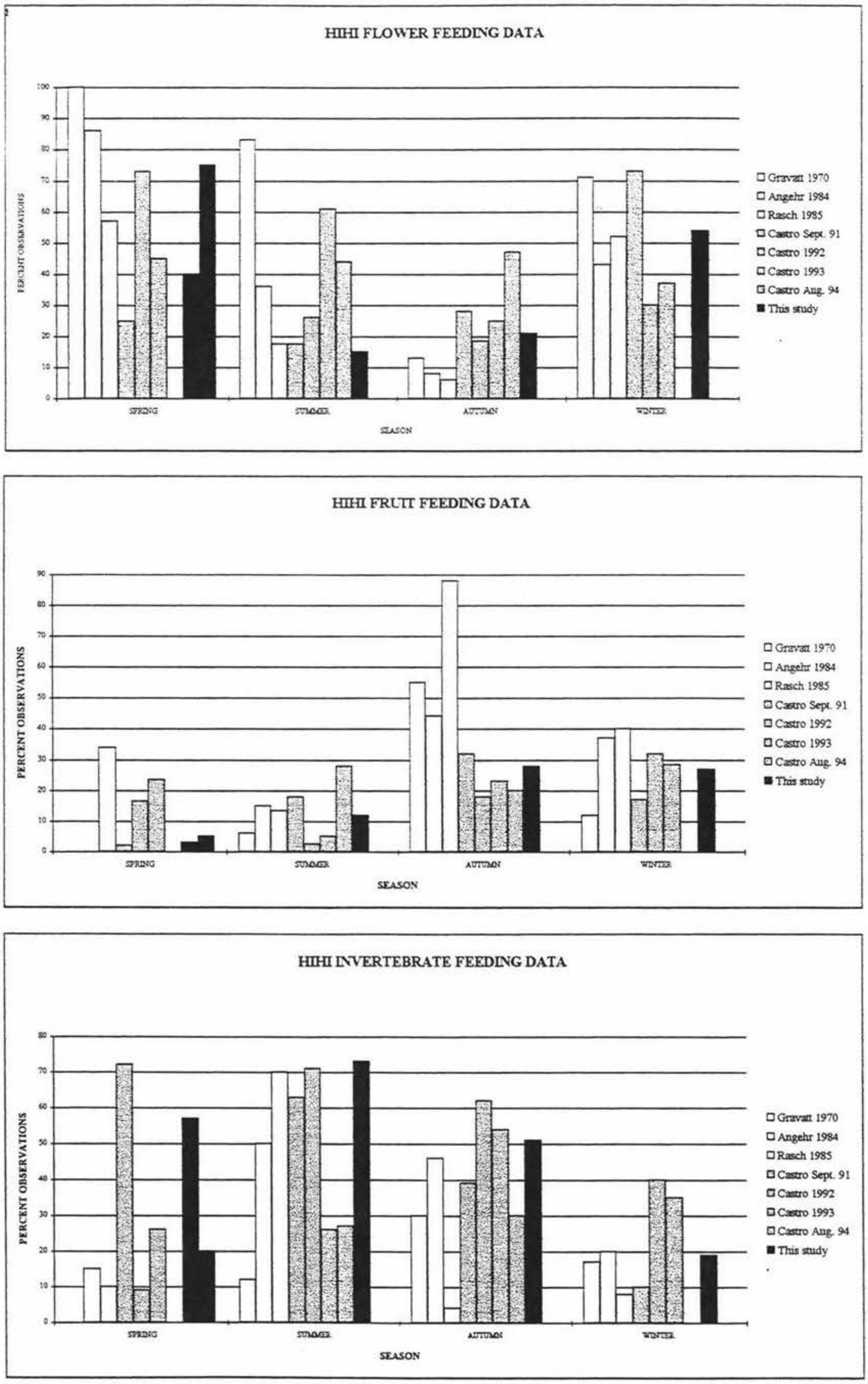

Fig. 3.9. Hihi feeding data for the islands, Little Barrier (white), Kapiti (grey), and Mokoia (black)

hihi would be expected to spend more time searching for them while visiting the nectar sites which allow them to extract energy at the fastest rates. This does not necessarily mean hihi are limited by nectar availability as more scattered flowers and fruits are likely to be available but offer rewards at lower rates. It seems that those hihi with access to feeders spend the least proportion of time foraging anyway, so a greater proportion of time given to invertebrate feeding may not actually mean they are consuming more insects. It may be that hihi are very responsive to nectar extraction rates when time given to nectar feeding has to be minimised. If invertebrates around feeders become heavily depleted by hihi, then hihi may need to continually forage further away for invertebrates, or spend more time searching for invertebrates around the feeders.

For the first two months on Mokoia hihi fed predominantly on invertebrates. Spring 1994 data shows hihi spent twice as much time invertebrate feeding than they did at the same time the following, and half the time nectar feeding. Castro's (1995) data shows the same but more pronounced difference between the first and second Spring. This again may be related to the artificial feeders, but could also be related to foraging strategies adopted by hihi in unfamiliar or unpredictable habitats following a translocation.

Many studies in Australia have shown that although areas inhabited by honeyeaters have pronounced seasonal changes in nectar availability, many honeyeater species remain sedentary (Collins et al. 1984a,b; Ford & Paton 1985; Newland & Wooller 1985; Paton 1985; Pyke 1985; McFarland 1986, Pyke & Recher 1986, 1988; Ramsey 1989). Tui are a very mobile species, and fly large distances in search of nectar (Stewart 1980; Angehr 1986; Bergquist 1985; Stewart & Craig 1985). Bellbirds and hihi seem to be more sedentary (Craig et al. 1981). A consequence of birds being highly nectarivorous and sedentary is that they will deplete their nectar resources when nectar production is low. Armstrong (1991) found foraging time was inversely correlated with nectar availability in New Holland and White-cheeked Honeyeaters. Hihi on Mokoia also spent more time foraging when nectar availability dropped (during spring and autumn). Winter foraging though did not follow this pattern, as time spent foraging and nectar availability were both low. This may imply carbohydrate availability is sufficiently high on Mokoia for most of the year except maybe the breeding period, and/or that hihi adopt different feeding strategies during the breeding and nonbreeding periods.

Angehr (1984), studying the ecology and behaviour of hihi on Little Barrier wrote, " the seasonality of flower and fruit use by Stitchbirds appears to be governed by the availability of fruit. Flowers are available all year on Little Barrier, but the availability of fruit is more restricted. Substantial amounts of ripe fruit first become available in January, and fruit is almost gone by July. Stitchbirds feed primarily on fruit as long as it is available, and switch to nectar only when most fruit is gone".

Most fruits offer higher rewards per item than most flowers (Fig 3.1, 3.2). For example, an average single *Fuchsia* tree on Mokoia at peak flowering will have an available nectar standing-crop between 1700 and 7,500 joules. An average single Wineberry tree with fruit on Mokoia will have an available standing-crop between 24,400 and 213,000 joules. Additionally, fruits are distributed over a wider area than flowers, mainly because fruiting species are more abundant than most flowering species on Mokoia (Chapter 2). If invertebrates are scattered to rare also, then hihi may prefer to obtain their energy needs from the scattered fruit and flower sources while in search of invertebrates. In this sense hihi may be viewed more as flower opportunists, rather than primarily nectarivorous.

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Chapter 4

Effects of food supplementation on foraging behaviour, survival, and reproduction of hihi

Introduction

The primary aim of this project was to test whether hihi were limited by natural food availability on Mokoia, and therefore whether supplementary feeding would be needed to sustain the Mokoia population. As noted in Chapter 1, it is not sufficient to correlate natural variation in food availability with survival, reproduction, and behaviour. It was important to obtain good data on natural food availability (Chapters 2, 3) to understand why food was limiting at particular times i.e., because overall availability was poor, because available nectar and fruit sources are widespread and unprofitable, because tui were excluding hihi from available carbohydrate sources or because hihi energy demands were high at the time. These data also allowed us to predict whether patterns of food limitation were likely to be consistent from year to year. However, the only way to demonstrate that food is limiting is to do experiments (Armstrong & Pyke 1991; Armstrong 1992a,b).

To test the hypothesis that any food is limiting, it is necessary to increase the availability of that resource and see if a parameter changes in the predicted direction (e.g., a change in body mass). There needs to be controls (e.g., individuals excluded from resources), and replicates. In wildlife ecology, the parameters of interest are usually survival, reproduction, territory or home-range size, or aspects of behaviour. Our experiment involved using feeders to periodically increase food availability to hihi to test whether access to feeders affected bird's foraging behaviour, weights, survival and/or reproduction.

With recovery programmes of any endangered species, it's difficult to balance the need to do experiments with the desire to do the management that seems best for the population (Armstrong et al. 1997). Without experiments, we run the risk of doing expensive long-term management that has little or no benefit, wasting critical resources. However, doing experiments means controls are needed, which may amount to sacrificing some individuals or populations if the management turns out to be necessary.

While it was important to find out if the hihi survival rate was limited by food supply, it wasn't desirable for birds to starve to death because they were excluded from supplementary food (both for ethical reasons and to maintain a reasonable sample size. The approach adopted was to assess starvation indirectly by measuring weight loss during short-term absence of supplementary food. Using curvlinear models for weight loss during starvation (Kleiber 1975). These data could be used to extrapolate the amount of weight loss that would have taken place before the natural food supply improved. The number of birds that would have lost condition or died without supplementary food being replaced could then be estimated.

The experiment assessing effect of food on behaviour, weights, and survival rate therefore involved providing supplementary food on an on-off basis, determining what times (if any) these factors varied in the predicted direction. In doing this, it was necessary to use a time scale that was long enough to detect significant weight loss but short enough to avoid killing birds. It would have been necessary to quickly modify or stop the experiment if birds had obviously been dying when supplementary food was removed. In addition to weighing birds, census data were used to compare disappearance rates during times when food was available and unavailable.

Another issue was to decide whether to test for food limitation in general, or carbohydrate limitation. This study has focused on carbohydrates because: (1) previous researchers had hypothesised that failure of hihi translocations were due to lack of adequate year-round supply of nectar and fruit (e.g., Angehr 1984a,b; Lovegrove 1986; Rasch 1991; Castro

1995), (2) Mokoia seemed likely to have limited diversity of flowers and fruit, being a small island with young vegetation, and (3) the success of insectivorous robins and saddlebacks translocated to Mokoia suggested that there was good supply of invertebrate food (Armstrong & Craig 1995; unpublished data and personal observations). However, during the breeding season (i.e., October-March, Castro 1995) there are elevated demands protein and minerals.

The experiments therefore tested: (1) whether survival and foraging behaviour outside the breeding period was limited by carbohydrate availability and at what times it was limiting, (2) whether reproduction was limited by food availability (i.e., including other dietary components). While an on-off experiment was appropriate for behaviour and survival, it wasn't appropriate for measuring whether reproduction was food limited, i.e., such an experiment would simply result in part of the reproductive cycle period taking place with supplementary food, and part of it without supplementary food. It was necessary to have birds either supplemented or not supplemented for the whole reproductive period. Therefore, the best experiment was to supplement some birds and not others. During the breeding period we compared reproductive success of birds with easy access to feeders with birds that had poor access to feeders (Armstrong et al. 1997). This was possible during the breeding period because birds were attached to their nest sites, and some birds needed to travel a long distance to the nearest feeder.

Methods

The data described in this Chapter overlaps with similar studies by other authors on Mokoia hihi. Parts of the methods and analysis for this Chapter were obtained from the work of associate researcher Dr. I. Castro. During the breeding season 1994/95 the feeding stations were maintained mostly by Dr. I. Castro. Additionally, all reproductive data and analysis presented in this chapter is the work of Dr. I. Castro and Dr. P. Armstrong.

Food composition and presentation

Outside the breeding season, the supplementary food was 20% W/W sugar solution. During the breeding season the supplementary food was Wombaroo (20% w/w sugar solution with other supplements designed to give a complete diet for honeyeaters). The food was presented in commercial hummingbird feeders (Perky Pet #212-P) which hold up to 1400ml. Feeders were changed and disinfected every 2-4 days when sugar water was used, and daily when Wombaroo was used.

The feeders were always accessible to hihi. Plastic mesh would have been used to exclude tui if they had. However, this was never necessary. It seems tui were reluctant to come under a plywood board, and even placing one board over a feeder was enough to exclude tui.

