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**Resource partitioning between two competitive species, the hihi
(*Notiomystis cincta*) and bellbird (*Anthornis melanura*), during
the non-breeding season on Tiritiri Matangi Island**

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Abstract

Understanding the level of competition and resource partitioning between New Zealand's ecological honeyeaters is important for hihi (*Notiomystis cincta*) conservation management. Hihi management on Tiritiri Matangi Island has been thought to be hindered by competition with bellbirds (*Anthornis melanura*), particularly at the supplementary sugar water feeders. With some inconsistent results in differences between their foraging ecology at different locations and seasons, I collected data on the foraging ecology of both hihi and bellbirds on Tiritiri Matangi Island to compare with previous studies at other locations. Nectar was the main constituent of both species diet with fruit only being consumed in the autumn-winter months for both species. The main difference between the species was that hihi consumed more fruit than bellbirds and bellbirds consumed honeydew. Bellbirds foraged more in the higher vegetation layers and on higher nectar value flowers than hihi which corresponded with previous studies. This suggested that resource partitioning is likely to be in the form of bellbirds defending the best resources of higher nectar value in the higher vegetation layers with interference competition and hihi obtain resources with exploitation competition by utilising flowers which are often smaller, less abundant or produce less nectar in the lower vegetation layers. Male bellbirds and hihi were the most frequent visitors to the supplementary feeders. With few interspecific interactions it suggests that male bellbirds are unable to defend the feeders due to the feeders being overwhelmed with hihi and also showing how dependent hihi are on supplementary feeding. Female bellbirds were the least frequent visitors suggesting that intraspecific competition is greater at the feeders but only for bellbirds as there was little evidence of high competition between the hihi sexes. There may be some resource partitioning between habitat types as hihi were consistently found at higher densities in the mature forest habitat likely due to their dependence on the feeders and artificial nest boxes, whereas bellbird densities changed with resource availability and breeding season territoriality. The densities of both species were affected by the presence of feeders and nectar availability with positive correlation between the species in the non-breeding season, suggesting that hihi habitat preference was not affected by competitive exclusion from bellbirds. The removal of 100 bellbirds for a translocation had no evident impact on hihi and bellbird densities at capture sites.

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In dedication and loving memory of Gladys Esme Bedingfield, October 1923 – September 2011. Photo: Michelle Roper, 2010.

PERMITTING

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Chapter 1:

General Introduction



A female hihi on Tiritiri Matangi Island.

Photo: Michelle Roper, 2010.

1.1 Habitat selection and resource partitioning

Knowledge of the habitat requirements of a species is fundamental for their conservation. Habitat loss, degradation and fragmentation are a major cause for the decline and extinction of many species world wide (Wilson, 1988 cited in Maken, 2006; Saunders, 2001). The loss of habitat, particularly high quality habitat, can directly result in reduced breeding success, survivorship and population productivity (Pulliam & Danielson, 1991). Habitat degradation and fragmentation can also exacerbate edge effects by altering the abiotic and biotic environment (Murcia, 1995). The biotic factors can cause direct biological changes to the distribution and abundance of species and influence species interactions, for example, competition, predation, herbivory, seed dispersal, biotic pollination and brood parasitism (Murcia, 1995). Therefore, understanding the habitat requirements of a species is important in conservation for species' survival, restoring habitat and reintroducing species.

Habitat can be defined as an area that contains the specific resources an organism needs to be able to reproduce and survive (Fretwell & Lucas, 1970; Hall, Krausman & Morrison, 1997). The total area available to a species can be made of different habitat types (or more accurately referred to as vegetation types; Hall *et al.*, 1997) resulting in the concept of habitat distribution and selection where different habitat types support a different number and diversity of species (Fretwell & Lucas, 1970). The suitability of the habitat types must be taken into consideration in conservation practise and it is assumed that individuals when given a choice will choose habitat that maximises their fitness (Possingham, 1992). Another assumption of habitat selection is that all individuals within the habitat will have the same expected success rate and are free to enter any habitat, hence called 'ideal free distribution' (Fretwell & Lucas, 1970). However, this assumption is usually violated. For example, if a habitat has limited nests sites and they have all been claimed, new individuals will be unable to breed and will have a reduced reproductive success (Fretwell & Lucas, 1970).

The resources that a species needs for its survival and reproduction can be described as their niche (Molles Jr, 2005). Ecologists use this term for describing the environmental factors that influence a species reproduction, growth and survival (Molles Jr, 2005). The ideal free distribution theory relates to the fundamental niche of a species

where there is a region of resources needed for survival and reproduction and the individuals can persist without competition (Hannan, Carroll & Pólos, 2003). However, the term niche has developed over many years within the context of interspecific competition (Molles Jr, 2005). Gause (1934, cited in Molles Jr, 2005) developed the concept of competitive exclusion which states that species cannot coexist with identical niches when resources are limited. Competition resulting from resource limitations restricts species to particular environments and generally reduces niche size resulting in a realised niche (Molles Jr, 2005).

Applying Gause's principle, this means that coexisting species must partition in time or space. This is achieved on an evolutionary scale by adaptations such as morphological differences (e.g. bill size) and specialisation on certain food types or feeding sites (Recher, 1971; Ford & Paton 1976a). The study of resource partitioning (referred to as cases of complementarity by Shoener, 1974) aims to understand how species coexist in the presence of interspecific competition (Hannan *et al.*, 2003; Nichols & Racey, 2006).

Resource partitioning can occur in a number of forms. Shoener (1974) describes five cases of resource partitioning where species can coexist: 1) Food type and habitat: Species that tend to have overlapping habitat will eat different foods. 2) Food type and time: They have similar food types but some form of temporal separation on a daily and/or yearly basis reduces resource competition. 3) Habitat and time: Where climatic factors influence a species activity and the different species show nonsynchronous spatial overlap. 4) Habitat and habitat: Species' habitat that overlaps horizontally will often differ vertically e.g. foraging height (Edington & Edington, 1972). 5) Food type and food type: Where species' eat similar food types but they each eat different sized food particles e.g. bigger bats eat bigger fruit than smaller bats (McNab, 1971). The causes of resource partitioning are often thought to be a result from interspecific competition (Ford & Paton, 1976a). The evidence for this comes from studies that demonstrate that in the absence of competitors, a species will increase its use of a habitat range that would be unseen in the presence of competitors (Grant, 1972 cited in Ford & Paton, 1976a).

1.2 Competition

Competition for resources can occur at two levels: intraspecific where individuals of the same species compete with each other and interspecific where individuals of different species compete for resources (Molles Jr, 2005). In both types of competition, there is the pressure for individuals to select the preferred habitat. It is assumed that individuals have a hierarchy of habitat preferences based on the level of reproduction and survival they can attain in each habitat type (Newton, 1998). When the most preferred habitat is saturated, surplus individuals must move to the second most preferred habitat and so on until they reach a habitat where they can survive but not reproduce (Newton, 1998). These less favourable habitats however provide a 'buffer' where over the years the individuals in this so called 'secondary habitat' can be potential immigrants to the 'primary habitat' to fill any gaps (Newton, 1998). Therefore, the 'primary habitat' will maintain more stable densities than the 'secondary habitats' (Newton, 1998) hence providing a sustainable population.

Interspecific competition is however thought to be a major force in the evolution of ecological niches (Ford, 1979). Interspecific competition is predicted to occur when species niches significantly overlap (Grant, 1972 cited in Ford, 1979). This form of competition can occur between species when common resources, such as food, are limited and exploited by two or more species (exploitation competition) or when resources are not in short supply but where one species excludes others (interference competition; Park, 1962). Exploitation competition occurs when an organism uses a particular limited resource and the more limited the supply of the resource is, the greater the intensity of competition (Park, 1962). Interference competition involves direct antagonistic interactions between organisms (Molles Jr, 2005) and can also affect their reproduction and survival (Park, 1962). Resource partitioning is hence thought to reduce the amount of competition by reducing niche overlap and lowering the intensity of competition (Toft, 1985 cited in Wilson, 2010). However, it is also thought that species within similar habitats may be able to coexist by a balance between exploitation and interference competition (Ford, 1979).

1.3 Interspecific competition in Honeyeaters

A good example of interspecific competition and resource partitioning can be found in honeyeaters (Meliphagidae). The family of honeyeaters consist mainly of nectarivorous birds found in Australia, New Zealand, New Guinea and Indonesia (Pyke, Christy & Major, 1996). Australia has about 72 species of honeyeaters (Ford, 1985 cited in Perrot, 1997) the majority of which are not totally nectarivorous and include insects, fruit and pollen in their diet (Recher, 1971; Ford, 1979). The proportion of nectar in their diet varies between species (Ford, 1979) and studies have observed that species who consume more insects generally feed in more varied locations (Keast, 1968; Ford & Paton, 1976a). Generally, honeyeaters show little specialisation and require similar nectar food resources (Terborgh & Diamond, 1970, Paton & Ford, 1976, Ford & Paton, 1977 and Recher, 1977 cited in Ford, 1979). Therefore, species that have high proportions of nectar in their diet will likely compete more (Recher, 1971, 1977, Ford & Paton, 1977, Paton & Ford, 1977 cited in Ford, 1979) especially given that nectar is often a limited resource (Ford, 1979).

Territorial behaviour occurs in many honeyeater species (Pyke *et al.*, 1996) and is a form of interference competition where individuals exclude others from resources. Most interspecific interactions involve larger species dominating smaller species (Immelmann, 1961 cited in Ford, 1979). Nonetheless, large and small honeyeaters can coexist in similar habitats (Keast, 1968) and it is hypothesised that larger species of honeyeaters are able to defend high quality resources (Ford, 1979). Smaller honeyeaters are thought to be more efficient at feeding, require less energy, and can feed on poorer nectar resources more profitably than larger species (Ford, 1979; Slater, 1994). Ford (1979) made predictions about how honeyeaters coexist in similar habitats: when flowering starts there is only a small amount of nectar available which can be utilised by smaller (more efficient) bird species and as nectar production increases the larger species will start to exclude the smaller species (Ford, 1979). When nectar production starts to decline, the first to leave the flowering plant should be the larger species (Ford, 1979). With smaller species having lower energy requirements, Ford (1979) predicts that they could breed in a wider range of sites and for a longer duration. Plant species with the richest nectar supply, either per flower or as flower clumps, would be visited more by larger species (Ford,

1979). This pattern of larger species being territorial (interference competition) and smaller species showing less territorial behaviour (exploitation competition) has also been found in hummingbirds (Wolf, Stiles & Hainsworth, 1976; Ford, 1979).

1.4 New Zealand Honeyeaters

New Zealand has three ecological honeyeater species. The tui (or Parsons bird; *Prosthemadera novaeseelandia*) and bellbird (or korimako; *Anthornis melanura*) belong the honeyeater family Meliphagidae. Hihi (or stitchbird; *Notiomystis cincta*) was once classed in the honeyeater family but has now been placed in its own family, Notiomystidae, as they are closer to New Zealand's wattle birds (family Callaeidae) than honeyeaters in phylogenetic trees of passerines (Ewen, Flux & Ericson, 2006; Driskell *et al.*, 2007). For this study I use the term honeyeaters in its ecological context i.e. nectarivorous birds.

Interference competition is known to occur between New Zealand's three honeyeater species as they all feed on nectar (Castro, Minot & Alley, 1994). Tui are dominant and exclude bellbirds and hihi from major nectar sources resulting in the smaller honeyeaters foraging on less productive flowers (Castro, 1995; Castro & Robertson, 1997). Bellbirds are also observed excluding hihi from food resources (Castro, 1995). There is a clear dominance hierarchy between these three species from tui to bellbirds to hihi, despite bellbirds being slightly smaller than hihi (Craig, Douglas, Stewart & Veitch, 1981a). As nectar is often considered a limiting resource (Ford, 1979), hihi risk negative impacts where the two more dominant species occur. Hihi are the most threatened species out of three with IUCN (2011) listing them as 'vulnerable' and with tui and bellbirds listed as 'least concern.' Therefore it is important to know the ecological niche and habitat requirements for hihi and the circumstances of these three species coexistence to enable future successful reintroductions of hihi and to create self-sustaining populations.

1.4.1 Habitat

All three honeyeaters occur in dense native forest but tui and bellbirds can also inhabit regenerating forest and urban environments, particularly when close to remnant

native forest (Higgins, Peter, & Steele, 2001). Tui are generally resident year round (Stildoph, 1923, Moncrieff, 1929 and Bull, 1959 cited in Higgins *et al.*, 2001) but they can have seasonal movements and disperse long distances dependent on food availability (Edgar, 1978, Owen and Sell, 1985, Wilson *et al.*, 1988 and Guest and Guest, 1993 cited in Higgins *et al.*, 2001). Tui also aggregate when food is abundant (McCann, 1952, St Paul, 1975 and Onley, 1980 cited in Higgins *et al.*, 2001). Bellbirds are also described as year round residents (Moncrieff, 1929, Turbott, 1953, Kikkawa, 1960, 1966, and Thoresen, 1967 cited in Higgins *et al.*, 2001) with local movements (Sagar, 1985 cited in Higgins *et al.*, 2001), seasonal changes in distribution (Moncrieff, 1929, St Paul, 1975, and Guest and Guest, 1977 cited in Higgins *et al.*, 2001), and dispersal (Moncrieff, 1929 and Wilson *et al.*, 1988 cited in Higgins *et al.*, 2001). However, hihi are known to be more sedentary than tui and bellbirds (Gravatt, 1970) with only limited movements (<2 km) in response to the availability of nectar and fruit several kilometres between good feeding sites (Gravatt, 1970; Angher 1984, 1985 cited in Higgins *et al.*, 2001; Heather & Robertson, 2005). The limited dispersal abilities of hihi compared to the other honeyeaters suggests that a local and year round supply of nectar/fruit producing plant species is required in sites being assessed for translocation (Perrot, 1997). Hihi are obligate cavity nesters (Rash, 1985, 1989) and require mature forest where such cavities exist. All three species show considerable overlap in habitat and responses to food resources, hence there must be other differences that allow them to coexist in similar habitats.

1.4.2 Foraging ecology

All three species feed on nectar, fruit and invertebrates (primarily insects and arachnids; Gravatt, 1970, 1971). Tui and bellbirds also include honeydew in their diet and tui occasionally eat pollen and seeds (Gravatt, 1971; Higgins *et al.*, 2001). The proportions of each dietary component differ between species (Merton, 1966; Gravatt, 1971). A study by Gravatt (1971) on Little Barrier Island, found that tui consume more nectar (81%) than hihi (75 %) and bellbirds consume the least (51 %) whereas hihi consume more fruit (15 %) than either tui (7 %) or bellbird (5 %) and bellbirds consume more invertebrates (44 %) than tui (13%) and hihi (9 %). A study on tui, bellbird and hihi

faecal content on Little Barrier Island by Gaze & Fitzgerald (1982) also supported Gravatt's (1971) work showing bellbirds consumed the most insects and hihi consumed the most fruit. An earlier study on tui and bellbirds by Merton (1966) on Hen Island found similar results with tui having the highest proportion of nectar and bellbirds had a higher proportion of insects in their diet. A study by O'Donnell (1980, cited in Gravatt, 1971) on tui and bellbird diet also found similar results in the Nelson region. This led to the conclusion that the diet of tui is primarily nectarivorous, the bellbird diet is primarily insectivorous, and the hihi diet is primarily nectarivorous but it more frugivorous than the other two.

This appears to be a good example of resource partitioning as each species depends more on different food types. However, the study by Merton (1966) was done in May and the faecal analysis by Gaze & Fitzgerald (1982) in autumn. Gravatt (1971) found that although the three species have different diets, they all show seasonal trends with all three species consuming higher proportions of nectar in spring and summer, fruit and invertebrates in winter. Stewart (1980, cited in Craig *et al.*, 1981b) also showed seasonal variation in the consumption of the different food types by tui and bellbirds on Tiritiri Matangi Island but less difference between these two species than occurred on Little Barrier Island. On Tiritiri Matangi, invertebrates were common in both species diets, particularly in winter and over the breeding season (Stewart, 1980 cited in Craig *et al.*, 1981b). Diet can therefore differ considerably between nearby locations (Stewart, 1980 cited in Craig *et al.*, 1981b). Hihi foraging (Angher 1984 cited in Castro, 1995; Castro, 1995; Perrot, 1997) also varies over the seasons and between sites. The results from the studies mentioned so far compared observations of single events of birds consuming particular foods. However, the study by Merton (1966) involved following individuals and recording how long they spent feeding on each food type. These results showed marked differences from observations of individual events. For example, bellbirds foraged for nectar in 46 % of the individual events but only 1% of an individual's total feeding time was spent foraging on nectar (Merton, 1966). Therefore, the idea that each species depends on one different component more than the others is not consistent on a temporal and spatial basis suggesting that this may not be a significant factor in the resource partitioning between these three species.

Resource partitioning can also occur spatially (vertically) within (forest) habitat. Gravatt (1971) divided the mature forest on Little Barrier into 6 layers and looked at feeding events in these layers by tui, bellbirds and hihi. Tui forage primarily in the canopy (47.8 %) with none observed in the lower understorey and ground layers (Gravatt, 1971). Bellbirds most commonly forage in the upper understorey (34.7 %) but occur in all vegetation layers (Gravatt, 1971). Hihi forage mainly in the middle storey (29.1 %) and lower understorey (26.5 %) and not at all on the ground (Gravatt, 1971). Similar results were also found by O'Donnell & Dilks (1994). Results from these studies suggest consistent patterns of vertical partitioning of forest habitat by these three species. It remains unknown though, particularly for hihi, how consistent these trends will be over seasons and in less mature forest habitats. There is also a study (Rasch & Craig, 1988) showing that tui most commonly forage on flowers of the highest nectar production, bellbirds on flowers of moderate nectar production and hihi forage on the lowest nectar producing flowers although they will try to feed on higher nectar producing flowers that tui also forage on. They also showed tui foraged most commonly in the canopy compared to bellbirds and hihi (Rasch & Craig, 1988), suggesting that there may be a link between foraging height and high quality nectar producing flowers.

1.5 Conservation in New Zealand

1.5.1 Impacts of human colonisation and introduced species

Before human colonisation, New Zealand was covered with about 75 % forest (Saunders & Norton, 2001). The terrestrial fauna consisted of birds, lizards, tuatara, invertebrates, frogs and bats (Veblen & Stewart, 1982; Holdaway, 1989). With the lack of terrestrial mammals, New Zealand's flora and fauna is highly endemic and the fauna evolved many flightless species (Bell, 1991 cited in Clout & Craig, 1995). The flora and fauna hence had no or few adaptations to recent introductions/invasions of mammals, particularly predatory mammals (Veblen & Stewart, 1982; Holdaway, 1989). Today New Zealand forest cover has been reduced to only about 25 % (Saunders & Norton, 2001).

Polynesians were the first to colonise New Zealand and form permanent settlements (Craig, Anderson, Clout, Creese, Mitchell, Ogden, Roberts & Ussher, 2000). They introduced the kiore (Polynesian rat; *rattus exulens*), Polynesian dog (*Canis familiaris*) and food plants (Veblen & Stewart, 1982; Craig *et al.*, 2000). The land was cleared of forests by fire resulting in habitat degradation, loss and fragmentation which contributed to the extinction of various bird species, such as the moa (*Dinornis* spp.; Veblen & Stewart, 1982; McGlone, 1989). Hunting by the Polynesians (Maori) is thought to have caused the extinction of 30 endemic bird species (Craig *et al.*, 2000). Hunting contributed to the loss of mainly larger ground dwelling birds, potentially with the help of Polynesian dogs (Cassels, 1984 cited in McGlone, 1989; McGlone, 1989). Kiore were a contributor to the extinction of smaller species (Fleming, 1969 cited in McGlone, 1989) along with the loss of habitat (Craig *et al.*, 2000).

New Zealand was then colonised by Europeans who came to hunt sea lions and seals (Craig *et al.*, 2000). The sealers brought a range of livestock, with the first being pigs and goats then sheep, cattle and horses, all of which established feral populations on both the North and South Islands (Veblen & Stewart, 1982). In the latter half of the nineteenth century, there was a more rapid onset of European settlement (Veblen & Stewart, 1982). They further cleared forest for timber and pastures, introducing European grasses and many other plant species (Craig *et al.*, 2000). They brought more livestock and formed acclimatization societies to introduce more animals and plants (Veblen & Stewart, 1982). They introduced a variety of deer species (*Cervus* spp.), European rabbits (*Oryctolagus cuniculus*), Australian brush-tailed possums (*Trichosurus vulpecula*) and a variety of exotic birds (Veblen & Stewart, 1982). Three species of European rodents also colonised New Zealand (Atkinson, 1973 and Taylor, 1975 cited in O'Donnell, 1996; Veblen & Stewart, 1982). With increased grasslands and poor management, the population of rabbits became uncontrolled (Craig *et al.*, 2000). To control the rabbits, mustelids were released in the 1880s; however, this was unsuccessful (Veblen & Stewart, 1982; Moors, 1983 cited in O'Donnell, 1996). The domestic cat (*Felis catus*) was also introduced as pets and formed feral populations (Thomson, 1922 cited in O'Donnell, 1996).

European settlement and introduced exotic species caused further detriment to the native species of New Zealand. It led to the extinction and decline in population numbers of many species of birds, lizards, invertebrates, bats, fish and frogs (Ministry for the Environment, 1997 and Towns & Daugherty, 1994 cited in Craig *et al.*, 2000). The main causes for this being predation, competition with introduced species, habitat loss, degradation and fragmentation, hunting and specimen collecting by humans (Clout & Craig, 1995). The predatory mammals (mustelids, rats and cats) preyed on the native animals (Veblen & Stewart, 1982; Craig *et al.*, 2000). Many species that declined were seed dispersers and pollinators, hence also having a detrimental effect on native plant species (Craig *et al.*, 2000). Herbivorous mammals (deer, brush-tailed possums, rabbits) have caused significant changes to the structure of the native vegetation, especially the understorey (Veblen & Stewart, 1982; Craig *et al.*, 2000), and some deer compete with the endangered takahe (*Notornis mantelli*) in grasslands (Owen, Mills, Lee & Lavers, 1989; Lee, Fenner, Loughan & Lloyd, 2000). Brush-tailed possums browse in the foliage of canopy trees and on a variety of invertebrates and small vertebrates (e.g. birds; Veblen & Stewart, 1982; Brown, Innes, & Shorten, 1993). Brush-tailed possums cause significant detriment to the native bird species as they prey on nests, consuming the eggs, chicks and parents (Brown *et al.*, 1993) and potentially have an effect on tree mortality (Veblen & Stewart, 1982). These possums and other herbivorous mammals (deer and goats) also compete for food (leaves and fruit) with native birds such as the North Island kokako (*Callaeas cinerea wilsoni*; Leathwick, Hay & Fitzgerald, 1983).

1.5.2 Conservation value of offshore islands

The decimation of native species on the mainland (North Island, South Island and Stewart Island) meant that many species were confined to offshore islands (Daugherty, Towns, Atkinson & Gibbs, 1990). New Zealand has over 700 offshore and outlying islands with 237 being greater than 5 ha in size (Atkinson 1989 cited in Veitch & Bell, 1990). Not all islands escaped the effects of human colonisation. Many islands were used by the Maori for agriculture and hunting seabirds and seals (Bellingham Bellingham, Towns, Cameron, Davis, Wardle, Wilmschurst & Mulder, 2010). Hence, the habitat was degraded and eventually kiore reached some islands, either by swimming, accidental

introduction from humans or potentially introduced for food (Atkinson, 1986 cited in Veitch & Bell, 1990; Bellingham *et al.*, 2010). When Europeans arrived, they used the islands for activities associated with natural resource exploitation (Veitch & Bell, 1990; Bellingham *et al.*, 2010).

Fortunately, many islands were never invaded by exotic predatory mammals (Armstrong *et al.*, 2002). Some islands contained island endemic species, for example the Chatham Island black robin (*Petroica traversi*; Robertson, 1985 cited in Daugherty *et al.*, 1990). These islands were also the only refuge for those who were once present on the mainland but were extirpated after the arrival of humans; including tuatara (*Sphenodon* spp.), many lizards (e.g. Duvaucel's gecko *Hoplodactylus duvaucelii*), many bird species (e.g. hihi, *Notiomystis cincta*, and saddleback, *Philesturnus carunculatus*), invertebrates (e.g. giant weta, *Deinacrida heteracantha*) and frogs (e.g. Hamilton's frog, *Leiopelma hamiltoni*; Daugherty *et al.*, 1990; Craig *et al.*, 2000). Therefore, without these offshore islands, many more species could have become extinct as a result of human colonisation.

The islands that were affected by human settlement have been the focus for ecological restoration (Veitch & Bell, 1990; Bellingham *et al.*, 2010). Most offshore islands have been free from human occupation for several decades allowing natural regeneration of vegetation (Armstrong *et al.*, 2002). Ecological restoration of islands has focused on eradicating exotic species (Veitch & Bell, 1990) and replanting vegetation which started in the 1920s (Bellingham *et al.*, 2010). The purposes for restoring island ecosystems is to help retain the high endemic value of islands as many have their own variety of animal and plant species (Veitch & Bell, 1990) and are used for the reintroduction of threatened native species (Saunders, 1994 and Armstrong & McLean, 1995 cited in Armstrong *et al.*, 2002). However, the full history of the islands is not always known and full restoration to its original state is unlikely (Meurk & Blaschke, 1990; Simberloff, 1990; Veitch & Bell, 1990). Islands can also not fully represent mainland conditions, only a small part, as islands have their own distinct habitat from varying climatic conditions and vegetation (Meurk & Blaschke, 1990). Some threatened species are introduced to islands that they may have not existed on, called 'conservation introductions' (Armstrong *et al.*, 2002), but their survival on these islands may be needed

for their continued existence and hence the vegetation replanted may need to suit these species more than replicating the original ecosystem.

Offshore islands hence provide a great opportunity for conservation, with some limitations. Islands only represent a small part of mainland New Zealand which means that when finding islands suitable for translocating species, only the ‘best match’ to the species original geographical range can be achieved (Meurk & Blaschke, 1990). Many reintroductions fail due to changes to the habitat where these changes may or may not be obvious (Simberloff, 1990). Therefore, the prior knowledge of a species habitat, experimentation and continued monitoring of translocations is important in the success of translocations.

1.5.3 Example of conservation efforts in New Zealand on the hihi (*Notiomystis cincta*).

The hihi represents a good example of conservation efforts in New Zealand and the importance of offshore islands as conservation reserves as well as their limitations. Hihi were once distributed throughout the North Island and offshore islands such as Kapiti, Great Barrier and Little Barrier Islands (Angher, 1984a). The Maori settlers were known to feed on hihi and use the yellow feathers from males to ornament their cloaks (Angher, 1985). After the arrival of European settlers, hihi were one of the first known species to become extinct on the mainland in 1883 (Buller, 1888 cited in Angher, 1984a; Angher, 1984a) and only a small population remained on Little Barrier Island (Angher, 1984a, 1985). The cause for hihi decline is not known but thought to be most likely due to rats, disease or a combination of both (Angher, 1984a; Rasch, Boyd & Clegg, 1996). Hihi are cavity nesters (Rasch, 1985) therefore they were more vulnerable to nest predation by the arboreal nest predators, ship rats (*Rattus rattus*; Angher, 1984a). As only females incubate (Angher, 1985), rodent predation on females can cause sex ratio biases in the population (O'Donnell, 1996). Cats could have also been a potential predator but cats were also present on Little Barrier Island where the hihi population persisted (Angher, 1984a). The Europeans introduced many exotic bird species (Wodzicki, 1950 cited in Angher, 1984a) which could have brought diseases that hihi were susceptible to (Angher, 1984a). At the same time hihi declined, the bellbird and tui populations also

showed declines, particularly in the north of the North Island indicating that disease may have impacted on all three honeyeater species (Rasch *et al.*, 1996). Bellbird and tui numbers did recover unlike the hihi (Rasch *et al.*, 1996), although bellbirds did not recover in Auckland, Northland, Great Barrier Island and Waiheke Island (Lee, 2005).

With a restricted range, the hihi population on Little Barrier Island was still vulnerable (Angher, 1984b). The New Zealand Wildlife Service had a policy to translocate and establish new populations of endangered species in one or more new locations; hence this was applied to hihi (Angher, 1984b). Hen Island was the first island chosen for translocation as it had some common vegetation and topography to Little Barrier Island (Angher, 1984b) and it was free of introduced mammals except for kiore (Angher, 1985). Reintroductions occurred in 1980 and 1981 and expeditions to the island to monitor hihi in 1982 and 1983 showed that hihi appeared to be breeding well (Angher, 1984b). Hihi were then introduced to Cuvier Island in 1982 which also had kiore and to Kapiti Island in 1983 which had kiore, Norway rats (*Rattus norvegicus*), and brush-tailed possums (Angher, 1984b, 1985). The vegetation on both of these islands had been subjected to browsing and structural change from introduced mammals in the past but the vegetation was regenerating (Angher, 1985). Successful breeding occurred on these islands as well in the following years after the translocation (Angher, 1985). However continued monitoring was needed for all three islands as there were concerns that these small islands with a smaller range of food resources could cause problems if there were poor flowering and fruiting years (Angher, 1985). These populations eventually began to decline after each translocation and did not establish stable populations (Rasch *et al.*, 1996; Armstrong & Perrot, 2000). Brush-tailed possums were removed from Kapiti Island in 1985 but the hihi population continued to decline (Rasch *et al.*, 1996).

With food limitation being a concern for the survival of hihi populations, their behavioural ecology was further studied by Castro (1995) following two translocations (1991 48 birds, 1992 47 birds) to Kapiti Island. Their behaviour and foraging ecology was monitored from 1992 to 1994 with the number of flowering and fruiting plants of their known food types also being monitored (Castro, 1995). Long term supplementary feeding was provided, primarily as sugar water (Castro, 1995). Castro (1995) concluded that interspecific competition for nest sites (with kakariki) contributed to low hihi

breeding success and artificial nest boxes were recommended. She also concluded that food supply and competition with other nectar feeders was a major limitation on the hihi population on Kapiti Island (Castro, 1995). Competition with bellbirds and tui, particularly for nectar resources, also had negative impacts on hihi (Castro, 1995). Castro (1995) found that hihi use of artificial feeders, and natural fruit and flowers varied throughout the year (Castro, 1995). Their seasonal foraging ecology showed different patterns to those found on Little Barrier Island, particularly in winter where on Little Barrier they consumed high proportions of fruit (Gravatt, 1971) but on Kapiti they consumed higher proportions of invertebrates (Castro, 1995). This is thought to be most likely due to the smaller range of fruiting plants on Kapiti and potentially competition with the other honeyeaters for the short supply of both fruit and nectar (Castro, 1995). This competition for natural forage explained the increased use of the sugar water feeders by hihi, particularly during egg laying and fledging, as tui and other large nectar feeding birds such as kaka could not enter the feeders (Castro, 1995).

Hihi were next translocated to Tiritiri Matangi and Mokoia Islands where extensive monitoring and experiments on supplementary food were conducted as part of the translocation process (Armstrong & Perrot, 2000; Armstrong & Ewen, 2001). Both islands had a history of intense mammalian browsing and were regenerating but Tiritiri Matangi had also been farmed with large areas of grassland and had been only recently replanted (Rasch *et al.*, 1996; Armstrong & Ewen, 2001). Mammalian predators (except for mice, *Mus musculus*, on Mokoia) had been eradicated but the islands had different competitors: Tiritiri Matangi having both bellbirds and tui and Mokoia only has tui. A supplementary feeder experiment involving alternating days with feeders available (16 days) and feeders absent (12 days) was conducted on Mokoia (1994) and the mass, survival and foraging behaviour of the individuals using the feeders was tracked (Armstrong & Perrot, 2000). Feeder use varied throughout the year (lowest in winter) and did not alter foraging time away from the feeders (Armstrong & Perrot, 2000), although, they did tend to feed on more invertebrates when the feeders were available (Armstrong & Perrot, 2000). Body mass of hihi with and without feeders did not change and it is concluded that hihi condition and survival was not affected by food limitation (Armstrong & Perrot, 2000). However, Castro *et al.* (2003) found the presence of feeders

on Mokoia significantly affected female nesting behaviour (life history changes). With supplementary feeding, females lay larger clutches, egg incubation time is reduced, fledgling and recruitment success is at least doubled and there is a reduced time period until the second clutch is laid (Castro *et al.*, 2003). Hence, hihi reproductive success is enhanced with supplementary feeding showing that they may have been food-limited, which is defined as at least some individuals having a greater chance of reproductive and/or survival success with added food (Carpenter, 1987). However, hihi mortality rate was still relatively high regardless of feeder presence and the respiratory illness caused by the fungus aspergillus was determined to be a common cause of mortality on Mokoia Island (Alley, Castro & Hunter, 1999). Recent studies (Low, 2010) suggest that predation from morepork (*Ninox novaeseelandiae*) could also be contributing to hihi mortality on Mokoia.

In September 1995, hihi were released on Tiritiri Matangi Island (Armstrong & Ewen, 2001). Similar feeder removal experiments as on Mokoia Island were conducted after the initial 6 months (breeding season) at which time sugar water was made available for 23-27 days and removed for 11-12 days (Armstrong & Ewen, 2001). In contrast to Mokoia, no seasonal patterns in the proportion of individuals using the feeder was detected, with up to 100% of hihi observed using the feeders, and the average proportion over the seasons ranged from 72-73 % (Armstrong & Ewen, 2001). Although survival was higher on Tiritiri Matangi Island, when feeders were absent, considerable body mass was lost and hihi mortality increased suggesting food limitation is more prominent on Tiritiri Matangi than on Mokoia (Armstrong & Ewen, 2001). The higher use of the feeders on Tiritiri Matangi Island compared to Mokoia could also be due to competition with bellbirds as bellbirds were absent on Mokoia (Armstrong & Ewen, 2001). Bellbirds were also observed using the feeders (Armstrong & Ewen, 2001) and may face similar food limitations.

Evidence following translocations to Kapiti Island and Tiritiri Matangi Island support the hypothesis that hihi face food limitation and competition on offshore islands (Castro, 1995; Armstrong & Ewen, 2001). Unlike Mokoia Island, both of these islands have resident bellbird populations that also use the supplemental feeders. At present, when visiting Tiritiri Matangi Island many bellbirds can be seen using these feeders

(personal observation). With bellbirds being known to exclude hihi from natural resources, there is the potential for bellbirds to be excluding hihi from the feeders. There have been no recent studies on the concurrent foraging ecology of both hihi and bellbirds on Tiritiri Matangi Island and no research on how each species use and interact at the feeders. Therefore, the overall aim of this thesis was to study the foraging ecology, feeder use and habitat distribution of hihi and bellbirds on Tiritiri Matangi Island. This provides a basis for comparisons of the foraging ecology of these two species on other islands (with and without feeders) and to determine what level of competition is occurring between these two species and how they coexist with similar ecological niches.

1.6 Study species

1.6.1 Hihi (*Notiomystis cincta*)

The hihi (or stitchbird) is a New Zealand endemic forest dwelling passerine (Rasch *et al.*, 1996; Armstrong & Ewen, 2001). They are of medium size and are sexually dimorphic, ranging from 18-19 cm in length and 30-40 g in weight, with males being larger and having different plumage colouration (Angher, 1985; Rasch *et al.*, 1996). Males have a black head, white ear tufts on the side of the head, yellow band across the breast, yellow on the shoulders and a distinct white bar on the wings (Angher, 1985; Rasch *et al.*, 1996). Females are a duller brownish-grey and have a more distinct white bar on the wing (Angher, 1985; Rasch *et al.*, 1996). Both sexes have whiskers around the base of the beak and they often hold their tail tilted upwards (Angher, 1985; Rasch *et al.*, 1996). Males can also erect their ear tufts when they are engaged in aggressive interactions (Angher, 1985). Juveniles resemble females at fledging (Angher, 1985).

Hihi local movements throughout the year are determined by food availability and the breeding season (Angher, 1985). Breeding pairs do not remain together throughout the year and forage independently outside of the breeding season (Angher, 1985). They have a range of breeding strategies including monogamy, polyandry, polygyny and polygynandry (Castro *et al.*, 1996). In addition to conventional avian copulation via the male mounting the female's back, hihi also copulate face to face (male mounting the female's belly), a form of forced copulation (Castro *et al.*, 1996). Hihi populations have a

tendency towards male bias and mate guarding of females and nests is an important aspect of male hihi behaviour during the early part of the breeding season (Low, 2005a; Low 2006b; Ewen, Thorogood & Armstrong, 2011). Extrapair copulations from 'floater' males are often successful (Ewen, Armstrong & Lambert, 1999). Hihi are cavity nesters and only females incubate but males help to feed chicks (Angher, 1985). A clutch of 3-5 eggs are laid, taking about two weeks to hatch and then another 26-30 days until chicks fledge (Angher, 1985).

As mentioned earlier, they are much more sedentary than bellbirds and tui. They prefer mature habitat and overall have an omnivorous diet (Angher, 1985). They are also less aggressive than bellbird and tui but males have been observed defending trees with an abundance of fruit in winter against other hihi (including females) and parakeets (Angher, 1985). However, hihi are known to be territorial and show intraspecific aggression within the breeding season (Castro *et al.*, 1996; Higgins *et al.*, 2001). There are reports of males being dominant over females outside of the breeding season and older hihi dominant over younger hihi of the same sex (Stewart, 1980, Craig *et al.*, 1981, Angher, 1984, Craig, 1984 and Rasch, 1985 cited in Higgins *et al.*, 2001).