Experimental design

Supplementary food was available at three permanent feeding stations (Fig. 4.1). During the on-off experiment, feeders were available for 16 days at the three permanent stations, then absent for 12 days. The feeders were available for the first three weeks after the release. They were then removed and replaced 12 days later. The plan was to continue the on-off experiment until breeding began. However, it became clear in mid-October that the birds were suffering leg injuries due to bands used on them (Armstrong et al 1997). Supplementary food was therefore supplied continuously until birds had recovered from their injuries as much as possible. The on-off experiment was re-initiated in January 1995, when most females had completed one nesting attempt. Feeders were removed on 10 January, and were then available on an on-off basis until October 1995. After which food was available continuously.

Weights and use of feeders

Birds were weighed at feeders using electronic scales. For the on-off experiment, 'fed' weights were measured on at least one day at the end at the end of each period when feeders were available. 'Unfed' weights were measured by weighing birds over the first three days

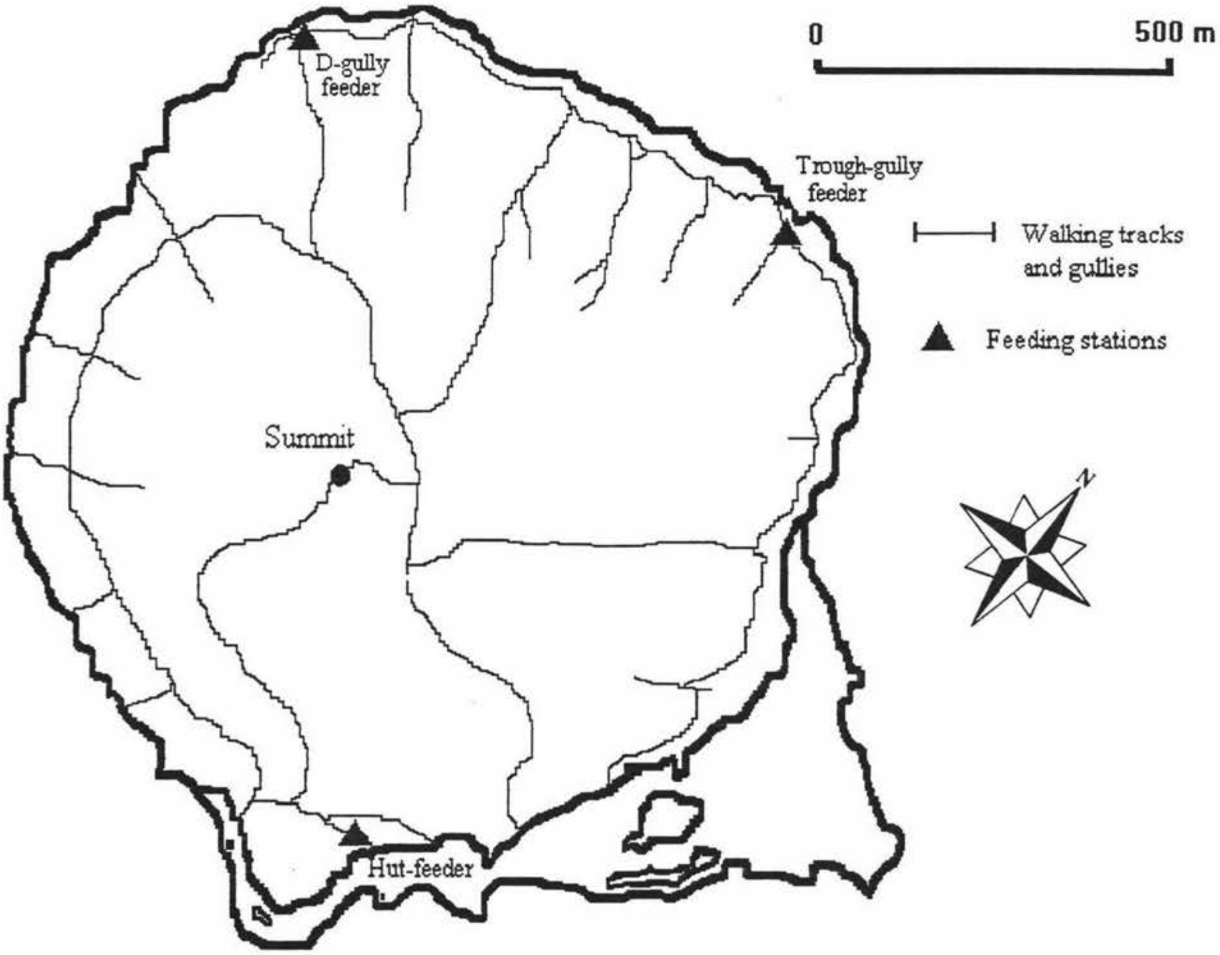

Fig. 4.1. Map of Mokoia Island showing the location of the three permanent feeding stations.

that feeders were available, noting each bird's weight the first time it used a feeder. Weights recorded every two weeks during the breeding season. All birds were identified by individual colour-band combinations.

The amount of feeding by each bird was also recorded. For each visit, we recorded the number of seconds from the time the bird started feeding until the time it left the feeder. Therefore, feeding time includes the time standing up to swallow the solution in addition to the time actually licking at the solution.

The scales were specifically designed for weighing birds in the field (Weighing Systems Ltd.). When each bird fed, it perched on a piece of dowelling connected to a loadbar (Fig. 4.2). This produced a digital readout of its weight to the nearest 0.5 g. Birds could not feed without sitting on the perch, and usually did so one at a time. It was possible for two (and occasionally three) birds to sit on the perch. When this happened, the weight of the bird already on the perch was subtracted.

The feeder was also mounted on the loadbar, so the feeder was weighed as well as the bird. Therefore, the starting weight (before the bird landed) was subtracted from the total weight to get the bird's weight. This was necessary to get accurate weights. If the feeder was separate from the weighing system, the bird's weight would oscillate every time it dipped its beak in the solution. It was also useful because we could measure the weight of solution removed by each bird, and from this measure the amount of energy removed per second of feeding time. However, when the feeders were busy, birds sometimes fed in rapid succession so that it was impossible to get the starting weight for each bird. In these cases, we assumed that the weight of solution removed was proportional to the amount of time that each bird fed. For example, one bird might feed 30 s then another feed for 60 s in rapid succession, removing 1.5 g of solution between them. We then assumed that 0.5 g had been removed by the first bird, and used that to estimate the starting weight before the second bird.

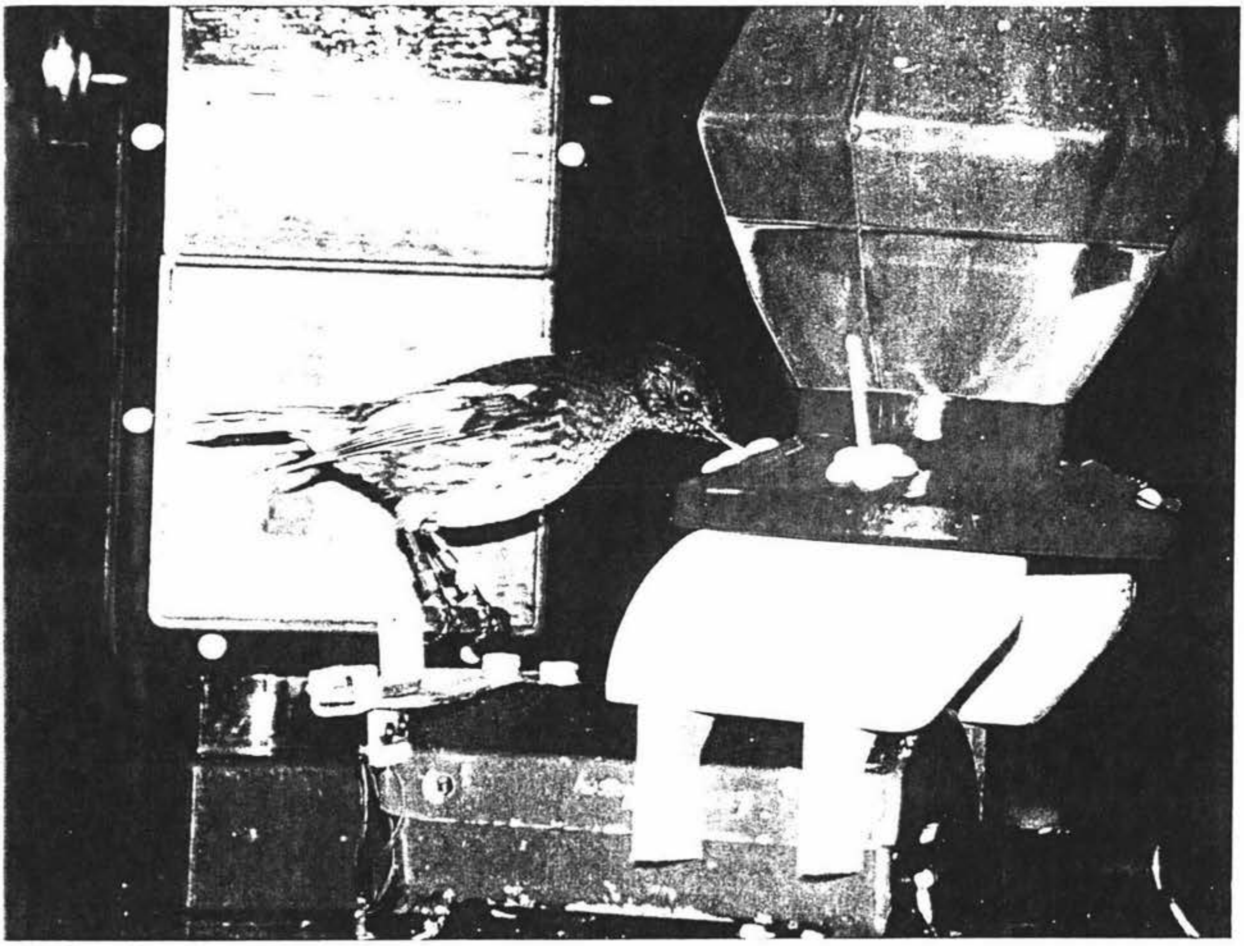

Figure 4.2. System for weighing hihi at feeders and recording how long they fed. The bird is perched on a loadbar which is connected to the digital readout above the bird. The loadbar also weighs the feeder, which becomes lighter as birds remove the sugar solution. In this case the reading was -18.0 g before the bird hopped on the scale, so the bird's weight is 29.0 g. When the bird hops on the perch, she also depresses a microswitch which signals a video camera to start recording.

Initially, there was an observer at each station to record weights. However, birds re-discovered feeders too slowly to measure unfed weights this way. When this method was used on 10 October 1994 only one bird re-discovered a feeder in 9 hours of observation (at all 3 feeders) on that day. Starting in January 1995 we used three video recorders (Panasonic NV-A1A) to record at feeders. Each camera was housed in a wooden box with a glass front, supported by a 1.5 m pole 1.5 m from the feeder. Cameras were focused to record the largest image possible that included the digital readout and the bird's colour bands. The body of the digital readout provided a background for the image, and was painted black for maximum contrast (Fig 4.2).

Because the tapes were only 90 minutes, we used electronic controllers (designed by Barry Spring-Rice) to pause the cameras when birds weren't feeding. Each controller was connected to the perch at the feeder. When a bird landed on the perch it depressed a microswitch, sending a pulse which caused the camera to start recording. When the bird left the perch, the camera continued to record for 3 s, allowing us to record the weight with no bird, then paused. These cameras could not actually detect whether or not the microswitch was depressed, but could only receive pulses. If the perch was depressed twice within 3 s (e.g., if a bird landed just after another had left), the recording would go out of synch, i.e., pause when birds landed and record again when they left. However, the controller was programmed to re-set itself every 40 s, to avoid staying out of synch. This system was only likely to go out of synch when the feeders were busy. We avoided the problem by running the feeders continuously at busy times. Very few weights were missed due to a controller going out of synch, and we never missed the unfed for any bird. When few birds were using feeders, cameras could be left all day without changing the tape.

The day was divided into four time periods: sunrise to mid-morning, mid-morning to noon, noon to mid-afternoon, and mid-afternoon to sunset. When measuring fed weights, we recorded one 90-min. tape for each time period if feeders were too busy. If few birds were feeding, we recorded all day with the controllers up to two days. When measuring unfed weights, we always recorded all day and blocked up the feeding holes over night to prevent any unrecorded visits.

When recording data off the video tapes, the weight on the digital readout we noted every 2 s and the median weight for each visit.

Behaviour

The methods used to record bird observations is outlined in Chapter 3. In this chapter observation data is split into times when feeders had been available for at least 13 days (fed birds), and times when feeders had been unavailable for at least 10 days (unfed birds). A lot of the 'unfed' data was recorded in the first few days after feeders were available again, but data were excluded for birds that had discovered a feeder (as indicated by video tape)

Reproduction

Fifty five nest boxes were erected around the island by students from Rotorua Highschool before birds began breeding. These were checked regularly, and nests monitored after females initiated breeding. We used the number of young fledged from the nest as the measure of reproductive success, and compared success of feeders nesting close to and far from feeders.

Analysis

ANOVA was used to test whether weights, feeder use, or time budgets varied according to (1) whether supplementary food was available ("fed"), and (2) the month. differences among individuals were controlled for in all analyses by treating the bird's identity ("individual") as a third factor in ANOVA. All three factors were treated as fixed. This means that the conclusions apply only to the particular set of birds studied. However, this is appropriate as most of the population was regularly observed.

The fed month interaction term was included in all tests, to determine whether the effect of supplementary food varied according to the time of year. Bird*fed? or bird*month interaction terms were not included. If a bird had multiple observations per field trip, these were merged or averaged into a single observation, and these were treated as the units of replication.

There was a lot of turnover of birds early in 1995, due to both mortality and recruitment. Therefore, analyses were done separately for 1994 and 1995. All observations in 1994 were done when feeders were available, except for some time budget analyses which were excluded from statistical analysis. Therefore, the 1994 analyses do not include "fed?" as a factor. Because there were two fieldtrips per month in 1994, the analyses test for differences among fieldtrips rather than differences among months.

With time budget data, the proportions were given arcsin square root transformations. No transformations were used on the other data sets, since the residuals always conformed closely to normality and there was no apparent heteroscedasticity.

Mortality was estimated using the Manly-Parr method (Manly & Parr 1968). For each field trip, the population (N_i) is divided into two categories: those seen on later trips (C_i) and those not seen on later trips (N_i - C_i). The birds seen on that trip (n_i) are also divided into those seen on later trips (c_i) and those not seen on later trips (n_i-c_i). Therefore, c_i/C_i gives an estimate of the proportion of birds sighted out of those alive (p_i). With the Manly-Parr method, N_i is estimated by n_i/p_i. This includes an estimate of the number of birds that were alive, but were not seen on that or subsequent trips. It may therefore be higher than the minimum number alive, given by $C_i + n_i - c_i$. However, it will be close or identical if p_i is high, mortality if low, or fieldtrips are frequent.

Results

Use of feeders

Hihi showed a clear seasonal pattern in their use of feeders (Fig. 4.3). The proportion of birds using the feeders per trip averaged (70%). However, there was a clear drop in the number of birds using feeders and the number of birds alive after the breeding season (i.e. after January). From January to March only 30% of birds were using feeders, and this dropped to 8% from April to early July, then rose to 50% from late July to early November. Therefore, its unlikely feeder availability had any effect on most birds after the first three months following their release. Low feeder use after January can't be explained by exclusion. Feeder use was minimal for most hihi outside the breeding period, and hihi did not stay by feeders or defend them. Tui were rarely observed using feeders, and never seen defending them.

The amount of feeder use per bird (excluding those not using feeders at all) also varied seasonally (Fig 4.4). The time per bird spent visiting feeding stations varied significantly between field trips from September-December 1994 ($P < 0.001$; Table 4.1), and between months from January-October 1995 ($P < 0.001$; Table 4.2). The overall feeder visitation rate for birds using feeders (from October 1994 to October 1995) was 48 s/h (Mean, males = 59 s/h, females = 39 s/h). Birds spent the least time visiting the feeding stations in winter. The high feeder use per bird in early May (Fig. 4.4) was due to two birds that fed extensively. Otherwise the average feeder use in winter was less than 25 s/h per bird. Birds on average drank about 0.03 g of solution per second of feeding time, obtaining about 5.2 mg of sucrose (20% W/W). This gives a mean energy intake rate of 86 J/s birds obtained at the feeders (assuming 1 mg of sucrose corresponds to 16.5 joules of energy).

Given that hihi foraged for about 10 hours of the day this equates to a mean daily visitation rate of 590 s/day for males and 390 s/day for females. This in turn equates to an average 50.7 kJ of energy per day for males and 33.5 kJ/day for females. This can be compared to predicted energy requirements based on Collins & Newland's (1986) equation derived from measurements on brown honeyeaters *Lichmera indistincta*. Assuming a 13 ^{0}C day

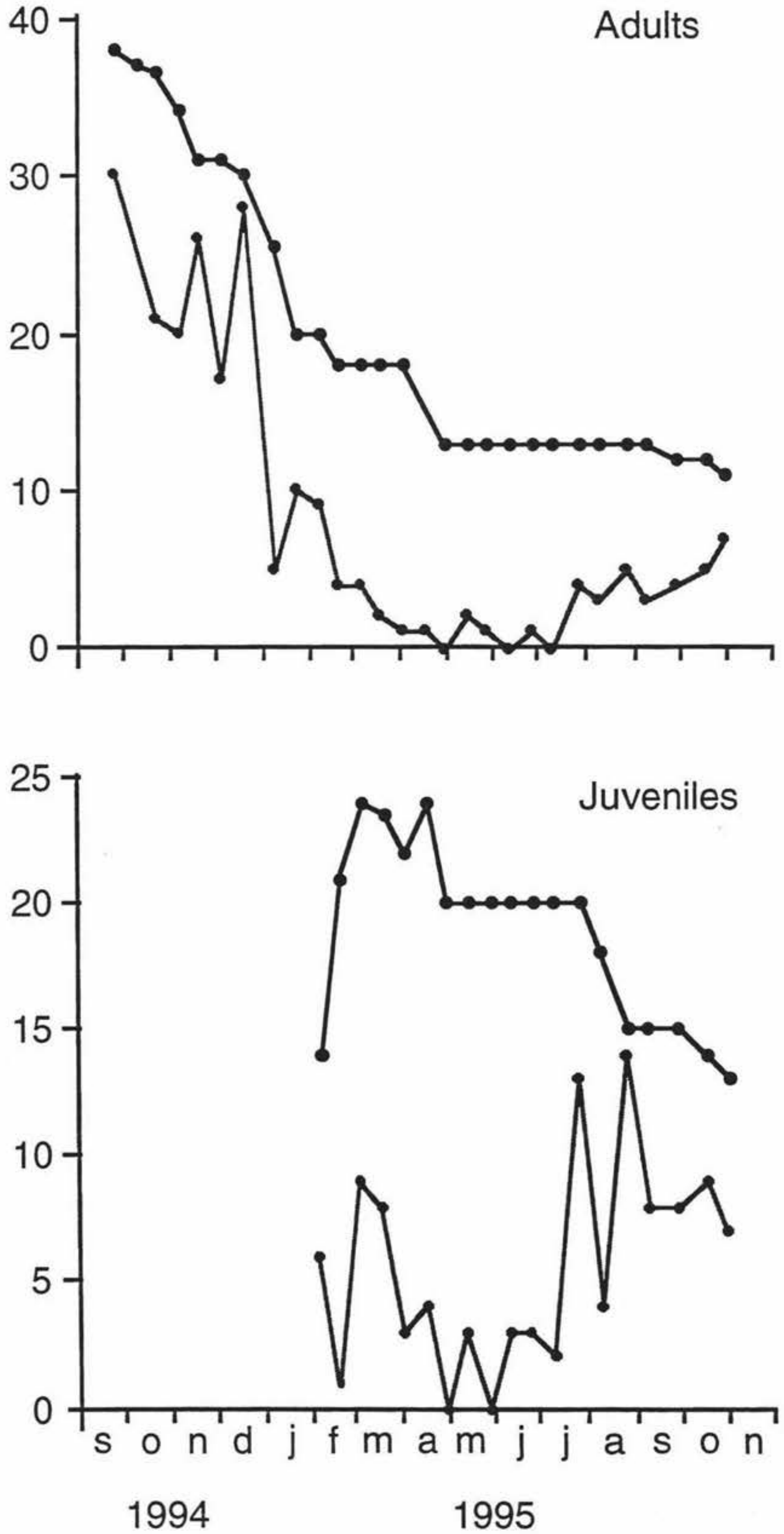

Fig. 4.3. Number of birds using feeders (lower lines) out of the number of birds alive (upper lines). Juveniles were only counted after 28 days post-fledging. Numbers alive were estimated with the Manly-Parr method, in combination with the minimum known to be alive on each date.

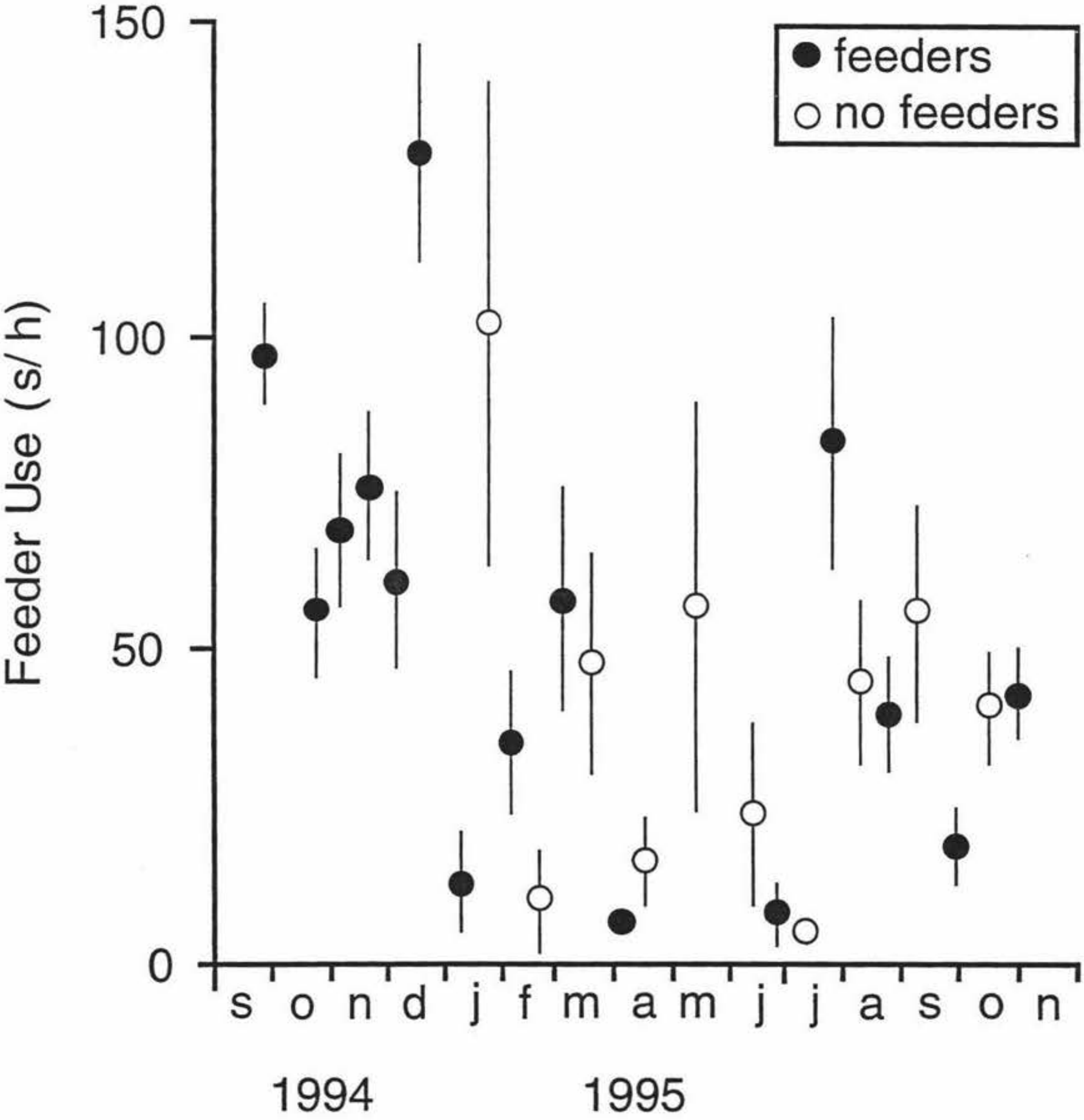

Fig. 4.4. Amount of feeder use by hihi that visited feeders (i.e., those that visited at least once during that field trip). Values shown are means +- standard error, using individuals as replicates.