1.6.2 Bellbird (*Anthornis melanura*)

The bellbird (or korimako) is also a sexually dimorphic New Zealand endemic passerine (Bartle & Sagar, 1987). They are widely distributed throughout New Zealand (Bartle & Sagar, 1987) and four subspecies have been identified (Higgins *et al.*, 2001). The most commonly distributed is *Anthornis melanura melanura* found on the North Island, South Island, Stewart Island and many offshore islands (Higgins *et al.*, 2001). The other three subspecies are endemic to particular smaller island groups with *A. m. oneho* on Poor Knights Island, *A. m. obscura* on the Three Kings Islands, and the extinct *A. m. melanocephala* on the Chatham Islands (Higgins *et al.*, 2001). From now on reference will be made only to the study species, *A. m. melanura*.

Bellbirds are of medium size, although slightly smaller than hihi, and sexually dimorphic by size and plumage colour. Males are larger than females and their length can range from 17-20 cm, with longer tails than hihi (Higgins *et al.*, 2001). Males weigh on average 32.5 g and females 25 g (Craig *et al.*, 1981a; Higgins *et al.*, 2001). The males

head and neck is a dark olive-green with a blue-purple iridescent sheen which is most prominent on the forehead (Higgins *et al.*, 2001). Their back is the same dark olive-green whilst the underbody grades from the same dark colour to a lighter olive-green (Higgins *et al.*, 2001). The primary and secondary feathers range from light brown to black and the tail feathers are a black-brown and are edged with iridescence (Higgins *et al.*, 2001). Females are overall a duller olive-brown with only weak iridescence on the forehead (Higgins *et al.*, 2001). The wings and tail are of similar colouration to males, although females have no iridescence on the tail feathers (Higgins *et al.*, 2001). The main distinguishing feature from males is the thin white moustachial stripe on the cheeks (Higgins *et al.*, 2001). Both sexes have red irises as adults whereas juveniles have brown irises (Higgins *et al.*, 2001). The juveniles also most resemble females but the moustachial stripe is pale yellow and they have very little or no iridescence (Higgins *et al.*, 2001).

As mentioned earlier, bellbirds have a varied diet and are considered residential but can disperse various distances depending on food availability (Higgins *et al.*, 2001). As for hihi, they do not remain in the breeding pairs and forage independently outside of the breeding season (Higgins *et al.*, 2001). However, they are also known to flock at resources, particularly mixed female and juveniles groups at the end of the breeding season (Sagar, 1985 cited in Higgins *et al.*, 2001; Higgins *et al.*, 2001). Bellbirds are aggressive and competitive, so they will either defend resource patches or form intraspecific hierarchies within a resource (Craig & Douglas, 1986; Higgins *et al.*, 2001). In general, males are dominant over females and females are dominant over juveniles (Craig, 1984, 1985 cited in Higgins *et al.*, 2001; Craig & Douglas, 1986). However, resident females will dominate over non-resident males (Higgins *et al.*, 2001). Both sexes defend their territories and resources with song and song type differing between the sexes (Brunton & Li, 2006). They also chase subordinates away (Craig & Douglas, 1986). Both sexes have wing slots, an emarginate ninth primary wing feather, which are used to make noise during aggressive encounters and the slots vary in size for the sexes and ages with the slot absent in juveniles (Craig & Douglas, 1986; Bartle & Sagar, 1987).

Bellbirds form territories during the breeding season to defend resources and the nest (Higgins *et al.*, 2001). On Tiritiri Matangi the breeding season is generally from

August to February (Cope, 2007). Courting begins at the end of winter from August to September and nest building often does not start until October (Higgins *et al.*, 2001; Cope, 2007). Females build well concealed nests and can be built in a variety of different plant species and at various heights from the ground (Higgins *et al.*, 2001; Cope, 2007). Although, on Tiritiri Matangi Island females seem to have a preference for nesting in cabbage trees (*Cordyline australis*; Cope, 2007). Females can lay up to four eggs, can relay if a nest fails and can have multiple clutches (Higgins *et al.*, 2001; Cope, 2007). Only females incubate but males help to feed her and the chicks (Higgins *et al.*, 2001; Cope, 2007). Females tend to spend more time feeding the chicks and spend less time away from them than the males (Cope, 2007). Eggs hatch within 14 days and can fledge within another 14 days (Higgins *et al.*, 2001; Cope, 2007). Bellbirds are generally thought to be monogamous as they often retain the same partner each year (Higgins *et al.*, 2001). However, extrapair copulations and paternity are known to occur (Cope, 2007).

1.7 Study site

Tiritiri Matangi Island is a low-lying 220 ha island in the Hauraki Gulf 4 km off the coast of the Whangaparaoa Peninsula and 25 km north of Auckland, New Zealand's largest city. It is 2.7 km long and has an average width of 0.7 km (Elser, 1978). Under the Reserves Act 1977 it was classed as a Scientific Reserve and is an open sanctuary, one of the few offshore islands that allow public visitation. As mentioned earlier, the island was subjected to mammalian browsing and farming, it also has a lighthouse (Elser, 1978). Farming ceased in 1971 and the farm stock was removed in 1972 (Elser, 1978). At that time the island consisted of 52 % grasslands, 20 % tree stands and the rest was fern and scrub (Elser, 1978). A restoration programme began in 1983 and volunteers from various national conservation organisations assisted in an extensive replanting programme (Galbraith, 1990). Since then, around 300,000 trees have propagated from local seeds and planted on the island (Galbraith, 1990). Cats, goats and rabbits were also removed although kiore were not eradicated until 1993 (Veitch, 2002). In 1988 the Supporters of Tiritiri Matangi Island (Inc) was founded by volunteers with the aims of developing the island as an open sanctuary, promoting public awareness and providing physical, material and financial support for projects on the island (Galbraith, 1990).

There are a number of native, exotic and reintroduced birds on Tiritiri Matangi Island. Approximately 77 bird species have been observed on the island (Graham & Veitch, 2002). There are approximately 27 native species that are naturally present on the island, including tui, bellbirds and fantails (Graham & Veitch, 2002). There are 19 native species that occur on the island but are not known to breed there and 22 introduced exotic species that have arrived on the island by themselves (Graham & Veitch, 2002). Reintroductions of native bird species include North Island saddleback (*Philesturnus carunculatus rufusater*), red-crowned kakariki (*Cyanoramphus novaezelandiae*), North Island robin (*Petroica australis*), kokako (*Callaeas cinerea*) and of course hihi (Graham & Veitch, 2002).

Bellbird numbers were very low on Tiritiri Matangi Island, with only 24 individuals observed in 1969 (Rimmer, 2004 cited in Cope, 2007) and the population has suffered a genetic bottleneck (Baillie & Brunton, 2011). Following kiore eradication, regular bird counts by Graham & Veitch (2002) were carried out from 1996 to 1998. The number of bellbirds and other birds such as saddleback increased significantly after the kiore eradication (Graham & Veitch, 2002). However, hihi were introduced in 1995 along with the sugar water feeders. Bellbirds dramatically increased in numbers following the removal of kiore but also likely benefitted from the presence of sugar water feeders. These factors plus the regeneration of forest have likely contributed to the large increases in the bellbird population on Tiritiri Matangi Island (Cope, 2007). The hihi population has grown significantly from the release of 38 individuals in the first 1995 translocation and then another 13 in 1996 (although only 16 remained following the first release and 5 following the second; Armstrong & Ewen, 2001), growing to a population of approximately 176 in September 2010 (102 male, 74 female; Ewen, J.G. and Walker, L. pers. comm.). However, the hihi population on Tiritiri has also been used as a source population for new reintroductions (e.g. to Maungatautari mainland reserve; Ewen, Parker, Richardson, Armstrong & Smuts-Kennedy, 2011).

1.8 Research objectives

This research aims to expand current knowledge of the foraging ecology of hihi and bellbirds and to help understand the level of competition and resource partitioning

between these two ecologically similar species on Tiritiri Matangi Island. Variation in foraging ecology has been found between different locations; therefore I aimed to see how the foraging ecology of hihi and bellbirds on Tiritiri Matangi Island compares to other locations. Natural diet of both species was measured; their short- and long-term temporal patterns were compared. Hihi and bellbirds both use the sugar water feeders on Tiritiri Matangi: how much, when and how they interact was also an aim of this study and has not previously been quantified. As all hihi on the island are colour banded the population abundance is well known, hence I tested variations and assumptions of a simple bird count methodology on hihi to determine the best method of estimating population abundance and then used these findings to help estimate the abundance of bellbirds on the island. The density and distribution of both species across different habitats during the non-breeding season along with estimates of the food available in those habitats was examined to compare spatial and temporal patterns. The removal of bellbirds for a translocation also occurred at the beginning of the research project; densities were compared pre- and post-removal to determine if the removal of 100 birds from the population could be detected. The structure of this thesis will consist of a methodology chapter with a specific introduction to each chapter, followed by result chapters including an abstract and discussion, and then a conclusions chapter with an overview of all results, future research recommendations and implications for hihi management. The specific research objectives are as follows:

- 1) To measure bellbird and hihi diet and their foraging behaviour on Tiritiri Matangi Island (Chapter 3)
- 2) To assess the abundance of known food plants and the level of nectar resources available throughout the research period (Chapter 3)
- 3) To assess visitation rates and behavioural interactions at the feeders by bellbirds and hihi in the short- and long-term to determine any differences and competition between the species and sexes (Chapter 4)
- 4) To estimate the abundance and density distribution patterns of hihi and bellbirds on Tiritiri Matangi Island and to assess what factors (habitat type, natural resources, feeders) may influence these (Chapter 5)

- 5) To assess whether the removal of 100 bellbirds had any detectable effect on the distribution of hihi in the areas of bellbird removal (Chapter 6)
- 6) Overview of the foraging ecology and habitat distribution of hihi and bellbirds to assess how these two species coexist with resource partitioning with future research recommendations and the implications for hihi management (Chapter 7)

Chapter 2:

Methodology



A male hihi at a water trough on Tiritiri Matangi Island.

Photo: Michelle Roper, 2010.

2.1. The foraging ecology of bellbirds and hihi with a plant survey of study sites on Tiritiri Matangi Island

2.1.1 First Food Eaten

2.1.1.1 Introduction

Bellbirds and hihi are both considered to have a primarily nectivorous diet. Their diet consists of a wide range of nectar producing flowering plant species and large overlap in the food sources on these two species has been reported (Castro & Robertson, 1997; Baker, 1999; Perrot & Armstrong, 2000). Bellbirds and hihi (as well as tui) have been shown to have differences in the proportion of nectar, fruit and invertebrates that they consume (Gravatt, 1970; Gaze & Fitzgerald, 1982). It is also known that the more dominant and aggressive tui can displace bellbirds and hihi from larger more productive flowers with the result that the two smaller species collect nectar from plants with smaller flowers and lower nectar concentrations when tui are present at high densities (Craig, 1984 cited in Castro & Robertson, 1997; Rasch and Craig 1988). However, little is known on whether these honeyeaters forage selectively (Castro & Robertson, 1997) apart from the ability of bellbirds and tui to recognise nectar availability for some species based on the flower colour (Delph & Lively, 1989 and Ladley *et al.*, 1997 cited in Castro & Robertson, 1997).

With these three ecological honeyeaters co-existing on the relatively small Tiritiri Matangi Island with only a small amount of mature remnant forest (45 ha; Brunton & Stamp, 2007), there is likely to be intense competition, resource partitioning and displacement by more aggressive species. As stated above, it is known that tui can displace bellbirds and hihi towards plants with smaller flowers, but what partitioning is occurring between bellbirds and hihi? Bellbirds are known to be more dominant over hihi (Perrot & Armstrong, 2000) so from what flowers are bellbirds displacing the hihi and what are the nectar sources used by hihi? Theory suggests that intense overlap in resource requirements between species and limitation of these resources will result in spatial and/or temporal variations in foraging patterns between competing species. Differences in foraging height (Gravatt, 1971) and nectar quality (Rasch & Craig, 1988) have also

been found between the three species but more research is needed to assess whether these results are consistent with location and season.

I conducted a foraging survey which would allow me to record the foraging behaviour of bellbirds and hihi and assess the proportions of different food types within their diets. I also recorded the species of plants from which bellbird and hihi were obtaining nectar and their seasonal patterns of nectar use along with the heights in which foraging occurred. Males and females of both species were observed to look at intraspecific variation in foraging behaviour and diet. This will give us some clues as to how bellbirds and hihi co-exist on this small island and how they may have once co-existed together on the mainland.

2.1.1.2 Procedure

To assess the foraging behaviour of bellbirds and hihi on Tiritiri Matangi Island, a simple procedure called ‘first food eaten’ was used. This procedure simply involved walking through an area until an individual of the targeted species was found, observing the individual until they consume a food item, recording sex of bird, food source, foraging height (in terms of forest strata) and species of plant and then moving on to another individual. This procedure aims to obtain independent data from different individuals of the same species by only recording one feeding observation from each individual.

‘First food eaten’ was carried out through the entire field period from April to October (autumn to spring) 2010. Generally, the second field week of each month was dedicated to ‘first food eaten’ observations but observations were also made while walking between transects during the bird count field week and any other opportunities whilst walking around the island. ‘First food eaten’ observations were conducted using up to 3 observers at any one time for the first three months, >3 in June, and one observer from July until October.

When either a bellbird or hihi was found, the observer remained a reasonable distance from the bird (so as not to disturb it) and used binoculars where necessary to follow the behaviour of the focal until it was unequivocally observed to consume a known food item. If the bird flew out of sight before observed feeding, then the search

continued for another bird. The data sheet in Appendix 2.1 outlines the variables recorded for each feeding event. Food type and foraging height were defined as follows:

- Food type
 - nectar
 - honeydew
 - fruit
 - invertebrate (positive identification)
 - probable invertebrate (could not see the food item but the behaviour of the bird suggested a invertebrate was consumed)
- Foraging height (in forest strata; definitions from Gravatt, 1971 and Poirot, 2004)
 - canopy (foliage of the vegetation which is exposed from above)
 - sub-canopy (foliage and twigs directly beneath the canopy)
 - upper understorey (typically twigs, branches and trunks that are continuous with sub-canopy which extends to the tops of smaller trees in the second layer of vegetation)
 - middle storey (canopy and sub-canopy of the second layer of vegetation)
 - lower understorey (typically the region of small shrubs and trunks below the middle layer)
 - ground (includes small plants, herbs, litter, logs and bare ground)

2.1.1.3 Analysis

2.1.1.3.1 Dietary components

The proportion of feeding events that targeted nectar, fruit, invertebrate or honeydew were calculated to compare the diet composition of different categories (species, sexes and seasons). As earlier months had lower sample sizes and as seasons are more biological meaningful than months, months were pooled into seasons: autumn-winter (April to August) and spring (September and October). Chi-square tests were then

used to make the appropriate comparisons between categories in the ratio of dietary components.

2.1.1.3.2 Foraging height

The proportion of all feeding events at each foraging height in the forest strata was calculated to compare the foraging height of different categories (species, sexes and seasons). Chi-square tests were used to test for any significant differences between the sexes and species at each foraging height. The observations were then categorised into the seasons (autumn-winter and spring) as above where chi-square tests were used to compare between the seasons for each sex and compare between the species for each season.

2.1.1.3.3 Sources of nectar

With small sample sizes in the earlier months, only observations from June to October were used for comparing the sources of nectar between bellbirds and hihi. The months were categorised into seasons: winter (June to August) and spring (September and October). The proportion of each nectar source (plant species) per season was calculated for both bellbirds and hihi from the number of nectar feeding observations per season. Chi-square tests were used to test for any significant differences between bellbirds and hihi for each plant species within each season. The proportion of each nectar source (plant species) per season was calculated then for the sexes of each species. Chi-square tests were again used to test for any significant differences between the sexes within each species and for each season.

2.1.2 Plant surveys of transect and feeder sites

2.1.2.1 Introduction

A plant survey of the transect and feeder sites was obtained to compare the level of local resources available with the estimated local densities of bellbirds and hihi from the bird counts and the number of visits to the artificial feeders. There are approximately 48 plant species known to be on Tiritiri Matangi Island (Supporters of Tiritiri Matangi

Inc, 2010) that are potential food sources for bellbirds and/or hihi (Castro & Robertson, 1997; Baker, 1999; Perrot & Armstrong, 2000). There were only 18 plant species on which bellbirds and hihi were observed feeding on throughout the study period (from ‘first food eaten’ data) and these were of most interest for determining resource availability during the study period. Therefore, the plants that bellbirds and hihi had been observed feeding on were the main focus for the plant survey which was carried out in August 2011. Three additional plant species were included which are well documented food sources and dominant in some locations on Tiritiri (Castro, 1997; Baker, 1999; Perrot and Armstrong, 2000), pohutukawa (*Metrosideros excelsa*), mahoe (*Melicytus ramiflorus*) and kanuka (*Kunzea ericoides*). Although bellbirds and hihi were not seen feeding on the latter three, bellbirds do collect honeydew from kanuka bark.

2.1.2.2 Procedure

Plant surveys were carried out slightly differently in transect versus feeder sites. Surveying the transects was carried out by walking slowly along each transect and tallying the number of target plant species within 10 m either side of the transect (as was done for the bird counts). For the feeder sites I tallied the number of each plant species within a 10 m radius of the feeder.

2.1.2.3 Analysis

The proportion of each plant species was calculated and categorised into the DAFOR scale: Dominant (>75%), Abundant (50–75%), Frequent (25–50%), Occasional (5–25%) and Rare (<5%; Affre *et al.*, 2009). From the ‘first food eaten’ data I knew what plant species were fruiting and flowering each month and combined this with the abundance index of each plant species at each transect and feeder site. Combining these data, I calculated a *food resources level* at each site per month using a DAFOR score of 1 to 5 (rare = 1, occasional = 2, frequent = 3, abundant = 4, dominant = 5). Due to the low number of feeding observations for fruit, scores were calculated for nectar producing plant species only and kanuka (for its honeydew) was included in the score for bellbirds only. Hence for each month, the *food resources level* was the cumulative DAFOR scores for all nectar producing plant species at each site. These scores were then compared to

estimated densities from the bird counts and the number of visits by hihi and bellbirds to the feeders in the respective chapters.

2.2. Feeder visitation and interactions

2.2.1 Introduction

Sugar water feeders are provided on Tiritiri Matangi Island as a supplementary food resource for hihi. It was shown on Mokoia Island that supplementary feeding increases clutch size and is an essential resource for the survival of hihi populations on offshore islands (Armstrong & Ewen, 2001; Castro *et al.*, 2003). Offshore islands may not be able to meet the resource requirements of hihi due to limited vegetation and competition with tui and bellbirds (Castro, 1995; Castro *et al.*, 2003). Therefore, the sugar water feeders may be essential for the long-term viability of the hihi population on small islands until enough mature forest has regenerated for a self-sustaining population.

On Tiritiri Matangi Island, the feeders are also used by bellbirds. Bellbirds are slightly smaller than hihi (Craig *et al.*, 1981) and can therefore fit through the openings to the feeders. Tui are unable to fit through the openings and are therefore excluded from the feeders. Bellbirds are known to dominate hihi in the dominance hierarchy that occurs between three of New Zealand's nectivorous birds, with tui being at the top of the hierarchy (Craig, 1985). Therefore, there is concern that bellbirds may have the potential to exclude hihi from the supplementary feeders upon which hihi rely. However, with the limited amount of nectar producing vegetation throughout the year on Tiritiri Matangi, the bellbirds may be just as dependent on these supplemental feeders when food resources are low. Therefore, as resource partitioning could be occurring at natural food resources, this may also be occurring at the feeders, particularly in the form of temporal variation (daily and seasonally) which may lead to different patterns of feeder use by the two species and by males and females within each species.

In 2010, there were 6 sugar water feeder stations available at various locations on Tiritiri Matangi Island (excluding one feeder placed near the visitor centre which provides access to tui and is dominated by tui and bellbirds only; Figure 2.1). These are situated in and around the mature/regenerated bush habitat (hihi preferred habitat;

Angher, 1985). Feeders are refilled and checked daily by Department Of Conservation staff and volunteers and the amount of sugar water placed within each feeder station varies. In general, the amount of sugar water deployed at a feeder each day (1 to 3 x 1.25 or 2 litres) was determined by how much sugar water was consumed on the previous day (except for one feeder which was limited to a single 1.25/2 litre bottle).

Most of the feeder stations consist of a wooden frame surrounded by plastic wire netting (Figure 2.2). On two sides there are three small openings. Inside the feeder stations, sugar water feeders (consisting of a plastic 1.25 or 2 litre bottle and plastic *hummingbird feeder* base allowing access to the sugar water through multiple small openings) are centrally placed. One feeder is made of plastic netting where the squares of the netting are large enough for hihi to enter from any direction and has a plastic base supporting the weight of one sugar water feeder.

To assess any potential impacts on hihi feeder use by bellbirds, we first needed to attain basic information on feeder use by the two species. Using video sampling, we filmed the feeders throughout the day and at various times of the year to obtain data on the number of birds visiting the feeders, the number of hihi and bellbird visits, the number of each sex and any interspecific and intraspecific behavioural interactions occurring inside the feeder stations. These factors were hypothesised to help us gain an understanding of how these birds use the feeders and whether any temporal variation or competitive exclusion is occurring between either species or sex.

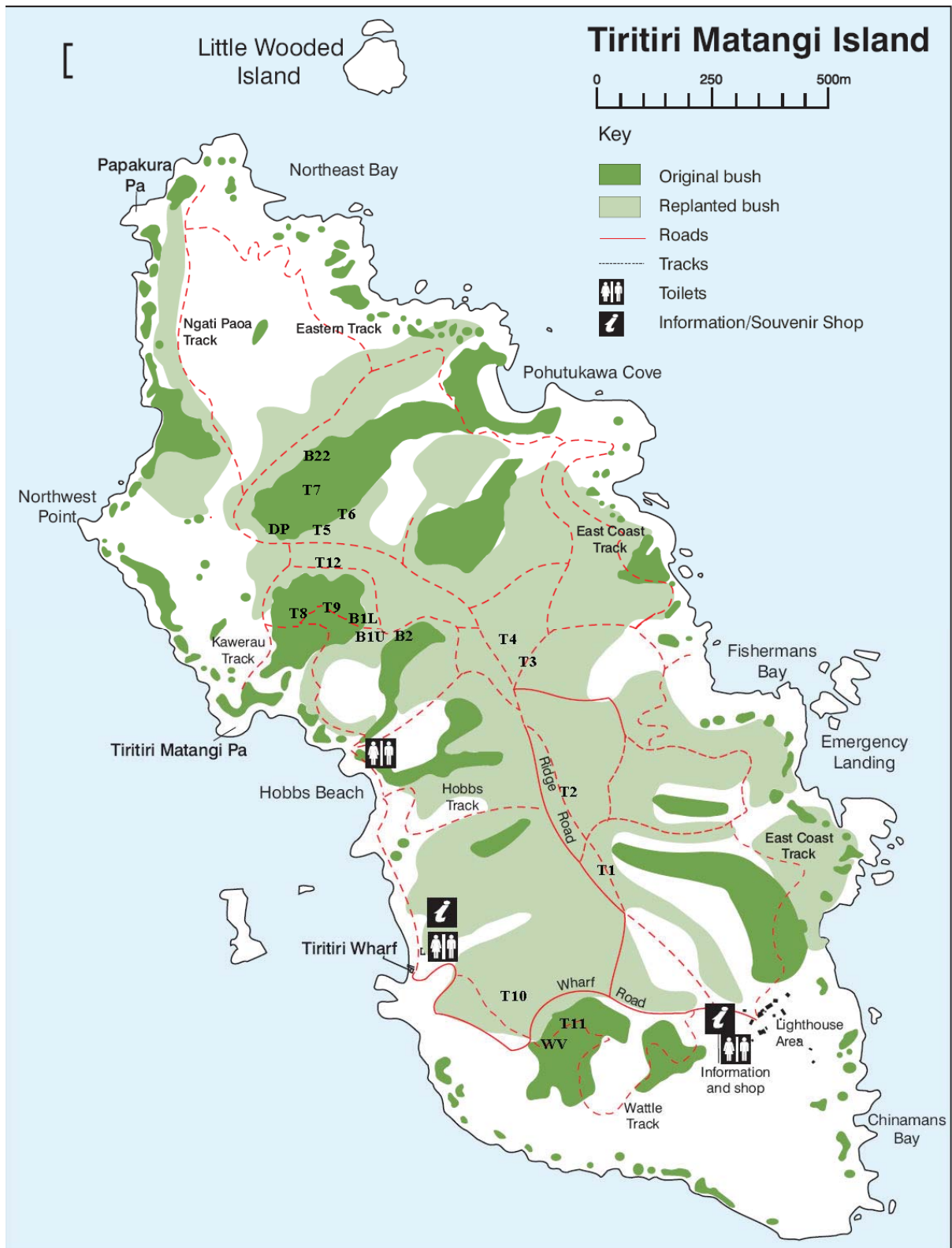


Figure 2.1. Map of Tiritiri Matangi Island with the location of transects (T1-T12) and feeders (B1L=Bush 1 Lower; B1U=Bush 1 Upper; B2=Bush 2; B22=Bush 22; DP=Dupont, WV=Wattle Valley).



Figure 2.2. An example of the general sugar water feeder station structure on Tiritiri Matangi Island. Photo: Michelle Roper, 2010.

2.2.2 Video sampling

2.2.2.1 Equipment and setup

For filming the feeder stations, we used two digital video recorder (DVR) units on separate feeder stations at any one time. These were powered by lead batteries. One to two cameras were connected to each DVR unit. One colour/infrared camera was placed on a tripod in front of the feeder station as close as possible for viewing inside the feeder station. Another camera, black and white, was placed further away from the feeder propped up in a tree with bamboo poles for extra support and at a position where the feeder and its surroundings could be seen. This background camera was primarily used for observing people passing by the feeders, especially those near public tracks, to see what influence they have on the birds inside the feeder stations. Occasionally cable faults occurred and cables for the colour cameras were prioritised. Feeders close to public walking tracks were also given priority for background cameras as feeders away from public tracks are only rarely disturbed by the rangers, researchers and volunteers passing through the area.

Video sampling began on the 22nd April 2010 and ended in October 2010. Video units were rotated between feeders so that sampling covered all feeders with each being recorded during at least 3 different months. Visits to the island were made twice per

month and usually lasted between 5 to 7 days. The period of filming depended on how quickly equipment could be accessed, moved and set up at each feeder (depending in some cases on access to transport and distances between feeders) and batteries changed. Filming was set to record from 6am to 6pm (Standard Time). The length of filming during the day depended on battery life and set up time. Generally, recharged batteries were taken out to feeders every morning at 8am when the rangers and volunteers changed the sugar water.

2.2.2.2 Recording observations

The video was viewed with the USB Playback Console programme that was provided with the DVR units. The programme had various functions where the video could be enhanced in brightness and colour, for example, to increase the quality of the video. The video quality was often reduced by sunlight interference causing the video to look very dark. Increasing the brightness was needed in these situations to be able to see the birds more clearly. A downfall with using the enhancements was that it could only be watched at half speed, hence taking twice as long to view. Watching at half speed was also sometimes necessary when large numbers of birds were entering the feeder during some periods of the day and some feeders tended to have more visits than others. When visitation to the feeders was very low, the periods of when the feeders were empty could be watched at higher speed and slowed back down when birds entered the feeder.

The programme *JWatcher* (<http://www.jwatcher.ucla.edu/>) was used for recording visitations, feeder occupation categories and behaviours. *JWatcher* works by assigning a key on your computer keyboard for each event you are recording. Visitations were divided into male bellbird, female bellbird, male hihi and female hihi. The feeder occupation categories were based on the combinations of each type of bird and sex in the feeder at any one time (Table 2.1). The type of behaviours recorded were primarily based on acts of aggression and/or dominance over any other bird which included displays, displacements and fighting. Copulation between males and females was also recorded. Other variables recorded included the presence of tui, people or other birds near the feeder.

Table 2.1. Feeder occupation categories based on the presence and number of bellbirds (BB) and hihi (HH) and males (M) and females (F) in the feeder at any one moment.

	Categories
Individuals	BB M
	BB F
	HH M
	HH F
More then one individual of same species and sex	BB M >1
	BB F >1
	HH M >1
	HH F >1
Groups of different species/sexes	BB M + F
	HH M + HH F
	BB M + HH M
	BB M + HH F
	BB F + HH M
	BB F + HH F
	BB M + BB F + HH M
	BB M + BB F + HH F
	BB M + HH M + HH F
	BB F + HH M + HH F
	All

The video was separated into each hour of the day for recording events. Visitations were recorded by identifying every bird that entered the feeder. This occasionally included birds that may have entered but not consumed any sugar water. Entering birds were counted as I could not keep track of movements (in/out) of individual birds when feeder use was high. This method provided an overall number of visitations of birds (by sex and species) for each hour of video. When a full hour (but more than 15 minutes) was not obtained due to the battery being replaced or loosing power, visitation rates were multiplied to get an estimated value for the hour period.

Initially all recordings were viewed however time constraints quickly become apparent. Average visitation rates were plotted to compare full day sampling with alternate hour sampling and the same daily patterns were detected. Therefore alternate hours only were viewed starting from 0700 hours and ending with 1700 hours.

Behaviours associated with dominance and aggression was also recorded. For bellbirds, dominance is often associated with song and body posture. The male bellbirds

inhale causing their chest and overall posture to rise, puffing up their feathers and singing a loud song. This is often directed at another bird. Male hihi tend to display by raising the white tufts of feathers on the side of their head, raising their tail and sometimes letting out a vocalisation (Angher, 1985). Female bellbirds are known to sing in response to other females singing, especially if they pose any threat to their territory (Brunton, Evans, Cope & Ji, 2008). Female hihi were considered to be displaying when raising their tail and overall posture as well as sometimes letting out a vocalisation as in males. Behaviours associated with aggression were primarily the displacement (including chasing) of another bird and direct fighting. Displacement was regarded when one bird directed itself at a fast pace towards another bird causing a response from that bird to remove itself from its position at the feeder or even exiting the feeder. Displacement also included when one bird continued moving towards the other bird resulting in a chase. Whether a displacement was observed was somewhat subjective and based on the experience of the observer (myself). Therefore, only occasions where the displacement was clearly viewed to be aggressive were recorded. Fighting behaviour was similar for bellbirds and hihi and occurred when one bird grasped another bird (usually with its feet). Not all behaviours and occupation categories could be recorded with *JWatcher* as I was limited by the number of keys on the keyboard available for all the events being recorded. Therefore, those that were not assigned a key were written down when observed. The time and date of some events such as fights were also written down for repeat viewing, if necessary.

External factors that could potentially influence the events at the feeder stations were also recorded. Tiritiri Matangi Island is an open sanctuary meaning it is open to the public from Wednesday to Sunday and public holidays. Three of the feeders were exposed to main public walking tracks and hence were passed by various sized groups of people throughout the day (between about 10:30am to 15:30pm). Rangers, researchers and volunteers staying on the island also occasionally passed the feeders. In April there were other researchers at the feeders catching hihi at certain periods of the day. Therefore, I recorded when people passed feeders to see what effect they had on the bird visitation to feeders. The background camera provided most of this information. Tui were also recorded when they visited the feeder. Tui often attempt to enter the feeders or see if

any sugar water has leaked below the feeder station and they occasionally excluded other birds even though they could not directly access the feeders. I also recorded if any other species of birds were sighted at or near a feeder station. Other general notes were made on, such as, the first birds to enter the feeder stations in the morning and the last to leave at night.

2.2.2.3 Analysis

2.2.2.3.1 Visitation patterns

2.2.2.3.1.1 Summary of feeders

Data from all feeders was combined to give the overall average (\pm SE) feeder usage per hour for every second hour of the daily observation period (0700 to 1700 hours), over all recording sessions per month and over all months to identify daily, monthly and overall patterns. A Mann-Whitney U-test was used to compare the visitation rates of all hours per month between each category (species and sex) to test for any significant differences in visits between them. A Spearman rank correlation was then used to test for any significant positive or negative correlation between the visitation rate of each species and sex. Overall average monthly visitation rates were then compared between the months with a one-way analysis of variance (ANOVA) and graphed to assess the long-term monthly trends.

Average visitation rates per hour were graphed from 0700 to 1700 hours to look at short-term trends in the number of visitations throughout the day for each month where substantial data was available (excluding August for the 'Bush 2' and 'Wattle Valley' feeders and October for the 'Bush 1' feeders as enough data had been obtained for analysis for 3 months per feeder). A one-way analysis of variance (ANOVA) was used to test for any significant differences in visitation rates throughout the day for each month of observations for each species and sex.

2.2.2.3.1.2 Individual feeders

The same analysis as used above was carried out for each feeder to compare visitation rates at each feeder. Data for each week and month (3 months per feeder) was combined to give the overall average (\pm SE) feeder visitation per hour. Welch's t-tests (normal distribution) and Mann-Whitney U-tests (non-normal distribution) were used to compare the visitation rates per month by species and sex to test for differences in visits between categories. A Spearman rank correlation was used to test for any significant positive or negative correlations between each species and sex. A one-way analysis of variance (ANOVA) was used to test for differences in daily and monthly visitation rates separately by species and sex. Where sufficient data were available, average visitation rates per month and hour from 0700 to 1700 hours were graphed.

2.2.2.3.2 Visitation patterns in relation to natural food resource availability

Visitation patterns of each species and sex were compared to resource availability in the surrounding area to assess any patterns between feeder use and resource availability. The average visitation rate of each species and sex were plotted against the cumulative DAFOR score (*food resources level*; refer to section 2.1.2.3 for details) for each feeder site. Trends in visitation rates and resource availability were assessed visually for any positive or negative correlation.

2.2.2.3.3 Behavioural interactions between species and sexes

The frequencies of displays, displacements and fighting behaviour were graphed and compared between months over all feeders to compare non-breeding and early breeding seasons. Data from all feeders was combined for each month and a Kruskal-Wallis test was used to compare the number of aggressive interactions by both species and sexes between months. Feeder occupation categories were not analysed due to time constraints and enough data on intra- and interspecific competition had been obtained for answering the questions of this thesis.

2.3 Bird counts

2.3.1 Introduction

Density and distribution is an important factor in understanding the interspecific interactions between species. While the population size of hihi is known (100% of the population is banded) due to an extensive monitoring programme, the numbers of bellbirds on Tiritiri Matangi Island has only been estimated (up to 1500, pers. comm. Brunton, D.H.). To be able to compare the density of hihi versus bellbirds, a robust survey methodology was required. Given that bellbird and hihi are of similar size and use similar resources a survey method that provides an accurate estimate for hihi (with its known population size) should also provide a robust method for bellbirds. The distribution of both hihi and bellbirds across the range of island habitats (mature/regenerated bush, regenerating bush, open shrub, and grasslands) and artificial resources (feeders) was also assessed. The distribution of these species and location of resources will help to identify whether any interspecific competition exists between the endangered hihi and more common bellbird on this small offshore island. It may also provide clues about co-existence by quantifying microhabitat distribution.

There are various methods for estimating population density (Buckland *et al.*, 2001). I chose a relatively simple method, strip transect or fixed width sampling (Buckland *et al.*, 2001; Azhar *et al.*, 2008), suited for surveying hihi and bellbirds as well as all other birds. The method is based on dividing the study area into a grid of spaced lines (Buckland *et al.*, 2001) creating transects of a fixed width and length. The observers walk slowly (about 150 m h⁻¹; Brunton and Stamp, 2007) along the transect and count all individuals in a fixed area either side of the centre line. This method does assume that all individuals in the transect are detected and counted (Buckland *et al.*, 2001). Although no data were collected to test this assumption, a width of 10 m either side of the zero line provides good visual coverage and New Zealand bird species are exceptionally tame and often do not respond to human presence.

2.3.2 Setup and procedure

Twelve permanent transects were setup at various locations across the island in a range of mature, regenerated and regenerating forest (Figure 2.1). The transects were setup along pre-existing narrow tracks where possible throughout various patches of forest as they provided easy access and reduced our impact on regenerating vegetation as in Brunton *et al.* (2007). The transects ranged in length from 100 to 250 m. Each was given a fixed width of 10 m on either side of the transect, giving a total width of 20 m. Transects were setup using flagging tape and a hip chain which were first calibrated against a measuring tape. Flagging tape was placed from the start and every 10 m until the end and marked with a number.

The transects were surveyed repeatedly generally over a period of a week. The aim was 10 repeats per month over the duration of the study period from April to October 2010. Transects were surveyed by up to 3 observers at any one time for the first three months (except for June where a group of students helped; they were trained by experienced observers). The following four months were surveyed by me. At the start of each survey, the time and weather conditions were recorded. Surveys were not conducted in poor weather conditions that could have affected the survey by reducing our visual field and ability to hear birds (strong rain and wind). Other notes were also occasionally taken, for example, what plants were in flower, certain areas that the hihi or bellbirds were favouring and any potential disturbances such as other people walking through the transect and vehicles passing by. The observers walked the transect slowly looking from side to side and recording all birds seen and heard within 10 m either side. Birds were recorded as either being seen and/or heard. Birds seen or heard from behind were not to be recorded as they could have been potentially biased by our presence. Bellbirds and hihi are sexually dimorphic so sex of sighted birds were recorded. Bellbird males and females have distinct differences in their song (Brunton & Li, 2006) and hence each observer was taught to recognise the different songs to be able to identify whether a male or female was heard when we were unable to see the bird clearly. Hihi also have some sex based differences in vocalisations (Higgins *et al.*, 2001) and could occasionally be identified by hearing only. Nikon 10 x 25 binoculars were most commonly used to identify birds in the canopy or further ahead on a transect. When a bellbird or hihi was

too high in the canopy to see or the lighting conditions made identifying the sex difficult, the bird was recorded as unknown sex. Start and finish times were recorded.

2.3.3 Calculating density

The calculation for estimating density using strip transect sampling from Buckland *et al.* (2001) and Azhar *et al.* (2008) is in the form of:

$$D = n/2WL$$

where density (D) per unit area (ha) equals the sum of individuals (n) divided by the total area of the transect (W = width, L = length).