Table 4.1. Two-way ANOVA testing whether feeder use per bird (s/h) varied over 6 fieldtrips from September-December 1994. Zeros are not included -- i.e., birds are excluded from the data set for a fieldtrip if they never used a feeder (see Figure 4.3 for proportion of birds using feeders on each trip). If a bird didn't use feeders on two or more trips, all data for that bird are excluded.

SOURCE	SS	DF	MS	F	P
INDIVIDUAL	190362	31	6141	2.031	0.005
FIELDTRIP	117875	5	23575	7.799	0.000
ERROR	279261	99	3022		

Table 4.2. Three-way ANOVA testing whether feeder use per bird (s/h) varied from January-October 1995. Zeros are excluded, as in Table 4.1. The 'Fed?' variable indicates whether it was a 'fed' trip (feeders available for the previous 15 days) or 'unfed' trip (feeders unavailable for the previous 12 days). Birds are excluded if they didn't use the feeders during two or more months, or didn't use feeders on both 'fed' and 'unfed' trips.

SOURCE	SS	DF	MS	F	P
INDIVIDUAL	159585	23	6938	3.100	0.000
MONTH	86054	8	10757	4.807	0.000
FED?	294	1	295	0.132	0.718
MONTH*FED?	93380	8	11672	5.216	0.000
ERROR	214834	96	2238		

temperature and 9 ^{0}C night temperature, this equates to a predicted requirement of 68 kJ/day for a 37 g bird (typical male) and 60 kJ/day for a 31 g bird (typical female). Based on the overall measured amounts of energy males and females extracted from feeders, and their predicted energy requirements, of the birds using feeders males obtained on average a predicted 74.5% of their daily energy needs from feeders while females obtained on average about 56% of their daily energy needs from feeders.

Changes in bird weights

For males, weights of birds used in analyses ranged from 34.7 to 41.8 g (mean = 37.8, sd = 1.7, n = 27). For females, they ranged from 28.9 to 35.6 g (mean = 31.9, sd = 1.6, n = 22). The estimated weight for each bird is a least squares mean that takes into account when the bird was weighed. The analysis included the individual as a variable, and therefore took into account differences in weight among birds.

To determine if weights were affected by feeders, it was necessary to know whether weights varied with the time of day. Bird's weights were initially separated into four times of day and treated each as independent observations, and time of day was included as a factor in ANOVA (Tables 4.3, 4.4). Because 'unfed' weights were obtained only the first time a bird used the feeder, the time effect data came from 'fed' weights. Time of day had a significant influence on birds weights ($P < 0.05$), and this time effect didn't change seasonally ($P > 0.35$ for date-month interaction term). Weights increased over the course of the day, and birds were on average 0.6 to 0.7 g heavier in late afternoon than early morning (Table 4.5).

For subsequent analysis, for time of day was corrected by subtracting the estimated effects shown in Table 4.5. For 'fed' trips, this was done for each time of day a bird was weighed. The corrected weights were then averaged to get the birds weight for that fieldtrip. For 'unfed' trips, the single weight for each bird according to its time of day. A single weight datum per bird was therefore obtained for both 'fed' and 'unfed' trips. These were then treated as independent observations.

Table 4.3. Three-way ANOVA testing whether hihi weights (g) varied with time of day in 1994 (early AM, late AM, early PM, or late PM). It excludes individuals that were not weighed at all four times of day, or were not weighed on at least three different trips.

SOURCE	SS	DF	MS	F	P
INDIVIDUAL	3425	27	126.8	38.71	0.000
FIELDTRIP	498	5	99.6	30.40	0.000
TIME	45	3	15.0	4.57	0.004
FIELDTRIP*TIME	10	15	0.7	0.21	0.999
ERROR	1124	343	3.3		

Table 4.4. Three-way ANOVA testing whether hihi weights (g) varied with time of day in 1995 (early AM, late AM, early PM, or late PM). The data set only includes 'fed' trips, and excludes months that didn't have data at all four times of day (April, May, June). It excludes individuals that were not weighed at all four times of day, or were not weighed on at least three different months.

SOURCE	SS	DF	MS	F	P
INDIVIDUAL	1215	12	101.3	104.6	0.000
MONTH	92	6	15.4	15.9	0.000
TIME	9	3	2.9	3.0	0.038
MONTH*TIME	19	18	1.1	1.1	0.374
ERROR	69	71	1.0		

Table 4.5. Effect of time of day on hihi weights (g), as estimated by ANOVA (Tables 4.3, 4.4). Means (± standard error) show how much heavier or lighter hihi are at each time of day, compared to the overall least squares mean. These means were subtracted in the subsequent analyses (Tables 4.6, 4.7) to eliminate the effect of time of day.

	1994		1995	
	N	Mean	N	Mean
EARLY AM	85	-0.29 ± 0.31	23	-0.37 ± 0.18
LATE AM	92	-0.19 ± 0.31	24	-0.26 ± 0.15
EARLY PM	108	-0.02 ± 0.30	33	+0.21 ± 0.19
LATE PM	109	+0.41 ± 0.29	31	+0.25 ± 0.16

Table 4.6. Two-way ANOVA testing whether hihi weights (g) varied over 6 fieldtrips from September-December 1994. Birds were excluded if they were only weighed on one trip. Females carrying eggs were also excluded.

SOURCE	SS	DF	MS	F	P
INDIVIDUAL	1221	32	38.16	10.24	0.000
FIELDTRIP	182	5	36.39	9.77	0.000
ERROR	365	98	3.72		

Table 4.7. Three-way ANOVA testing whether hihi weights (g) were affected by supplementary food, and whether this varied between months from January-October 1995. The 'Fed?' variable indicates 'fed' weights (taken after feeders available for 15 days) or 'unfed' weights (taken the first time each bird used a feeder after 12 days in which they were unavailable). Birds are excluded if they were not weighed during two or more months, or were not weighed on both 'fed' and 'unfed' trips.

SOURCE	SS	DF	MS	F	P
INDIVIDUAL	2262	25	90.49	50.01	0.000
MONTH	43	9	4.74	2.62	0.010
FED?	23	1	23.40	12.93	0.000
MONTH*FED?	27	9	3.02	1.67	0.110
ERROR	183	101	1.81		

If natural foods are limiting in some months, weights would be expected to go down when there were no feeders, and go up after feeders were available. The exception to this was one bird who lost 9 g after feeders were removed from 27 September to 9 October 1994, then regained this weight after feeders were available again. This was the only bird whose unfed weight was obtained in October 1994, hence this was not included in the analysis.

Weights varied month-to-month, both in 1994 ($P < 0.001$) and 1995 ($P = 0.01$) (Tables 4.6, 4.7) (Fig 4.5). Overall, fed weights were significantly lighter than the unfed weights ($P < 0.001$), and this did not change significantly from January through October ($P > 0.35$ for date/month interaction term). This suggests there was no time hihi were losing weight feeding on natural foods as compared to the *ad libitum* energy supplied. Weights were always lower when feeders were available from January through August 1995, except for June. The sample size in June was very low (3 vs 4 birds), so the difference is probably not significant (Fig 4.6).

There was a big increase in weights in December 1994, mid-way through the breeding season, and a big drop in August, about six weeks before the breeding season. Otherwise, the seasonal pattern is unclear (Fig 4.5).

Relationships between feeder use, bird's weights, and reproduction

The data, to this point, suggests that availability of food on Mokoia did not limit condition of adult hihi, especially during the greater part of the non-breeding season. However, birds during the breeding season are site attached (Castro 1995). Therefore, it's possible feeder use between birds during the breeding season may not be equal, or primarily relate to natural carbohydrate availability.

Nest sites were widely distributed over the island, and the distance to the nearest feeder ranged from 10 m to 650 m. Twelve females laid at least one clutch in the 1994/95 breeding season (Table 4.8). One of these was only incubated for a few days, and was abandoned when another female laid her second clutch in the same box. The other 11 females raised

Table 4.8. Two-way ANOVA testing whether the % time hihi spent foraging varied between months, from September-December 1994. Observations were done at least 50 m from the nearest feeder, and were for a minimum of 60 s on each bird. The analysis only includes times when feeders were available, and exludes observations on birds that hadn't discovered feeders yet. Birds were were also excluded if they were only observed on one trip. Data were subjected to arcsin square root transformation.

SOURCE	SS	DF	MS	F	P
INDIVIDUAL	7.64	16	0.48	1.87	0.052
MONTH	4.66	3	1.56	6.09	0.002
ERROR	10.98	24	0.26		

Table 4.9. Two-way ANOVA testing whether the % of foraging time spent on nectar and fruit varied between months, from September-December 1994. Observations with no feeding were excluded. Otherwise for Table 4.8.

SOURCE	SS	DF	MS	F	P
INDIVIDUAL	2.64	8	0.33	0.74	0.658
MONTH	0.58	3	0.19	0.43	0.732
ERROR	5.81	13	0.45		

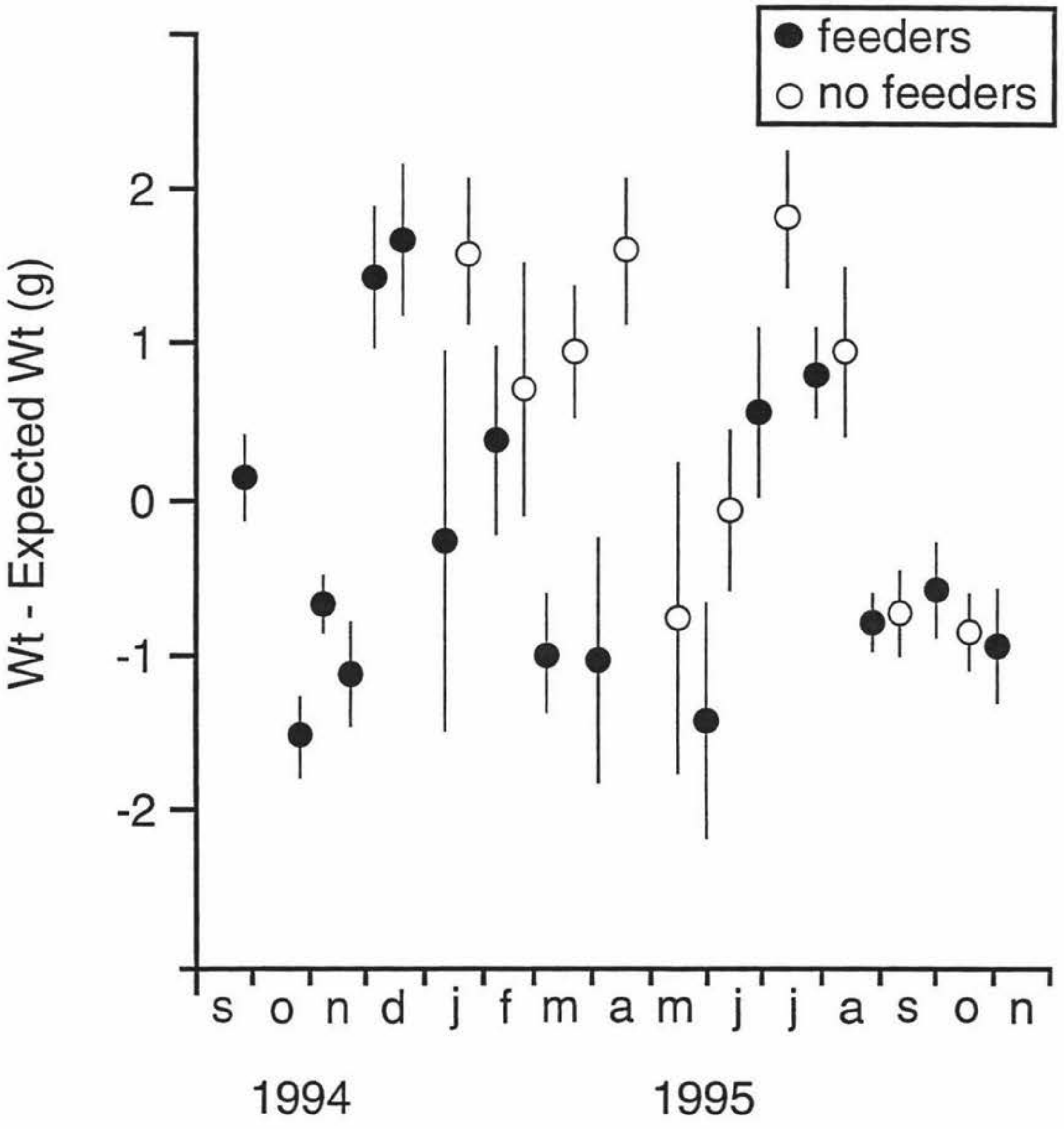

Fig. 4.5. Effect of feeders on hihi weights. The expected weight for each bird is its least squares mean estimated from the whole data set for 1994 or 1995 (years were analysed separately due to extensive turnover of birds). Values shown are the mean residual +- standard error, using individuals as replicates.

eggs to hatching, and the number of young fledged per female ranged from zero to six. Eight of the females started nesting early enough that most of their first nesting attempt was completed before the on-off feeding experiment was re-initiated

Among those eight females, those with nests closest to feeders used them the most, while those with nests more than 500m away almost never used them (Fig. 4.6). Females with nests closest to feeders fledged more young (Fig. 4.7). In addition, the amount of weight they put on during incubation (i.e., weight while incubation minus their previous weight) was greater than for females away from feeders.