The number of bellbirds and hihi were averaged for each transect from the repeated surveys during each month (May was divided into during (early May) and post- (mid May) bellbird translocation; refer to section 2.4 for details). The average from each transect was then used to calculate the estimated density per hectare. I also calculated the densities using seen birds only data for comparison.

An overall average was then calculated from all transects combined. Using the average density per hectare we could then estimate the total population density (abundance) for the island. Tiritiri Matangi Island has a total area of 220ha. However, there is a substantial proportion of the island that is not suitable habitat for bellbirds and hihi, such as the grasslands. Bellbirds are seen all over the island in regenerated and regenerating forest, even around the visitors bunkhouse (personal observation), therefore we estimated their total habitat area of the island to be 195 ha (included mature, replanted and open shrub areas, excluded grassland; measurements from Brunton and Stamp, 2007). However, hihi have been shown to have a strong preference for forested areas which occupy 100ha of the island area (Ewen *et al.*, 2011).

It was also hypothesised that the sugar water feeders may have an influence on nearby transects. We therefore divided transects into feeder (<85m) and non-feeder areas (≥85m). Based on the distance from the feeders to the transects obtained from Global Positioning Satellite (GPS) coordinates using a Garmin handheld navigation system, online mapping tools (<http://www.zonums.com/gmaps/maptool.php>) and Google Earth software, 6 transects were considered to be in ‘feeder areas’ and 6 were considered to be in ‘non-feeder areas’. Since most feeders were in forested areas, transects were also

divided into track/regenerating patches and established forest locations with 6 transects considered as tracks/regenerating patches (4 transects on open tracks, 2 transects in very sparse pohutukawa dominant regenerating patches) and 6 considered as forest areas (mature and regenerating native and exotic forest).

2.3.4 Analysis

2.3.4.1 Overall abundance

Estimated hihi densities were compared using a paired t-test with the known population density (176 hihi) from a survey conducted in September 2010 based on the number of banded birds found. Densities based on ‘seen and heard’ and ‘seen only’ were compared to see whether there was any sampling error when including ‘heard only’ birds. A paired t-test was used to test for any significant differences between ‘seen and heard’ estimates and ‘seen only’ estimates and to compare ‘non-feeder and feeder areas’ and ‘tracks/regenerating patches and established forest areas’. Densities were also calculated from mature remnant and replanted regenerating forested areas for comparison. Once a robust estimate was determined for hihi the same principles were applied to the bellbird density estimates. The same principles were also applied to the hihi sexes (sex ratio of hihi known) with paired t-tests for comparison between the most robust estimates and the known population size of each sex to test whether the same principles apply to the sexes. Bellbird sex densities were also estimated with similar principles applied.

2.3.4.2 Distribution

2.3.4.2.1 Habitat

The estimated densities were compared spatially and seasonally. The density (+ SE) from each transect during the month were graphed to examine distribution. To establish how the distribution of hihi and bellbirds relate to each other, the number of hihi and bellbirds counted at each transect were compared on a daily basis with a Spearman rank correlation. ‘Seen only’ counts were used for hihi estimated densities and ‘seen and

heard' counts were used for bellbird estimated densities in the current and following sections.

The impact of habitat type on densities and distribution of both species and sexes on the island over the months were compared using six habitat types:

- Mature forest (remnant/regenerated)
- Exotic and native regenerating forest
- Kanuka abundant regenerating forest
- Pohutukawa abundant regenerating forest
- Open track through mature and regenerating forest
- Open tracks through regenerating forest

A 3D bar chart was plotted with the density per ha at each transect against habitat type and month. Plots were made for species and sex's density estimates for comparisons from April to October 2010. A Spearman rank correlation was used to compare different trends in monthly variation between hihi and bellbird densities and Wilcoxon signed-rank tests were used to compare hihi and bellbird densities each month. The same tests were used to compare the sexes.

Densities were also compared to the estimated level of resources available each month. The estimated density at each transect was plotted against the cumulative DAFOR score (*food resources level*; see section 2.1.2.3 for details). A Spearman rank correlation was used to test for any significant correlation between resource availability and density for both bellbirds and hihi.

2.3.4.2.2 Density distribution and feeders

Factors that could have influenced hihi and bellbird density at transects were distance to feeder, sugar water consumption and visits to feeders. The average density (\pm SE) and average distance from nearest feeder (\pm SE) at 'non-feeder areas' and 'feeder areas' were compared for hihi and bellbirds on a scatter plot. The average density and nearest distance from a feeder for each transect were then plotted for each month to observe any further differences in density between 'non-feeder areas' and 'feeder areas.' A Spearman rank correlation was used to test for any significant correlation between densities and distances to nearest feeder.

The average density was then compared with the level of sugar water consumption at the nearest feeder. Records of how much sugar water was consumed each day were available for comparison (data collected by Department of Conservation rangers and volunteers). However, some records were missing or incomplete during the weeks when the bird counts were conducted. Therefore, the sugar water consumption for each week and at each feeder was converted into proportions and divided into categories of low (0-10 %), medium (11-20 %) and high (21-100 %) consumption. The average hihi and bellbird densities (\pm SE) and average distance (\pm SE) to closest feeder over all feeders and months were categorised based on the level of sugar water consumption and plotted for comparison. A Kruskal-Wallis test was used to compare densities between each sugar water consumption category for each species.

The estimated density at 'feeder area' transects was also compared to the number of visits to the closest feeder. The densities for males and females of both species for each month were plotted against the monthly average number of visits per hour obtained from the feeder video data (Chapter 5). A Spearman rank correlation was used to test for any significant correlation between the estimated densities and the average number of visits to the closest feeder. Average visits per hour over all feeders near transects in 'feeder areas' were also plotted against sugar water consumption levels and a Kruskal-Wallis test compared feeder visits within each sugar water consumption category to assess the relationship between these two factors.

2.4 Impact of the removal of bellbirds on hihi distribution

2.4.1 Introduction

In addition to estimating the overall density of bellbirds and hihi in different habitats on the island, I also used this method to assess the impact of removing 100 bellbirds from the population on the density and distribution of hihi (and bellbirds). The removal of 100 bellbirds for a translocation was conducted between the 3rd and 6th of May during the field period. As bellbirds are the dominant species in this relationship, there is the potential for competitive exclusion towards hihi (Perrot & Armstrong, 2000). If bellbirds are removed from an area it could then be assumed that hihi may then be

found in the area at higher densities after a period of time if competitive exclusion was occurring. The other possibility is that with bellbirds using song to defend their resources and territories (Brunton & Li, 2006) other bellbirds may re-inhabit the area quicker than hihi due to the absence of song protecting the areas where resident bellbirds were removed.

2.4.2 Methods

The estimated densities of both species at each transect for before (April), immediately following (mid May) and one month after (June) the bellbird translocation were obtained from chapter 5. The locations of where bellbirds were removed from the population was known, therefore each transect could be categorised as near (7 transects) or far (5 transects) from a capture site. The densities at each transect were also calculated from morning (AM) and afternoon (PM) counts to assess any temporal differences.

2.4.3 Analysis

Estimated densities of bellbirds and hihi at each transect were compared graphically before, after and one month after the bellbird translocation. A table was made comparing whether the density of bellbirds and hihi increased, had no change or decreased immediately after and one month after bellbird removal from capture sites and non-capture sites. The same was applied to the AM and PM densities. The number of capture and non-capture sites where bellbird and hihi densities changed were compared and the densities before, immediately after and one month after were compared with a Wilcoxon signed-rank test.

Appendix 2.1 Worksheet used for the foraging ecology of hihi and bellbirds

Data sheet 1. 'First food eaten' data sheet.

First Food Eaten								
Name of observer								
Species	Date	Time	Sex	Location	Habitat	Food type	Plant/invertebrate name*	Height

* Species names given to plants, general names given to invertebrates e.g. fly, moth, caterpillar.

Chapter 3:

The foraging ecology of bellbirds and hihi with a plant survey of study sites on Tiritiri Matangi Island



Female bellbird feeding on flax on Tiritiri Matangi Island.

Photo: Michelle Roper.

3.1 Abstract

The foraging ecology of bellbird and hihi often differs between location and seasons. The composition of their diet varies between the species as well but how different they are also depends on location and season. One aspect of their foraging ecology, foraging height, has been consistent between studies although little research has been done in different locations and seasons. Little study has been conducted on bellbirds and hihi foraging ecology and how they differ on Tiritiri Matangi Island. The aim of this study was to collect data on the foraging ecology of bellbirds and hihi on Tiritiri Matangi Island to assess differences between the species, sexes and to compare with previous studies in other locations. Nectar was the most frequently consumed component for both bellbirds (78.6 %) and hihi (80.6 %) with invertebrates the second most frequently consumed component (13.1 and 16.0 % respectively). Bellbirds consumed honeydew (7.6 %) unlike hihi and had a lower consumption of fruit (0.69 %) than hihi (3.5 %). Between the seasons from autumn-winter to spring, bellbird consumption of nectar increased (70.8 to 85 %), invertebrate consumption remained similar (13.08 to 13.13 %), honeydew consumption decreased (14.6 to 1.9 %) and fruit was only observed being consumed in autumn-winter (1.5 %). Hihi only had a slight increase in nectar consumption (79.5 to 81.7 %), invertebrate consumption increased (7.7 to 18.3 %) and fruit was also only observed being consumed in autumn-winter (12.8 %). No significant differences were found between the sexes of each species for the total results and for each season. The foraging height differed between the two species with bellbirds most commonly foraging in the canopy (48.7 %) and sub-canopy (40.6 %) layers of the vegetation whereas hihi were most commonly foraging in the middle storey (38.1 %) and sub-canopy (31.9 %) layers. There were slight differences between the seasons with male bellbirds foraging in the sub-canopy and ground more in autumn-winter than spring whereas females were in the canopy and ground more in autumn-winter, with the middle storey being visited more by both sexes in spring. Hihi were most commonly in the sub-canopy and canopy layers in autumn-winter whereas in spring they were more often foraging in the middle storey and sub-canopy layers with no significant differences between the sexes. The frequency of nectar consumption from different plant species also slightly differed between the species with bellbirds frequently consuming five finger (*Pseudopanax arboreus*) and

manuka (*Leptospermum scoparium*) in autumn-winter and karo (*Pittosporum crassifolium*) and manuka in spring. In contrast, hihi were most frequently observed consuming kohekohe (*Dysoxylum spectabile*) and five finger in autumn-winter and hangehange (*Geniostoma ligustrifolium*) and karo in spring. No significant differences were found between the hihi sexes but male bellbirds more often consumed golden wattle (*Acacia pycnantha*) than females. From the plant survey, resource availability scores were calculated and showed that in general nectar availability increased from autumn-winter to spring which corresponds to the wider range of plants species in their diet in spring and increased nectar consumption by both bellbirds and hihi. Compared to other studies, there were similarities and differences showing that their foraging ecology depends on the vegetation present. Foraging height was somewhat consistent with other studies although bellbirds were found more often in the higher vegetation layers which may be due to the low population of tui or the smaller size of trees allowing tui to defend a whole resource with bellbirds and hihi sharing resources when tui absent. They may also need to forage for invertebrates on the ground and in the air more due to smaller trees and competition with other bird species. Hence, vertical resource partitioning is likely to be a contributing factor to how bellbirds and hihi coexist with bellbirds defending the best resources in the higher vegetation layers potentially of higher nectar value with interference competition and hihi obtaining resources with exploitation competition by utilising flowers (which are often smaller, less abundant or produce less nectar) in the lower vegetation layers.

3.2 Aims

- To assess and compare the diet and foraging behaviour of bellbird and hihi on Tiritiri Matangi Island
- To determine any potential differences in the proportion of dietary components and foraging behaviour between the sexes of each species
- To assess any potential differences in the proportion of dietary components and foraging behaviour between bellbirds and hihi
- To assess the abundance of known food plants and the level of nectar resources available throughout the research period

3.3 First Food Eaten

3.3.1 Dietary components

3.3.1.1 Bellbird

Over all months nectar was the most frequently consumed component of bellbird natural diet (78.6 %). Invertebrates were the second most observed component of the diet (13.1 %) followed closely by honeydew consumption (7.6 %) and a small amount of fruit was consumed (0.69 %). This pattern in consumption percentages was consistent for both male and female bellbirds (Figure 3.1; $\chi^2 = 0.74$, $df = 3$, $0.90 < P < 0.10$).

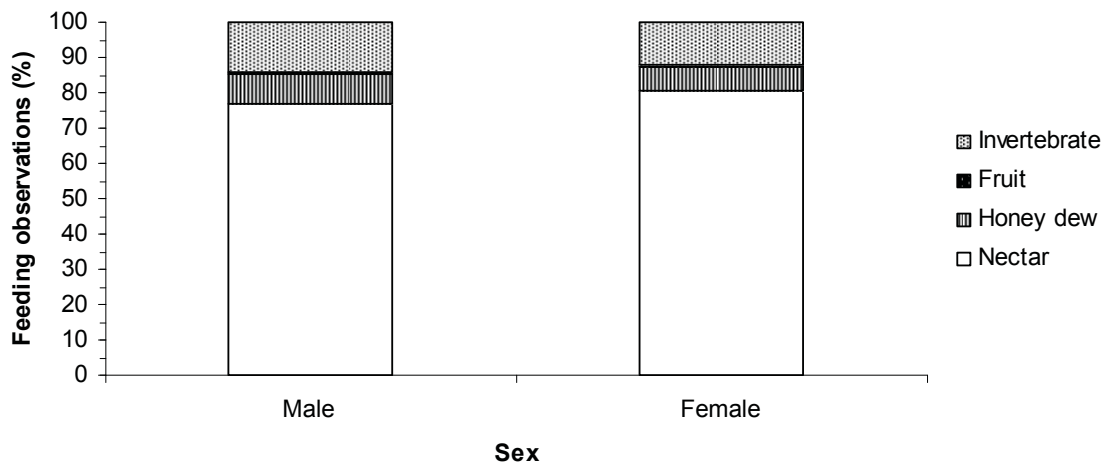


Figure 3.1. First food eaten observations for male and female bellbirds between April and October 2010.

The amount of each component consumed varied throughout the year (Figure 3.2). Earlier in the year (April to June) nectar consumption was low (between 33.3-65.1 %) and honeydew consumption was high (between 23.8-42.9 %). Later in the year (July to October), bellbirds consumed less honeydew (between 0-3.3 %) and more nectar (between 79.5-87.0 %). Invertebrate consumption was slightly lower earlier in the year (between 0-11.1 %) compared to later in the year (between 13.0-18.2%). Bellbirds were only observed eating fruit in April (66.7%, small sample size), which were likely to be the remnants of summer fruiting. As with the overall results, there was little difference between the types of food consumed by males and females each month (Table 3.1).

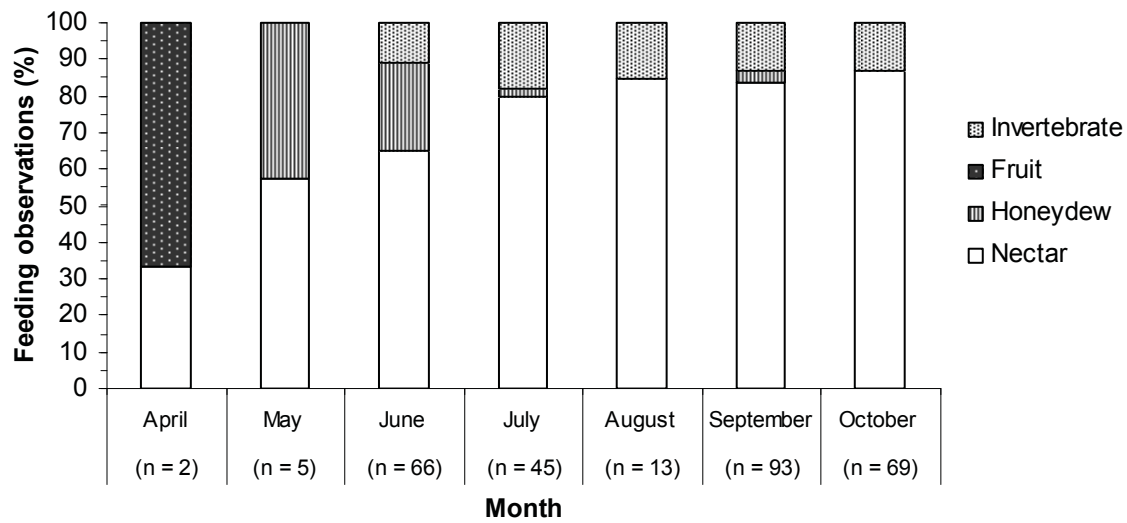


Figure 3.2. First food eaten observations for bellbirds from April to October 2010.

Table 3.1. Chi-square tests comparing the frequencies of different food (first food eaten) that made up the diet of male and female bellbirds from April to October 2010. Key: - insufficient data for test result.

		Nectar	Honeydew	Fruit	Invertebrate	χ^2	df	P
April	Male	0	0	1	0	-	-	-
	Female	1	0	1	0	-	-	-
May	Male	0	0	0	0	-	-	-
	Female	4	3	0	0	-	-	-
June	Male	26	11	0	5	0.57	2	0.753
	Female	15	4	0	2			
July	Male	21	1	0	5	0.66	2	0.90<P>0.10
	Female	14	0	0	3			
August	Male	3	0	0	0	0.71	1	0.90<P>0.10
	Female	8	0	0	2			
September	Male	42	1	0	6	0.64	2	0.726
	Female	34	2	0	6			
October	Male	27	0	0	6	1.47	1	0.225
	Female	33	0	0	3			

Due to small sample sizes in earlier months, the observations were combined seasonally into autumn-winter (April to August) and spring (September and October) for further analysis (Figure 3.3). Significant differences were found between autumn-winter and spring in the proportion of each food type consumed ($\chi^2 = 19.67$, $df = 3$, $P = <0.005$). In autumn-winter, nectar consumption was lower (70.8 %) than in spring (85 %). The opposite trend was found for honeydew with higher consumption in autumn-winter (14.6 %) and lower in spring (1.9 %). Fruit consumption was only observed in autumn-winter

(1.5 %) and invertebrate consumption was consistent across seasons (autumn-winter, 13.08 % and spring, 13.13%). These same trends were found for both males and females separately (Table 3.2) and there were no differences in the food types consumed between males and females in autumn-winter ($\chi^2 = 0.58$, $df = 3$, $0.95 < P > 0.90$) or spring ($\chi^2 = 0.69$, $df = 2$, $P = 0.708$).

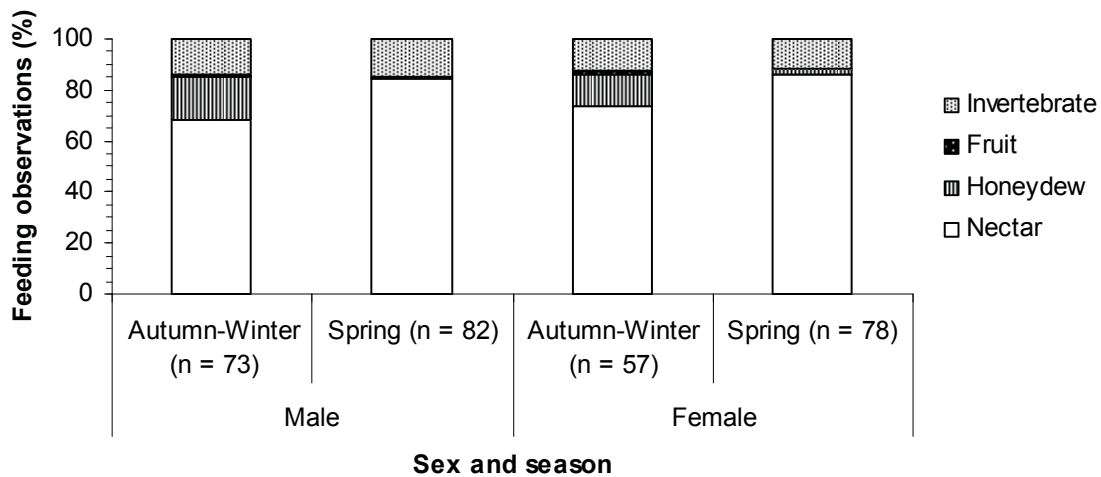


Figure 3.3. First food eaten observations for male and female bellbirds for autumn-winter and spring 2010.

Table 3.2. Chi-square tests comparing the first food eaten observations of male and female bellbirds between autumn-winter and spring 2010.

		Nectar	Honeydew	Fruit	Invertebrate	χ^2	df	P
Male	Autumn-winter	50	12	1	10	13.05	3	<0.005
	Spring	69	1	0	12			
Female	Autumn-winter	42	7	1	7	6.66	3	0.05<P>0.025
	Spring	67	2	0	9			

3.3.1.2 Hihi

Similarly to bellbirds, nectar was the most common component of hihi natural diet (80.6 %). Overall, invertebrates were the next most consumed component (16.0 %) with a small amount of fruit also consumed (3.5 %). The proportion of each food type in the diet was not significantly different between males and females (Figure 3.4; $\chi^2 = 1.04$, $df = 2$, $P = 0.595$).

The proportion of dietary components consumed by hihi varied slightly throughout the year (Figure 3.5). Fruit consumption was highest earlier in the year (between 5.3-100 %) and no observations of fruit consumption were made from August

to October. In general, observations of invertebrate consumption increased throughout the year (between 0-23.9 %) and nectar consumption was relatively consistent (Figure 3.5). Where samples sizes were large enough for statistical comparisons, little difference was found between male and female consumption rates each month (Table 3.3).

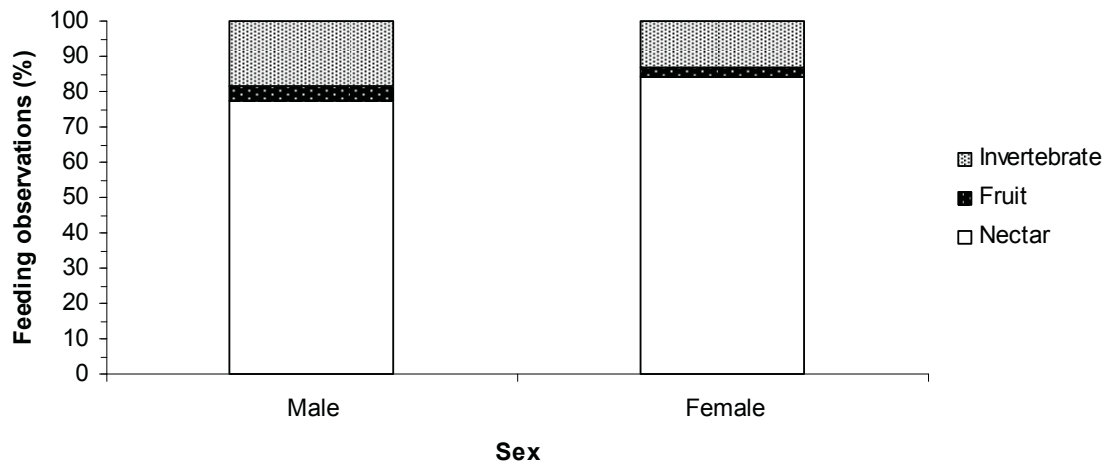


Figure 3.4. First food eaten observations for male and female hihi over all months in 2010.

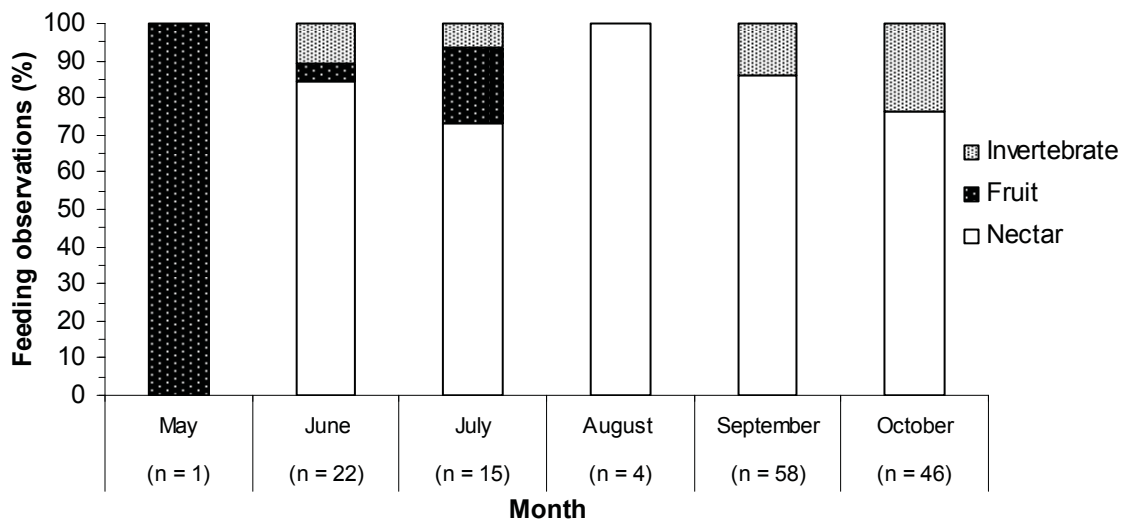


Figure 3.5. First food eaten observations for hihi from April to October 2010.

Hihi observations were combined seasonally into autumn-winter (April to August) and spring (September and October; Figure 3.6)) due to small sample sizes in some months. In autumn-winter, hihi diet was more varied with the presence of fruit

(12.8 %). Nectar consumption was similar in autumn-winter (79.5 %) and spring (81.7 %) but invertebrate consumption increased in spring (from 7.7 to 18.3 %). This difference between the seasons was significantly different ($\chi^2 = 15.41$, $df = 2$, $P = 0.000$) with higher consumption of fruit in the autumn-winter months and higher consumption of invertebrates in spring. These same trends were found within each sex (Table 3.4) and there were no differences found in the ratio of food types consumed between males and females in autumn-winter ($\chi^2 = 0.80$, $df = 2$, $P = 0.671$) and spring ($\chi^2 = 0.23$, $df = 1$, $P = 0.628$).

Table 3.3. Chi-square tests comparing the frequencies of different food (first food eaten) that made up the diet of male and female hihi from April to October 2010.

		Nectar	Honeydew	Fruit	Invertebrate	χ^2	df	P
April	Male	0	0	0	0	-	-	-
	Female	0	0	0	0			
May	Male	0	0	0	0	-	-	-
	Female	0	0	1	0			
June	Male	7	0	0	2	3.21	2	0.90<P>0.10
	Female	9	0	1	0			
July	Male	5	0	3	0	4.04	2	0.90<P>0.10
	Female	6	0	0	1			
August	Male	2	0	0	0	-	-	-
	Female	2	0	0	0			
September	Male	24	0	0	4	0.011	1	0.916
	Female	26	0	0	4			
October	Male	20	0	0	7	0.15	1	0.703
	Female	15	0	0	4			

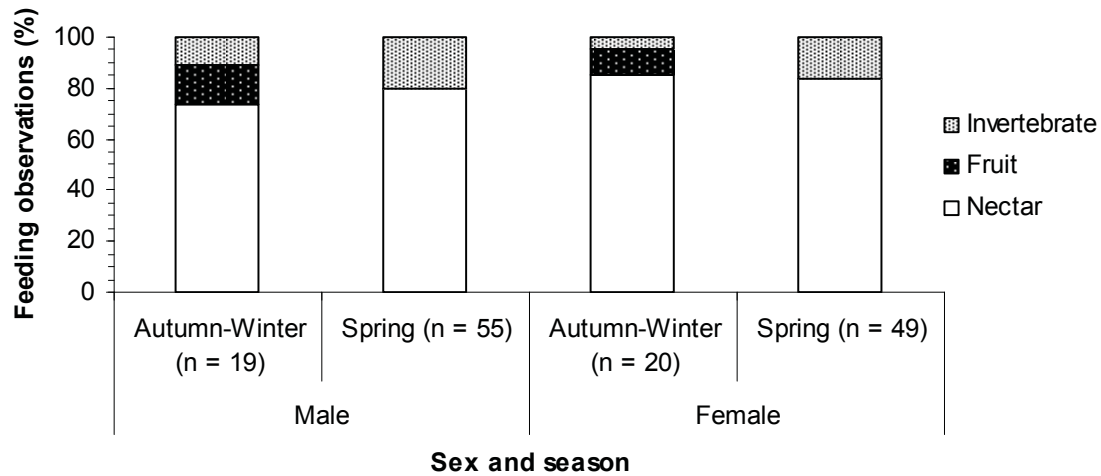


Figure 3.6. First food eaten observations for male and female hihi for autumn-winter and spring 2010.

Table 3.4. Chi-square tests comparing the first food eaten observations of male and female hihi between autumn-winter and spring 2010.

		Nectar	Fruit	Invertebrate	χ^2	df	P
Male	Autumn-winter	14	3	2	9.49	2	0.01<P>0.005
	Spring	44	0	11			
Female	Autumn-winter	17	2	1	6.30	2	0.05<P>0.025
	Spring	41	0	8			

3.3.1.3 Interspecific Comparison

Overall, there were some notable differences between the diets of bellbird and hihi (Figure 3.7). The most evident difference was that hihi do not feed on honeydew. In addition, hihi consumption of fruit was significantly greater (3.5% compared to bellbird 0.7%; $\chi^2 = 16.15$, $df = 3$, $P = 0.001$) and occurred throughout the entire autumn to spring period of the study. In contrast, bellbirds and hihi had very similar consumption ratios of nectar (78.6 and 80.6 % respectively) and invertebrates (13.1 and 16.0 % respectively).

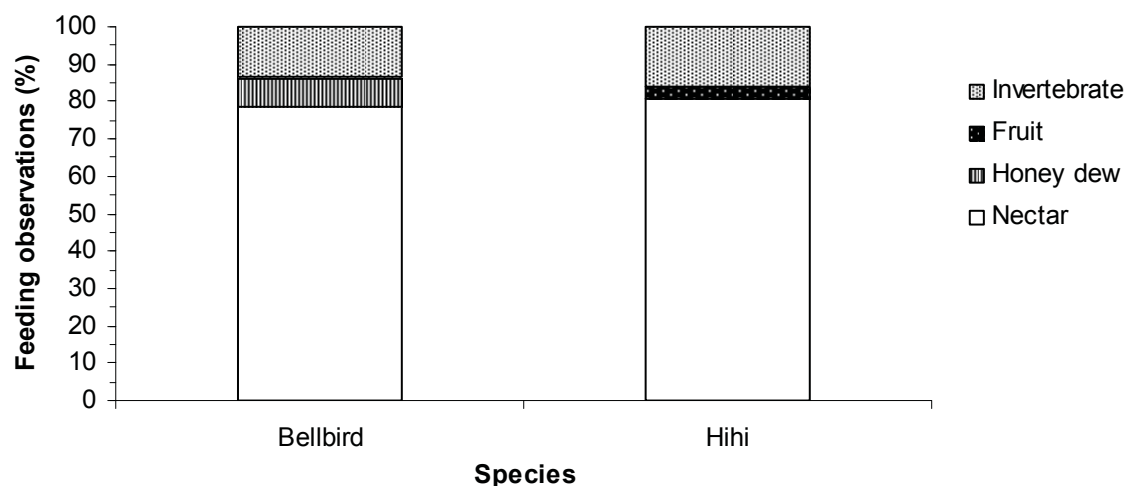


Figure 3.7. First food eaten observations for bellbirds and hihi from April to October 2010.

As the consumption percentages varied throughout the period of the study for both species, comparisons were made between them monthly and seasonally. Until August, the food types consumed by the two species were significantly different (Table 3.5). However, in September and October no significant differences in diet were found (Table 3.5). When months were combined into seasons, species differences only occurred in autumn-winter (Figure 3.8; Table 3.6) due to fruit and honeydew consumption.

Table 3.5. Chi-square tests comparing the first food eaten observations of bellbirds and hihi from April to October 2010.

		Nectar	Honeydew	Fruit	Invertebrate	χ^2	df	P
April	Bellbird	1	0	2	0	-	-	-
	Hihi	0	0	0	0			
May	Bellbird	4	3	0	0	9	3	0.05<P>0.025
	Hihi	0	0	1	0			
June	Bellbird	41	15	0	7	8.16	3	0.05<P>0.025
	Hihi	16	0	1	2			
July	Bellbird	35	1	0	8	10.17	3	0.025<P>0.01
	Hihi	11	0	3	1			
August	Bellbird	11	0	0	2	0.70	1	0.90<P>0.10
	Hihi	4	0	0	0			
September	Bellbird	76	3	0	12	1.95	2	0.377
	Hihi	50	0	0	8			
October	Bellbird	60	0	0	9	2.27	1	0.132
	Hihi	35	0	0	11			

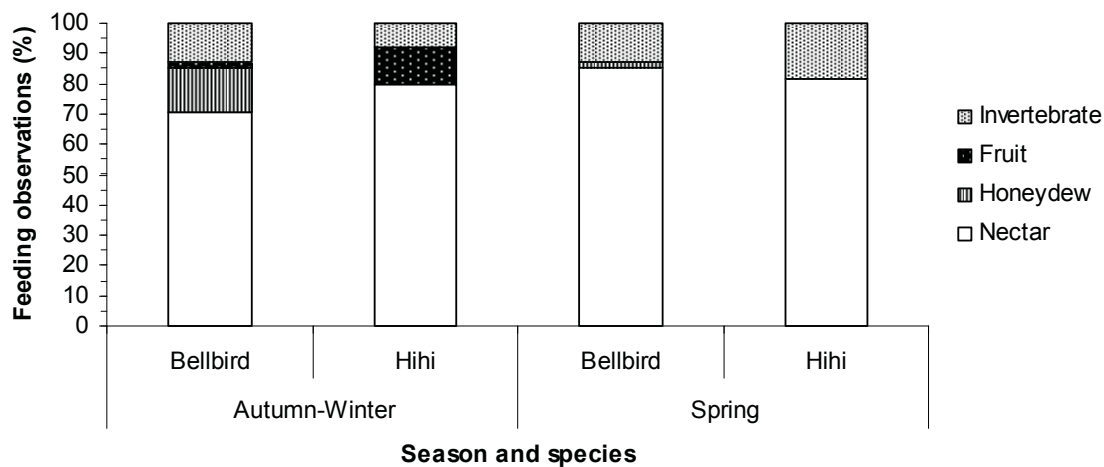


Figure 3.8. First food eaten observations for bellbirds and hihi for autumn-winter and spring 2010.

Table 3.6. Chi-square tests comparing the first food eaten observations of bellbirds and hihi for autumn-winter and spring 2010.

		Nectar	Honeydew	Fruit	Invertebrate	χ^2	df	P
Autumn-winter	Bellbird	92	19	2	17	15.97	3	0.001
	Hihi	31	0	5	3			
Spring	Bellbird	136	3	0	21	3.13	2	0.209
	Hihi	85	0	0	19			

3.3.2 Foraging Height

3.3.2.1 Bellbird

Bellbirds were most commonly observed foraging in the canopy and sub-canopy vegetation layers (Figure 3.9). Both males and females were observed foraging in the canopy (45.4 and 53.0 % respectively), closely followed by the sub-canopy (41.7 and 38.8 %). Fewer observations were made of males and females feeding in the upper understorey (0 and 0.7 %), middle storey (3.7 and 4.5 %) and lower understorey (0.6 and 0.7 %). Males were however observed foraging on the ground layer more than females (8.6 and 2.2 %). Ground layer foraging was the only significant difference found between males and females (Table 3.7).

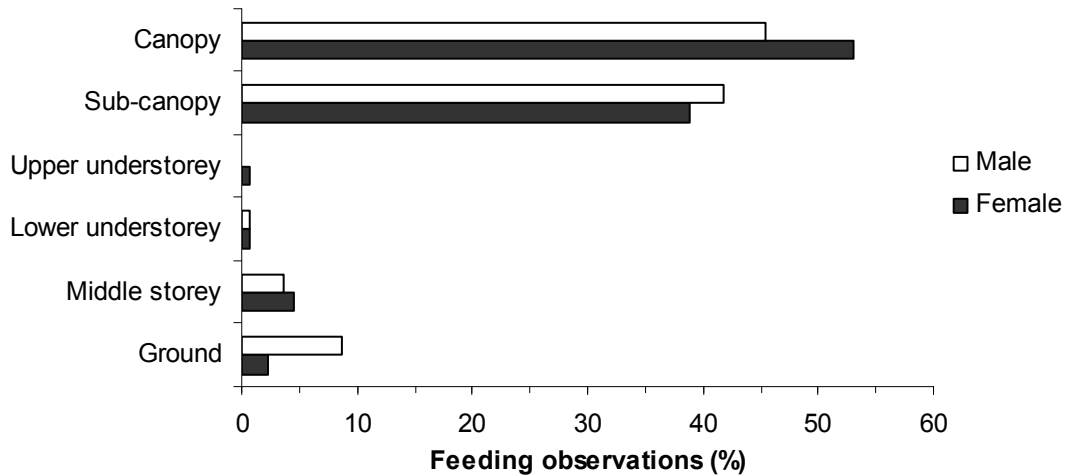


Figure 3.9. Male and female bellbird foraging heights between April and October 2010.

Table 3.7. Chi-square tests comparing first food eaten observations at each foraging height between male and female bellbirds from April to October 2010.

Height	Male	Female	χ^2	df	P
Canopy	74	71	0.062	1	0.803
Sub-canopy	68	52	2.13	1	0.144
Upper understorey	0	1	1.00	1	0.317
Middle storey	6	6	0.00	1	1.000
Lower understorey	1	1	0.00	1	1.000
Ground	14	3	7.12	1	0.008

Seasonal comparisons between foraging heights were also made (Figure 3.10). The distribution of observations at each foraging height did not vary between autumn-winter and spring for males but did for females (Table 3.8). Females foraged significantly more within the sub-canopy layer in spring (46.8 %) compared to winter (27.3%) and less at the ground level in spring compared to winter (0 versus 5.5 % respectively).

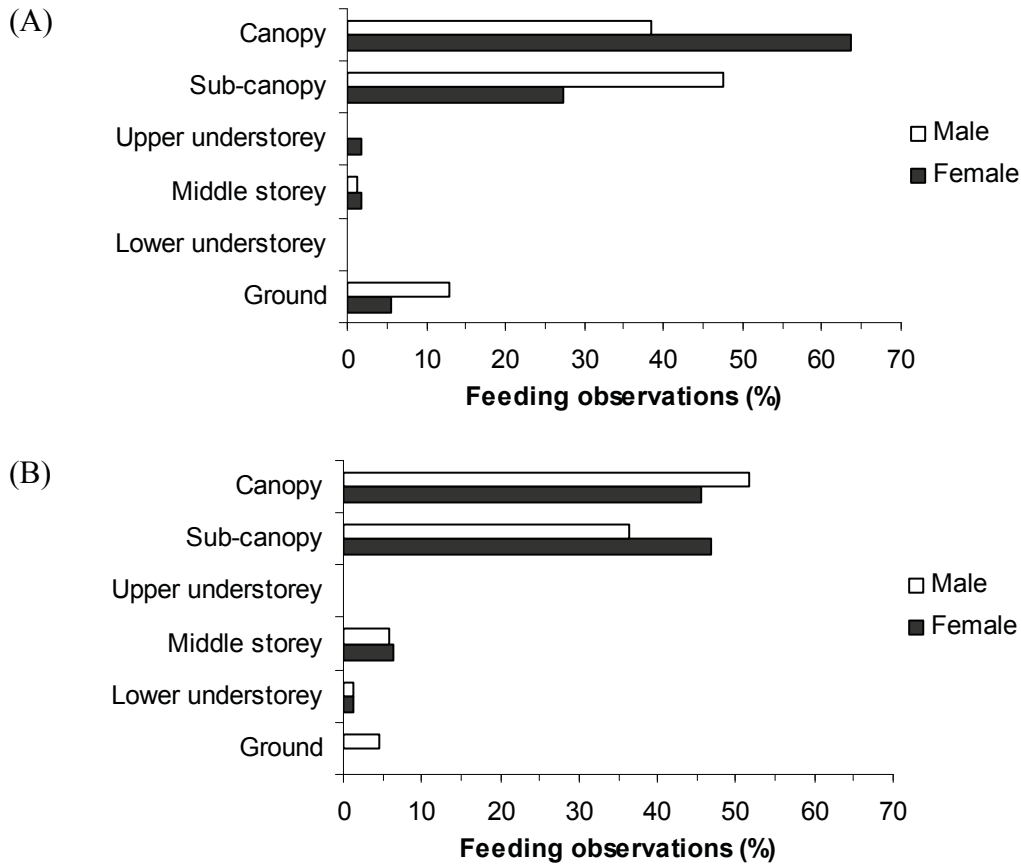


Figure 3.10. Male and female bellbird foraging height observations for autumn-winter (A) and spring (B) 2010.

Table 3.8. Chi-square tests comparing first food eaten observations at each foraging height between autumn-winter and spring 2010 for male and female bellbirds.

Season	Height	Autumn-winter	Spring	χ^2	df	P
Male	Canopy	30	44	2.65	1	0.104
	Sub-canopy	37	31	0.53	1	0.467
	Upper understory	0	0	-	1	-
	Middle storey	1	5	2.67	1	0.102
	Lower understory	0	1	1.00	1	0.317
	Ground	10	4	2.57	1	0.109
Female	Canopy	35	36	0.014	1	0.906
	Sub-canopy	15	37	9.31	1	0.002
	Upper understory	1	0	1.00	1	0.317
	Middle storey	1	5	2.67	1	0.102
	Lower understory	0	1	1.00	1	0.317
	Ground	3	0	3.00	1	0.083

3.3.2.2 Hihi

Hihi were mostly commonly observed feeding in the middle storey and sub-canopy layers. Both males and females were observed at similar rates (Figure 3.11) with most feeding occurring in the middle storey (36.1 and 40.3 % respectively) and sub-canopy (33.7 and 29.9 %) layers. Feeding at the canopy layer was also fairly common for both males (15.7 %) and females (14.3 %). Fewer observations were made of males and females feeding at the ground (7.2 and 6.5 %), upper understory (3.6 and 3.9 %) and lower understory (3.6 and 5.2 %) layers. No significant differences were found between males and females at each foraging height (Table 3.9).

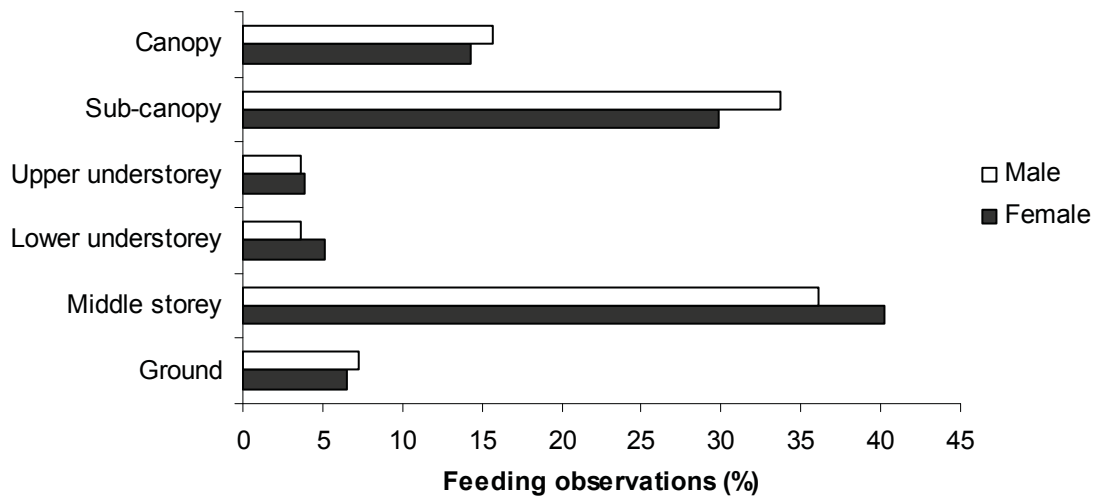


Figure 3.11. Male and female hihi foraging heights between April and October 2010.

Table 3.9. Chi-square tests comparing first food eaten observations at each foraging height between male and female hihi from April to October 2010.

Height	Male	Female	χ^2	df	P
Canopy	13	11	0.17	1	0.683
Sub-canopy	28	23	0.49	1	0.484
Upper understory	3	3	0.00	1	1.000
Middle storey	30	31	0.016	1	0.898
Lower understory	3	4	0.14	1	0.705
Ground	6	5	0.091	1	0.763

Seasonal comparisons between foraging heights were also made (Figure 3.12). For both sexes, there was little difference at each foraging height between autumn-winter and spring except for the middle storey (Table 3.10). No observations of feeding were made at the middle storey layer in autumn-winter but there was a significant increase in spring (49.2 %; Table 3.10). There was also a nearly significant result for an increase in feeding at the lower understorey layer in spring (0 to 4.9 %). Similar results were found for females who were also seen feeding significantly more at the middle storey layer in spring (0 to 53.6 %) but they were also seen significantly more at the ground layer (0 to 8.9 %; Table 3.10).

Table 3.10. Chi-square tests comparing first food eaten observations at each foraging height between autumn-winter and spring 2010 for male and female hihi.

Season	Height	Autumn-winter	Spring	χ^2	df	P
Male	Canopy	4	9	1.92	1	0.166
	Sub-canopy	13	14	0.037	1	0.847
	Upper understorey	1	2	0.33	1	0.564
	Middle storey	0	30	30.00	1	0.000
	Lower understorey	0	3	3.00	1	0.083
	Ground	3	3	0.00	1	1.000
Female	Canopy	6	5	0.091	1	0.763
	Sub-canopy	12	11	0.043	1	0.835
	Upper understorey	1	2	0.33	1	0.564
	Middle storey	0	30	30.00	1	0.000
	Lower understorey	1	3	1.00	1	0.317
	Ground	0	5	5.00	1	0.025

3.3.2.3 Interspecific comparison

The number of feeding observations at each foraging height varied between bellbirds and hihi (Figure 3.13). Bellbirds feed in the canopy and sub-canopy layers (48.7 and 40.6 % respectively) significantly more than hihi (15 and 31.9 %; Table 3.11). Whereas, hihi were seen feeding significantly more in the middle storey layer (38.1 %) than bellbirds (4.0%; Table 3.11). Hihi were also observed feeding slightly more in the upper understorey and lower understorey (3.8 and 4.8 %) than bellbirds (0.3 and 0.7 %; Table 3.11). At the ground layer no significant difference in feeding observations were found between bellbirds (5.7 %) and hihi (6.9 %; Table 3.11).

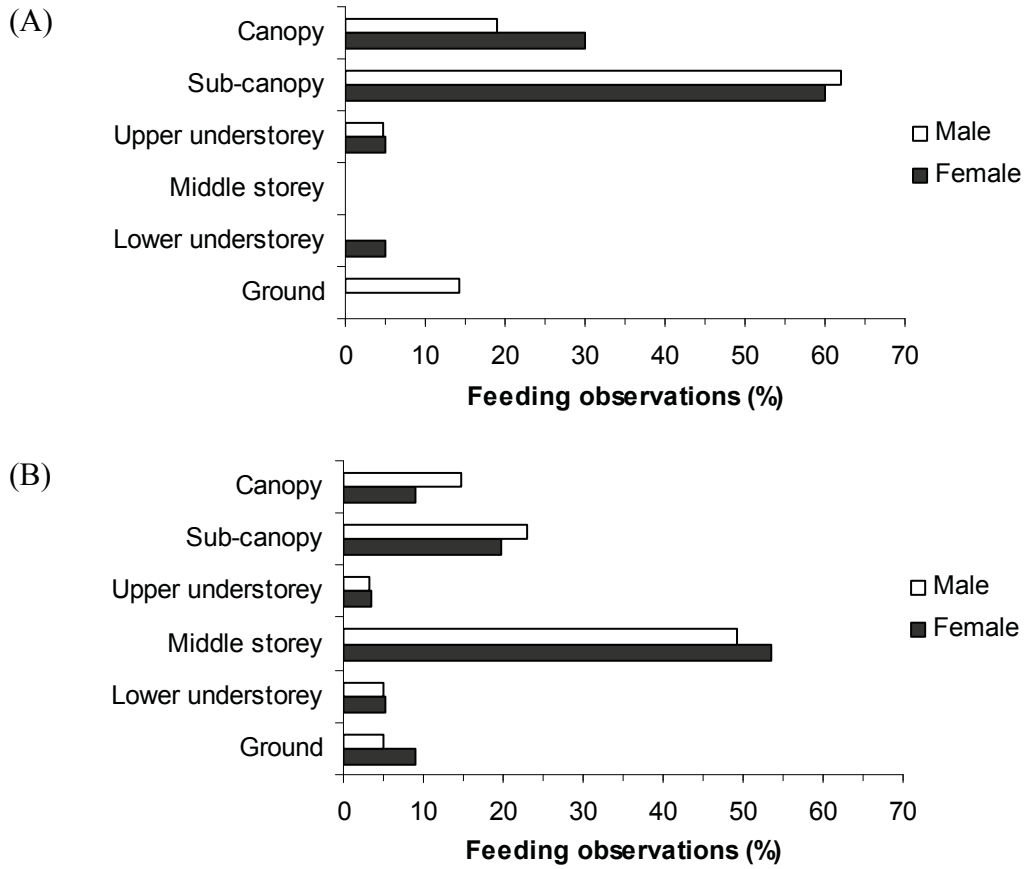


Figure 3.12. Male and female hihi foraging height observations for autumn-winter (A) and spring (B) 2010.

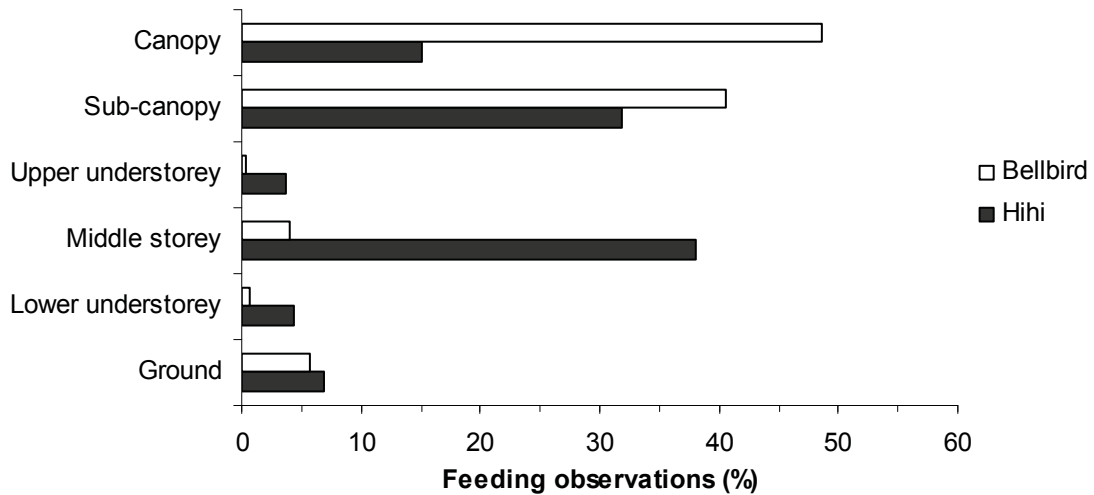


Figure 3.13. Bellbird and hihi foraging heights between April and October 2010.

Table 3.11. Chi-square tests comparing first food eaten observations at each foraging height between bellbirds and hihi from April to October 2010.

Height	Bellbird	Hihi	χ^2	df	P
Canopy	145	24	86.63	1	0.000
Sub-canopy	121	51	28.49	1	0.000
Upper understorey	1	6	3.57	1	0.059
Middle storey	12	61	32.89	1	0.000
Lower understorey	2	7	2.78	1	0.096
Ground	17	11	1.29	1	0.257

Comparisons were also made by season between species (Figure 3.14). In autumn-winter bellbirds were observed feeding significantly more at the canopy, sub-canopy and ground layers (Table 3.12). No significant differences between hihi and bellbirds in other foraging heights during autumn-winter (Table 3.12). In spring, bellbirds were still observed feeding significantly more at the canopy and sub-canopy (Table 3.12) and hihi were observed feeding significantly more at the middle storey and upper understorey (Table 3.12). Bellbirds were consistently seen feeding more in the canopy and sub-canopy (possibly except for sub-canopy in autumn-winter). Hihi were only seen feeding more than bellbirds at the middle storey and upper understorey layers in spring.

Table 3.12. Chi-square tests comparing first food eaten observations at each foraging height between bellbirds and hihi during autumn-winter and spring 2010.

Season	Height	Bellbird	Hihi	χ^2	df	P
Autumn-winter	Canopy	65	10	40.33	1	0.000
	Sub-canopy	52	25	9.47	1	0.002
	Upper understorey	1	2	0.33	1	0.564
	Middle storey	2	0	2.00	1	0.157
	Lower understorey	0	1	1.00	1	0.317
	Ground	13	3	6.25	1	0.012
Spring	Canopy	80	14	46.34	1	0.000
	Sub-canopy	68	25	19.88	1	0.000
	Upper understorey	0	4	4.00	1	0.046
	Middle storey	10	60	35.71	1	0.000
	Lower understorey	2	6	2.00	1	0.157
	Ground	4	8	1.33	1	0.248

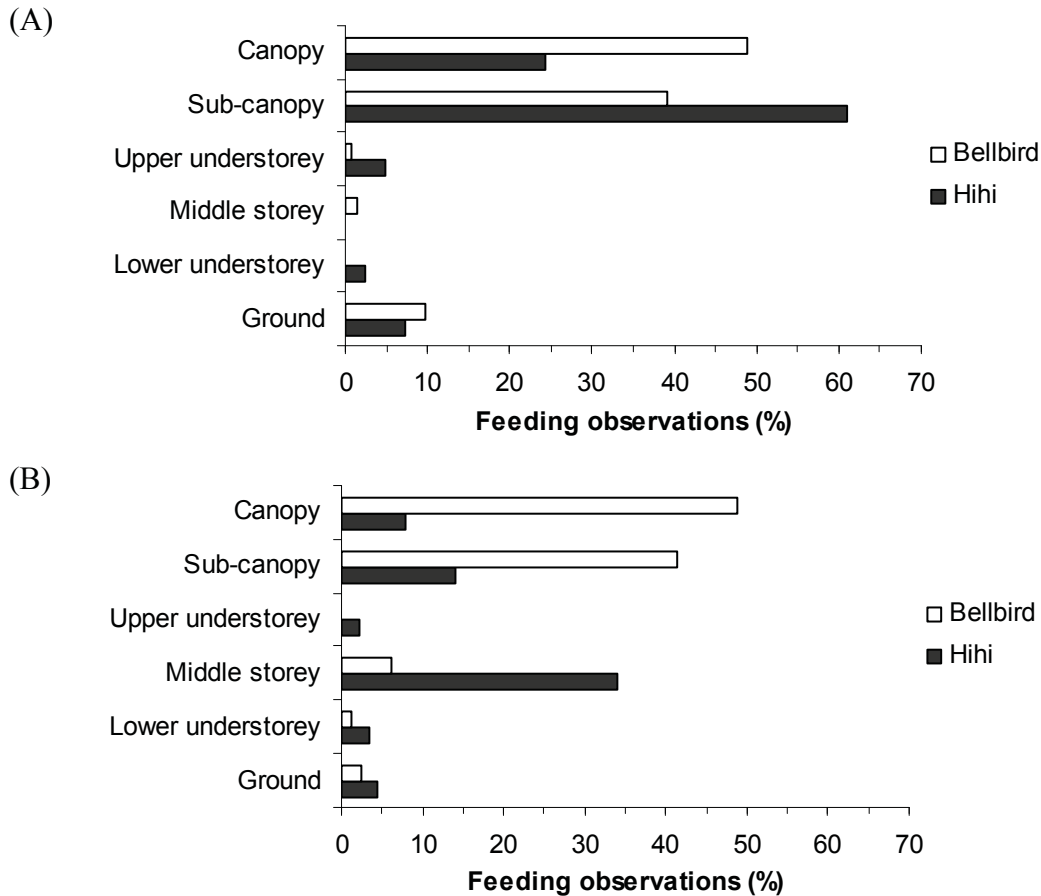


Figure 3.14. Bellbird and hihi foraging height observations for autumn-winter (A) and spring (B) 2010.

3.3.3 Sources of nectar

The plant sources of nectar varied throughout the year for both bellbirds and hihi as different plants came into flowering. However, the proportion of feeding observations at these plant species varied between bellbirds and hihi (Figure 3.15). During the winter months (June to August), nectar feeding observations were obtained from 7 plant species that were in flower during this period. Bellbirds were most commonly seen nectar feeding on five finger (*Pseudopanax arboreus*) and manuka (*Leptospermum scoparium*) whereas hihi were found nectar feeding mostly on kohekohe (*Dysoxylum spectabile*) and five finger (Figure 3.15). Bellbirds were found nectar feeding significantly more than hihi on golden wattle (*Acacia pycnantha*), manuka and five finger (Table 3.15). The number of feeding observations on the other plant species was similar for bellbirds and hihi (Table 3.15). In spring (September and October) more plant species were flowering and nectar feeding was observed on a total of 13 plant species (Figure 3.15). Bellbirds were

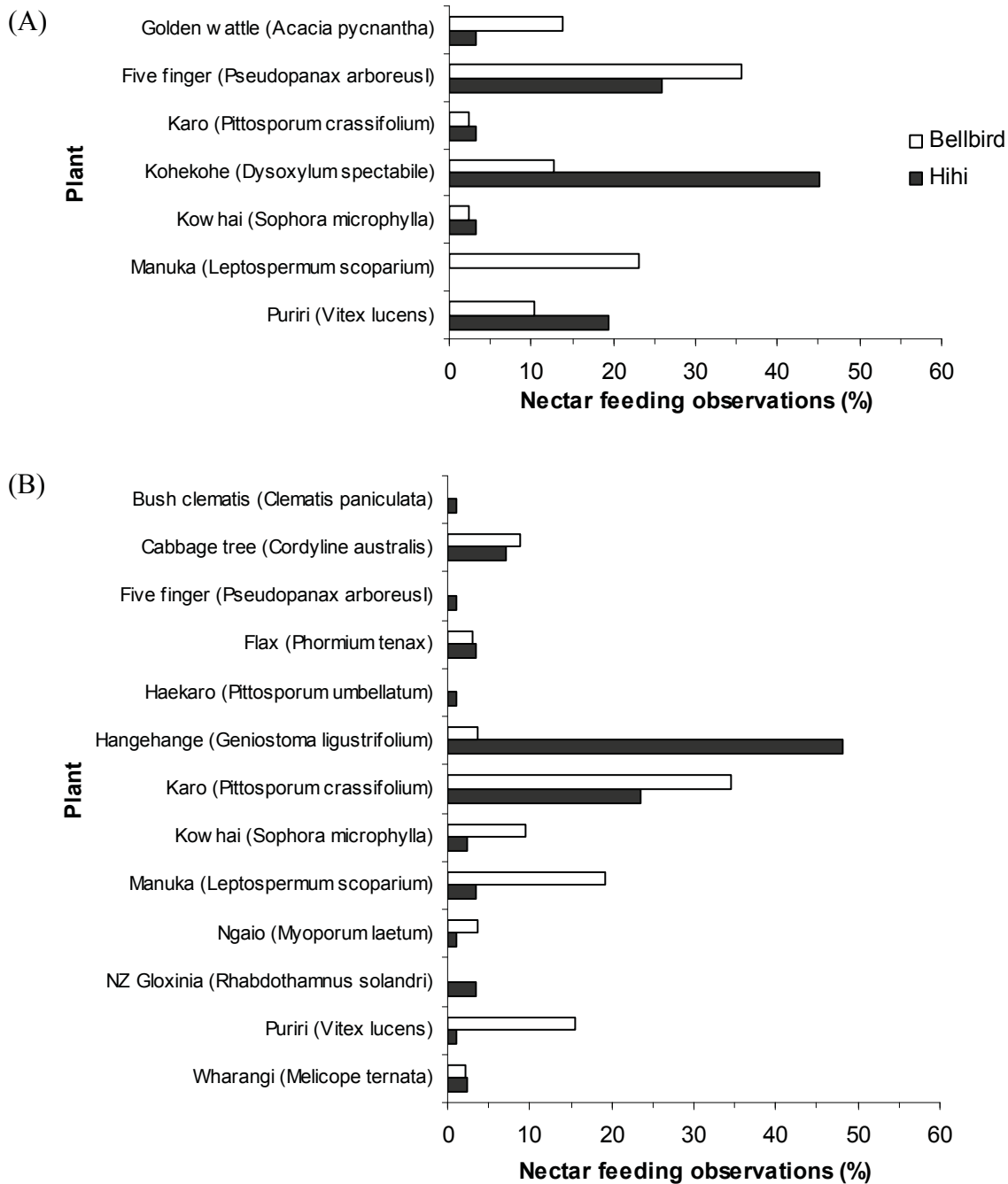


Figure 3.15. Nectar feeding observations at different plant species for bellbirds and hihi during winter (A) and spring (B) 2010.

observed feeding mostly on karo (*Pittosporum crassifolium*) and manuka whereas hihi were observed feeding mostly on hangehange (*Geniostoma ligustrifolium*) and karo (Figure 3.15). Of these 13 species, bellbirds consumed significantly more nectar than hihi from manuka, karo, kowhai (*Sophora microphylla*) and puriri (*Vitex lucens*; Table 3.13).

In spring, hihi consumed significantly more nectar from hangehange than bellbirds and although a significant result was not found between bellbird and hihi for bush clematis (*Clematis paniculata*), haekaro (*P. umbellatum*), five finger and New Zealand gloxinia (*Rhabdothamnus solandri*), only hihi were observed nectar feeding from these three plant species (Table 3.13). Bellbird and hihi were observed nectar feeding in similar proportions on cabbage tree (*Cordyline australis*), wharangi (*Melicope ternata*), ngaio (*Myoporum laetum*), and flax (*Phormium tenax*; Table 3.13).

Table 3.13. Chi-square tests results comparing nectar feeding observations at flowering plant species between bellbirds and hihi during winter and spring 2010.

Season	Plant	Bellbird	Hihi	χ^2	df	P
Winter	Golden wattle (<i>Acacia pycnantha</i>)	12	1	9.31	1	0.002
	Five finger (<i>Pseudopanax arboreus</i>)	31	8	5.83	1	0.016
	Karo (<i>Pittosporum crassifolium</i>)	2	1	0.33	1	0.564
	Kohekohe (<i>Dysoxylum spectabile</i>)	11	14	0.36	1	0.549
	Kowhai (<i>Sophora microphylla</i>)	2	1	0.33	1	0.564
	Manuka (<i>Leptospermum scoparium</i>)	20	0	20.00	1	0.000
	Puriri (<i>Vitex lucens</i>)	9	6	0.60	1	0.439
Spring	Bush clematis (<i>Clematis paniculata</i>)	0	1	1.00	1	0.317
	Cabbage tree (<i>Cordyline australis</i>)	12	6	2.00	1	0.157
	Five finger (<i>Pseudopanax arboreus</i>)	0	1	1.00	1	0.317
	Flax (<i>Phormium tenax</i>)	4	3	0.14	1	0.705
	Haekaro (<i>Pittosporum umbellatum</i>)	0	1	1.00	1	0.317
	Hangehange (<i>Geniostoma ligustrifolium</i>)	5	41	28.17	1	0.000
	Karo (<i>Pittosporum crassifolium</i>)	47	20	10.88	1	0.001
	Kowhai (<i>Sophora microphylla</i>)	13	2	8.07	1	0.005
	Manuka (<i>Leptospermum scoparium</i>)	26	3	18.24	1	0.000
	Ngaio (<i>Myoporum laetum</i>)	5	1	2.67	1	0.102
	NZ Gloxinia (<i>Rhabdothamnus solandri</i>)	0	3	3.00	1	0.083
	Puriri (<i>Vitex lucens</i>)	21	1	18.18	1	0.000
	Wharangi (<i>Melicope ternata</i>)	3	2	0.20	1	0.655

Comparisons of nectar sources were also made between the sexes of each species. Overall, there were very few differences in nectar sources used by males and female within in each species. In winter, bellbird males were found consuming mostly from five finger and golden wattle (Table 3.14). Female bellbirds also consumed mostly from five finger but they also consumed just as much from manuka (Table 3.14). The only significant difference between males and females was that males consumed significantly more golden wattle nectar and slightly more puriri nectar (Table 3.14). In spring, no significant differences in nectar sources between males and females were found and both

sexes were mostly observed nectar feeding on karo and manuka (plus puriri for females). In winter, both male and female hihi were most commonly observed nectar feeding on kohekohe and puriri with no significant differences between males and females for all plant species (Table 3.14). In spring, male and female hihi were both observed nectar feeding most commonly and in similar proportions on hangehange and karo although females were also observed feeding significantly more than males on flax (Table 3.14).

Table 3.14. Chi-square tests comparing nectar feeding observations at flowering plant species between the sexes of bellbirds and hihi during winter and spring 2010.

Season	Plant	Bellbird					Hihi				
		Male	Female	χ^2	df	P	Male	Female	χ^2	df	P
Autumn-winter	Golden wattle (<i>Acacia pycnantha</i>)	12	0	12.00	1	0.001	0	1	1.00	1	0.317
	Five finger (<i>Pseudopanax arboreus</i>)	18	13	0.81	1	0.369	5	3	0.50	1	0.480
	Karo (<i>Pittosporum crassifolium</i>)	0	2	2.00	1	0.157	1	0	1.00	1	0.317
	Kohekohe (<i>Dysoxylum spectabile</i>)	6	5	0.09	1	0.763	6	8	0.29	1	0.593
	Kowhai (<i>Sophora microphylla</i>)	1	1	0.00	1	1.000	0	1	1.00	1	0.317
	Manuka (<i>Leptospermum scoparium</i>)	7	13	1.80	1	0.180	0	0	-	1	-
	Puriri (<i>Vitex lucens</i>)	7	2	2.78	1	0.096	2	4	0.67	1	0.414
Spring	Bush clematis (<i>Clematis paniculata</i>)	0	0	-	1	-	1	0	1.00	1	0.317
	Cabbage tree (<i>Cordyline australis</i>)	6	6	0.00	1	1.000	4	2	0.67	1	0.414
	Five finger (<i>Pseudopanax arboreus</i>)	0	0	-	1	-	1	0	1.00	1	0.317
	Flax (<i>Phormium tenax</i>)	1	3	1.00	1	0.317	0	3	3.00	1	0.083
	Haekaro (<i>Pittosporum umbellatum</i>)	0	0	-	1	-	1	0	1.00	1	0.317
	Hangehange (<i>Geniostoma ligustrifolium</i>)	2	3	0.20	1	0.655	20	21	0.02	1	0.876
	Karo (<i>Pittosporum crassifolium</i>)	26	21	0.53	1	0.466	11	9	0.20	1	0.655
	Kowhai (<i>Sophora microphylla</i>)	8	5	0.69	1	0.405	1	1	0.00	1	1.000
	Manuka (<i>Leptospermum scoparium</i>)	14	12	0.15	1	0.695	1	2	0.33	1	0.564
	Ngaio (<i>Myoporum laetum</i>)	4	1	1.80	1	0.180	1	0	1.00	1	0.317
	NZ Gloxinia (<i>Rhabdanthus solandri</i>)	0	0	-	1	-	2	1	0.33	1	0.564
	Puriri (<i>Vitex lucens</i>)	7	14	2.33	1	0.127	1	0	1.00	1	0.317
	Wharangi (<i>Melicope ternata</i>)	1	2	0.33	1	0.564	0	2	2.00	1	0.157

3.4 Plant surveys of transect and feeder sites

A list of plant species that were potential food sources for bellbirds and hihi was compiled from various sources (Castro, 1997; Baker, 1999; Perrot & Armstrong, 2000) and combined with what plant species are known to exist on Tiritiri Matangi Island (Supporters of Tiritiri Matangi Inc, 2010; Appendix 3.1). Of these 48 species, bellbirds and hihi were only seen feeding on nectar and fruit from 18 of these (Appendix 3.1). The 21 plant species included in the survey were categorised using the DAFOR scale for each

transect (Table 3.15) and feeder area (Table 3.16). The DAFOR scale was then converted to a number to calculate an overall score to represent a *food resources level*, an example on how the score was calculated is given in Table 3.17. Total *food resources level* for each transect and feeder site from April to October 2010 are displayed in Table 3.18 for bellbirds and total resource level scores excluding kanuka are displayed in Table 3.19 for hihi. The total scores showed that in general resource availability increased from April to October as more plant species came into flower and nectar production however there were some areas where the *food resources level* was higher in winter (Tables 3.18 & 3.19).

Table 3.15. DAFOR scales (D = dominant, A = abundant, F = Frequent, O = occasional, R = rare) for each plant species known to be fed on by bellbirds and hihi (plus the three dominant species) for each transect.

Plant species	Transect											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Acacia pycnantha</i>											R	
<i>Clematis paniculata</i>												R
<i>Coprosma robusta</i>	R	R										R
<i>Cordyline australis</i>	O	F	O	O	F	R	O			F	A	O
<i>Dysoxylum spectabile</i>							O	O	D			
<i>Geniostoma ligustrifolium</i>	R		R	R	R	O	F	O	O		O	R
<i>Kunzea ericoides</i>	O	O	R		F	A	O	F			R	F
<i>Leptospermum scoparium</i>		R	R		R						R	
<i>Melicope ternate</i>			R	R	R							
<i>Melicytus ramiflorus</i>	O	O	O		O		R			O	O	O
<i>Metrosideros excelsa</i>	F	O	F	A			O	O	R	A	O	R
<i>Myoporum laetum</i>		R	O	R	R	R					R	O
<i>Myrsine australis</i>					O	F	F	F	R		R	O
<i>Phormium tenax</i>	F	R	R									
<i>Pittosporum crassifolium</i>	R	R	R	R						R	R	
<i>Pittosporum umbellatum</i>												
<i>Pseudopanax arboreus</i>					R	R		O			R	R
<i>Pseudopanax lessonii</i>					R							
<i>Rhabdothamnus solandri</i>							R					
<i>Sophora microphylla</i>	R	O	R	R	R	R				R	R	R
<i>Vitex lucens</i>	R	R	R	R				R		R		R

Table 3.16. DAFOR scales (D = dominant, A = abundant, F = Frequent, O = occasional, R = rare) for each plant species known to be fed on by bellbirds and hihi (plus the three dominant species) for each feeder area.

	Feeder					
	Bush 1 Lower	Bush 1 Upper	Bush 2	Bush 22	Dupont	Wattle Valley
<i>Acacia pycnantha</i>						
<i>Clematis paniculata</i>						
<i>Coprosma robusta</i>						
<i>Cordyline australis</i>	O	O		O		A
<i>Dysoxylum spectabile</i>						
<i>Geniostoma ligustrifolium</i>	A	O	O	O		O
<i>Kunzea ericoides</i>			O	O	D	
<i>Leptospermum scoparium</i>						O
<i>Melicope ternata</i>		R				
<i>Melicytus ramiflorus</i>		O				F
<i>Metrosideros excelsa</i>	O	F		O		
<i>Myoporum laetum</i>						
<i>Myrsine australis</i>	F		O	F	O	
<i>Phormium tenax</i>		O	O	O		
<i>Pittosporum crassifolium</i>						
<i>Pittosporum umbellatum</i>						
<i>Pseudopanax arboreus</i>			O	R		
<i>Pseudopanax lessonii</i>						
<i>Rhabdothamnus solandri</i>						
<i>Sophora microphylla</i>		R				
<i>Vitex lucens</i>		O				

Table 3.17. Example of how the score for the *food resources level* was calculated from the DAFOR scale for Transect 1 from April to October 2010 (D = dominant(5), A = abundant(4), F = Frequent(3), O = occasional(2), R = rare(1)).

Plant species	DAFOR	Month						
		April	May	June	July	August	Sept	October
<i>Coprosma robusta</i>	R							
<i>Cordyline australis</i>	O							2
<i>Kunzea ericoides</i>	O	2	2	2	2	2	2	
<i>Melicytus ramiflorus</i>	O							
<i>Metrosideros excelsa</i>	F							
<i>Phormium tenax</i>	F							3
<i>Pittosporum crassifolium</i>	R					1	1	1
<i>Sophora microphylla</i>	R					1	1	1
<i>Vitex lucens</i>	R		1	1	1	1	1	1
Total score		2	3	3	3	5	5	8

Table 3.18. *Food resources level* (including kanuka) for each transect and feeder area from April to October 2010.

		Month						
		April	May	June	July	August	September	October
Transect	1	2	3	3	3	5	5	8
	2	2	4	4	4	7	7	10
	3	1	3	3	3	5	7	10
	4	0	1	1	1	3	5	7
	5	3	4	5	5	6	6	6
	6	4	4	5	5	6	7	4
	7	2	2	4	4	2	6	6
	8	3	4	8	8	6	6	3
	9	0	0	5	5	0	2	2
	10	0	1	1	1	3	3	6
	11	1	2	4	4	6	6	10
	12	3	4	5	5	6	7	7
Feeder	Bush 1 Lower	0	0	0	0	0	4	6
	Bush 1 Upper	0	2	2	2	3	6	9
	Bush 2	2	2	4	4	4	4	4
	Bush 22	2	2	3	3	3	4	6
	Dupont	5	5	5	5	5	5	0
	Wattle Valley	0	2	2	2	2	4	8

Table 3.19. *Food resources level* (excluding kanuka) for each transect and feeder area from April to October 2010.

		Month						
		April	May	June	July	August	September	October
Transect	1	0	1	1	1	3	3	8
	2	0	2	2	2	5	5	10
	3	0	2	2	2	4	6	10
	4	0	1	1	1	3	5	7
	5	0	1	2	2	3	3	6
	6	0	0	1	1	2	3	4
	7	0	0	2	2	0	4	6
	8	0	1	5	5	3	3	3
	9	0	0	5	5	0	2	2
	10	0	1	1	1	3	3	6
	11	0	1	3	3	5	5	10
	12	0	1	2	2	3	4	7
Feeder	Bush 1 Lower	0	0	0	0	0	4	6
	Bush 1 Upper	0	2	2	2	3	6	9
	Bush 2	0	0	2	2	2	2	4
	Bush 22	0	0	1	1	1	2	6
	Dupont	0	0	0	0	0	0	0
	Wattle Valley	0	2	2	2	2	4	8

3.5 Discussion

3.5.1 Dietary components

The composition of food types that made up the diet of bellbird and hihi varied between the species but also varied throughout the year. Bellbirds were observed most often feeding on nectar followed by invertebrates, honeydew and fruit and no differences were found between the sexes. Seasonal differences were observed in that nectar consumption increased from the autumn-winter period to spring whereas honeydew consumption decreased. Invertebrate consumption was consistent throughout the study period and fruit was only consumed in the autumn. Hihi also preferred nectar followed by invertebrates and fruit and as with bellbirds no differences between the sexes was detected. Nectar consumption was consistent across the study period but invertebrate consumption increased and fruit was only consumed in autumn-winter.

Dietary differences between the species related to the seasons with the differences occurring mostly in the autumn-winter. The major difference between bellbirds and hihi were that bellbirds consume honeydew and hihi did not. In the autumn-winter period, bellbirds and hihi consumed similar proportions of nectar and invertebrates but hihi had a higher proportion of fruit in their diet. In the spring, no fruit was available and the bellbirds did not consume as much honeydew which may be due to the seasonal variation in honeydew production (Gaze & Clout, 1983) and/or the increase in nectar availability (more plant species were in flower; see section 3.4).