Survival

All 40 birds survived the first 5 days, 38-39 survived the first 3 weeks, and 37-38 survived the first 6 weeks. It's unlikely any of these early deaths were attributable to food. The first bird found dead was a female on day 6, whose transmitter was found on the ground with a piece of wing nearby. She was found in a closed-canopy gully area suggesting she was a victim of predation by ruru (morepork, *Ninox novaeseelandiae*), harrier *(Circus approximans)*, or weka (*Gallirallus australis*). The second bird identified as dead was a male found 8 October (the fifth week). This male was last seen alive 11 days before. While he appeared active and vigorous at the time, his weight had dropped 4.5 g since capture even though he had had continuous access to feeders and used them regularly. The third bird that probably died during the first 6 weeks was a female last seen on 15 September 1994 (10 days after release). No birds died between 27 September-9 October 1994, the only period when supplementary food was not available in 1994. In addition, there was no correlation between survival of birds in 1994 and the degree to which they used feeders (Armstrong et al. 1997). In 1995, winter was the period of lowest mortality, with the highest mortality taking place in late summer and spring (Fig 4.8). There was no apparent tendency for birds to die when feeders were available vs unavailable.

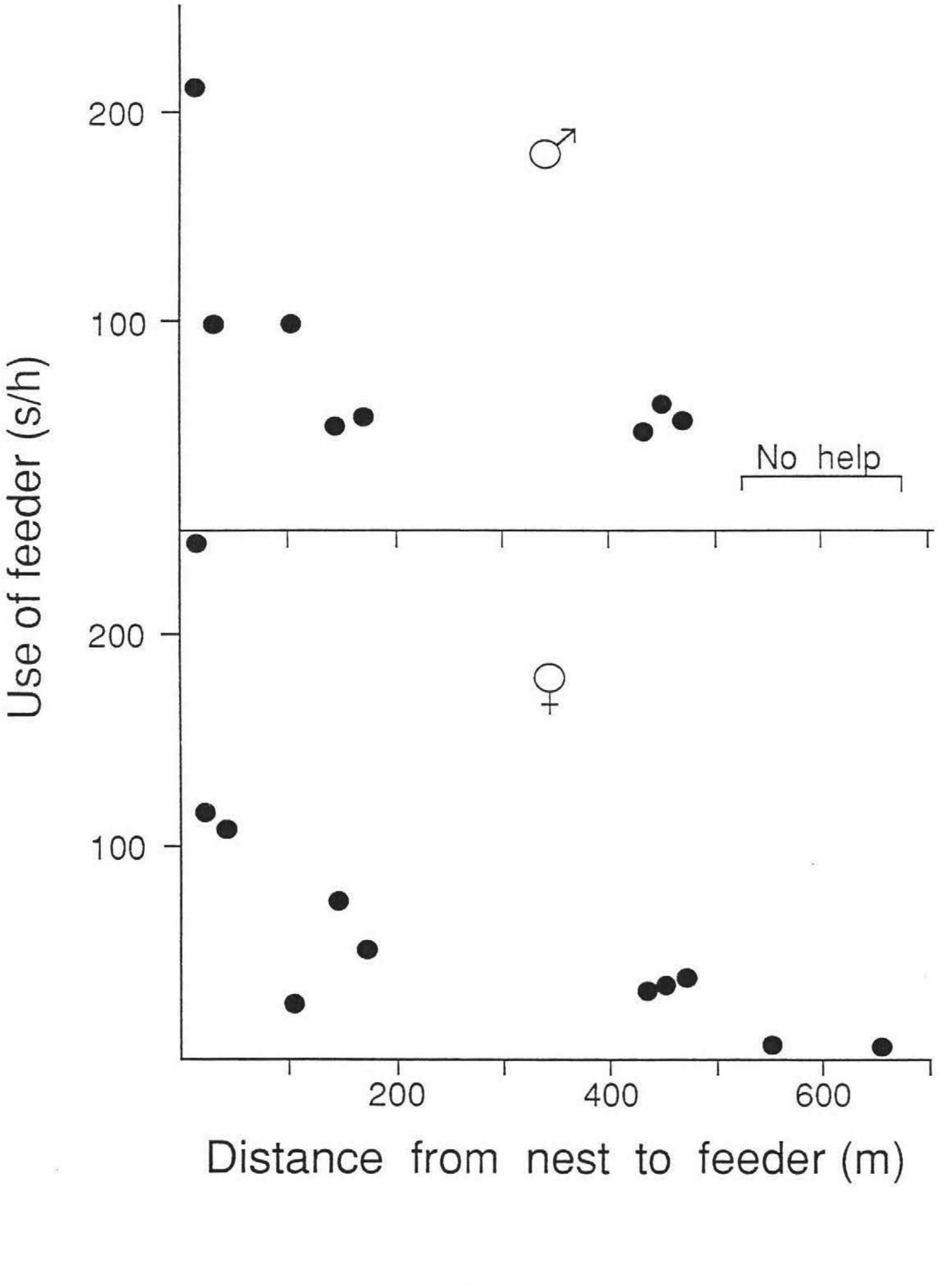

Fig. 4.6. Effect of nest box position (see Fig. 4.1) on degree to which hihi used feeders. Feeder use is averaged from three dates, from late November through mid December. Data are included here for all females that laid clutches, except for one female that abandoned her clutch within the first week.

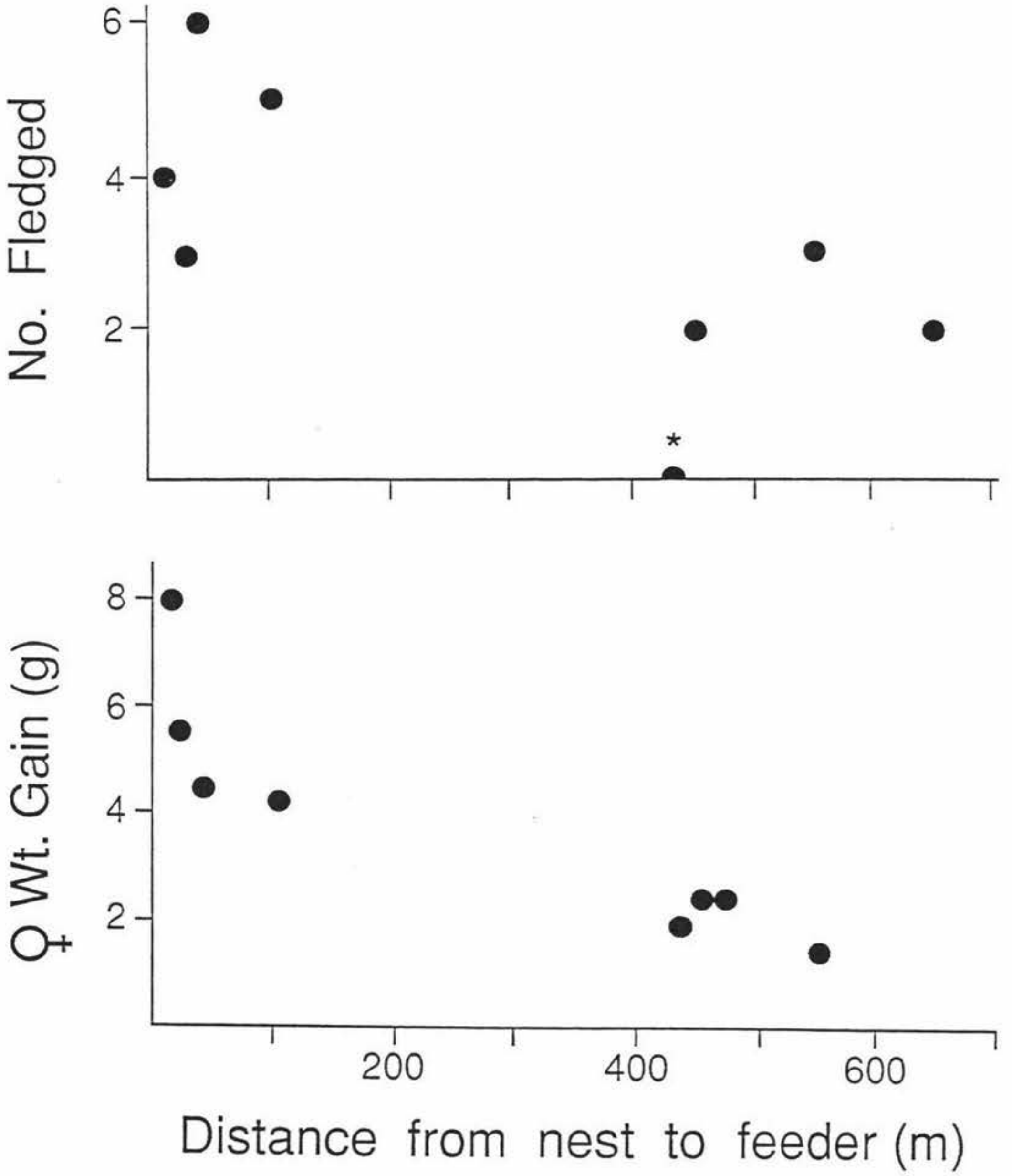

Fig. 4.7. Apparent effect of access to feeders on (1) reproductive success and (2) weight gained by incubating females. Weight gain compares weights during incubation with those before incubation. * = a nest in which the chicks were killed by mite infestation. Three chicks would probably have fledged from this nest otherwise.