The results of this study produced similarities and differences to previous studies on hihi dietary composition (Figure 3.16). In autumn there was only one sample for hihi and the comparison is most likely invalid, but the one sample was of fruit which was a major component of the hihi diet on Little Barrier Island (Gravatt, 1971; Angher, 1985 and Rasch, 1985 cited in Castro, 1995). In winter the results for hihi most resemble those of Castro (1995) in 1991 on Kapiti Island with a high proportion of nectar and similar amounts of fruit and invertebrates. Although the results from Little Barrier Island (Gravatt, 1971; Angher, 1985 and Rasch, 1985 cited in Castro, 1995) also show similar trends with nectar being the highest proportion, the proportions of fruit and invertebrates are not quite as similar. In spring the results for hihi most resemble the results from Little

Barrier Island (Gravatt, 1971; Angher, 1985 and Rasch, 1985 cited in Castro, 1995) with a high proportion of nectar, very little or no fruit and a moderate proportion of invertebrates in the diet (Gravatt, 1971; Angher, 1985 and Rasch, 1985 cited in Castro, 1995). Therefore, the diet of hihi on Tiritiri Matangi Island most resemble that of hihi on Little Barrier Island but the resemblance to the diet of hihi on Kapiti Island in winter 1991, shows that their diet is likely to be more linked to the availability of resources than location.

The results of this study for bellbirds also showed some similarities and differences with other studies (Figure 3.17). However, the comparisons may be slightly affected by the fact that Gravatt (1971) did not record feedings on honeydew and Poirot (2004) did not record feedings on fruit (although it is assumed that there was no fruit available due to very few flowering trees in this area as no nectar feedings were recorded until the summer). Overall, the same trend in changes of proportions of dietary components over the seasons was found over various locations (Figure 3.17). The proportion of nectar in the bellbird diet recorded in my study on Tiritiri Matangi Island and on Little Barrier Island (Gravatt, 1971) increased from autumn to spring whereas the proportion of fruit decreased. The proportion of honeydew recorded in my study and in Nelson (Poirot, 2004) also showed a decrease from autumn to spring. The proportion of invertebrates recorded were quite similar between the seasons for the data from Tiritiri Matangi and the Nelson locations but on Little Barrier Island (Gravatt, 1971) the proportion of invertebrates in the diet decreased. The major difference between the results from Tiritiri Matangi and the other locations is the actual proportions. The results from this study showed higher proportions of nectar and much lower proportions of invertebrates in the bellbird diet. There were lower proportions of honeydew feeding observations compared to the Nelson locations (Poirot, 2004), most likely because honeydew was the main source of carbohydrates in Nelson unlike on Tiritiri Matangi Island where nectar was available throughout the year, and lower proportions of feeding on invertebrates than in Nelson. Therefore, overall the bellbird diet on Tiritiri Matangi Island was observed to have much higher proportions of nectar, a small amount of invertebrates and a very small amount of fruit. As shown by the diet of hihi, this could be due to variation of resources and their availability between locations and seasons.

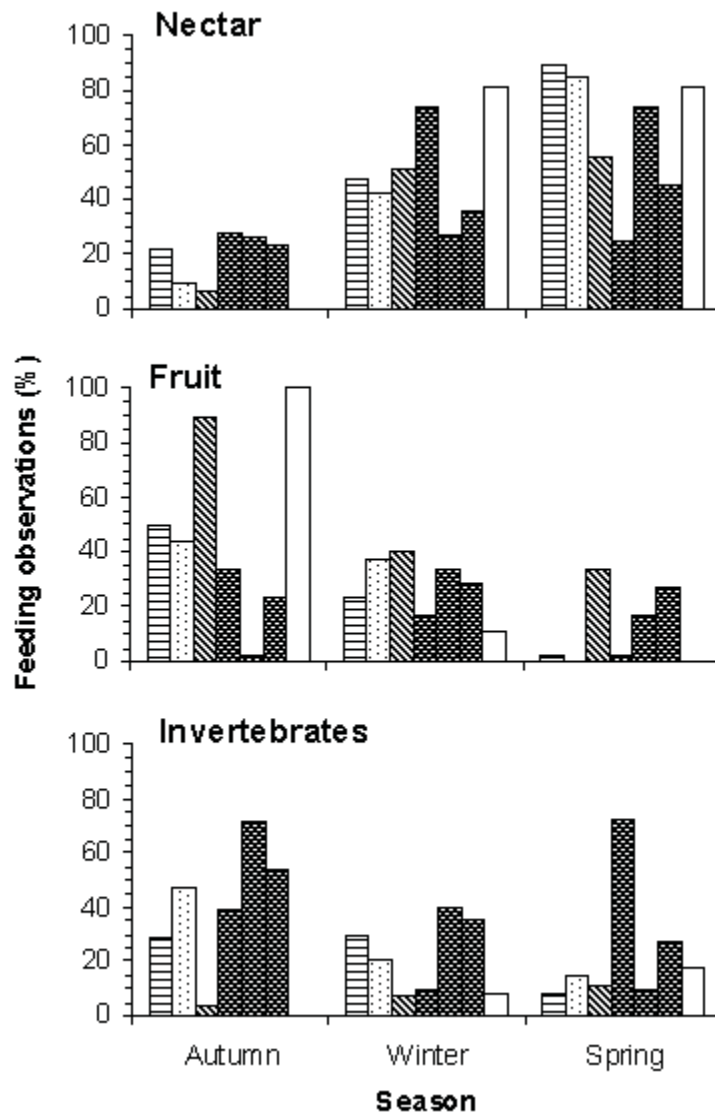


Figure 3.16. Comparisons of hihi feeding observations between Little Barrier Island, Kapiti Island and Tiritiri Matangi Island. Data from left to right: Little Barrier- Gravatt (1971; data for 1969; horizontal stripes), Angher (1985, cited in Castro, 1995; data for 1982; black spots), Rasch (1985, cited in Castro, 1995; data for 1984; diagonal stripes); Kapiti Island- Castro (1995; data from left to right for 1991-1993; black bars); Tiritiri Matangi Island- this study (data for 2010; white bars).

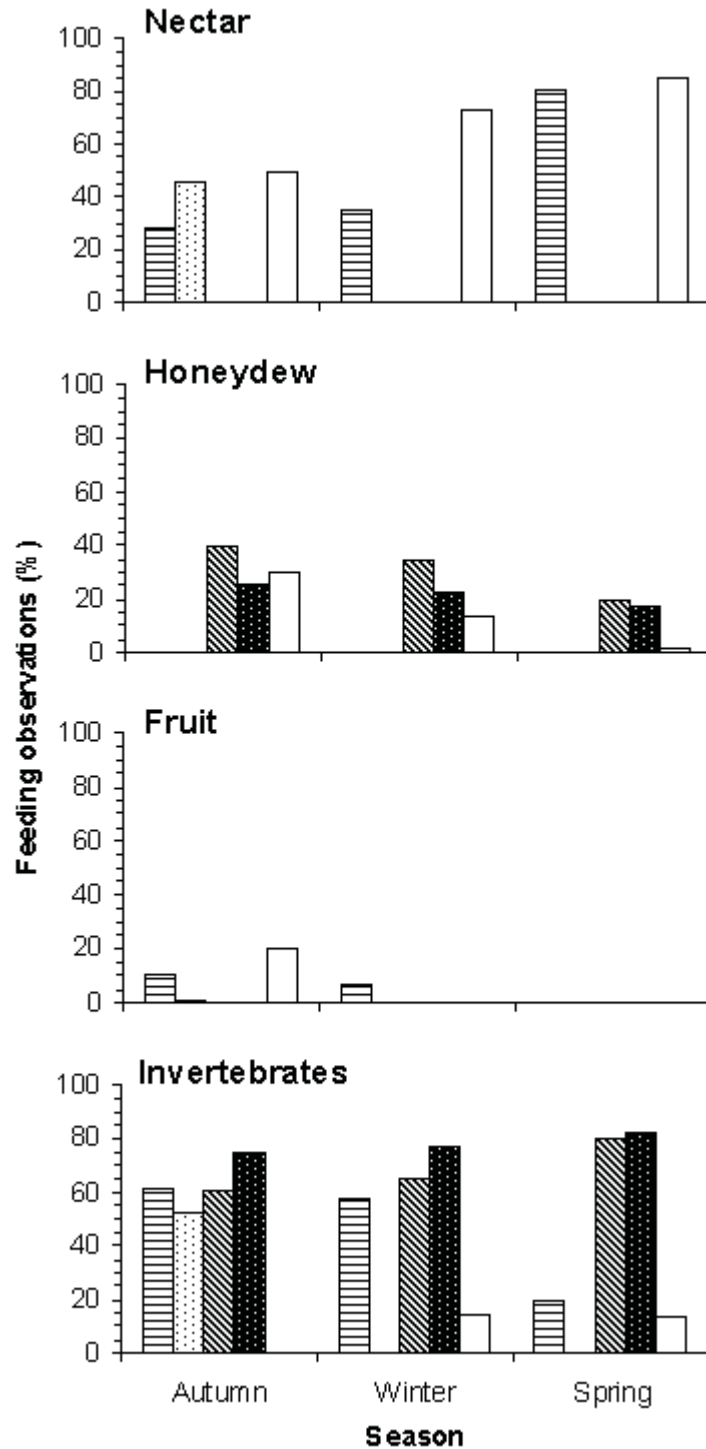


Figure 3.17. Comparisons of bellbird feeding observations between Little Barrier Island, Hen Island, two locations in Nelson and Tiritiri Matangi Island. Data from left to right: Little barrier- Gravatt (1971; data for 1969; horizontal stripes); Hen Island- Merton (1966; data for 1965; white spots); Nelson- Poirot (2004; data for 2003; Rotoiti Nature Recovery project diagonal stripes; Mt. Misery Nelson Lakes National Park white spots); Tiritiri Matangi Island- this study (data for 2010; white bars).

Gravatt (1971) also found that females of both species tended to consume more insects than males, particularly in winter, however this was not found in my results. Hihi sexes had a similar number of observations for consuming invertebrates and this is potentially because they were often seen foraging together (personal observation). Bellbird males were observed more than females feeding on invertebrates which could be due to males being more often seen foraging on the tracks near the feeders. With overall there being less females visiting the feeders (Chapter 4), they were more likely to be feeding on invertebrates off tracks in less observed areas. Therefore, the results from this study may not accurately reflect the differences in invertebrate consumption between the sexes due to biasing factors.

3.5.2 Foraging height

Foraging heights in the forest strata varied significantly between bellbirds and hihi. In general, bellbirds appeared to forage more at higher vegetation levels and hihi spent more time feeding in the middle canopy layers, with both species foraging in similar proportions in the lower and ground layers. Bellbirds were mostly seen foraging in the canopy, sub-canopy and ground layers. Little seasonal variation was found but female bellbirds did forage less than males on the ground in spring and less in the sub-canopy in autumn-winter. Hihi were observed feeding mostly in the middle storey and sub-canopy layers and this varied with season. In autumn-winter hihi were mostly found feeding in the sub-canopy and canopy layers with no differences between the sexes. In spring, both males and females showed a slight preference for foraging at the middle storey layer. Female hihi were found feeding on the ground layer more in spring than in autumn-winter. The major differences between the species were that 1) bellbirds were observed feeding more at the canopy and sub-canopy layers, and 2) hihi were observed feeding significantly more than bellbirds at the middle storey and upper understorey in spring.

Again, some similarities and differences in the proportion of feeding observations at the different vegetation layers were found between this study and with Gravatt's (1971) study on Little Barrier Island. Overall, both studies found that there were

proportionally more bellbirds feeding in the higher vegetation levels than hihi (Figure 3.18). However, on Tiritiri Matangi bellbirds were proportionately most commonly

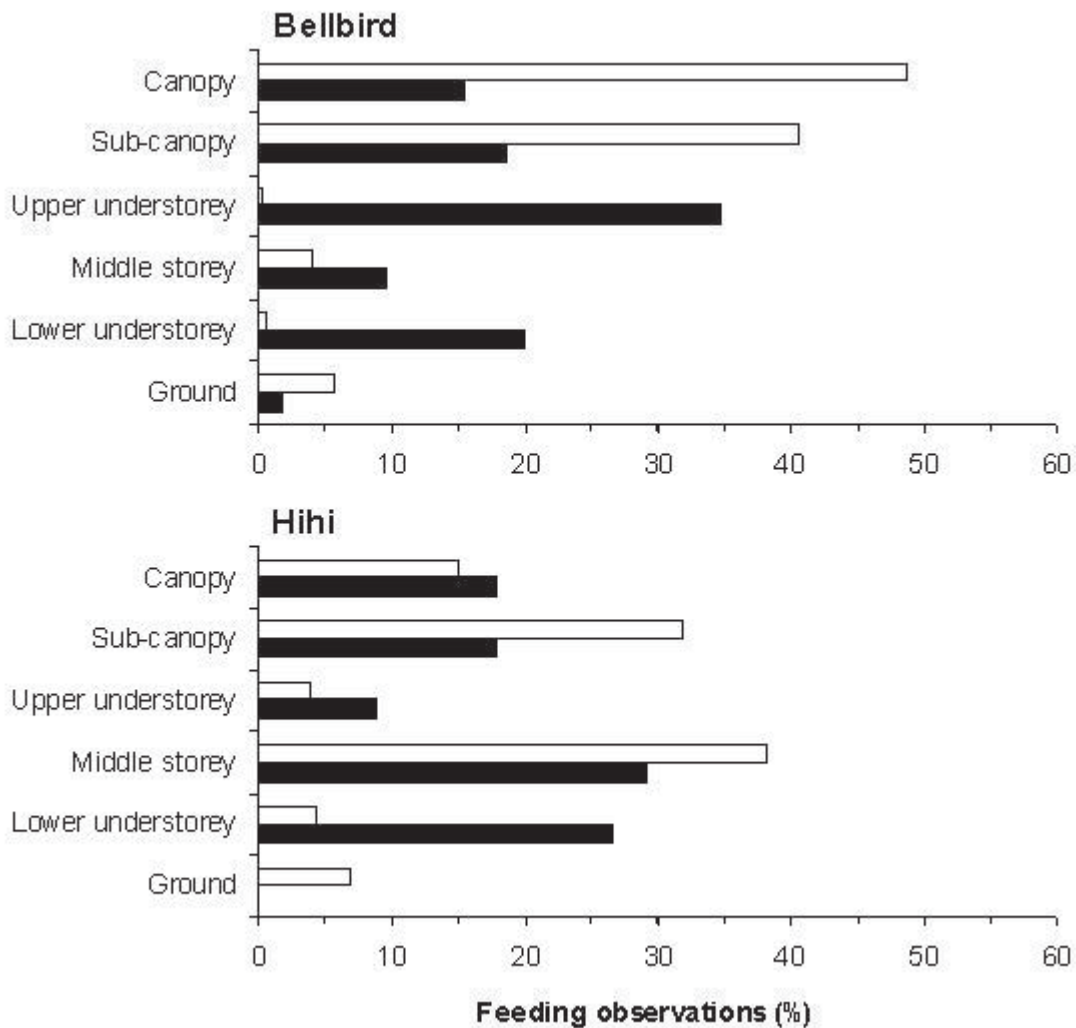


Figure 3.18. Comparisons of bellbird and hihi foraging height between Tiritiri Matangi Island (this study; data for 2010; white bars) and Little Barrier Island (Gravatt, 1971; data for 1969; black bars).

foraging in the canopy and sub-canopy whereas on Little Barrier they were most commonly feeding in the upper understory. More bellbirds were also seen on the ground on Tiritiri Matangi. Hihi were feeding most commonly in the middle storey layer for both islands. However, on Tiritiri hihi were foraging second most commonly in the sub-canopy layer whereas on Little Barrier it is the lower understory. The foraging observations were similar at the other levels except hihi were observed feeding on the ground unlike on Little Barrier. There are two potential factors contributing to the

differences found between these two locations. The first is that Tiritiri Matangi has much younger vegetation and a smaller variety of plants hence the birds may be confined to trees that produce the most resources in the canopy and sub-canopy layers. Smaller trees could also potentially be why they forage more on the ground compared to Little Barrier as they might not be able to get their required intake of invertebrates off the trunks in the lower and upper understorey layers of smaller trees. The other factor could be that there may be less tui on Tiritiri Matangi compared to Little Barrier. On Little Barrier Island tui dominated the canopy and sub-canopy layers with less bellbirds and hihi in these layers. However, on Tiritiri there were proportionately more bellbirds and hihi in the canopy and sub-canopy layers. Tui numbers seemed to vary on Tiritiri and they were not abundant for most parts of study period, only the occasional flock seemed to pass by. With fewer tui, bellbirds and hihi may be able to occupy the higher vegetation levels in more resources where tui were not present and not able to push bellbirds and hihi towards the lower levels. On Tiritiri Matangi, tui were also observed dominating a single tree and not allowing other species to feed on the same tree (personal observation) as the smaller size of regenerating trees may not be able to support many species feeding on nectar and the small size means tui could defend the whole resource. This means that bellbirds and hihi could only occupy trees with no tui which allowed them to reside in the upper vegetation layers. Hence, on Tiritiri Matangi Island bellbirds took the role of most dominant (at least in resources absent of tui) as they showed a similar pattern to the that of tui on Little Barrier with the most foraging occurring in the canopy and sub-canopy layers with hihi still most frequently foraging in the middle storey but also more in the canopy and sub-canopy unlike on Little Barrier Island.

Data was also available to compare bellbird sexes foraging heights between Tiritiri Matangi Island (spring months, September and October) and two locations in the Nelson region (spring/summer months, October and December) by Poirot (2004). Both sexes show considerable more feeding observations in the canopy and sub-canopy layers on Tiritiri than in both Nelson regions (Figure 3.19). Bellbirds in the Nelson region were observed foraging more in the middle story and lower understorey layers. Females spent much more time on the ground in Nelson than on Tiritiri where none were observed

feeding on the ground in spring. Previously in Figure 3.17 we could see that diet varied between these locations with Tiritiri bellbirds consuming more nectar, less honeydew and

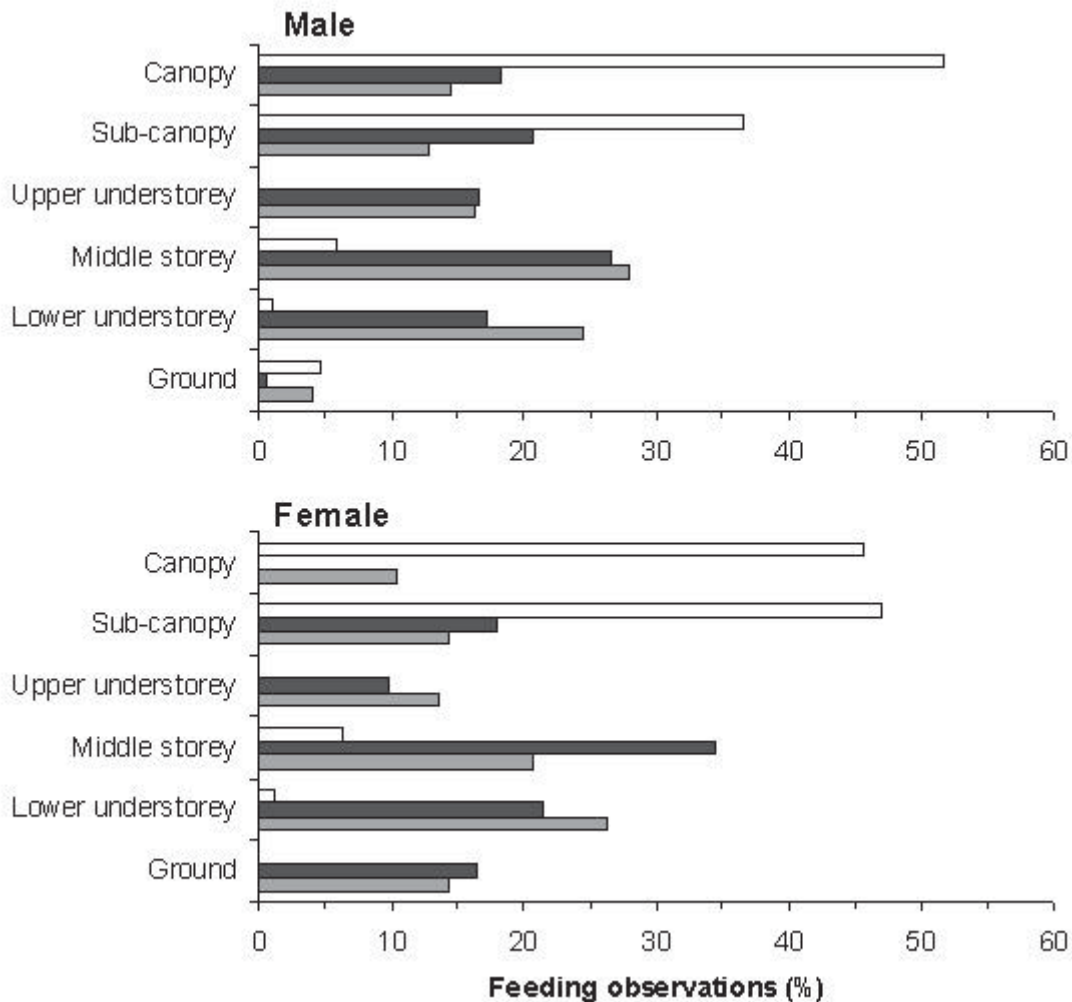


Figure 3.19. Comparisons of bellbird feeding height between Tiritiri Matangi Island (this study; data for 2010; white bars) and Nelson (Poirot, 2004; Rotoiti Nature Recovery project black bars; Mt. Misery, Nelson Lakes National Park grey bars).

fewer invertebrates than in Nelson. Hence, these differences in foraging heights could be explained by the differences in diet. With Tiritiri bellbirds consuming more nectar, they are more likely to be foraging in the higher vegetation levels where the flowers are and this was found in the results. The bellbirds in Nelson feeding more in the lower vegetation layers is most likely due to them feeding on a high proportion of invertebrates which are more likely found in higher abundances in the lower vegetation layers as bellbirds have been known to consume invertebrates while spiralling their way up tree

trunks (Gravatt, 1971). On Tiritiri, females were most commonly observed hawking for invertebrates. Hawking is a more energy consuming activity and can be regarded as uneconomical (Ford & Paton, 1976b). With Tiritiri having a much greater abundance of nectar as well as honeydew and the sugar water feeders, perhaps the bellbirds can more easily regain the energy loss from hawking unlike in Nelson where their only sugar source was honeydew. This would also help explain why the proportion of nectar consumption is so much higher on Tiritiri because they needed to consume nectar more often to regain energy losses from hawking. On Tiritiri, bellbirds also have more competition on the ground and lower layers because Tiritiri has many omnivorous and insectivorous species, such as saddlebacks (*Philesturnus carunculatus*), North Island robins (*Petroica longipes*) and whiteheads (*Mohoua albigilla*) which may be why they rely more on hawking. The level of competition with tui in the Nelson region is unknown, as competition with tui could also contribute to the foraging height of bellbirds. Therefore, the differences in vegetation type, resource availability and competition are likely factors that can affect the bellbirds distribution in the various vegetation layers.

3.5.3 Sources of nectar

The nectar sources varied slightly between the species. Bellbirds were most commonly observed feeding on five finger and manuka in winter months and on karo and manuka in the spring, with only males found consuming golden wattle in winter. Hihi were most commonly observed feeding on kohekohe and five finger in the winter and hangehange and karo in the spring. No significant differences were found between the sexes. The amount of feeding at these sources correlates well with the observed feeding heights. All plant species mentioned above had an abundance of flowers in the canopy and sub-canopy layers except for hangehange which is mostly found in the middle storey layer of the vegetation. Bellbirds fed significantly more on five finger, manuka, and karo; plants comprising the canopy and sub-canopy layers on Tiritiri. In contrast, hihi fed significantly more on spring flowering hangehange, a middle storey layer plant. Therefore, the dietary components, foraging heights and sources of nectar all vary throughout the year according to the resources available.

In relation to the coexistence of honeyeaters, Ford (1979) predicted that the larger species would leave a nectar resource first due to their higher energy demands. Bellbirds however left first and although they are slightly smaller, they are the more dominant species and perhaps have a higher energy demand for being the dominant species as aggressive interactions require an increased metabolic rate (Newton, 1998). With bellbirds being more dominant (interference competition) and potentially having more energetic costs, they will have better access to resources with the highest availability of nectar and higher levels of nectar are needed to maintain their dominant status. With hihi being the subordinate species in this relationship, they must be able to coexist with bellbirds by exploitation competition. This means that hihi must be more efficient foragers which is somewhat shown by their use of plant species with small flowers such as hangehange. Hihi are known to be acrobatic with being able to feed upside down, for example (Angher, 1985), which may contribute to why they are more efficient feeders with being able to access flowers in various positions. Hihi also have slightly longer beaks which may make them more efficient at collecting nectar than the shorter billed bellbird as the short-billed honeyeaters in Australia tend to be more insectivorous than nectivorous (Keast, 1968). Therefore, Ford's (1979) prediction may be better stated as the most dominant species will leave a resource first before the subordinate.

It is difficult to make comparisons to previous studies on plant species preferences as the different locations vary in their range and abundance of different vegetation but some similarities were found. On Little Barrier island (Gravatt, 1971) both hihi and bellbirds were commonly found visiting puriri (*Vitex lucens*) and as in our results, more bellbird observations were made of foraging in puriri than hihi. Haekaro (*Pittosporum umbellatum*) was another common source of nectar for hihi and bellbirds on Little Barrier (Gravatt, 1971) but only hihi were observed feeding on this on Tiritiri Matangi. This is most likely due to that this plant is not very common on the island unlike its relative karo (*Pittosporum crassifolium*) which was a very common source of nectar for hihi and bellbirds. The plant species visited that Kapiti Island (Castro, 1995) and Tiritiri Matangi Island have in common were all visited frequently by hihi and bellbirds whenever flowers were available except no observations were made of hihi visiting *Sophora microphylla* on Kapiti Island. Only a few visitations to this species was made on Tiritiri as it was often

dominated by tui (personal observation) but there are likely to be more tui and bellbirds on Kapiti as it is a much larger island (1,965 ha) meaning there could be more competition for hihi and hence could be excluded from *Sophora microphylla*.

Rasch & Craig (1988) observed the plant species that all three honeyeaters foraged on Little Barrier Island and classed each plant species based on the quality of nectar they produced: Type 1 were clumped flowers with the highest nectar production to Type 5 which were entomophilous flowers with the lowest nectar production. Tui foraged on types 1 and 2, bellbirds most commonly fed on types 1-3 and hihi mostly foraged on types 4 and 1 (Rasch & Craig, 1988). Comparing the plants bellbirds and hihi foraged on Tiritiri and Little Barrier (Rasch & Craig, 1988), in this study bellbirds foraged on Puriri more than hihi which is type 2 and hihi fed more on Kohekohe (type 3), NZ Gloxinia (type 4) and Haekaro (type 1), showing some similarities found by Rasch & Craig (1988) supporting their conclusions that the most dominant birds will feed on the highest ranked flowers and the most subordinate will feed on the lowest ranked flowers, although hihi do try to feed on higher ranked flowers. Rasch & Craig (1988) found that hihi often avoid feeding on plants that bellbirds fed on, potentially because they are their nearest competitor. Therefore, plant species preferences by hihi and bellbirds are more likely due to their availability and high production of flowers which will provide the most nectar as well as being affected by competition with bellbirds potentially foraging more on higher nectar producing flowers than hihi.

3.6 Conclusion

The foraging ecology of hihi and bellbirds showed variation between each other and over the seasons. The diet of both consisted of a high proportion of nectar with a smaller amount of invertebrates and fruit with no differences between the sexes. The difference between these two species was that only bellbirds consumed honeydew and hihi were more often observed consuming fruit. This correlates well with other studies that have shown hihi tend to be more frugivorous than the Meliphagidae honeyeaters but it did not correlate with the notion that bellbirds are more insectivorous. Considerable differences were found between the frequencies of foraging observations in the different vegetation layers. Bellbirds were most commonly foraging in the canopy and sub-canopy

layers with hihi most commonly foraging in the middle storey. However, this was only so for the spring months. In autumn, bellbirds were most common in the canopy layer whereas hihi were most common in the sub-canopy layer. Hence, in general bellbirds were more common in the higher vegetation layers whereas hihi were in the lower layers. No differences were found between the sexes for hihi but in bellbirds there were more males observed feeding on the ground than females. Particular plant species were visited more often than others which was most likely due to their abundance and productivity of flowers, with some plants being used more by each bird species. The foraging ecology of hihi and bellbirds on Tiritiri Matangi Island had similarities and differences between other studies showing the adaptability of these birds to different resources. The plant survey showed that in general resource availability increased from April to October as more plant species came into flower and nectar production however there were some areas where the resource availability was higher earlier in the year. Overall, resource partitioning between these two species appears to occur in the form of 'habitat and habitat' where when the species' habitats overlaps horizontally it will often differ vertically (Shoener, 1974). Bellbirds defend the best resources in the higher vegetation layers potentially of higher nectar value with interference competition and hihi obtain resources with exploitation competition by utilising flowers (which are often smaller, less abundant or produce less nectar) in the lower vegetation layers. The differences between studies also show the importance of assessing the vegetation structure and level of competition in an area where hihi may be reintroduced to ensure a stable and self-sustaining population will form.

Appendix 3.1. Bellbird and hihi food sources on Tiritiri Matangi Island

Table 1. Known potential food sources for bellbirds and hihi on Tiritiri Matangi Island and which plant species were observed producing nectar (N), fruit (F) and honeydew (H) from first food eaten observations.

Plant	April	May	June	July	August	September	October
<i>Acacia</i> spp.			N	N	N		
<i>Alectryon excelsus</i>							
<i>Alseuosmia macrophylla</i>							
<i>Astelia banksii</i>							
<i>Beilschmiedia tawa</i>							
<i>Clematis paniculata</i>						N	
<i>Clianthus puniceus</i>							
<i>Coprosma areolata</i>							
<i>Coprosma macrocarpa</i>							
<i>Coprosma propinqua</i>							
<i>Coprosma repens</i>							
<i>Coprosma rhamnoides</i>							
<i>Coprosma robusta</i>	F						
<i>Cordyline australis</i>							N
<i>Corynocarpus laevigatus</i>							
<i>Cyathodes juniperina</i>							
<i>Dodonaea viscosa</i>							
<i>Dysoxylum spectabile</i>			N	N			
<i>Elaeocarpus dentatus</i>							
<i>Entelea arborescens</i>							
<i>Geniostoma rupestre</i>							
<i>Geniostoma ligustrifolium</i>						N	N
<i>Hebe stricta</i>							
<i>Hedycarya arborea</i>							
<i>Knightia excelsa</i>							
<i>Kunzea ericoides</i>	H	H	H	H	H	H	H
<i>Leptospermum scoparium</i> (incl. var <i>keatlyii</i>)		N	N	N	N	N	N
<i>Macropiper excelsum</i>							
<i>Melicope ternata</i>						N	
<i>Melicytus novae-zelandiae</i>							
<i>Melicytus ramiflorus</i>							
<i>Metrosideros excelsa</i>							
<i>Muehlenbeckia australis</i>							
<i>Myoporum laetum</i>							N
<i>Myrsine australis</i>		F					
<i>Phormium tenax</i>							N
<i>Pittosporum crassifolium</i>					N	N	N
<i>Pittosporum umbellatum</i>						N	
<i>Podocarpus totara</i>							
<i>Pseudopanax arboreous</i>			N	N	N		
<i>Pseudopanax lessonii</i>			F	F			
<i>Rhabdothamnus solandri</i>						N	N
<i>Rhopalostylis sapida</i>							
<i>Ripogonum scandens</i>							
<i>Schefflera digitata</i>							
<i>Sophora microphylla</i>					N	N	N
<i>Streblus heterophyllus</i>							
<i>Vitex lucens</i>		N	N	N	N	N	N

Chapter 4:

Feeder visitation and interactions



Sugar water feeder station and camera setup on Tiritiri Matangi Island.

Photo: Michelle Roper, 2010.

4.1 Abstract

On Tiritiri Matangi Island, successful hihi survival and reproduction depends on supplementary sugar water feeders (Armstrong and Ewen, 2001). Bellbirds are a more dominant species that also use these feeders and there is the potential that they are competitively preventing hihi from truly utilising the feeders. There is also concern that male hihi may be reducing female hihi access to the feeders. The aim of this chapter was to compare visitation rates in the short- and long-term to determine any differences between the species and sexes. Along with assessing intra- and interspecific aggressive interactions, I could then assess the level of competition occurring at the feeders. On average, per feeder, male bellbirds were the most frequent visitors (114 ± 6 visits hr^{-1}), followed by male hihi (49 ± 3 visits hr^{-1}), female hihi (46 ± 3 visits hr^{-1}) and female bellbirds (6 ± 1 visits hr^{-1}). Their use of the feeder in the short-term was similar with increasing visits throughout the day and declining by evening. However, this pattern was mainly found in the autumn and winter months and the change in visitation rates throughout the day was often less significant for females of both species. In contrast, spring visits were consistent throughout the day for both species and sexes at most feeders. Long-term monthly trends showed differences between the species and sexes. Male bellbird and female hihi visits were relatively consistent from autumn to spring (99 to 129 and 40 to 44 visits hr^{-1} respectively) whereas male hihi visits increased (24 to 69 visits hr^{-1}) and female bellbird visits declined (16 to 3 visits hr^{-1}). Positive correlations between the species and sexes visits with few intra- and interspecific aggressive interactions in the non-breeding season showed that there was little competition between the species and hihi sexes. There was more intraspecific competition between bellbirds with no correlation between the sexes at some feeders and very few female visits observed. Aggressive interactions increased at the start of the breeding season (September) which was most likely due to breeding territoriality for both species and forced copulations by male hihi onto female hihi. Feeder use was often influenced by the presence of tui and people but overall it is suggested that resource availability and breeding behaviour contribute to the short and long-term trends found. Therefore, dominant male bellbirds cease to highly defend the feeders from subordinate males and

hihi due to the overwhelming number of visits, although female bellbirds appear to still be at risk from male bellbird dominance.

4.2 Aims

- To compare visitation rates to the feeders by bellbirds and hihi to determine any differences between the species and sexes.
- To observe for any daily and monthly variation in feeder use by both species and sexes to understand short- and long-term temporal patterns of feeder use.
- To compare daily patterns of feeder visits by both species and sexes to determine whether any short term competitive exclusion is occurring.
- To observe the behaviour of bellbirds and hihi to assess the types of aggressive intraspecific and interspecific interactions occurring at the feeders.

4.3 Overall visitation patterns

Long-term trends

Visits to the feeders varied between the species and sexes. Over all months and feeders male bellbirds were the most frequent visitors at 114 ± 6 visits hr^{-1} per feeder. Hihi were the next most frequent visitors with males having an average of 49 ± 3 visits hr^{-1} and females with 46 ± 3 visits hr^{-1} per feeder. Female bellbirds were the least frequent visitors with an average of 6 ± 1 visits hr^{-1} per feeder. However, average visitation rates varied over the months and throughout the day. Similar daily and monthly trends in visitation rates were found between the different feeders although there were differences at some feeders. Variation in visitation trends between the feeders could possibly be explained by various factors (e.g. presence of tui or people) but sometimes there was no obvious cause.

Throughout the study period there was some variation in visitation rates (Figure 4.1). Different feeders were observed each month hence only months with adequate data could be combined to give the overall results (Table 4.1). Male bellbirds were the most frequent visitors over all months and their visits were significantly higher than hihi visits

in all months except June (Mann-Whitney U-test; Table 4.2). Female hihi in general visited more frequently than male hihi from May to July but their visits were not significantly different until September when male hihi visited significantly more frequently than females (Table 4.2). Female bellbirds were the least frequent visitors over all months with their visits significantly lower than all other categories (sexes and species) in all months except in May they were not significantly lower than male hihi (Table 4.2). Significant positive correlations were found between all categories except in September male and female bellbirds did not show any significant correlation (Spearman rank correlation; Table 4.2).

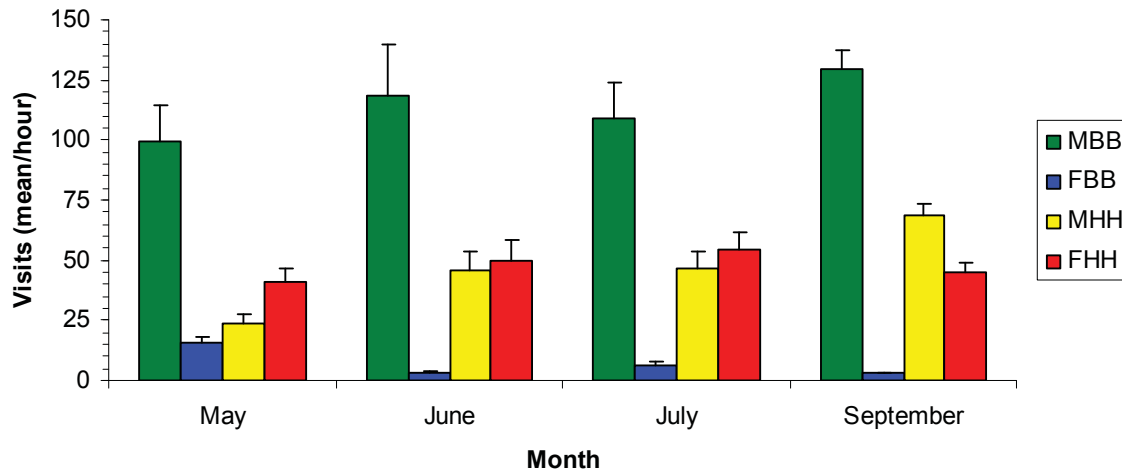


Figure 4.1. Mean visitation rate per hour per feeder each month for male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) at all feeders. Error bars represent standard error values.

Table 4.1. Number of hours of video recorded at each feeder per month.

	April	May	June	July	September
Bush 1 Lower	0	23	0	21	17
Bush 1 Upper	0	34	10	0	20
Bush 2	0	0	9	15	29
Bush 22	12	0	25	0	24
Dupont	0	20	0	23	25
Wattle Valley	0	0	13	11	27
Total	12	77	57	70	142

Table 4.2. Test results from a Mann-Whitney U-test and Spearman rank correlation between the visitation rate per hour for each species and sex per month from the combined results of all feeders observed in each month. Key: MBB = male bellbird; FBB = female bellbird; MHH = male hihi; FHH = female hihi; vs = versus.

		MBB vs FBB	MBB vs MHH	MBB vs FHH	MHH vs FHH	FBB vs MHH	FBB vs FHH
May	<i>U</i>	7236	6784.5	6485.5	5442	6329	6582.5
	<i>n</i>	76	76	76	76	76	76
	<i>P</i>	0.0000	0.0003	0.0128	0.1642	0.0510	0.0036
	<i>r_s</i>	0.88	0.82	0.81	0.93	0.87	0.88
	<i>n</i>	76	76	76	76	76	74
	<i>P</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
June	<i>U</i>	4326.5	3476	3428.5	3107	4227	4255
	<i>n</i>	56	56	56	56	56	56
	<i>P</i>	0.0000	0.0695	0.1240	0.7418	0.0000	0.0000
	<i>r_s</i>	0.36	0.79	0.78	0.86	0.31	0.27
	<i>n</i>	56	56	56	56	56	54
	<i>P</i>	0.006	<0.0001	<0.0001	<0.0001	0.022	0.042
July	<i>U</i>	6762	5756	5421.5	4817	6121.5	6169.5
	<i>n</i>	70	70	70	70	70	70
	<i>P</i>	0.0000	0.0006	0.0421	0.6205	0.0000	0.0000
	<i>r_s</i>	0.47	0.87	0.82	0.90	0.65	0.71
	<i>n</i>	70	70	70	70	70	68
	<i>P</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
September	<i>U</i>	30123	24059	26102	23033.5	28550	27838.5
	<i>n</i>	142	142	142	142	142	142
	<i>P</i>	0.0000	0.0000	0.0000	0.0001	0.0000	0.0000
	<i>r_s</i>	-0.05	0.78	0.37	0.64	0.19	0.52
	<i>n</i>	142	142	142	142	142	140
	<i>P</i>	0.519	<0.0001	<0.0002	<0.0003	0.022	<0.0001

Short-term trends

The daily pattern in visitation rates differed slightly with month (Figure 4.2). In May the daily pattern showed some degree of visits increasing towards the afternoon then declining towards the end of the day (Figure 4.2) but these results were only significant for bellbirds between 0700 and 1700 hours (not between 0900 and 1500 hours) but not for hihi although female hihi were close to the significance threshold ($P < 0.05$) for the daily variation between 0700 and 1700 hours (see Appendix 4.1). June showed an increase in visitation rates throughout the day with visits highest between 0900 and 1500 hours and declining by 1700 hours (Figure 4.2). This was only significant for the males

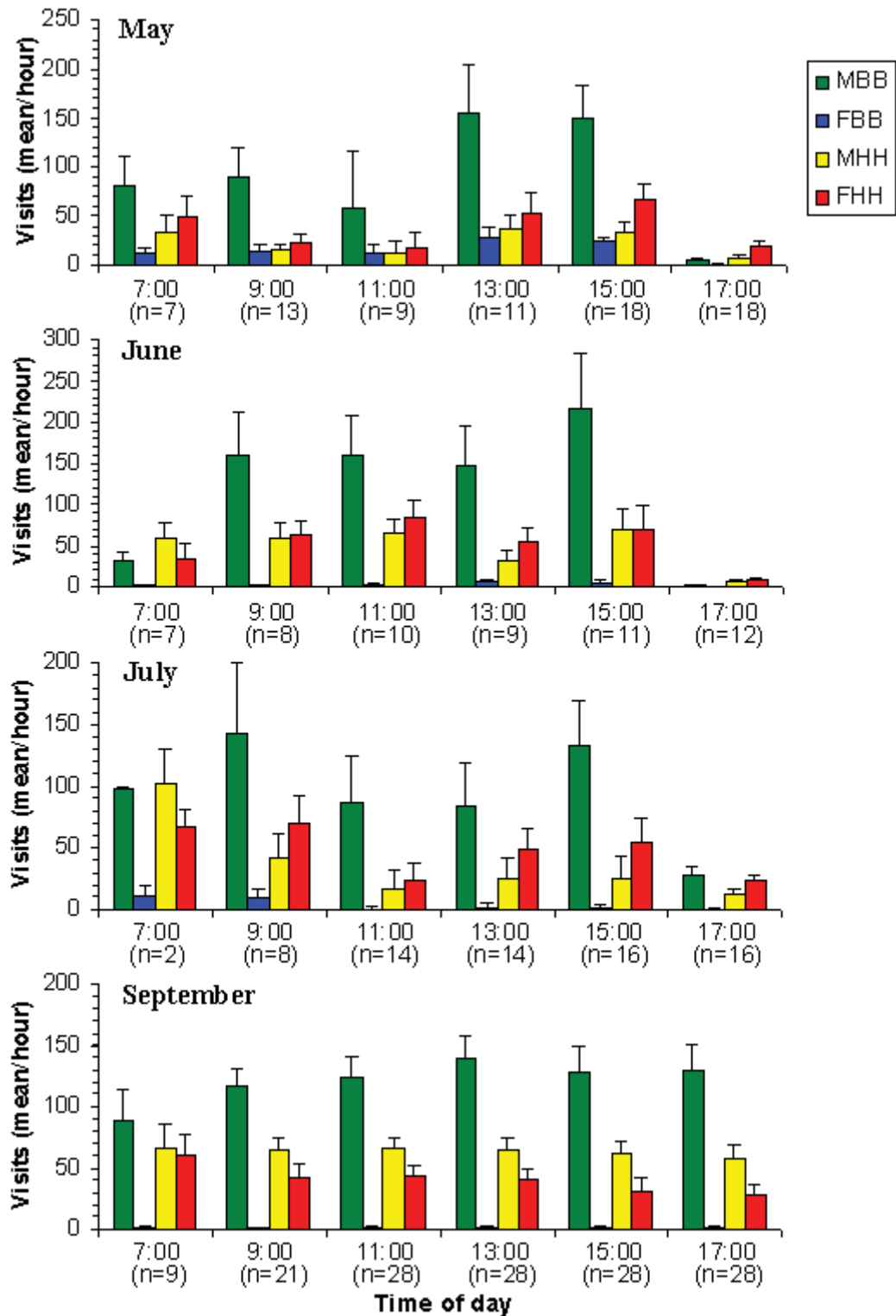


Figure 4.2. Mean number of visits per hour per feeder by male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) from combined results of all feeders during each month of observations. Error bars represent the standard error values.

of both species (Appendix 4.1). Visits throughout the day were becoming less variable in July. Only male bellbirds showed some slightly significant morning and afternoon peaks in visitation rate (Figure 4.2; Appendix 4.1; close to the significance threshold between 0700 and 1700 hours only) whereas the visits by the other birds were more consistent although they appear higher in the morning than in the afternoon (Figure 4.2). There was less variation in average visitation rates throughout the day in September with no significant trends found (Figure 4.2; Appendix 4.1).

4.4 Individual feeders

4.4.1 Bush 1 Lower

Long-term trends

Overall at the 'Bush 1 Lower' feeder there was an average visitation rate per hour (\pm SE) of 184 (\pm 18.6) male bellbirds, 90 (\pm 8.5) male hihi, 90 (\pm 7.1) female hihi and 25 (\pm 3.2) female bellbirds. Each month male bellbirds were the most frequent visitors (Figure 4.3) although their visits were not significantly higher than male hihi in July and both hihi sexes in September (Welch's t-test; Table 4.3). Female hihi visits were significantly higher than male hihi in May but over the months male hihi visits increased more than female hihi but there was no significant difference between them in July and September (Table 4.3). Female bellbirds were the least frequent visitors with their average visitation rate significantly lower than all other categories except in May when they were not significantly lower than male hihi (Table 4.3). Significant positive correlations were found between all species and sexes over all months except female bellbirds did not significantly correlate with the other categories in September, likely due to their low visitation rate (Spearman rank test; Table 4.3). Therefore, overall bellbirds showed a decline in visitation rates over the months which was significant for females ($F_{2,58} = 8.66$, $P = 0.001$) but not for males ($F_{2,58} = 1.06$, $P = 0.335$). In contrast, male hihi had a significant increase in visitation rates over the months ($F_{2,58} = 5.52$, $P = 0.006$) but female hihi visits were more consistent throughout the period of study ($F_{2,58} = 0.02$, $P = 0.983$).

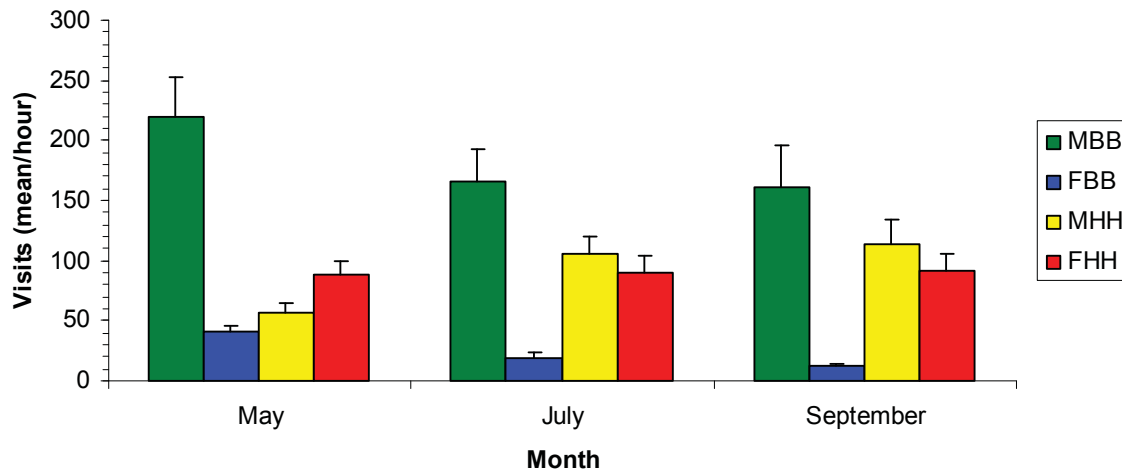


Figure 4.3. Mean visitation rate per hour each month for male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) at the ‘Bush 1 Lower’ feeder. Error bars represent standard error values.

Table 4.3. Test results of a Welch’s t-test and Spearman rank correlation comparing the number of visits by each species and sex for May, July and September, 2010 at the ‘Bush 1 Lower’ feeder. Key: MBB = male bellbird; FBB = female bellbird; MHH = male hihi; FHH = female hihi; vs = versus.

		MBB vs FBB	MBB vs MHH	MBB vs FHH	MHH vs FHH	FBB vs MHH	FBB vs FHH
May	<i>t</i>	5.16	4.66	3.65	-2.45	1.59	3.91
	df	23	24	26	40	41	35
	<i>P</i>	0.000	0.000	0.001	0.019	0.120	0.000
	<i>r_s</i>	0.91	0.80	0.72	0.89	0.75	0.68
	<i>n</i>	23	23	23	23	23	23
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000
	<i>t</i>	5.27	1.94	2.47	0.83	5.97	4.94
	df	21	29	29	39	24	24
July	<i>P</i>	0.000	0.063	0.020	0.411	0.000	0.000
	<i>r_s</i>	0.82	0.71	0.83	0.75	0.81	0.83
	<i>n</i>	21	21	21	21	21	21
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000
	<i>t</i>	4.34	1.18	1.88	0.93	5.08	5.96
	df	16	25	20	27	16	16
	<i>P</i>	0.001	0.248	0.074	0.360	0.000	0.000
	<i>r_s</i>	0.22	0.94	0.84	0.75	0.13	0.32
September	<i>n</i>	17	17	17	17	17	17
	<i>P</i>	0.407	0.000	0.000	0.000	0.611	0.214

Short-term trends

The daily pattern in visitation rates differed with month (Figure 4.4; see Appendix 4.2 for values). Male bellbird visits tended to increase from 0700 to 1700 hours in May ($F_{5,17} = 10.41$, $P = 0.000$) and July ($F_{5,15} = 4.59$, $P = 0.010$) but not in September ($F_{4,12} = 0.91$, $P = 0.490$) despite the sharp decrease in visits late in the day. However, the increase and decrease in visitation rates between 0900 and 1500 hours were not significant for both May ($F_{3,11} = 0.77$, $P = 0.533$) and July ($F_{3,11} = 0.15$, $P = 0.929$) showing the major changes in visitation rates occur early in the morning and late in the day. Female bellbirds had a similar increase and decrease in visits between 0700 and 1700 hours in May ($F_{5,17} = 18.23$, $P = 0.000$), although not between 0900 and 1500 hours ($F_{3,11} = 2.93$, $P = 0.081$), and their visits were consistently low throughout the day during July ($F_{5,15} = 1.96$, $P = 0.144$) and September ($F_{4,12} = 0.71$, $P = 0.598$). Male hihi had various peaks throughout the day, particularly early in the morning and in the afternoon in May, with significant declines in visitation at the end of the day for May ($F_{5,17} = 3.29$, $P = 0.029$) and July ($F_{5,15} = 18.23$, $P = 0.000$) with less difference in visits between 0900 and 1500 hours (May: $F_{3,11} = 1.48$, $P = 0.273$; July: $F_{3,11} = 0.36$, $P = 0.786$), and no significant difference between visitation rates throughout the day in September ($F_{4,12} = 2.51$, $P = 0.097$). Female hihi had less variation in visitation rates throughout the day, particularly for May ($F_{5,17} = 2.56$, $P = 0.067$) and September ($F_{4,12} = 0.39$, $P = 0.815$), but there was slightly more variation in visits in July ($F_{5,15} = 5.16$, $P = 0.006$) although not between 0900 and 1500 hours ($F_{3,11} = 0.22$, $P = 0.883$). Therefore, overall there was more variation in visitation rates throughout the day in late autumn (May) but by early spring (September) both species and sexes were using the feeding at more consistent rates throughout the day except for a drop in visitation rates at the end of day.

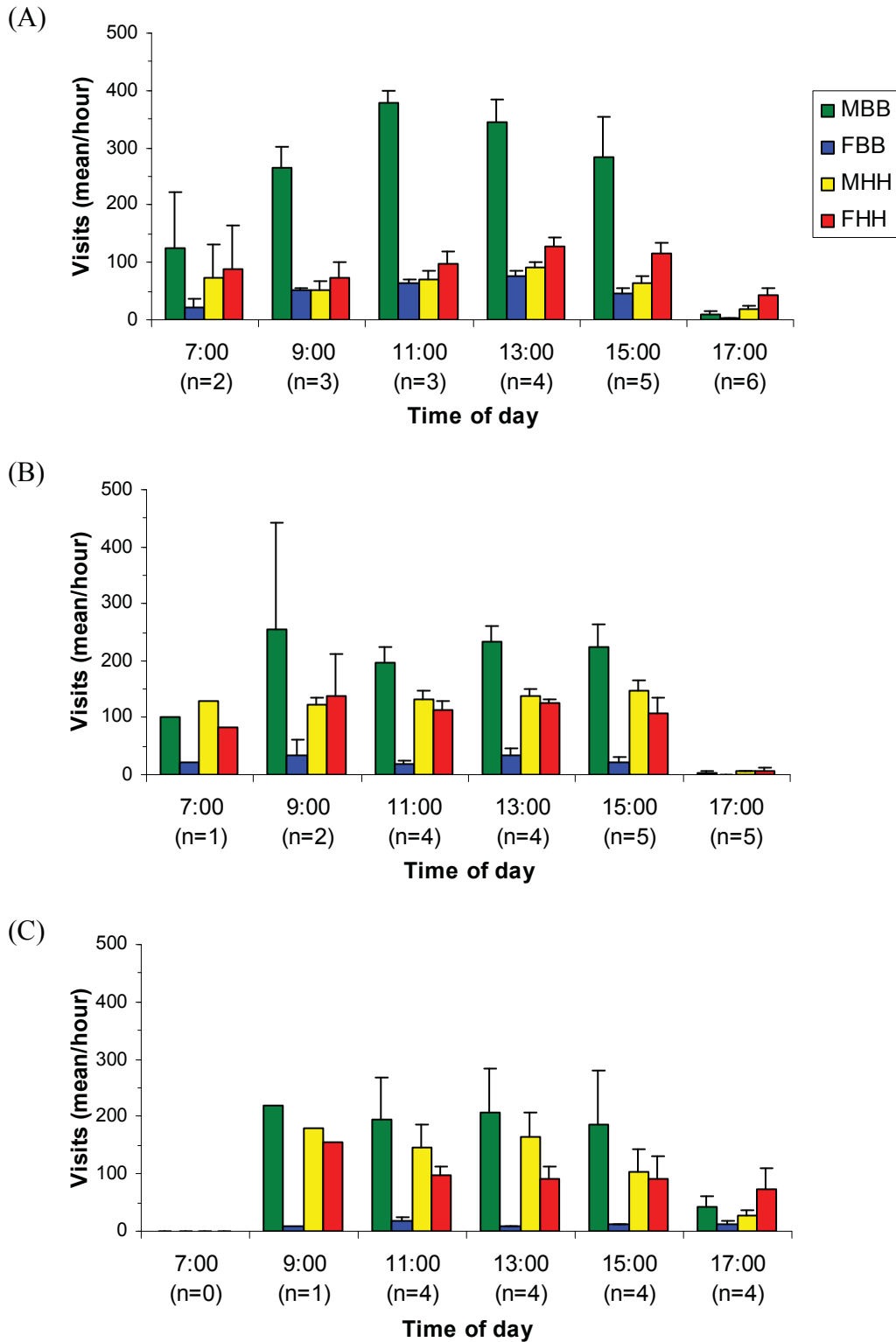


Figure 4.4 Mean number of visits per hour by male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) during the months of May (A), July (B) and September (C) at the 'Bush 1 Lower' feeder. Error bars represent the standard error values. n = sample size (number of hours).

4.4.2 Bush 1 Upper

Long-term trends

Overall at the 'Bush 1 Upper' feeder there was an average visitation rate per hour (\pm SE) of 98 (\pm 13.9) male bellbirds, 60 (\pm 7.3) female hihi, 43 (\pm 6.2) male hihi and 9 (\pm 1.2) female bellbirds. Each month male bellbirds were the most frequent visitors (Figure 4.5) although their visits were not significantly higher than female and male hihi in June and September (May and June: Mann-Whitney U-test; September: Welch's t-test; Table 4.4). Female hihi visited on average more frequently than male hihi but this was only significant in May (Table 4.4). Female bellbirds were the least frequent visitors with significantly less visits per hour than all other categories for all months except in June where male hihi visits were not significantly higher (Table 4.4). Significant positive correlations were found between all species and sexes in May and June except in June male and female hihi did not significantly correlate with female bellbirds (Spearman rank test; Table 4.4). However, in September there were no significant correlations between any of the species and sexes (Table 4.4). On average, bellbird visits increased from May to June then decreased in September (Figure 4.5) but this was only significant for males ($F_{2,61} = 4.37$, $P = 0.017$) not females ($F_{2,61} = 0.48$, $P = 0.62$) as their visitation to the feeder was relatively low. In contrast, average hihi visits increased from May to September and this increase was significant for both males ($F_{2,61} = 15.57$, $df = 2$, $P = 0.000$) and females ($F_{2,61} = 9.71$, $df = 9.71$, $P = 0.000$).

Short-term trends

The daily pattern in visitation rates differed with month (Figure 4.6; see Appendix 4.3 for values). In both May and June, there were significant peaks in visitation rates in the afternoon (1500 hours) for male bellbirds (May: $F_{5,28} = 6.37$, $P = 0.000$; June: $F_{5,28} = 6.37$, $P = 0.000$), female bellbirds (May: $F_{5,28} = 8.55$, $P = 0.000$; June: $F_{5,28} = 8.55$, $P = 0.000$), male hihi (May: $F_{5,28} = 2.73$, $P = 0.039$; June $F_{5,28} = 2.73$, $P = 0.039$) and female hihi (May: $F_{5,28} = 3.65$, $P = 0.011$; June: $F_{5,28} = 3.65$, $P = 0.011$). Without the early morning and late evening values, the variation between 0900 and 1500 hours was still significant for male bellbirds (May: $F_{3,19} = 4.08$, $P = 0.022$; June: $F_{5,28} = 4.08$, $P = 0.022$),

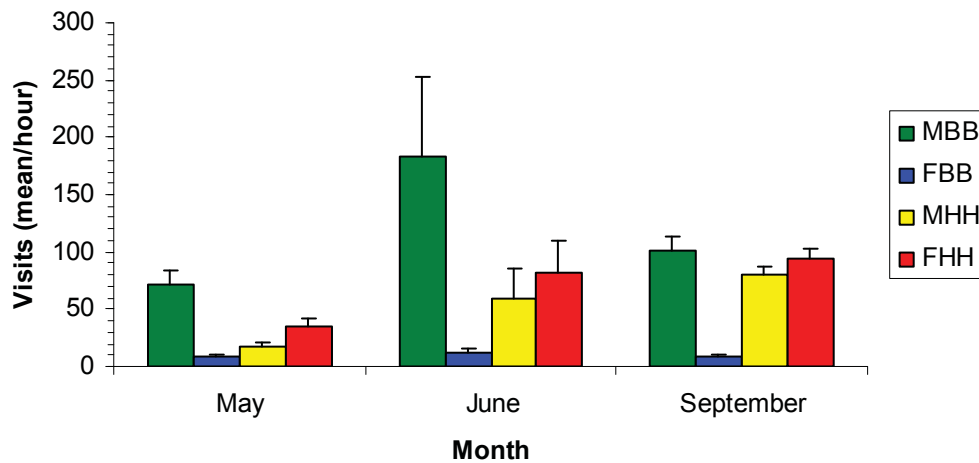


Figure 4.5. Mean visitation rate per hour each month for male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) at the ‘Bush 1 Upper’ feeder. Error bars represent standard error values.

Table 4.4. Test results of a Mann-Whitney U-test (non-normal distribution), Welch’s t-test (normal distribution) and Spearman rank correlation comparing the number of visits by each species and sex for May, July and September, 2010 at the ‘Bush 1 Upper’ feeder. Key: MBB = male bellbird; FBB = female bellbird; MHH = male hihi; FHH = female hihi; vs = versus.

		MBB vs FBB	MBB vs MHH	MBB vs FHH	MHH vs FHH	FBB vs MHH	FBB vs FHH
May	<i>U</i>	1527	1435.5	1347.5	1041.5	977.5	910.5
	<i>n</i>	34	34	34	34	34	34
	<i>P</i>	0.000	0.001	0.033	0.107	0.016	0.001
	<i>r_s</i>	0.80	0.67	0.73	0.87	0.66	0.73
	<i>n</i>	34	34	34	34	34	34
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000
June	<i>U</i>	135	120	113.5	92.5	82.5	67
	<i>n</i>	10	10	10	10	10	10
	<i>P</i>	0.0255	0.2729	0.545	0.364	0.0958	0.0046
	<i>r_s</i>	0.84	0.77	0.82	0.98	0.43	0.55
	<i>n</i>	10	10	10	10	10	10
	<i>P</i>	0.005>P >0.001	0.01>P> 0.005	0.005>P >0.001	P<0.001	P>0.10	0.1>P>0. 05
September	<i>t</i>	6.86	1.34	0.40	-1.28	9.20	10.35
	<i>df</i>	19	30	31	37	19	19
	<i>P</i>	0.000	0.189	0.692	0.207	0.000	0.000
	<i>r_s</i>	-0.11	0.22	0.14	0.14	0.14	-0.20
	<i>n</i>	20	20	20	20	20	20
	<i>P</i>	0.646	0.345	0.556	0.558	0.558	0.389

female bellbirds (May: $F_{3,19} = 8.73$, $P = 0.001$; June: $F_{5,28} = 8.73$, $P = 0.001$) and female hihi (May: $F_{3,19} = 4.96$, $P = 0.010$; June: $F_{3,19} = 4.96$, $P = 0.010$) but male hihi were not quite below the significant level threshold for both months (May: $F_{3,19} = 3.03$, $P = 0.055$; June: $F_{5,28} = 3.03$, $P = 0.055$). However, the difference between these two months was that in May the visits decreased from 0700 to 1100 hours before increasing to the peak at 1500 hours whereas in June there was a gradual increase from 0700 hours until the peak at 1500 hours. The decrease in visitation rates between 0700 and 1500 hours in May seems to be at least partially due to the presence of tui outside the feeder as when a tui would land on the feeder, all hihi and bellbirds would exit out of the feeder. There was no significant correlations between the number of tui visits and the number of male bellbird ($r_s = 0.15$, $n = 34$, $P = 0.383$), female bellbird ($r_s = 0.24$, $n = 34$, $P = 0.169$), male hihi ($r_s = -0.10$, $n = 34$, $P = 0.595$), and female hihi ($r_s = -0.06$, $n = 34$, $P = 0.718$) visits, however this does not take into account the duration of the tui surrounding the feeder. There was less variation in the visitation rates throughout the day in September for male bellbirds ($F_{5,14} = 0.44$, $P = 0.815$), female bellbirds ($F_{5,14} = 0.27$, $P = 0.920$), male hihi ($F_{5,14} = 0.68$, $P = 0.649$) and female hihi ($F_{5,14} = 0.50$, $P = 0.770$). Therefore, overall there was more variation in visitation rates throughout the day in late autumn (May) with significant afternoon peaks but by early spring (September) both species and sexes were using the feeders at consistent rates throughout day.

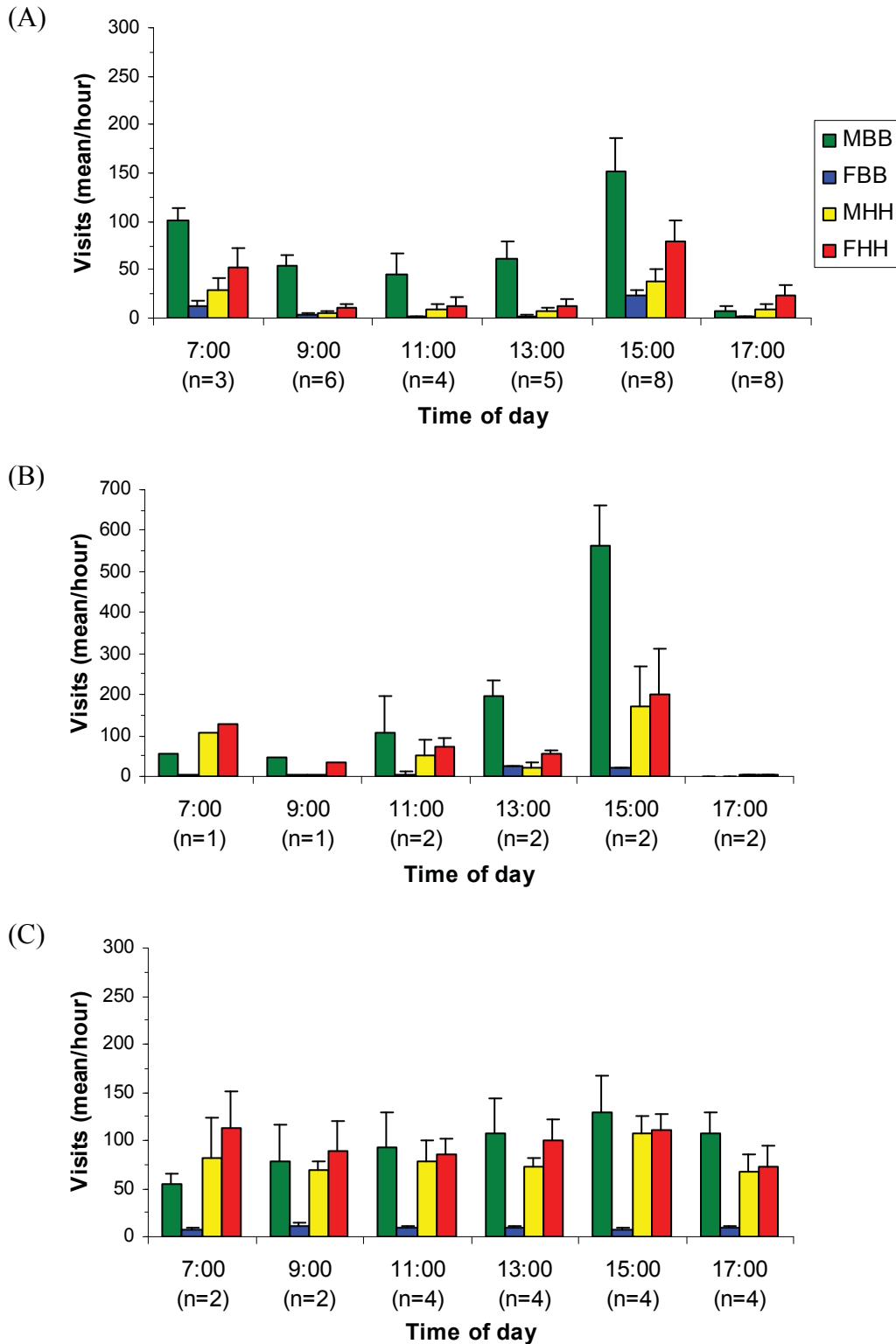


Figure 4.6. Mean number of visits per hour by male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) during the months of May (A), June (B) and September (C) at the 'Bush 1 Upper' feeder. Error bars represent the standard error values. n = sample size (number of hours).

4.4.3 Bush 2

Long-term trends

Overall at the ‘Bush 2’ feeder there was an average visitation rate per hour (\pm SE) of 89 (\pm 9.7) male bellbirds, 65 (\pm 8.5) female hihi, 45 (\pm 5.5) male hihi and 0.68 (\pm 0.2) female bellbirds. Male bellbirds were the most frequent visitors in June and September (Figure 4.7) although their visits were not significantly higher than hihi in June (Welch’s t-test; Table 4.5). In July female hihi visited most frequently which was significantly different from male bellbird and male hihi visits (Mann-Whitney U-test; Table 4.5). Female hihi visits were not significantly higher than male hihi visits in June but in September male hihi visits increased and they were significantly higher than female hihi (Welch’s t-test; Table 4.5). Female bellbird visits were very infrequent with their visits significantly lower than male bellbirds and hihi (Mann-Whitney U-test and Welch’s t-test; Table 4.5) and in September there were no female bellbird visits observed (Figure 4.7). Significant positive correlations were found between all species and sexes in all months except in June female bellbirds did not significantly correlate with male bellbirds and male hihi and there were no female bellbirds in September to test for correlation (Spearman rank correlation; Table 4.5). Overall, average male bellbird visitation rates to the ‘Bush 2’ feeder were similar in June and September with only slightly lower visits in July ($F_{2,50} = 2.94$, $P = 0.062$) hence they were visiting this feeder consistently during winter and spring whereas female bellbird visits were highest in winter (June and July) with no visits observed in spring (September; $F_{2,50} = 19.69$, $P = 0.000$). Male hihi had a similar monthly pattern to male bellbirds but they had a steeper decline in mid-winter (July) and were using the feeder considerably more in spring (September; $F_{2,50} = 7.68$, $P = 0.001$). Female hihi visits slightly declined from winter (June and July) to spring (September) but this was not significant ($F_{2,50} = 2.02$, $P = 0.143$) therefore they were using this feeder consistently through both seasons as did male bellbirds.

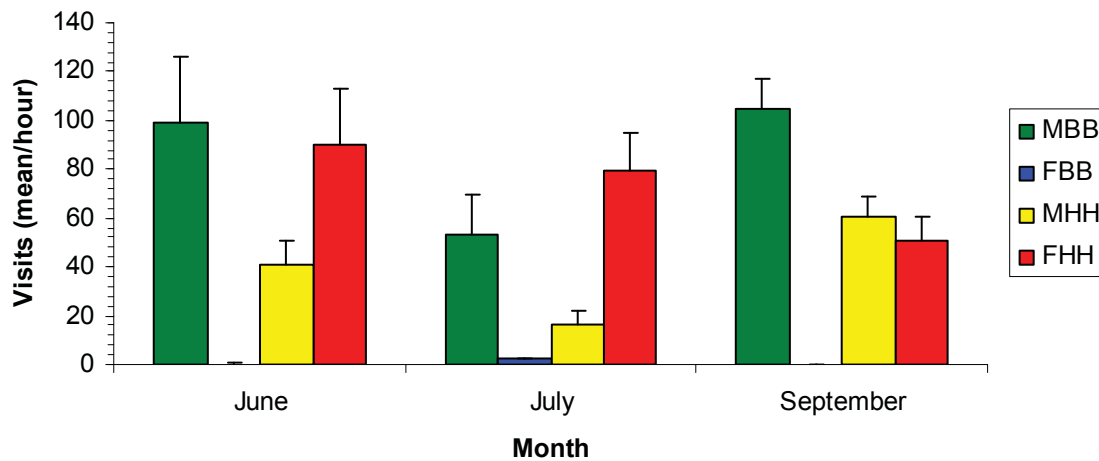


Figure 4.7. Mean visitation rate per hour each month for male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) at the 'Bush 2' feeder. Error bars represent standard error values.

Table 4.5. Test results of a Welch's t-test (normal distribution), Mann-Whitney U-test (non-normal distribution) and Spearman rank correlation comparing the number of visits by each species and sex for May, July and September, 2010 at the 'Bush 2' feeder. Key: MBB = male bellbird; FBB = female bellbird; MHH = male hihi; FHH = female hihi; vs = versus; n/a = not available.

		MBB vs FBB	MBB vs MHH	MBB vs FHH	MHH vs FHH	FBB vs MHH	FBB vs FHH
June	<i>t</i>	3.62	2	0.25	-1.94	3.93	3.84
	df	8	10	15	10	8	8
	<i>P</i>	0.007	0.073	0.810	0.082	0.004	0.005
	<i>r_s</i>	0.64	0.87	0.81	0.76	0.64	0.82
	<i>n</i>	7	7	7	7	7	7
	<i>P</i>	0.05> <i>P</i> > 0.025	0.005> <i>P</i> > >0.001	0.01> <i>P</i> > 0.005	0.025> <i>P</i> > >0.01	0.05> <i>P</i> > 0.025	0.01> <i>P</i> > 0.005
July	<i>U</i>	345	319	177.5	134.5	123	120
	<i>n</i>	15	15	15	15	15	15
	<i>P</i>	0.000	0.0004	0.0237	0.0001	0.000	0.000
	<i>r_s</i>	0.48	0.94	0.81	0.76	0.34	0.51
	<i>n</i>	13	13	13	13	13	13
	<i>P</i>	0.069	0.000	0.000	0.001	0.214	0.050
September	<i>t</i>	n/a	3.03	3.36	0.78	n/a	n/a
	df	n/a	47	54	51	n/a	n/a
	<i>P</i>	n/a	0.004	0.001	0.436	n/a	n/a
	<i>r_s</i>	n/a	0.90	0.85	0.93	n/a	n/a
	<i>n</i>	n/a	27	27	27	n/a	n/a
	<i>P</i>	n/a	0.000	0.000	0.000	n/a	n/a

Short-term trends

Daily visitation patterns differed slightly between the species and sexes over the months (Figure 4.8; see Appendix 4.4 for values). Male bellbirds visited the feeder frequently at similar rates during the day in June except for very low visits early and late in the day ($F_{5,3} = 4.13$, $P = 0.136$). A similar pattern was found in July but visits were much less frequent except for a large peak in the afternoon ($F_{4,10} = 1.39$, $P = 0.304$). In September there was a gradual increase in visitation rates throughout the day peaking at 1300 hours and then a gradual decline towards the end of the day ($F_{5,23} = 6.77$, $P = 0.001$) with the change in visitation rates also significant between 0900 and 1500 hours ($F_{3,16} = 3.44$, $P = 0.042$). There were only a few female bellbird visits observed in June at 1100 and 1300 hours but in July there were slightly more visits throughout the whole day ($F_{4,10} = 0.48$, $P = 0.750$) but no observations were made in September. Male hihi had a gradual increase in visits during the day before starting to decline in the afternoon in both June ($F_{5,3} = 265.53$, $P = 0.000$) and September ($F_{5,23} = 10.33$, $P = 0.000$) including when removing the early morning and later afternoon visits, from 0900 to 1500 hours (June: $F_{3,2} = 23.13$, $P = 0.042$; September: $F_{3,16} = 4.96$, $P = 0.013$). As with male bellbirds, male hihi visits were consistently low throughout the day in July except for a peak in the afternoon ($F_{4,10} = 1.43$, $P = 0.293$). Female hihi showed similar trends in June with a gradual increase then decrease in visits throughout the day ($F_{5,3} = 18.11$, $P = 0.019$), but unlike male hihi their visits were more frequent, the change in visitation rate was not significant between 0900 and 1500 hours ($F_{3,2} = 2.75$, $P = 0.278$), and the daily pattern in visits in September was not significant ($F_{5,23} = 2.10$, $P = 0.102$). However, female hihi did have the same trend in visits in July although with a much larger afternoon peak ($F_{4,10} = 1.77$, $P = 0.211$). Therefore, overall there were more visits to the feeder and more variation throughout the day in early winter (June) and spring (September) with consistently low visits in mid-winter (July) except for relatively large afternoon peaks although female bellbirds showed the opposite trend with more visits in mid-winter.