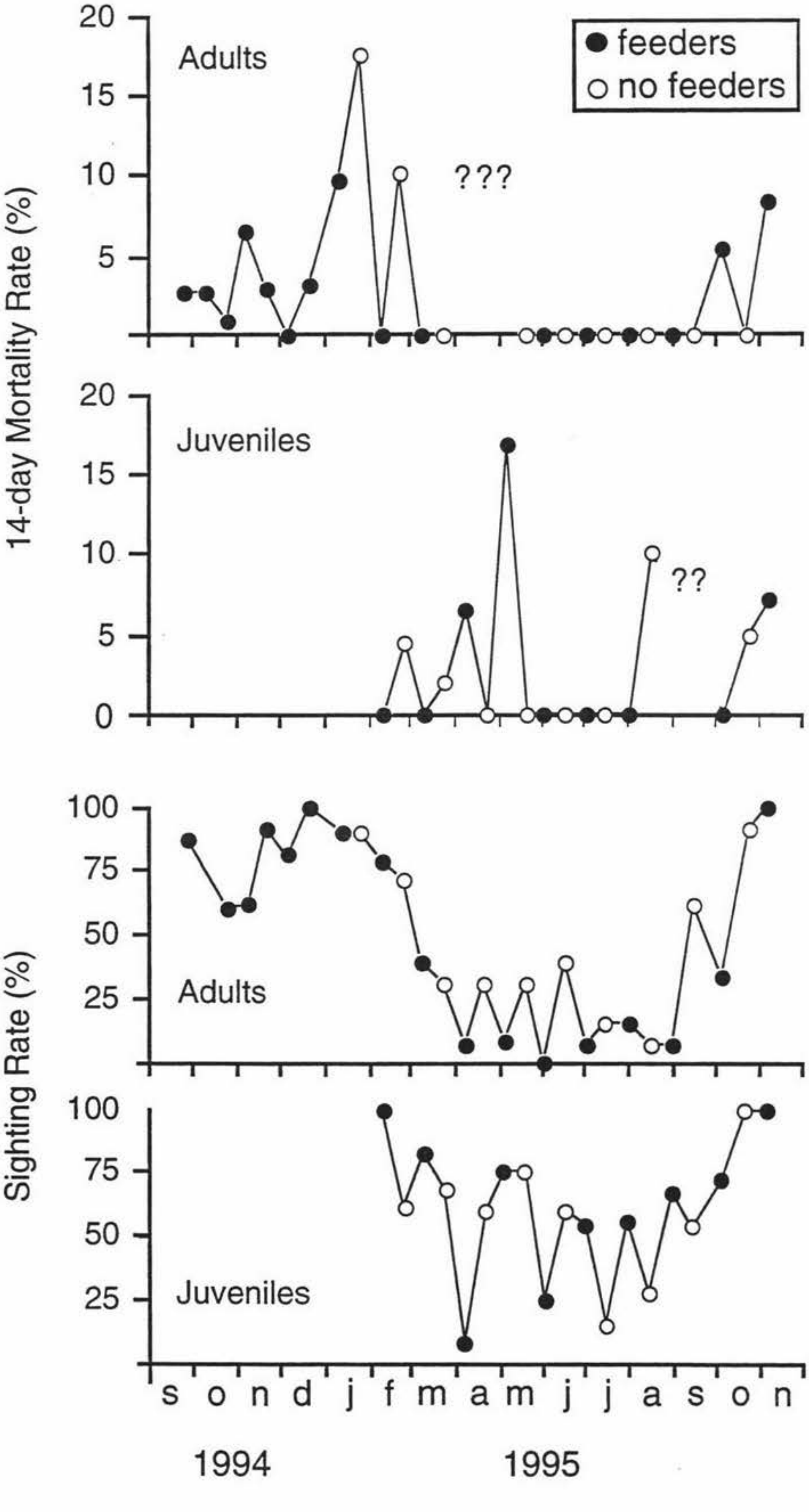

Fig. 4.8. Patterns in hihi mortality rate and sighting rate (% of birds seen per 3-day search). Mortality was estimated with the Manley-Parr method. ? = times when mortality occurred, but sighting rates were too low to estimate mortality for each field trip.

Table 4.10. Three-way ANOVA testing whether the % time hihi spent foraging was affected by supplementary food, and whether this varied between months from January-October 1995. The 'Fed?' variable indicates 'fed' trips (when feeders had been available for 13-16 days) or 'unfed' trips (when feeders had been unavailable for 10-12 days or when feeders had been put up in the last 3 days but the bird observed hadn't used them). Birds are excluded if they were not observed during two or more months, or were not observed both when 'fed' and 'unfed'. Data were subjected to arcsin square root transformation.

SOURCE	SS	DF	MS	F	P
INDIVIDUAL	6.01	27	0.22	2.36	0.000
MONTH	3.48	9	0.39	4.10	0.000
FED?	0.05	1	0.05	0.56	0.455
MONTH*FED?	4.36	9	0.48	5.13	0.000
ERROR	19.58	207	0.09		

Table 4.11. Two-way ANOVA testing whether the % of foraging time spent on nectar and fruit was affected by supplementary food, and whether this varied between months from January-October 1995. Observations with no feeding were exluded. Otherwise as for Table 4.10.

SOURCE	SS	DF	MS	F	P
INDIVIDUAL	5.60	24	0.23	0.91	0.589
MONTH	5.61	9	0.62	2.43	0.012
FED?	1.14	1	1.14	4.43	0.037
MONTH*FED?	4.01	9	0.45	1.74	0.083
ERROR	48.99	191	0.26		

Effects of supplementary food on birds foraging behaviour

In Chapter 3 observation data were described without reference to food supplementation, and compared with other studies. In this chapter time-budgets recorded during periods of feeder availability and unavailabilty are compared. Figure 4.9 shows the number of birds from which time-budgets were recorded each month. A total of 354 time-budgets (Fed = 214 total observations, unfed = 139) were obtained, with a mean of 25.3 separate observations greater than 30 s per month (Mean fed = 15.3 per month, unfed = 12.6) from September 1994 to October 1995. This totalled 25.9 hours with an overall mean of 1.85 h per month (Mean fed = 1.2 h per month, unfed = 50 min) and overall mean 4.4 minutes per observation period (Mean fed = 4.7 min, unfed = 3.9 min).

Birds tended to use feeders less outside the breeding period (Fig 4.3, 4.4), and most birds had gains in weight when feeders were unavailable (Fig 4.6). However, feeders had overall little effect on the amount of time birds spent foraging ($P = 0.455$; Table 4.10; Fig. 4.10). However, there is no obvious seasonal pattern to this suggesting the interaction is due to erratic temporal variation in foraging behaviour, rather than any effect of feeders. Birds spent more time foraging when feeders were unavailable in some months (e.g., June and October) and *vice versa* in other months (e.g., January and March).

While feeders didn't affect overall foraging time, they effected whether birds foraged for carbohydrates or invertebrates. The proportion of foraging time spent on carbohydrate feeding (nectar and fruit) was significantly less when feeders were available ($P = 0.03$; Table 4.11; Fig 4.10). Overall, this affect did not vary significantly between most months ($P = 0.083$ for interaction term) and the effect is in the same direction for most months. However, in September 1994 and February 1995 unfed birds spent significantly more time carbohydrate feeding compared to fed birds ($P < 0.05$). Overall, there is a clear seasonal trend to time birds spent carbohydrate feeding. Birds spent most of their feeding time visiting carbohydrate sources in winter and spring, and were mostly invertebrate feeding in summer and autumn (Fig 4.12).

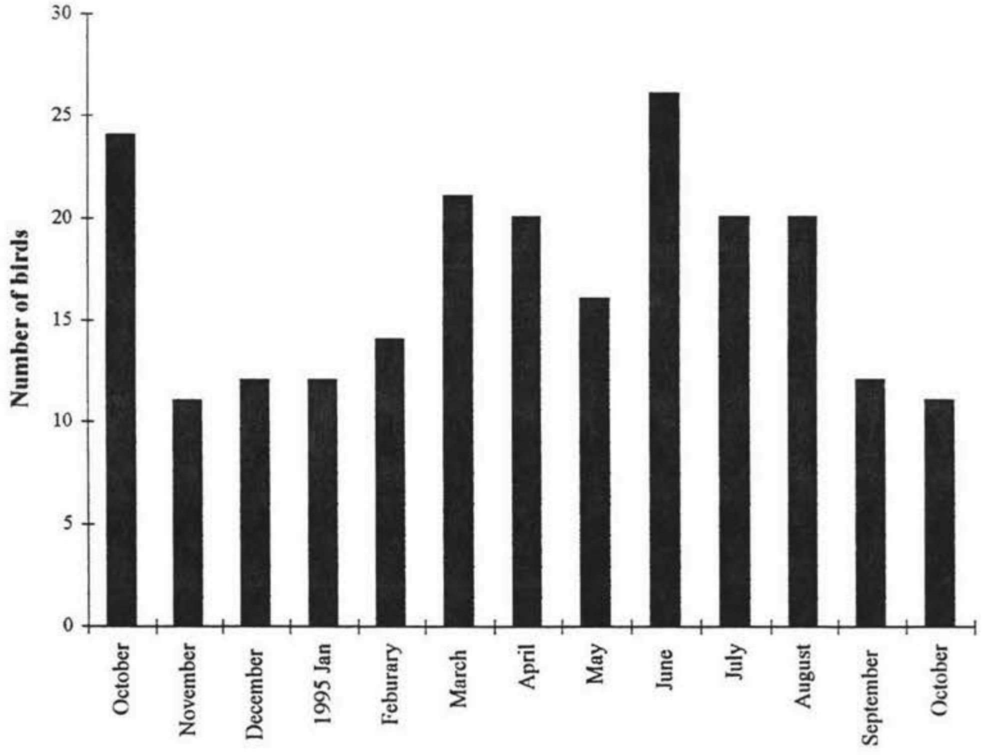

Fig 4.9. Number of birds from which time-budgets were obtained each month.

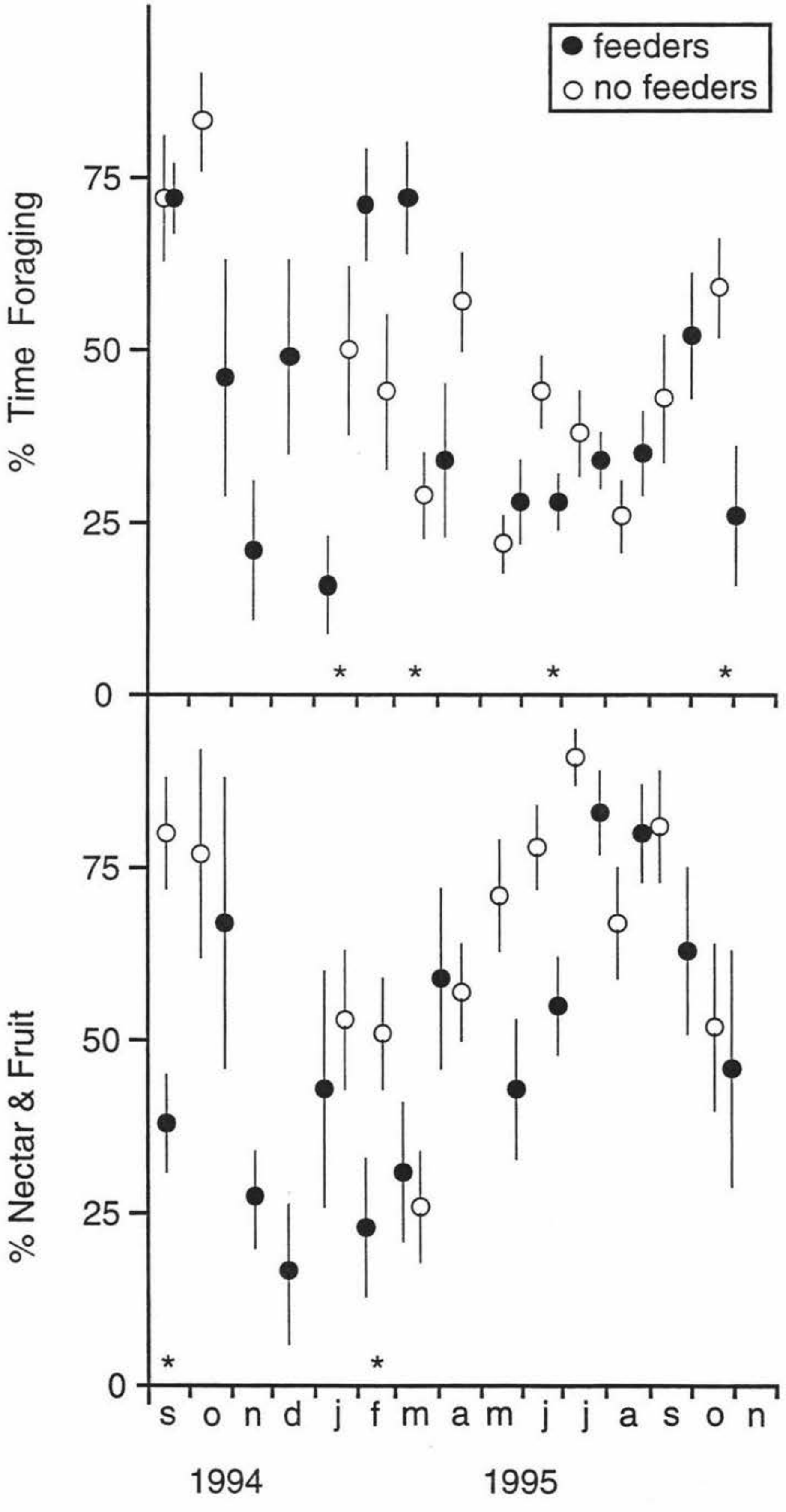

Fig. 4.10. Effect of feeders on % of time hihi spent foraging and % of foraging time on nectar and fruit sources. Values are means +- standard error, using individuals as replicates. * = individual months where there is a significant difference ($P<0.05$) with feeders present or absent.