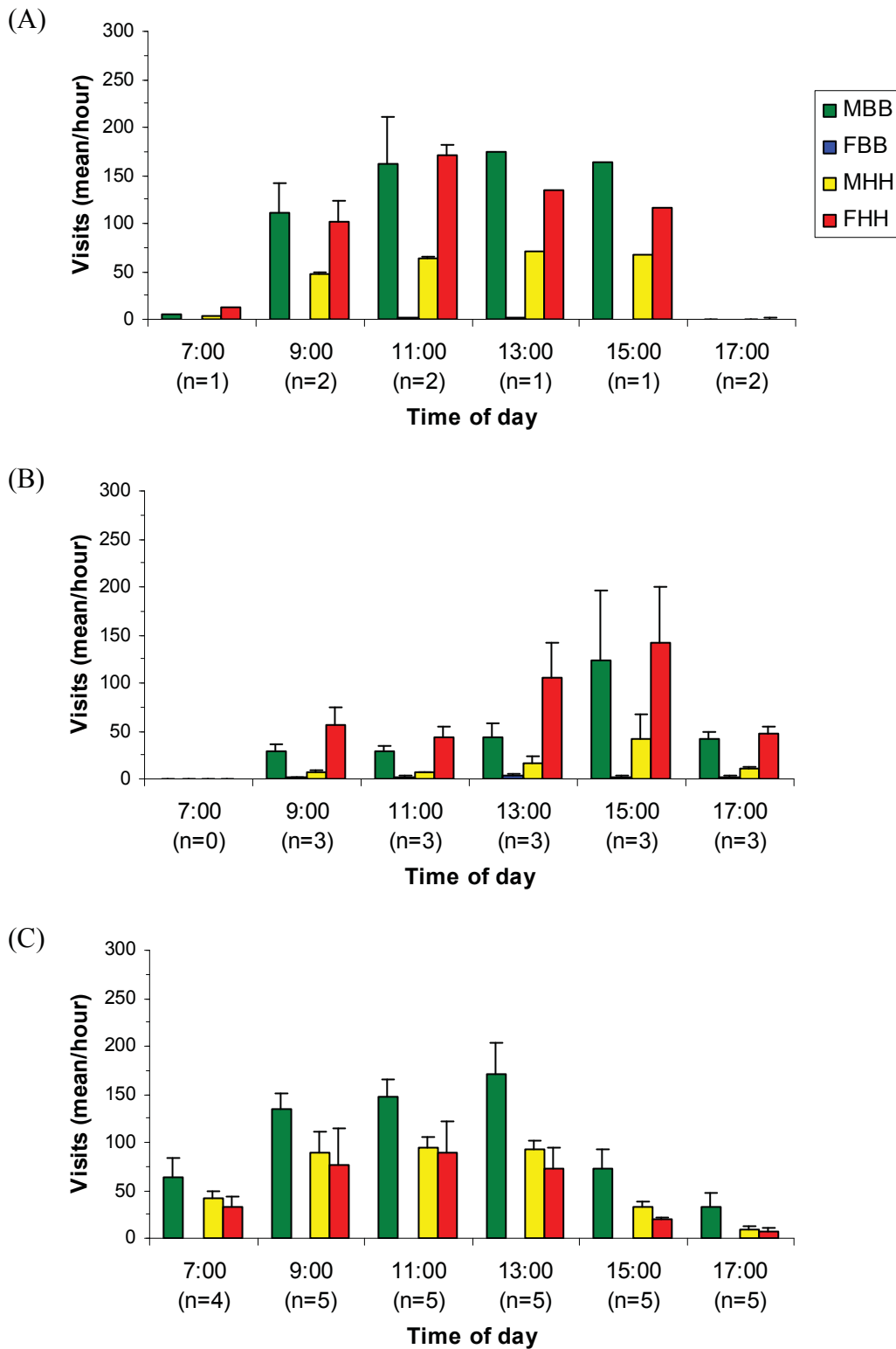


Figure 4.8. Mean number of visits per hour by male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) during the months of June (A), July (B) and September (C) at the 'Bush 2' feeder. Error bars represent the standard error values. n = sample size (number of hours).

4.4.4 Bush 22

Long-term trends

Overall at the ‘Bush 22’ feeder there was an average visitation rate per hour (\pm SE) of 129 (\pm 16.4) male bellbirds, 57 (\pm 6.5) male hihi, 15 (\pm 2.4) female hihi and 1.9 (\pm 0.5) female bellbirds. Male bellbirds were the most frequent visitors over all months observed (Figure 4.9) but they were only significantly more frequent than male and female hihi in June and September (Welch’s t-test and Mann-Whitney U-test; Table 4.6). Male hihi were the second most frequent visitors and they were also significantly more frequent than female hihi in June and September (Table 4.6). Female bellbird visits were significantly lower than male bellbirds and hihi over all months (Table 4.6). Significant positive correlations were found between all species and sexes in all months except in September female bellbirds did not significantly correlate with male bellbirds and hihi as there were very few female bellbird visits in September (Spearman rank correlation; Table 4.6; see Appendix 4.5 for values). Overall, average visitation rates declined from autumn (April) to winter (June) and then increased in spring (September) for male bellbirds ($F_{2,58} = 19.73$, $P = 0.000$) and male hihi ($F_{2,58} = 24.32$, $P = 0.000$). In contrast, female bellbird ($F_{2,58} = 14.26$, $P = 0.000$) and female hihi ($F_{2,58} = 14.07$, $P = 0.000$) visits gradually declined from autumn to spring.

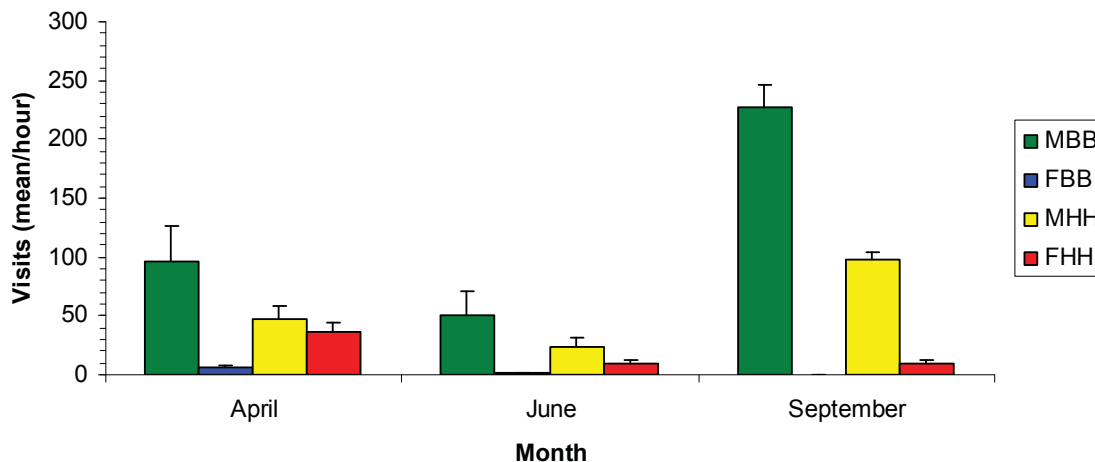


Figure 4.9. Mean visitation rate per hour each month for male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) at the ‘Bush 22’ feeder. Error bars represent standard error values.

Table 4.6. Test results of a Welch's t-test (normal distribution), Mann-Whitney U-test (non-normal distribution) and Spearman rank correlation comparing the number of visits by each species and sex for May, July and September, 2010 at the 'Bush 22' feeder. Key: MBB = male bellbird; FBB = female bellbird; MHH = male hihi; FHH = female hihi; vs = versus.

		MBB vs FBB	MBB vs MHH	MBB vs FHH	MHH vs FHH	FBB vs MHH	FBB vs FHH
April	<i>t</i>	3	1.55	1.92	0.76	3.67	3.74
	df	11	13	12	20	11	12
	<i>P</i>	0.012	0.146	0.078	0.456	0.004	0.003
	<i>r_s</i>	0.85	0.78	0.84	0.96	0.76	0.74
	<i>n</i>	12	12	12	12	12	12
	<i>P</i>	0.000	0.003	0.001	0.000	0.004	0.006
June	<i>U</i>	786.88	820.65	707.64	749.37	796.84	687.62
	<i>n</i>	25	25	25	25	25	25
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000
	<i>r_s</i>	0.47	0.50	0.47	0.82	0.64	0.57
	<i>n</i>	25	25	25	25	25	25
	<i>P</i>	0.018	0.010	0.019	0.000	0.001	0.003
September	<i>U</i>	876	825.5	876	876	300	300.5
	<i>n</i>	24	24	24	24	24	24
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000
	<i>r_s</i>	0.17	0.74	0.41	0.55	0.14	0.29
	<i>n</i>	24	24	24	24	24	24
	<i>P</i>	0.439	0.000	0.048	0.005	0.528	0.174

Short-term trends

The daily pattern in visitation rates differed with month (Figure 4.10; see Appendix 4.5 for values). In April visits by both species and sexes increased from 0700 to 0900 hours then had quite a drop at 1100 hours before increasing again at 1300 hours then declining towards the end of the day which was significant for male bellbirds ($F_{5,6} = 19.96$, $P = 0.001$) but not for female bellbirds ($F_{5,6} = 2.39$, $P = 0.246$), male hihi ($F_{5,6} = 1.66$, $P = 0.277$) and female hihi ($F_{5,6} = 2.25$, $P = 0.175$) although hihi visits increased again during 1700 hours and between 0900 and 1500 hours the variation in male hihi visits were more significant ($F_{3,3} = 9.25$, $P = 0.05$). A possible explanation for this daily pattern was the presence of other researchers who were catching hihi directly from the feeders. The researchers were present at 1100 hours and from 1500 hours until near the end of the day which correlates with the decrease in visitation rates. Their presence may have deterred some birds from entering the feeder but the most likely cause for decreased visitation rates is from when the researchers closed access to the feeders when removing

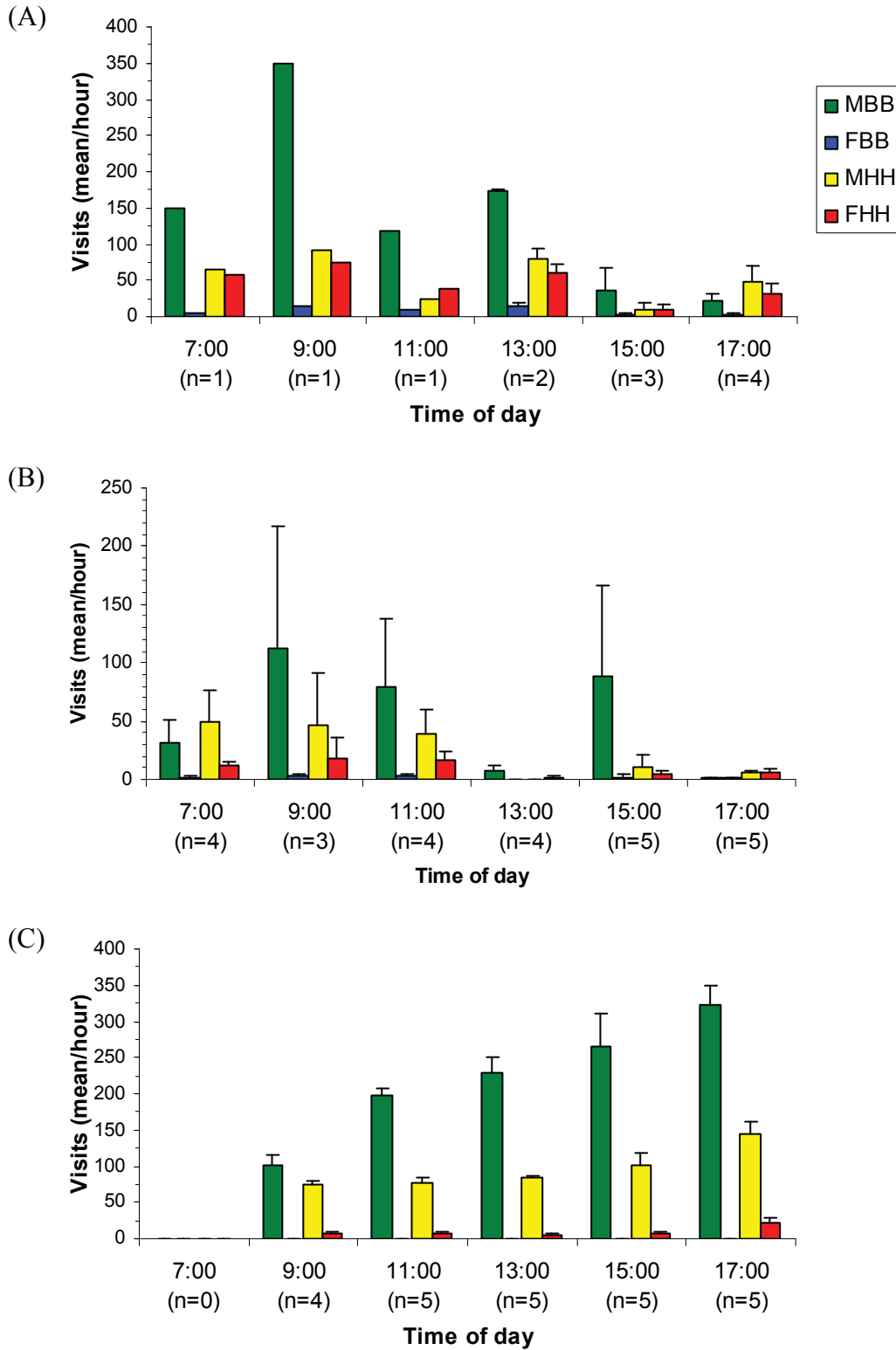


Figure 4.10. Mean number of visits per hour by male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) during the months of April (A), June (B) and September (C) at the ‘Bush 22’ feeder. Error bars represent the standard error values. n = sample size (number of hours).

trapped hihi. In June, visits were quite low by both species and sexes although visits increased by mid-morning and then decreased until a small peak in mid-afternoon (Figure 4.10). However, with such a low number of visits this change was not significant for both bellbirds (male: $F_{5,19} = 0.70$, $P = 0.628$; female: $F_{5,19} = 3.20$, $P = 0.876$) and hihi (male: $F_{5,19} = 1.30$, $P = 0.304$; female: $F_{5,19} = 1.02$, $P = 0.435$). In contrast, September had a greater number of male bellbird visits which significantly increased from morning to late in the afternoon ($F_{4,19} = 7.86$, $P = 0.001$). Female bellbirds were only observed visiting the feeder at 1700 hours (see Appendix 4.5 for values) but at such low values that this increase was not significant ($F_{4,19} = 0.94$, $P = 0.462$). Hihi visits were more consistent throughout the day between 0900 and 1500 hours (male: $F_{3,15} = 1.55$, $P = 0.244$; female: $F_{3,15} = 0.34$, $P = 0.794$) until a significant increase near the end of the day from 0700 to 1700 hours (male: $F_{4,19} = 6.46$, $P = 0.002$; female: $F_{4,19} = 3.83$, $P = 0.019$). Therefore, the males of both species most frequently visited the ‘Bush 22’ feeder in autumn (April) and spring (September) whereas visits by the females of both species gradually decreased from autumn to spring.

4.4.5 Dupont

Long-term trends

Overall at the ‘Dupont’ feeder there was an average visitation rate per hour (\pm SE) of 24 (\pm 7.1) male bellbirds, 2.4 (\pm 0.98) female hihi, 1.8 (\pm 0.53) male hihi and 0.12 (\pm 0.045) female bellbirds. Male bellbirds were the most frequent visitors over all months (Figure 4.11) with significantly higher visitation rates than hihi and female bellbirds (Mann-Whitney U-test; Table 4.7). Average male and female hihi visits were similar each month and there was no significant difference between the sexes (Table 4.7). No female bellbirds were observed in May but some were observed in July and September but their visitation rates were only significantly lower in September not July (Table 4.7). Significant positive correlations were only found between male bellbirds and hihi and between hihi sexes in July with no significant correlation found between female bellbirds and the other categories for all months where data was available (Spearman rank correlation; Table 4.7). Overall, male bellbirds had a insignificant increase ($F_{2,65} = 1.29$,

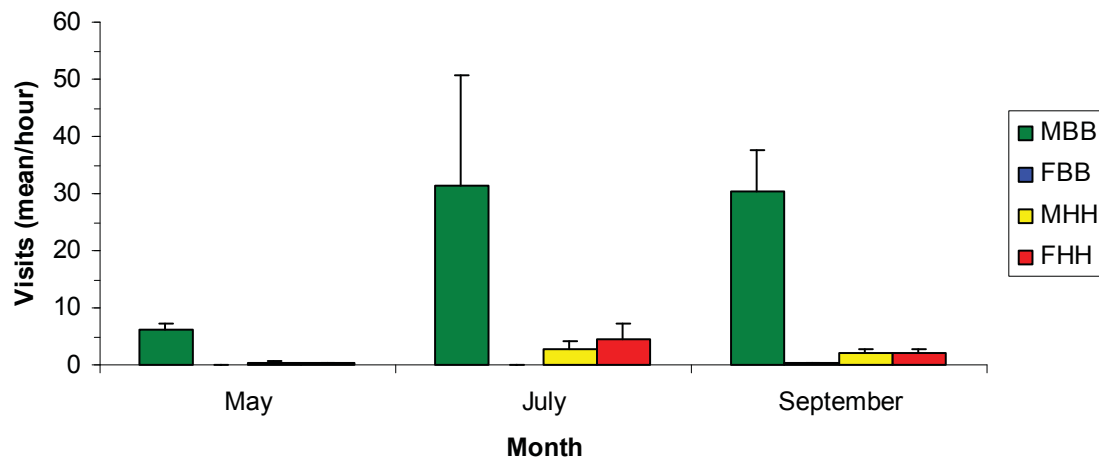


Figure 4.11. Mean visitation rate per hour each month for male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) at the ‘Bush 22’ feeder. Error bars represent standard error values.

Table 4.7. Test results of a Mann-Whitney U-test and Spearman rank correlation comparing the number of visits by each species and sex for May, July and September, 2010 at the ‘Dupont’ feeder. Key: MBB = male bellbird; FBB = female bellbird; MHH = male hihi; FHH = female hihi; vs = versus; n/a = not available.

		MBB vs FBB	MBB vs MHH	MBB vs FHH	MHH vs FHH	FBB vs MHH	FBB vs FHH
May	<i>U</i>	n/a	561	554	391.5	n/a	n/a
	<i>n</i>	20	20	20	20	20	20
	<i>P</i>	n/a	0.000	0.000	0.350	n/a	n/a
	<i>r_s</i>	n/a	-0.16	-0.21	-0.10	n/a	n/a
	<i>n</i>	18	18	18	18	18	18
	<i>P</i>	n/a	0.499	0.369	0.687	n/a	n/a
July	<i>U</i>	766.5	719.5	711.5	558.5	477	502
	<i>n</i>	23	23	23	23	23	23
	<i>P</i>	0.000	0.000	0.000	0.619	0.046	0.182
	<i>r_s</i>	0.28	0.47	0.56	0.88	0.13	0.18
	<i>n</i>	21	21	21	21	21	21
	<i>P</i>	0.196	0.024	0.006	0.000	0.559	0.419
September	<i>U</i>	950	949.5	947.5	654.5	524.5	544.5
	<i>n</i>						
	<i>P</i>	0.000	0.000	0.000	0.727	0.010	0.030
	<i>r_s</i>	-0.07	0.15	0.09	0.24	-0.28	0.00
	<i>n</i>	23	23	23	23	23	23
	<i>P</i>	0.750	0.469	0.658	0.254	0.171	0.997

$P = 0.281$) in visitation rates from autumn (May) to winter (July) with similar visitation rates in spring (September) and female bellbird visits were consistently low ($F_{2,65} = 2.61$, $P = 0.081$). Hihi visits insignificantly increased in July and declined in September (male: $F_{2,65} = 2.31$, $P = 0.108$; female: $F_{2,65} = 1.56$, $P = 0.218$).

Short-term trends

The daily pattern in visitation rates differed slightly with month (Figure 4.12; see Appendix 4.6 for values). In May, average male bellbird visits increased from the morning until a peak at 1100 hours then visits declined throughout the afternoon ($F_{5,14} = 10.75$, $P = 0.000$), with less variation between 0900 and 1500 hours ($F_{3,9} = 3.15$, $P = 0.079$), whereas visits were more consistent during the day in July ($F_{4,18} = 0.92$, $P = 0.474$) and September ($F_{5,19} = 1.04$, $P = 0.421$) except for some relatively high morning (September) and afternoon (July and September) peaks. There were very few female bellbird visits throughout the day (see Appendix 4.6 for values) in the months they visited so no significant daily trends were found in July ($F_{4,18} = 0.53$, $P = 0.715$) and September ($F_{5,19} = 1.04$, $P = 0.423$). Hihi visits were infrequent in April (male: $F_{5,14} = 0.52$, $P = 0.754$; female: $F_{5,14} = 1.22$, $P = 0.351$) and July (male: $F_{4,18} = 0.76$, $P = 0.567$; female: $F_{4,18} = 0.65$, $P = 0.635$) with visits mostly only observed late in the day but in September their visits were more consistent throughout the whole day, particularly between 0900 and 1500 hours (male: $F_{3,15} = 0.30$, $P = 0.826$; female: $F_{3,15} = 0.47$, $P = 0.709$), until a more significant peak in visits at the end of the day (0700 to 1700 hours; male: $F_{5,19} = 2.76$, $P = 0.049$; female: $F_{5,19} = 5.79$, $P = 0.002$). Therefore, at the ‘Dupont’ feeder visits during the day by both species and sexes in general increased from autumn (April) to spring (September).

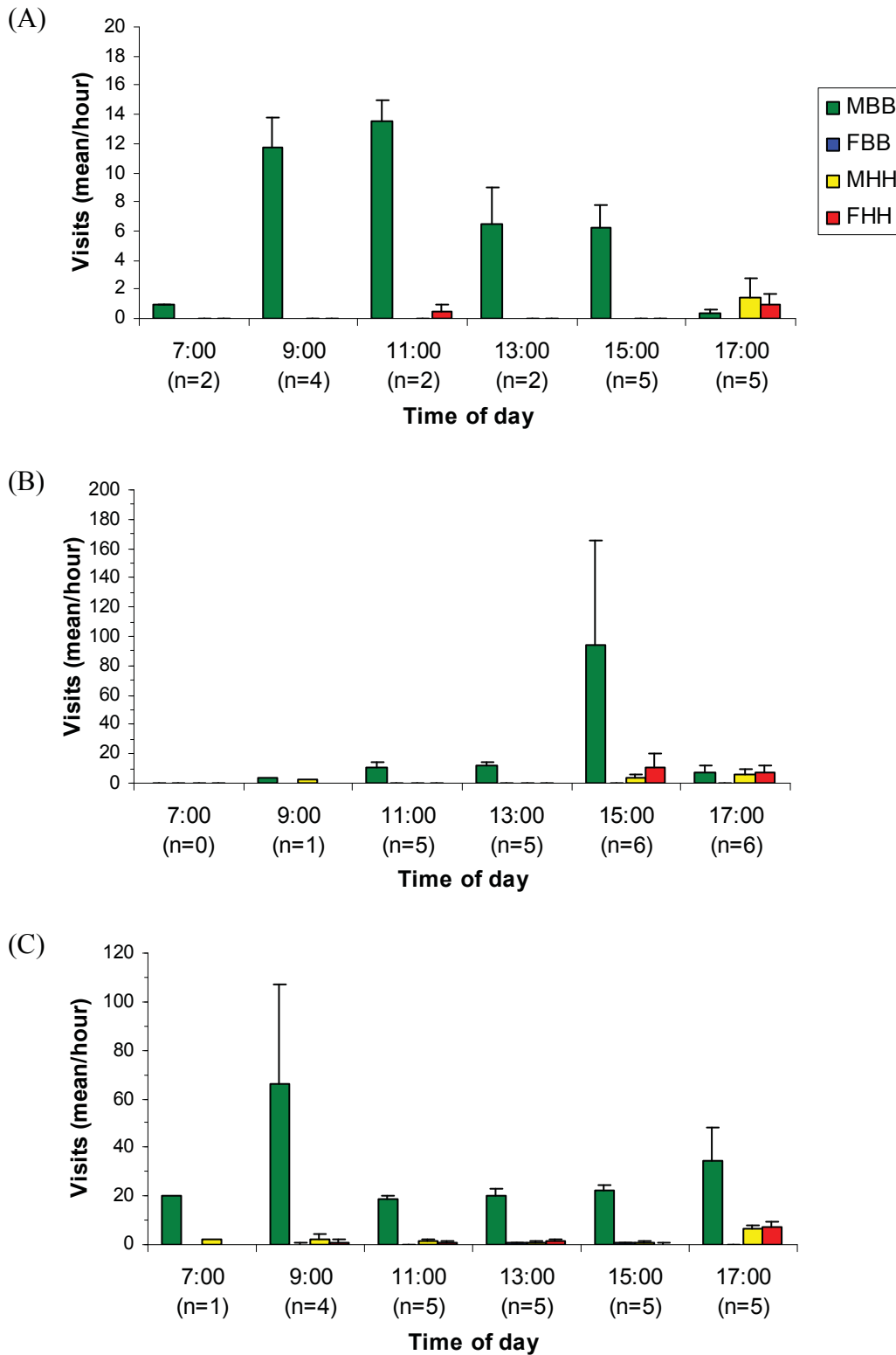


Figure 4.12. Mean number of visits per hour by male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) during the months of May (A), July (B) and September (C) at the ‘Dupont’ feeder. Error bars represent the standard error values. n = sample size (number of hours).

4.4.6 Wattle Valley

Long-term trends

Overall at the ‘Wattle Valley’ feeder there was an average visitation rate per hour (\pm SE) of 192 (\pm 15.7) male bellbirds, 77 (\pm 5.2) male hihi, 56 (\pm 5.1) female hihi and 0 (\pm 0) female bellbirds. Male bellbirds were the most frequent visitors over all months (Figure 4.13) with significantly higher visits than both male and female hihi (Welch’s t-test and Mann-Whitney U-test; Table 4.8). There was no significant difference between male and female hihi visits until September where male visits were significantly higher (Table 4.8). No female bellbirds were observed at this feeder over all months observed therefore no comparisons could be made. Significant positive correlations were only found between male bellbirds and hihi in July but the hihi sexes showed significant positive correlations over all months observed (Spearman rank correlation; Table 4.8). Overall, male bellbird ($F_{2,48} = 2.44$, $P = 0.098$) and male hihi ($F_{2,48} = 0.62$, $P = 0.542$) visitation rates were relatively consistent from winter (June and July) to spring (September) whereas female hihi had a significant decline in visitation rates from the start of winter to the start of spring ($F_{2,48} = 6.26$, $P = 0.004$).

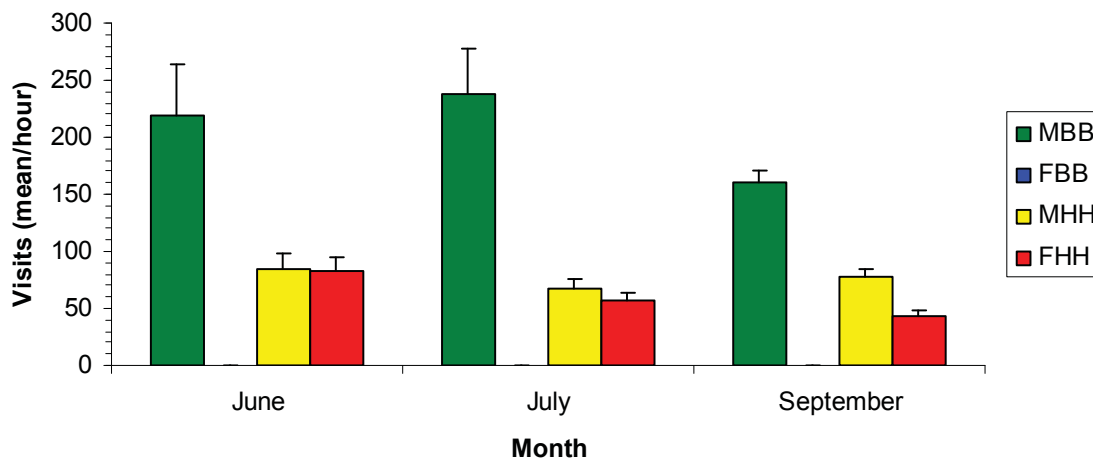


Figure 4.13. Mean visitation rate per hour each month for male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) at the ‘Wattle Valley’ feeder. Error bars represent standard error values.

Table 4.8. Test results of a Welch's t-test (normal distribution), Mann-Whitney U-test (non-normal distribution) and Spearman rank correlation comparing the number of visits by each species and sex for June, July and September, 2010 at the 'Wattle Valley' feeder. Key: MBB = male bellbird; FBB = female bellbird; MHH = male hihi; FHH = female hihi; vs = versus; n/a = not available.

		MBB vs FBB	MBB vs MHH	MBB vs FHH	MHH vs FHH	FBB vs MHH	FBB vs FHH
June	<i>t</i>	n/a	2.8	2.88	0.16	n/a	n/a
	df	n/a	13	13	23	n/a	n/a
	<i>P</i>	n/a	0.015	0.013	0.873	n/a	n/a
	<i>r_s</i>	n/a	0.63	0.94	0.65	n/a	n/a
	<i>n</i>	n/a	11	11	11	n/a	n/a
	<i>P</i>	n/a	0.022	0.000	0.015	n/a	n/a
	<i>t</i>	n/a	4.21	4.5	1.17	n/a	n/a
	df	n/a	10	10	19	n/a	n/a
	<i>P</i>	n/a	0.002	0.001	0.255	n/a	n/a
July	<i>r_s</i>	n/a	0.34	0.41	0.82	n/a	n/a
	<i>n</i>	n/a	9	9	9	n/a	n/a
	<i>P</i>	n/a	0.311	0.212	0.002	n/a	n/a
	<i>U</i>	n/a	1058	1093	965	n/a	n/a
	<i>n</i>	n/a				n/a	n/a
	<i>P</i>	n/a	0.000	0.000	0.000	n/a	n/a
	<i>r_s</i>	n/a	0.34	0.11	0.65	n/a	n/a
	<i>n</i>	n/a	25	25	25	n/a	n/a
	<i>P</i>	n/a	0.081	0.588	0.000	n/a	n/a
September	<i>U</i>	n/a	1058	1093	965	n/a	n/a
	<i>n</i>	n/a				n/a	n/a
	<i>P</i>	n/a	0.000	0.000	0.000	n/a	n/a
	<i>r_s</i>	n/a	0.34	0.11	0.65	n/a	n/a
	<i>n</i>	n/a	25	25	25	n/a	n/a
	<i>P</i>	n/a	0.081	0.588	0.000	n/a	n/a
	<i>U</i>	n/a	1058	1093	965	n/a	n/a
	<i>n</i>	n/a				n/a	n/a
	<i>P</i>	n/a	0.000	0.000	0.000	n/a	n/a

Short-term trends

The daily pattern in visitation rates varied with month (Figure 4.14; see Appendix 4.7 for values). In June, visitation rates increased towards the middle of the day and declined towards the end of the day for male bellbirds ($F_{5,7} = 11.57$, $P = 0.003$), male hihi ($F_{5,7} = 8.41$, $P = 0.007$) and female hihi ($F_{5,7} = 23.47$, $P = 0.000$) although the difference in visitation rates between 0900 and 1500 hours were not significantly different for male bellbirds ($F_{3,5} = 2.10$, $P = 0.219$) and male hihi ($F_{3,5} = 1.15$, $P = 0.414$) but was significant for female hihi ($F_{3,5} = 14.75$, $P = 0.006$). In July, male bellbirds had a similar trend as in June but early morning and late afternoon visits were more frequent so overall there was no significant difference in visitation rates throughout the day ($F_{5,5} = 2.55$, $P = 0.164$) with hihi visits also being consistent throughout the day (male: $F_{5,5} = 4.12$, $P = 0.073$; female: $F_{5,5} = 1.00$, $P = 0.499$). In September, visitation rates were again consistent throughout the day for male bellbirds ($F_{5,21} = 0.39$, $P = 0.850$) and hihi (male: $F_{5,21} = 1.04$, $P = 0.421$; female: $F_{5,21} = 1.23$, $P = 0.329$). Therefore, visitation rates

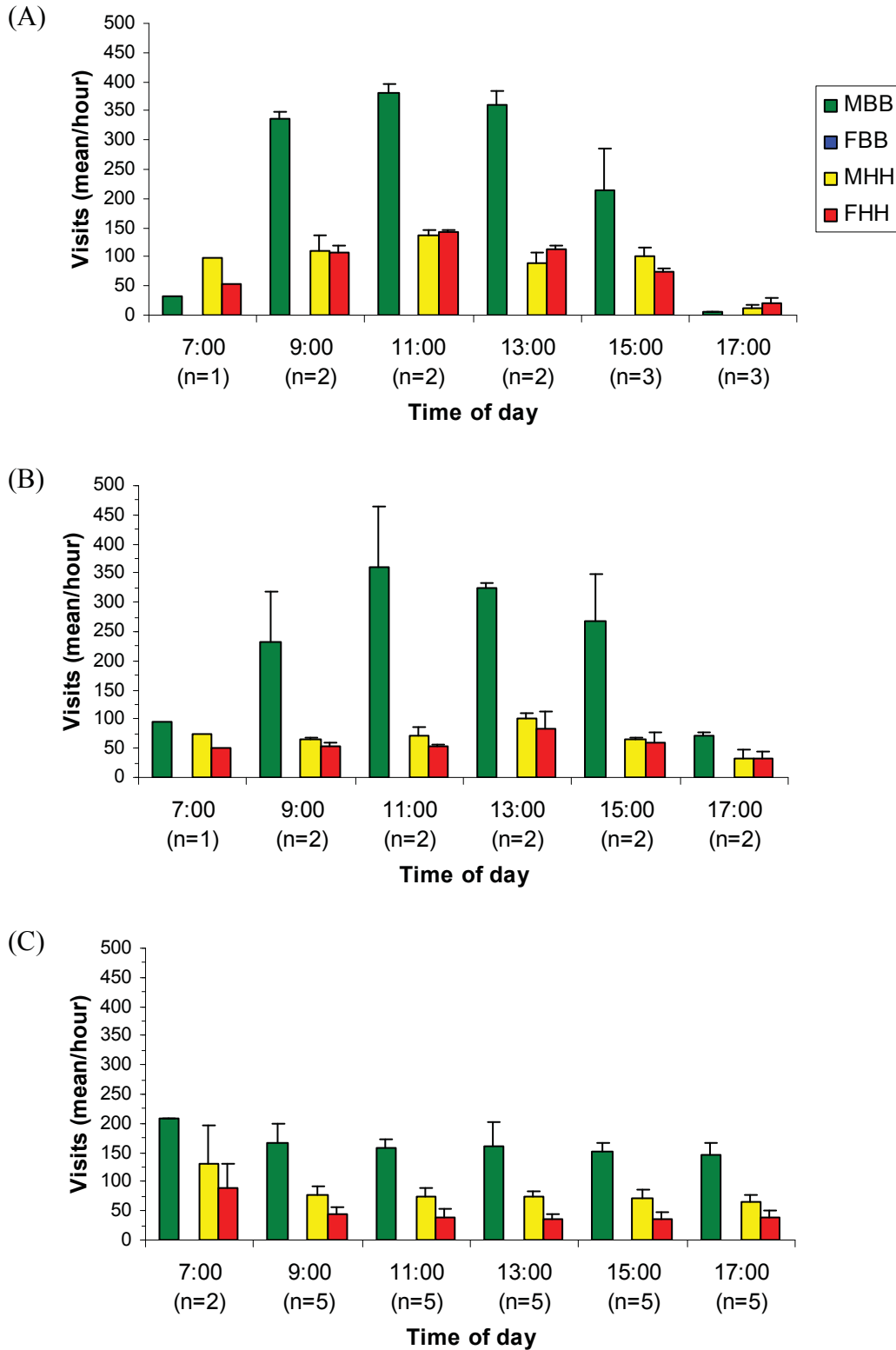


Figure 4.14. Mean number of visits per hour by male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) during the months of June (A), July (B) and September (C) at the ‘Wattle Valley’ feeder. Error bars represent the standard error values. n = sample size (number of hours).

throughout the day were more variable in early winter (June) and became more consistent towards spring (September).

4.5 Visitation patterns in relation to natural food resource availability

The visitation patterns have shown variation on a temporal basis, with some potential causes for the variation (tui and people). Another important factor in determining their use of the feeders is the availability of nectar resources. Using the data collected from the plant survey and first food eaten observations, I was able to plot resource availability in the area surrounding a feeder against the number of visits to the feeder over the months observed (Appendix 4.8). With such large variation in feeder use between both species and sexes over the months, no clear trends between monthly resource availability surrounding the feeder and feeder use could be established.

4.6 Behavioural interactions between species and sexes

4.6.1 Displacement

Through combining the results from all feeders for all times of the day, we could determine patterns in behavioural acts and interactions between the species and sexes over the months. Male bellbirds overall tended to show more displacement behaviour towards other males from April to September compared to displacement towards females (Figure 4.15). I found that displacements of male bellbirds by other male bellbirds significantly increased from April to September ($H = 38.54$, $df = 4$, $P = 0.000$) whereas their displacement of female bellbirds did not vary throughout the study ($H = 3.77$, $df = 4$, $P = 0.438$). Male bellbird displacement of male hihi ($H = 23.25$, $df = 4$, $P = 0.000$) and female hihi ($H = 13.04$, $df = 4$, $P = 0.011$) also increased autumn to spring.