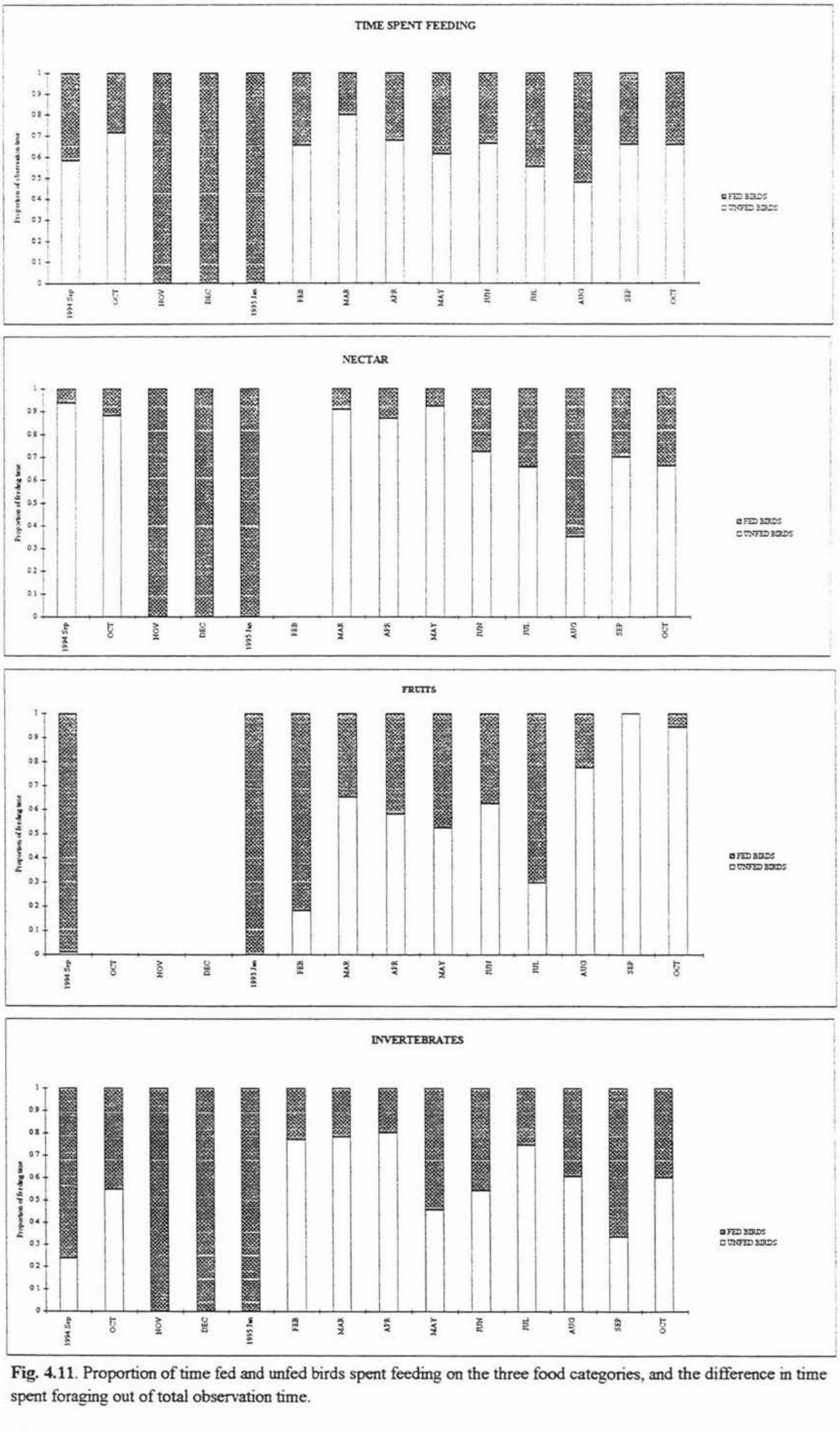

Fig. 4.11. Proportion of time fed and unfed birds spent feeding on the three food categories, and the difference in time spent foraging out of total observation time.

DISCUSSION

Supplementary feeding is common after translocations (Bright & Morris 1994; Armstrong & McLean 1995), and can be a way of achieving a "soft release" (Scott & Carpenter 1987). However, it is uncertain how significant supplementary feeding is to the survival of hihi. The frequent use hihi make of feeders immediately following their release on islands could be interpreted as evidence that feeders are an important resource at those times (Castro 1995).

The effect of feeder use on birds survival

We couldn't experimentally test the effects of supplementary feeding immediately after release as feeding stations were continuously available. However, we could compare the initial mortality (e.g., first six weeks) with how quickly birds discovered feeders. Most birds discovered feeders in the first two weeks, and there was no evidence of higher mortality in birds not using feeders (Armstrong et al. 1997). In 1995, there was no tendency for birds to die when feeders were absent *vs* when they were present, and this conclusion is supported by the weight data (see below).

Feeder use in relation to natural food sources

Data on nectar and fruit availability has shown hihi had access to natural sources of fruit and nectar all year, and that exclusion by tui was negligible (Chapter 3). Phenology results (Chapter 2) have shown there were months when natural carbohydrate availability was significantly lower compared to other months (e.g., October-November 1994/95, and June 1995). Fruit sources were available all year round. and/or restricted to two or three species. While there were periods natural nectar sources were scarce (e.g., Autumn, and early spring/late winter). While feeder use did vary significantly between months this did not correspond to monthly changes in the availability natural carbohydrate sources- i.e., birds were not more likely to visit feeders in the months that carbohydrate availability was low.

The rate at which birds can extract energy at feeders (Mean = 86 Js^{-1}) is much higher than rates estimated for most flower sources (Mean for all species = 3.8 Js^{-1}, 95% CI = 1.96, excluding pohutukawa). However, Mokoia hihi were often seen visiting low grade flowers even when feeders were available. This could imply that the supplementary food we provided was an inferior substitute for nectar, i.e., lacking trace elements and/or amino acids important to hihi. Alternatively, it's possible that birds were distributing themselves according to some factor/s other than carbohydrate availability, hence most birds were not near feeders. Nectar and invertebrate foraging may be so closely coupled in hihi that they distribute themselves according to both- i.e., the locality with the best trade off between carbohydrate and invertebrate availability. In this sense feeders may have been inferior to natural carbohydrate sources, because invertebrates were heavily depleted around them. However, it's difficult to know what aspects of honeyeater biology are directly influenced by carbohydrate availability. Castro (1995) found reproductive activities influenced feeder use also, increases in feeder use by Kapiti hihi corresponded to the months when egg laying started.

Non-feeding activities are probably higher for birds during the breeding season, and its likely these relate to higher energy requirements also. It maybe that during the breeding season, hihi are using feeders to obtain their energy requirements quickly because feeding time has to be minimised. It's possible birds are more time limited than energy limited during this time, favouring feeders because they could extract more energy in a shorter amount of time compared to natural carbohydrate sources. It may be that feeders allow breeding birds to better manage their time searching for invertebrates, and/or their non-foraging time, and it may be that these activities are more closely correlated with birds survival.

Changes in birds weights

While there is no indication feeders influenced bird's survival, bird's weights consistently dropped during periods of feeder availability. Although this is interesting, it seems irrelevant for management i.e., no apparent evidence birds needed supplementary food. Birds might get lighter during periods of feeder availability because they no longer take bulky foods stuffs (e.g., fruit seeds and insect parts). If true, unfed hihi should take more fruits and insects than fed hihi, and this weight difference should be more pronounced during months of nectar scarcity (e.g., autumn). The differences in the mean fed and unfed weights each month varied from 0.1 g in October 1995 to 2.6 g in April 1995. The autumn months show the greatest difference (birds were on average 2.1 g lighter when feeders were available, which equates to a 5-6% difference in body mass). In January the difference was also high (fed birds were on average 1.9 g lighter), while in winter (1.1 g) and spring (0.2 g) there was on average little differences in fed and unfed birds weights. This may support the idea that the weight differences are due to differences in the foraging behaviour of fed and unfed birds, as the difference is lowest when fed and unfed birds are mostly nectarivorous (e.g., winter and spring, Chapter 3) and highest in autumn when unfed birds were mostly eating invertebrates and fruits.

However, while feeders also affected bird's foraging behaviour, it seems unlikely bird's weight gains when feeders were unavailable can be explained by unfed birds consuming heavier food stuffs. Birds on average spent more time feeding when there were no feeders (Fig 4.11). However, this resulted mostly from birds elevating time given to nectar feeding. Additionally, feeders had little effect on the overall time given to fruit feeding for most birds (fed = 16%, unfed = 12%), and birds spent more time invertebrate feeding when feeders were available (59%) compared to when unavailable (35%).

Alternatively, removing feeders may at times significantly reduce the overall variability of food rewards available to hihi (i.e., the relative profitability). Perhaps the variation in rate of food intake (brought about by the presence and absence of feeders) may sometimes have a more important effect on bird's weights than birds average food intake rates. Perhaps those birds using feeders most are those most in need of supplementary food, and these birds could be responding to the risk of starvation when feeders are removed by storing relatively greater proportions of their ingested calories in the form of fat (i.e., hyperlipogenesis, Scott & Potter 1970). The drop in bird's weights could therefore be birds losing this fat layer during the period of feeder availability. This also seems unlikely in the light of how little energy birds actually extracted on average from feeders, but maybe those birds just needed to know that the feeders were available to have changes in body mass.

Changes in body mass of 5-35% over periods of several months have been recorded for populations of honeyeaters, sunbirds and hummingbirds (e.g., Carpenter et al. 1983; Stiles 1980; Ford & Pursey 1982; Collins & Briffa 1983a,b; Paton 1985; McFarland 1986, Ford 1991). In contrast to this study, most Australian honeyeaters show an increase in body mass outside the breeding period (e.g., Ford & Pursey 1982; McFarland 1986; Ford 1991). Variations in body mass are usually associated with adjustments in fat stores or water content (e.g., Collins 1981; Ford & Pursey 1982; Paton 1985a; McFarland 1986). The mean 1.1 g weight difference between fed and unfed hihi measured in this study only equates to about 2-3% variation in body mass.

Changes in body mass of 2-3% may not be uncommon on a daily basis for most hihi. McFarland (1986) estimated that a 13-15 g male Eastern Spinebill (Australian honeyeater *Acanthorhychus tenuirostris*) carrying about 3 g of fat in mid-winter would be able to generate about 100-120 kJ of energy, enough to maintain an inactive bird for about 48 hours at ambient temperatures. The predicted hihi energy requirements, based on Collins & Newland's (1986) equation derived from measurements on brown honeyeaters *Lichmera indistincta* are estimated at 68 kJ/day and 60 kJ/day for males and females respectively. Therefore, a 1.1 g increase in body fat would equate to about 37-44 kJ, enough to probably maintain an inactive hihi for about 36-48 hours assuming a 13^0C day temperature and 9^0C night temperature. This weight difference may be negligible when you consider some hummingbirds, sunbirds and honeyeaters studied during laboratory experiments in which nectar was available *ad libitum*, and had variations in weight equating to 3-4% of body mass over a 24 hour period.

Relating feeder use to reproductive success

During the first breeding season feeders were continuously available, and during that time there is tentative evidence that supplementary food effected birds reproductive success-i.e., females nesting nearest to feeders fledged more young. Although this may suggest food supply limits birds reproduction on Mokoia it's important to note that not all differences in reproduction can be explained in terms of access to food. In particular, some females will be in better condition than others, or otherwise pre-disposed to high breeding rates. It isn't clear whether the correlation between reproduction rate and feeder access reflects a cause or an effect. Birds nesting closest to feeders may have been high-quality birds, and gained the best nesting sites because of this. It's also possible that the habitat around the feeders, not the feeders themselves affected reproductive success, i.e., the nests near feeders had the best habitat. The nests by feeders were at two locations on the island and had more mature forest than most other locations.

Most importantly, we need to be cautious in interpreting a pattern from eight females. Data for 1995/96 (Armstrong et al. 1997) and 1996/97 (Dr. I. Castro, pers. comm) don't support the idea that birds near feeders have higher reproduction rates. There is also a surprising pattern in the first two years, in that fledglings produced near feeders had lower survival rates and the survivors tended to be males. The female recruitment rate was actually lower for nests near feeders.

Long-term prospects

The supplementation experiments produced no evidence that condition or survival of hihi on Mokoia was limited by food energy outside the breeding period. They produced tentative evidence that reproduction was limited by food, but this has not been supported by subsequent research on Mokoia. Nevertheless it's important to be aware that the time period studied for this thesis may not represent the long-term situation on Mokoia. Wiens (1977) coined the phrase 'ecological crunch' for a period of adversity which can lead to high mortality and intense intra- and interspecific competition. As mentioned, its possible 1994/95 were good flowering years on Mokoia, and that subsequent years may have marked variations in fruit and nectar availability (Castro 1995). Unlike tui, hihi are unable to leave Mokoia during crunch periods. Therefore, while natural carbohydrate availability didn't appear to be limiting hihi condition and/or survival during this study the possibility exists that their long-term prospects could be effected by annual variations in carbohydrate availability.

Additionally, cyclones and storms have the potential to effect food availability in the short term, shifting an otherwise good flowering year into a series of poor flowering/fruiting periods.

While food availability could limit hihi condition/survival in the long-term, Mokoia hihi may have more pressing problems. While there was no evidence that mortality was caused by shortages in carbohydrate availability, the mortality rate was high nevertheless. The mortality rate is high enough that the long-term survival prospects of hihi on Mokoia are doubtful (Armstrong et al. 1997). Even without food shortages, it's likely that the Mokoia hihi population will slowly dwindle away, much the same as hihi populations in previous translocations to Hen, Cuvier, and Kapiti. This thesis therefore does not support the conventional notion (Angehr 1984b; Lovegrove 1986; Rasch 1991; Castro 1995) that failure of hihi translocations have been due to food limitation. If translocated hihi populations are to survive, further research will be needed to determine why hihi suffer high mortality rates, and what (if any) can be done about it.

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Chapter 5

Management recommendations

Aim of recommendations

The main aim is to plant species and manage feeding stations on Mokoia island to make the habitat more suitable to the resident hihi population. This thesis specifically targets food supply, so my recommendations don't include issues such as nesting sites, and disease. Improving the food supply for hihi involves: (1) maintaining feeding stations during the required periods, and (2) planting flowering and fruiting species used by hihi to supplement species already present on the island, and/or adding species not presently found on Mokoia.

Those species recommended for planting are designed to fill observed nectar/fruit gaps on Mokoia, or periods when the natural food supply is most likely to be limiting hihi survival. This does not necessarily mean that hihi are only limited by food availability when it is at its lowest. Demand for food sources also influences their availability. In particular, during the hihi breeding period nectar sources peak for the year, but feeder use is also at its highest (Chapter 4). Hihi tend to spend more time on activities other than foraging, compared to the nonbreeding period and expend more resources. These activities include additional aggression (including defences of territories and females), nest building, egg-formation, incubation and chick rearing. Increased demand for the most profitable nectar sources may still be high enough to limit hihi condition and/or survival during the breeding period, even though nectar availability peaks during this time on Mokoia.

Additionally, tui may exclude hihi from the profitable flower sites during peak flowering, forcing hihi to forage for additional invertebrates, fruits and more dispersed flowers. However, this assumes nectar feeding is of primary importance to hihi, and that competition is the regulating factor. Competition is readily inferred, but rarely is it directly observed in the field (Ford 1979). Whether the size of honeyeater populations is governed by the physical conditions or by competition from other species trying to exploit the same resources has never been proved by any authors. Additionally, the presence of guilds may be seen as a contradiction to competition theory, in that species with high resource overlap (as described by the definition of guilds) manage to coexist (Pontin 1982). Such coexistence may be facilitated by community structuring forces such as predation and disease, so that competition has little effect on population dynamics (Sih et al. 1985) or the species in the guild may be partitioning the shared resources in such a way that competition is lessened (Wiens 1989). Birds simply displacing each other at feeding sites does not constitute in itself competition, as this is only true when the common resources being depleted are in short supply, and this influences birds survival and/or reproduction rates.

Feeding station recommendations

Chapter 4 showed that feeder access had little influence on birds weights or survival. This was especially so during the greater part of the non-breeding season (e.g., autumn and winter) when most birds didn't use feeding stations. Because birds tended to suffer high mortality anyway (annual > 50%) any benefits derived from feeder access is difficult to interpret. It is therefore equally difficult to propose any specific recommendations regarding managing feeding stations on Mokoia. As feeder use was high during the breeding period, and there is some evidence feeder access influenced birds reproductive success, we can recommend maintaining feeding stations over the hihi breeding period. However, sugar water was replaced with Wombaroo during the breeding period (October-January), which contains, sugar water, protein, fat, vitamins, and minerals. Considering feeder use was highest during the breeding period (when Wombaroo was provided), and birds lost weight outside the breeding period. It may be that birds are protein limited, not energy limited on Mokoia. Therefore, changes in birds weights may be more responsive to protein availability than carbohydrate availability. However, research continued since this thesis testing whether food is limiting birds breeding (by supplementing their diet with Wombaroo), and has not given any evidence that it is.

Given that the hihi long-term mortality rate was high, and most birds found dead had died from disease, we therefore need to minimise the risk of infection at feeding stations. It's important that feeders used to attract birds outside the breeding season so people can view them are kept clean.

Identifying nectar/fruit gaps on Mokoia

Mokoia is composed mostly of sub-canopy species which is typical of most regenerating habitats (Chapter 2). Species such as five-finger, mahoe, hangehange, *Coprosma spp.* and pate are fast growing, and are important hihi food sources during autumn and early spring when little nectar is available. The canopy species present on Mokoia provide flowers that hihi take, but their fruits are either unpalatable, or too large to be taken by hihi. In contrast, the flowers of sub-canopy species are generally small and low in their nectar content (Chapter 3). All the canopy species except kohekohe flower during the hihi breeding season (October-January). Although pohutukawa is relatively well represented on Mokoia, the other canopy species are mostly young trees that are confined and relatively few in number. Therefore, it may prove useful to plant additional summer flowering and fruiting species, as well as those species recommended to fill observed nectar/fruit gaps.

In addition, it may prove necessary to plant species to fill the periods when hihi are relying on the fewest plant species. Hihi reliance on kohekohe and *Albizia* is evident throughout winter. *Albizia* is not abundant on Mokoia but is an important food source over winter to hihi and tui. Kohekohe concludes its flowering period towards the end of winter, leaving only *Albizia*, *Fuchsia*, and five-finger providing practically all the natural occurring nectar sources from August to November. As the canopy develops, these species may die off in some areas. Without additional planting this could lead to a decrease in diversity and more pronounced nectar gaps from August to November. This is because all the flowering canopy species on Mokoia taken by hihi flower during Summer, with the exception of kohekohe.

In summary the major nectar gaps appear to be when the most profitable species are out of flower (e.g., species such as pohutukawa, rewarewa, *Albizia*, and *Fuchsia*). It's important to note that 1994/95 was a good flowering year in New Zealand, and that phenologies can be highly variable between years within the same community (Castro 1995). In Chapter 2, I showed that the number of species in flower drops during the colder months (when there are only two flowering species). This may be a crunch period, but since its likely demand for food is elevated for breeding birds, the early summer months may also be treated as a time of low food availability.

Mokoia lacks canopy species that flower outside the summer months, and the most profitable canopy species are rare. Therefore the most profitable species should be increased in number, and additional flowering species selected to fill the autumn nectar gaps, and spring/early summer fruit and nectar gaps.

Preliminary considerations for planting

a) What degree of revegetation will be attempted? Will there be a planting sequence? Mokoia has good ground cover and a well developed understory in most areas, this would probably make sequence planting unnecessary. However, the saplings to be planted may need to be of sufficient size to compete for light, and/or be regularly weeded around.

b) What negative impacts might the planned project have? (eg., impacts of programmes for weed control, changes to habitat used by other endangered species, loss of other land-use options). There may be the option of removing small areas of tree fern on some south facing slopes. This would be done to determine whether or not the succession of canopy species would be improved at these sites compared to the untreated areas.

c) Goals of tangata whenua. For Maori, the *tangata whenua* of New Zealand any discussion of historical or cultural issues must begin with the Treaty of Waitangi (Roberts et al. 1995). Recognising this fact, in 1975 Parliament passed the Treaty of Waitangi Act, which created legal rights for this Treaty, and upon which much legislation has since been based. For example, the 1986 Environment Act, the 1987 Conservation Act, and the 1991 Resource Management Act, each containing specific provisions for compliance with the principles of the Treaty of Waitangi. Therefore, any discussion regarding revegetation on Mokoia must be referred to the local *tangata whenua* (the Te Arawa people).

d) Has the planning considered soils, community ecology, hydrology, historic sites, wahi tapu sites? Wallace (1993) commented that many of the kohuhu on the Northwest of Mokoia appear to be dying off in some localities as well as some cabbage tree and mahoe. This is still occurring, and *Fuchsia* may also be dying off in the same areas. Soil loss and 'pan-rooting' may also be claiming some trees, these factors warrant further investigation to ensure whether soil quality, or disease is the main problem. This is important because if the causation is not understood there is the possibility that the essential features of the habitat will be missed, and its superficial features regarded as important.

e) What are the performance indicators ? Are they measurable, and directly linked to the aims? eg., survival and growth of the planted species. Cashmore (1995) recorded a mean survival rate of 36.8% for those species planted on Tiritiri Matangi.

f) Will management be required to maintain the planted sites ?

g) Which plant species would be most suitable to achieving the project aim. These would preferably be native species found locally with flowers rich in nectar (ornithophilous flowers), and species other than sub-canopy plants with fruits which hihi will eat.

Some plant species recommended for planting on Mokoia

1) Trees that flower during the hihi breeding season (Spring/Summer)

- Rewarewa *Knightia excelsa* ✻
- Kaikomako *Pennantia corymbosa*
- Hinau *Elaeocarpus dentatus*
- Kowhai *Sophora microphylla*
- Karo *Pittosporum crassifolium*
- Akeake *Dodonaea viscosa* ✻
- Maire *Mida salicifolia*
- Toru *Toronia toru*

- Titoki *Alectryon excelsus* ❊
- Toropapa *Alseuosmia macrophylla* ❊
- Haekaro *Pittosporum umbellatum*

2) Plants that flower during Autumn and Winter

- Puriri *Vitex lucerns*
- Maire tawaki *Syzygium maire*
- Kohekohe *Dysoxylum spectabile* ❊
- Rata *Metrosideros spp.* ❊
- Haekaro *Pittosporum umbellatum*
- Wattle tree varieties *Acacia* ❊
- *Eucalyptus*

3) Plants that fruit during Summer and Spring

- Toro *Myrsine salicina*
- *Passiflora tetranda*
- pigeonwood *Hedycarya arborea*
- Raukawa *Pseudopanax edgerleyi*
- Karangu *Coprosma lucida*

❊ Present on Mokoia

Australia has 72 honeyeater species and many ornithophilous flowering species (Ford 1979). New Zealand on the other hand has three honeyeater species and an equally small number of ornithophilous flowering species (Craig et al. 1981). This means in New Zealand our range in choice of ornithophilous flowering species is very much limited. Although New Zealand has 30 native flowering families Godley (1979) reported as being visited by native birds, most of these probably do not meet the hihi's energetic demands (Castro 1995). Because of this I suggest the possibility of planting exotic species (similar to that done with *Albizia* on Tiritiri Matangi, Cashmore 1995). It's likely that any plant species not 'naturally' found in the Rotorua area will be controversial, and may conflict with other restoration objectives on Mokoia. However, some *Eucalyptus* (Blue gum) and *Acacia* (wattle) were once native to New Zealand but went extinct during the last Ice Age (25,000-15,000 yr. ago, Stevens 1988). Its possible these eucalypt and wattle species were once an important nectar source to the hihi`s ancestors which Fleming (1962) estimated to have colonised New Zealand in the late Tertiary (2-25 m.yr.bp). For the present *Albizia* on Mokoia should not be cut down, especially the large individuals along some tracks, as these are the most profitable nectar sources on Mokoia over the winter months.

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