Female bellbird displacement became most observable in September (Figure 4.15). Female bellbird displacement of male bellbirds had a significant rise in September ($H = 26.12$, $df = 4$, $P = 0.000$) whereas there was little difference in the displacement between female bellbirds ($H = 1.79$, $df = 4$, $P = 0.774$) as there were only very few observations of this in June and September (Figure 4.15). Female bellbird displacement

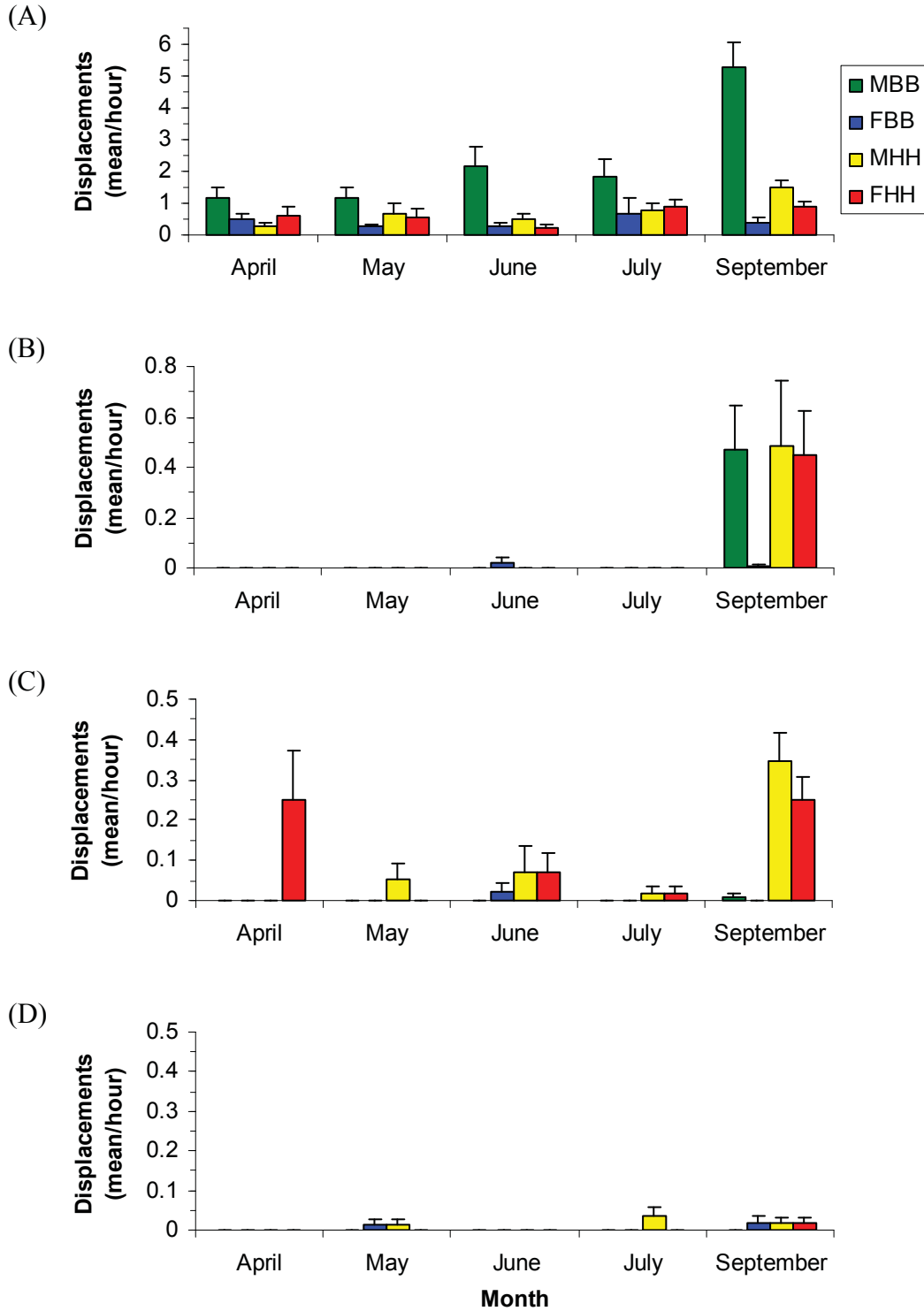


Figure 4.15. Mean number of displacements per hour per feeder each month made by male bellbirds (A), female bellbirds (B), male hihi (C) and female hihi (D) towards male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) at all feeders. Error bars represent standard error values.

of male ($H = 28.08$, $df = 4$, $P = 0.000$) and female hihi ($H = 24.18$, $df = 4$, $P = 0.000$) also increased in September.

Displacements by male hihi also increased at various times throughout the study, particularly towards other hihi. Male hihi displacement of other males increased significantly from May to September ($H = 41.99$, $df = 4$, $P = 0.000$) although there was a small decrease in July (Figure 4.15). Average male hihi displacement of female hihi gradually decreased from April to July where it then increased again in September ($H = 26.58$, $df = 4$, $P = 0.000$). There were very few observations of male hihi displacing bellbirds. There was a very small amount observed towards female bellbirds in June ($H = 6.23$, $df = 4$, $P = 0.183$) and an even smaller amount towards male bellbirds in September ($H = 1.77$, $df = 4$, $P = 0.779$).

Overall there were very few observations of female hihi displacing other birds (Figure 4.15). Intraspecific displacement of male hihi was observed in May, July and September ($H = 2.39$, $df = 4$, $P = 0.664$) whereas displacement of other female hihi was only observed in September ($H = 3.54$, $df = 4$, $P = 0.472$). Interspecific displacement of female bellbirds was observed in May and September ($H = 1.47$, $df = 4$, $P = 0.831$) but there were no observations of female hihi displacing male bellbirds ($H = 0.00$, $df = 4$, $P = 1.000$).

4.6.2 Displays

The degree of displaying amongst bellbirds and hihi observed varied throughout the year (Figure 4.16). Male bellbirds were most commonly seen displaying at the feeders which increased between April and September ($H = 77.09$, $df = 4$, $P = 0.000$). Female bellbirds were not observed displaying until September ($H = 37.51$, $df = 4$, $P = 0.000$) however this was only observed at the two feeders in 'Bush 1'. Male hihi were observed displaying a small amount in May (0.013 ± 0.013 displays hr^{-1}) but there was a significant increase in September ($H = 83.60$, $df = 4$, $P = 0.000$). Female hihi were only observed displaying a very small amount (0.009 ± 0.009 displays hr^{-1}) in September ($H = 1.77$, $df = 4$, $P = 0.779$).

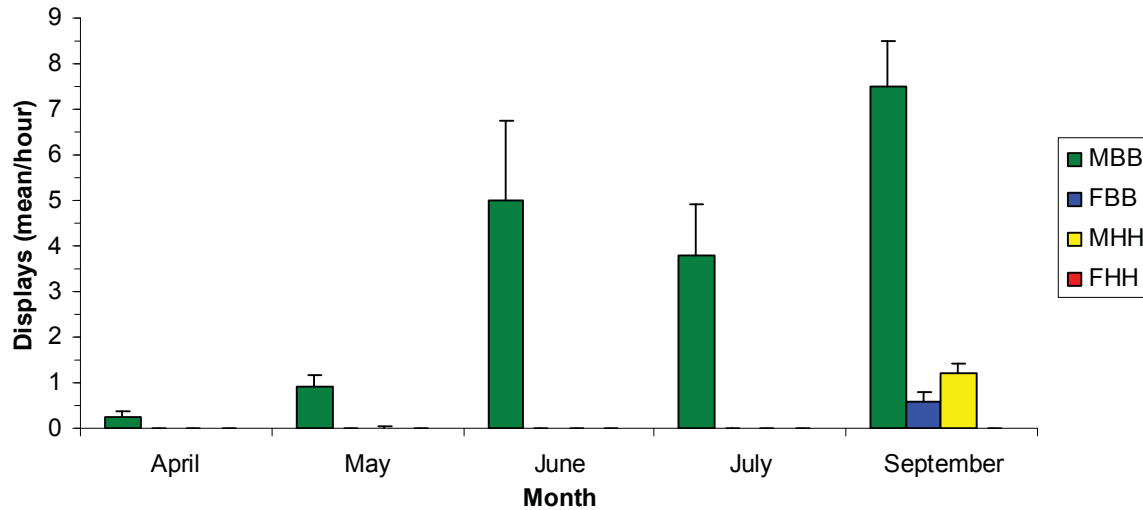


Figure 4.16. Mean number of displays per hour per feeder each month made by male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) over all feeders. Error bars represent standard error values.

4.6.3 Fights

Intraspecific fighting was observed at the feeders (Figure 4.17). The majority of fighting observed occurred between male bellbirds with peaks in May, July and overall the most fighting was observed in September ($H = 15.22$, $df = 4$, $P = 0.004$). There were no observations of fighting between female bellbirds ($H = 0.00$, $df = 4$, $P = 1.000$). Male hihi fighting was observed in June, July and September at a fairly consistent rate ($H = 5.95$, $df = 4$, $P = 0.203$). There were rare observations of fighting between female hihi in July and September ($H = 3.60$, $df = 4$, $P = 0.462$). There was the odd fight between male and female bellbirds in September (0.026 ± 0.026 fights hr^{-1} ; $H = 1.77$, $df = 4$, $P = 0.779$). The only fighting that occurred between male and female hihi was from the result of what appeared to be forced copulation from the male onto the female (0.035 ± 0.017 copulations hr^{-1} ; $H = 7.13$, $df = 4$, $P = 0.129$). There was only one observation of bellbird copulation in September but the female seemed to be receptive to the male (0.009 ± 0.009 copulations hr^{-1} ; $H = 1.77$, $df = 4$, $P = 0.779$). Interspecific fighting was rarely observed and all involved female bellbirds in September at the ‘Bush 1’ feeders. These fights observed appeared to be instigated by the female bellbird towards male hihi at an average of 0.043 ± 0.029 fights hr^{-1} ($H = 5.33$, $df = 4$, $P = 0.255$) and female hihi at an average of 0.017 ± 0.017 fights hr^{-1} ($H = 1.77$, $df = 4$, $P = 0.779$). No fights were observed between

male bellbirds and hihi as when a male bellbird and a hihi confronted, one would back down and these were categorised as displacements or they would both back down and just take turns at feeding from the same area.

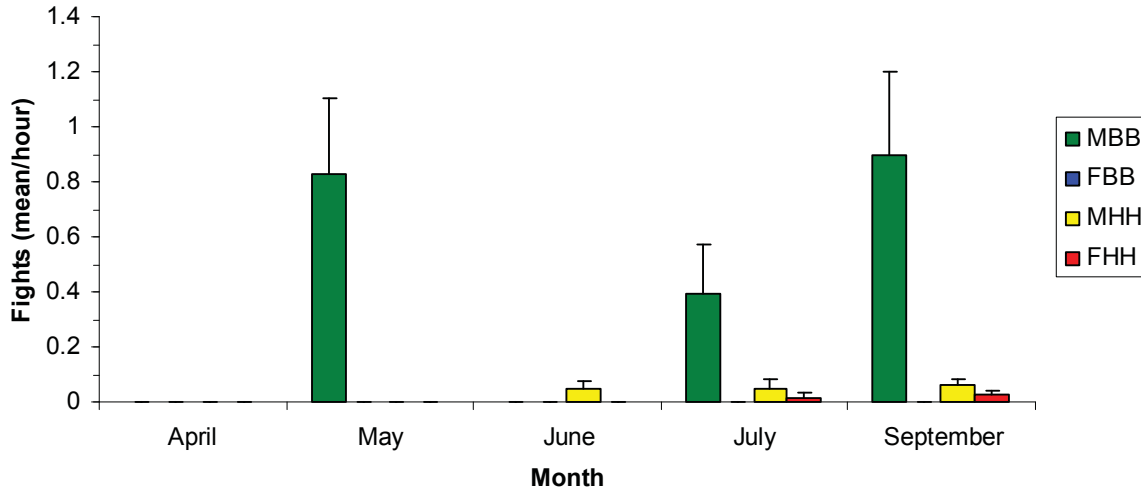


Figure 4.17. Mean number of intraspecific same sex fights per hour per feeder each month for male bellbirds (MBB), female bellbirds (FBB), male hihi (MHH) and female hihi (FHH) over all feeders. Error bars represent standard error values.

4.7 Discussion

4.7.1 Visitation patterns

Many significant differences were found between both species and sexes in how often they visited the feeders, when they visited and how they behaved at the feeders (see summary of visitation patterns in Table 2). Overall, male bellbirds were the most frequent visitors with an average of 114 visits hr^{-1} , male hihi next most frequent at 49 visits hr^{-1} , closely followed by female hihi with 45 visits hr^{-1} and female bellbirds were the least frequent visitors with only 6 visits hr^{-1} . Over all feeders this trend was also found for each month where average male bellbird visits were significantly higher than all other birds over all months observed (Table 4.9). The exceptions were for some individual feeders where male bellbird visits were not significantly higher than hihi in June (three out of four feeders), July (male hihi only; one out of four feeders) and September (two out of six feeders). Also, in July female hihi visited more frequently at one feeder (out of four) than both male bellbirds and male hihi. Male hihi visitation increased throughout the year and

their visits were not always higher than females. Average female hihi visits outnumbered male hihi visits earlier in the year in May (two out of three feeders), with little difference between their visits in June (all four feeders) and July (3 out four feeders) until the males significantly outnumbered females in September (two out of six feeders). There was little difference between male hihi and female bellbirds in May and at one feeder in June (out of four) plus little difference between both females in July at one feeder (out of four), but overall average female bellbird visitation was significantly lower than all other birds from autumn to spring and at most feeders, with some feeders and during some months having no female bellbird visitation observed.

Table 4.9. Summary of all feeders with mean visitation rates per hour (per feeder) plus standard error (over all hours of the day) each month for each species and sex, short-term patterns within each month and long-term (monthly) patterns.

		Bellbird		Hihi	
		Male	Female	Male	Female
Visitations rates	May	99.14 (\pm 15.04)	15.68 (\pm 2.82)	24.04 (\pm 3.88)	40.88 (\pm 6.01)
	June	120.26 (\pm 20.45)	2.73 (\pm 0.83)	46.63 (\pm 7.20)	51.89 (\pm 8.14)
	July	108.66 (\pm 15.47)	6.4 (\pm 1.68)	46.91 (\pm 6.91)	54.33 (\pm 6.93)
	September	129.25 (\pm 8.26)	2.82 (\pm 0.47)	68.83 (\pm 4.55)	44.75 (\pm 4.19)
Short-term patterns	May	Increase then decrease	Increase then decrease	No change	No change
	June	Increase then decrease	No change	Increase then decrease	No change
	July	Increase then decrease	No change	No change	No change
	September	No change	No change	No change	No change
Long-term patterns		No change	Decrease	Increase	No change

These patterns of feeder use relate to the interspecific and intraspecific dominance hierarchies of hihi and bellbirds. Bellbirds are dominant over hihi (Higgins *et al.*, 2001) and there are more bellbirds than hihi on Tiritiri Matangi Island (Chapter 5) therefore more bellbird visits would be expected under the assumption that they are also affected by food-limitation (defined as at least some individuals of a population having an increased chance of survival and/or reproduction with additional food; Carpenter, 1987). Bellbirds also display intraspecific competition with males dominant over females and females dominant over juveniles (Craig, 1984, 1985, cited in Higgins *et al.*, 2001; Craig & Douglas, 1986) which was shown by a much higher visitation rate by males than females (juveniles were not identified in the feeder footage but could have been

misidentified as females as they both have moustachial stripes). However, average female bellbird visitation rates were lower than hihi, potentially showing that intraspecific competition may be more common than interspecific competition at the feeders. Hihi are known to be territorial and show intraspecific aggression within the breeding season (Castro *et al.*, 1996; Higgins *et al.*, 2001). There are reports of males being dominant over females outside of the breeding season and older hihi dominant over younger hihi of the same sex (Stewart, 1980, Craig *et al.*, 1981, Angher, 1984, Craig, 1984 and Rasch, 1985 cited in Higgins *et al.*, 2001). Overall though, male and female hihi visitation rates were similar suggesting that there is little competitive exclusion between the hihi sexes at the feeders unlike bellbirds. Therefore, more intraspecific competition is occurring with bellbirds and considering that female bellbirds were visiting less than hihi, it is unlikely that the male bellbirds are competitively excluding hihi to a high degree.

Feeding territoriality in nectar-feeding birds has been linked to food abundance but whether they are linked by causation or coincidence has been debated (e.g., Carpenter, 1987; Armstrong, 1992a). Hawaiian honeycreepers territoriality behaviour outside of the breeding season varies with nectar abundance: less aggressiveness when nectar is most abundant (Carpenter, 1978). Honeycreepers are often found to no longer display territorial behaviour when there is more than 200 flowers in their foraging area which lead to the idea that there are thresholds for territoriality: the higher threshold is when food abundance is high and territoriality should disappear because they are not food-limited; the lower threshold is when food abundance is so low that territoriality disappears because the resources defended would not pay for the cost of defence (Carpenter & MacMillen, 1976; Carpenter, 1987). However, this does not apply to all nectar-feeding birds with some hummingbirds (Ewald & Carpenter, 1978) and honeyeaters (Armstrong, 1992a) showing little changes in territorial behaviour when provided with abundant nectar, and other reasons have been linked to why territoriality may cease when nectar is limited. A study on territoriality in the rufous hummingbird (*Salphorus rufus*) showed that territory size varies with the number of flowers within the area (Kodric-Brown & Brown, 1978). In a drought year where flower production was very low, additional sugar water feeders were supplied and whilst the rufous hummingbird initially tried to defend the feeders, the feeders became overwhelmed with

other species, particularly non-territorial hummingbirds, and the rufous hummingbird ceased defending the feeders, showing little aggression towards the other species (Kodric-Brown & Brown, 1978). Therefore, territoriality ceased because the feeders were so overwhelmed with competitors that defence was not economical (Kodric-Brown & Brown, 1978; Carpenter, 1987).

With such high visitation rates by both bellbirds and hihi at many of the feeders on Tiritiri Matangi, it is clear that these feeders are not being highly defended by the most dominant individuals. Bellbirds are the more dominant species, but hihi visits were often nearly as frequent as bellbird visitation at some feeders hence it was likely that, as in the rufous hummingbird example above (Kodric-Brown & Brown, 1978), the feeders were being overwhelmed with competitors to the extent that the most dominant bellbirds were unable to defend the feeders. Whilst aggressive displays by male bellbirds occurred, they were relatively low and most were directed towards other male bellbirds. Hence, some male bellbirds may have tried to defend but it was not economical to continue as hihi and other bellbirds were overwhelming the feeders. However, at the ‘Dupont’ feeder in April, for example, there were very few hihi visits during the day compared to male bellbird visits, suggesting that this feeder may have been defended, at least temporarily, by dominant male bellbirds. Therefore, when there is food limitation, defence ceases by dominant male bellbirds because the feeders are overwhelmed with hihi and subordinate bellbirds; whereas when food is not limited (although not superabundant), dominant male bellbirds may be able to defend feeders as they are not being overwhelmed with competitors.

The difference between hihi and bellbird sexes may be due to the risks of being displaced and the risk of starvation. Female bellbirds visiting the feeders so irregularly may be due to the risk of being displaced by males. Female bellbirds are often much smaller (Craig *et al.*, 1981a; Higgins *et al.*, 2001) than males and are subordinate to adult males (Craig & Douglas, 1986). The risk of not winning a fight and getting injured associated with being subordinate (Newton, 1998) may be why females do not risk visiting the feeders on a regular basis. Female bellbirds did however use the feeders more in autumn and early winter suggesting that they were food limited as resource availability was low (Appendix 9; Chapter 3) and they potentially required the extra energy for

recovering from the breeding season and post-breeding season moult (Higgins *et al.*, 2001) hence it was worth the risk of being displaced by males. However, juvenile males still retaining their moustachial stripe in autumn could have been misidentified as a female, hence contributing to higher female visitation rates. Although male hihi can be more dominant than females outside of the breeding season, this can vary with residential status (Stewart, 1980, Craig *et al.*, 1981, Angher, 1984, Craig, 1984 and Rasch, 1985 cited in Higgins *et al.*, 2001). Castro (1995) found that there were dominance hierarchies at feeders on Kapiti Island with dominant males or females and the hierarchies were different at each feeder. However, at the feeders on Tiritiri Matangi, there were such high visits by both males and females and little intraspecific aggression suggesting that they may have ceased dominance behaviour because they were at the lower threshold with food limitation and were at risk of starvation/reduced survival and defence was not economical. This is supported by Castro's (1995) observation of the dominance hierarchies ceasing on Kapiti Island when visits to the feeders were high. However, we cannot tell whether there was a hierarchy between the ages of hihi visiting the feeders. Hence, hihi may be more likely to overcome territoriality like the Hawaiian honeycreepers (Carpenter, 1978) as they have a greater reliance on the feeders because of food limitation from competition with bellbirds (and tui) and low availability of flowers from the regenerating vegetation.

In autumn and winter, patterns in daily variation were more significant. These patterns consisted of peaks in visitation rates during the middle of the day with significantly lower visitation rates early in the morning and late in the afternoon. The timing of peaks varied during the day and varied between feeders, but the overall result was higher use of the feeders in the middle of the day and afternoon. These peaks were most commonly significant in male bellbird visits but the patterns were still to some degree observed in female bellbirds and hihi. The exceptions were 'Dupont' in May with very infrequent visits and 'Bush 22' in June where visits were consistent throughout the day. Later in the year, particularly September, visits to the feeders by each species and sex were consistently similar throughout the day from 0700 to 1700 hours. The exceptions were 'Bush 2' and 'Bush 22' where there were still some peaks in the day, particularly in the afternoon. With nectar availability being lower in autumn and winter

than in spring (Chapter 3), it is likely that natural nectar production would be exhausted quicker as nectar concentrations can be higher in the morning (Ford, 1979); hence higher use of the feeders in the middle of the day and afternoon as lower nectar availability can correlate with increased feeder use (Armstrong, 1992b). Visits dropped by the evening potentially due to nectar levels being restored. Therefore, their visitation to the feeders appears to depend on daily and seasonal requirements with potentially factors such as nectar availability influencing their use of the feeders.

Some variation in visitation rates was found between the months with the sexes showing slightly different trends. Male bellbirds had a slight but insignificant increase in visits from May to September (four out of six feeders) but male hihi had a significant increase which was a common trend amongst most of the feeders (four out of six). Female bellbirds however showed various significant peaks and declines from May to September with an overall decline in visits for three feeders and insignificant change at the other three. Female hihi showed an insignificant increase and decline in visits throughout the year over all feeders. Most feeders showed some degree of decreased female hihi visits in September but this declining trend was only significant for two feeders and one showed an insignificant decline with the other two feeders showing no significant change and one feeder showed a significant increase. The increase in male visitation towards the breeding season in spring is likely due to the increase in energy demand for pre-breeding season behaviours such as courting and territory defence as animals will often gain body reserves (Welbergen, 2011) and increased body mass can affect, for example, egg quality (Wendeln, 1997). Male hihi are known to lose weight when under high intrusion pressure from other males in their territory (Low, 2006b) and actively defend their mate in her fertile period (Low, 2005a); hence the increase in feeder use could be attributed to an increase in mass to prepare for the costs of defending the female and territory which could cause loss in mass over the breeding season. A significant increase in male bellbird visitation did not occur perhaps because bellbirds disperse further from feeders to establish territories containing nest site and resources (Chapter 5; Higgins *et al.*, 2001). No increase in female hihi visits was perhaps due to the end of the feeder filming not being close enough to female nesting behaviour. The last video footage observed was for September when females were likely to be searching for

potential nest sites with pair formation and nesting behaviour not occurring until October (Castro *et al.*, 1996; Higgins *et al.*, 2001) with feeder use found to have a significant affect on their reproductive behaviour, such as larger clutches and reduced time to laying second clutch (Castro *et al.* 2003). At some feeders, female hihi visits decreased potentially due to the increase in natural resource availability (Chapter 3) or from avoiding males to reduce the risk of forced copulations from males (Low, 2005b) as forced copulation is more likely to occur in areas of high densities of hihi (Castro *et al.*, 1996). On Kapiti Island, often no hihi were observed using feeders in the winter months with increases in the number of hihi using the feeder(s) in spring (Castro, 1995), showing the reliance of hihi on the feeders in the breeding season and suggesting that hihi on Tiritiri were more food-limited in the winter. Female bellbird visits declined in spring perhaps because the risk of using feeders was higher with increased territorial behaviour associated with the breeding season and they could obtain their energy needs from natural sources as resource availability increased towards spring (Chapter 3). Therefore, changes in visitation rates over the months was most likely due to factors such as resource availability and changes in behaviour in the pre-breeding season (September) resulting in differences between both species and sexes.

Despite the monthly variations, over all months positive correlation was found between the number of visits made by both species and sexes except in September where male and female bellbirds did not show any correlation. There were some exceptions where female bellbirds did not correlate with male bellbirds and hihi, most likely due to the female's infrequent visits to the feeders. At the 'Wattle Valley' feeder there was little correlation between both species and sexes visiting the feeder, potentially suggesting some competition although the correlation coefficient was not negative. However, the overall level of positive correlation suggests little competitive exclusion was occurring between the species and sexes at the feeders.

4.7.2 Visitation patterns in relation to natural food resource availability

Other studies on feeder use have shown that the use of sugar water feeders declines when abundant nectar is available (Armstrong, 1992). In general, resource availability increased from earlier in the year to September (Appendix 4.9; Chapter 3)

and while at some feeders female feeder use declined with increasing nectar availability, male feeder use increased (particularly male hihi). Therefore, other factors were likely to be influencing their use of the feeders (such as breeding behaviour mentioned above). With the differences in feeder use between the days during each month, this shows that feeder use varied on a day by day basis (and sometimes an hourly basis) depending on factors such as daily availability of nectar and daily energy requirements. It has been observed that after periods of rain on the island feeder use increased, determined from the amount of sugar water consumed in one day (L. Walker, pers. comm.), indicating the potential effects of weather on feeder use.

4.7.3 Behavioural interactions between species and sexes

The number of behavioural interactions at the feeders also varied slightly over the months. Both male and female bellbirds showed significantly more displacement behaviour towards other male bellbirds and hihi in September compared to earlier in the year, potentially due to increased territorial behaviour as the breeding season began (Higgins *et al.*, 2001). Male hihi displacement behaviour also increased towards other male and female hihi as their territorial and defence behaviour also likely began in September (Higgins *et al.*, 2001). Male hihi displacement behaviour only slightly increased towards male bellbirds as in the breeding season males will defend their mates against other male hihi but not against harassment from male bellbirds (Low, 2005a) with only a small amount of displacement behaviour towards female bellbirds. Little displacement behaviour by female hihi was observed towards other female hihi, male hihi and female bellbirds but overall most of this did occur during September observations as their territorial behaviour may have also begun (Higgins *et al.*, 2001). The number of displays made by both species and sexes all increased from April to September associated with their increase in territorial behaviour in the breeding season (Higgins *et al.*, 2001; Low, 2005a; Brunton & Li, 2006) but this increase was not significant for female hihi who were rarely seen displaying at the feeders.

The occasional fight was observed between each sex of each species, most occurring spring. Male bellbirds, however, showed peaks in fighting behaviour throughout the whole observation period. Female bellbirds were the only ones observed

instigating a fight (or attack) towards hihi but not between themselves. They also had the occasional fight with male bellbirds in September. This aggressive behaviour was likely to be from resident female bellbirds defending their territory (Higgins *et al.*, 2001) as there were few female visits and it only occurred at the 'Bush 1' feeders. Fighting between male and female hihi appeared to be the result from forced copulation by the males which was also only observed in September. Copulation in feeders has also been observed on Kapiti Island and forced copulation can increase in areas of high hihi density (Castro *et al.*, 1996). Only one occasion of bellbird copulation was observed in September. From feeder observations it appeared that when sugar water bottles were empty or blocked, there was more aggressive interactions hence further research is needed on this as it may show that more regularly replacing empty sugar water feeders is important for reducing aggression at the feeders (currently the sugar water is only replaced once per day). Therefore, it appears that behavioural interactions by both species increased throughout the study from April to September which correlates with the start of the breeding season (bellbird: Brunton & Li, 2006; hihi: Low, 2006a).

4.8 Conclusion

Male bellbirds were on average the most frequent visitors to the supplementary sugar water feeders followed by male hihi, female hihi and then female bellbirds. Their use of the feeder in the short-term was similar with increasing visits throughout the day and declining by evening, however this pattern was mainly found in the autumn and winter months as spring visits were consistent throughout the day. Long-term trends showed differences between the species and sexes. Male bellbird and female hihi visits were relatively consistent from autumn to spring whereas male hihi visits increased and female bellbird visits declined. Positive correlation between the species and sexes with few interspecific aggressive interactions showed that there was little competitive exclusion between the species and hihi sexes, however there was more intraspecific competition between bellbird sexes with no correlation at some feeders and very few female bellbird visits observed. Hence, dominant male bellbirds can cease to defend the feeders from subordinate males and hihi due to the overwhelming number of visits, although female bellbirds appear to still be at risk from male bellbird dominance.

Appendix 4.1. Statistical outputs for the daily variation in visitation rates from all feeders

Table 1. Test results from a one-way ANOVA for the daily variation in visitation rates each month for all hours of the day and between 0900 and 1500 hours only.

	Month	All hours			0900 to 1500 hours		
		F	DF	P	F	DF	P
Male bellbird	April	7.42	5	0.001	5.96	3	0.013
	May	3.56	5	0.006	0.55	3	0.650
	June	3.48	5	0.009	0.32	3	0.808
	July	2.35	5	0.051	0.26	3	0.851
	September	0.67	5	0.647	0.33	3	0.807
Female bellbird	April	2.88	5	0.044	2.63	3	0.108
	May	2.66	5	0.029	0.57	3	0.640
	June	1.27	5	0.291	0.74	3	0.533
	July	0.94	5	0.463	0.28	3	0.841
	September	0.55	5	0.74	0.75	3	0.523
Male hihi	April	1.83	5	0.157	3.95	3	0.043
	May	1.93	5	0.100	1.00	3	0.401
	June	2.48	5	0.044	0.87	3	0.465
	July	2.24	5	0.061	0.16	3	0.924
	September	0.75	5	0.587	0.27	3	0.843
Female hihi	April	2.40	5	0.078	3.99	3	0.042
	May	2.21	5	0.062	1.80	3	0.160
	June	2.30	5	0.059	0.50	3	0.683
	July	2.07	5	0.081	0.39	3	0.761
	September	0.53	5	0.754	0.19	3	0.902

Appendix 4.2. Daily visitation rates at the ‘Bush 1 Lower’ feeder

Table 1. Mean (\pm SE) number of visits per hour throughout the day for each species and sex over the months of May, July and September at the ‘Bush 1 Lower’ feeder.

		Time of day					
	Month	7:00	9:00	11:00	13:00	15:00	17:00
Male bellbird	May	126.5 (\pm 95.5)	266.67 (\pm 34.26)	376.67 (\pm 23.1)	343.75 (\pm 41.05)	284 (\pm 69.02)	10.33 (\pm 4.96)
	July	100	254 (\pm 187)	197.75 (\pm 25.64)	234 (\pm 0)	222.6 (\pm 42.51)	4.4 (\pm 2.77)
	September		219	194.5 (\pm 74.40)	208.5 (\pm 73.54)	184.75 (\pm 95.97)	43.5 (\pm 18.26)
Female bellbird	May	20 (\pm 16)	51.33 (\pm 4.67)	64 (\pm 5.51)	74.75 (\pm 9.59)	46.2 (\pm 7.61)	1.83 (\pm 0.87)
	July	20	33.5 (\pm 27.5)	17.25 (\pm 6.87)	35 (\pm 11.45)	23 (\pm 8.20)	0.4 (\pm 0.24)
	September		8	17.5 (\pm 6.84)	8.75 (\pm 1.44)	11 (\pm 1.58)	13.5 (\pm 3.86)
Male hihi	May	73 (\pm 58)	51.67 (\pm 14.1)	69.67 (\pm 16.01)	91.5 (\pm 9.28)	62.6 (\pm 14.1)	17.5 (\pm 6.7)
	July	130	123.5 (\pm 10.5)	133 (\pm 15.37)	138 (\pm 11.90)	148.6 (\pm 17.86)	4.8 (\pm 2.63)
	September		181	146.75 (\pm 38.36)	163.5 (\pm 42.32)	104.5 (\pm 39.65)	26.5 (\pm 9.72)
Female hihi	May	89 (\pm 75)	72.67 (\pm 27.61)	99 (\pm 21.39)	129 (\pm 14.46)	116.8 (\pm 17.96)	41.5 (\pm 13.62)
	July	82	137.5 (\pm 73.5)	114.25 (\pm 13.38)	126.5 (\pm 6.20)	107.6 (\pm 26.85)	6.6 (\pm 4.53)
	September		155	96.5 (\pm 15.81)	90.5 (\pm 22.15)	92.25 (\pm 39.13)	73.5 (\pm 35.38)

Appendix 4.3. Daily visitation rates at the ‘Bush 1 Upper’ feeder

Table 1. Mean (\pm SE) number of visits per hour throughout the day for each species and sex over the months of May, June and September at the ‘Bush 1 Upper’ feeder.

		Time of day					
	Month	7:00	9:00	11:00	13:00	15:00	17:00
Male bellbird	May	101.33 (\pm 13.35)	54.83 (\pm 10.95)	45.25 (\pm 21.83)	61.6 (\pm 18.66)	152.63 (\pm 33.45)	8 (\pm 4.88)
	June	54	54	105.5 (\pm 90.5)	196 (\pm 39)	561.5 (\pm 98.5)	1 (\pm 1)
	September	54.5 (\pm 11.5)	78.5 (\pm 37.5)	93 (\pm 36.25)	106.75 (\pm 36.82)	129.5 (\pm 38.20)	107 (\pm 21.76)
Female bellbird	May	12.67 (\pm 4.70)	3.67 (\pm 1.54)	1 (\pm 1)	1.6 (\pm 1.17)	23.75 (\pm 5.43)	1.13 (\pm 0.74)
	June	3	4	6 (\pm 6)	24.5 (\pm 2.5)	23 (\pm 0)	0.5 (\pm 0.5)
	September	8 (\pm 1)	11 (\pm 3)	9.75 (\pm 1.03)	9.5 (\pm 2.22)	8 (\pm 1)	8.75 (\pm 2.46)
Male hihi	May	29.67 (\pm 11.05)	5.5 (\pm 2.17)	9.5 (\pm 5.69)	7.2 (\pm 3.26)	38.13 (\pm 13.23)	9.25 (\pm 4.43)
	June	106	5	49.5 (\pm 40.5)	20 (\pm 14)	170 (\pm 101)	3 (\pm 2)
	September	82 (\pm 41)	69 (\pm 10)	77.75 (\pm 22.13)	72 (\pm 9.19)	107.75 (\pm 17.12)	66.5 (\pm 18.23)
Female hihi	May	52 (\pm 19.43)	11.17 (\pm 2.69)	13.25 (\pm 7.78)	12.8 (\pm 6.57)	79.13 (\pm 22.36)	23.13 (\pm 10.99)
	June	126	35	70.5 (\pm 25.5)	56.5 (\pm 8.5)	199 (\pm 111)	4 (\pm 2)
	September	112.5 (\pm 38.5)	89.5 (\pm 30.5)	86.25 (\pm 15.47)	100.25 (\pm 21.39)	110.5 (\pm 17.11)	73.5 (\pm 20.35)

Appendix 4.4. Daily visitation rates at the ‘Bush 2’ feeder

Table 1. Mean (\pm SE) number of visits per hour throughout the day for each species and sex over the months of June, July and September at the ‘Bush 2’ feeder.

			Time of day					
	Month		7:00	9:00	11:00	13:00	15:00	17:00
Male bellbird	June	6	110 (± 31)	162 (± 49)	174	164	0 (± 0)	
	July		29.33 (± 7.84)	28.67 (± 5.78)	44 (± 15.01)	123.67 (± 73.04)	41.67 (± 6.69)	
	September	63 (± 20.68)	134.8 (± 16.01)	147 (± 18.64)	170.8 (± 32.35)	72.4 (± 19.93)	32.6 (± 13.82)	
Female bellbird	June	0	0 (± 0)	1 (± 0)	1	0	0 (± 0)	
	July		1 (± 0)	1.67 (± 1.20)	3.33 (± 1.76)	2.67 (± 1.45)	2.33 (± 1.33)	
	September	0 (± 0)	0 (± 0)	0 (± 0)	0 (± 0)	0 (± 0)	0 (± 0)	
Male hihi	June	4	46.5 (± 2.5)	64.5 (± 1.5)	71	68	0 (± 0)	
	July		7.33 (± 1.33)	6.67 (± 0.88)	15.67 (± 8.17)	41.67 (± 25.76)	11 (± 2.08)	
	September	41.25 (± 7.69)	89.2 (± 21.69)	95 (± 10.89)	92.6 (± 9.90)	33.4 (± 4.03)	8.6 (± 3.85)	
Female hihi	June	13	101 (± 23)	171 (± 10)	134	117	0.5 (± 0.5)	
	July		56.67 (± 18.59)	43.33 (± 10.91)	106.33 (± 36.38)	141.33 (± 57.97)	48 (± 6.56)	
	September	33 (± 10.17)	77.2 (± 37.79)	89 (± 32.87)	72 (± 22.72)	19.6 (± 2.80)	8 (± 2.26)	

Appendix 4.5. Daily visitation rates at the ‘Bush 22’ feeder

Table 1. Mean (\pm SE) number of visits per hour throughout the day for each species and sex over the months of April, June and September at the ‘Bush 22’ feeder.

		Time of day					
	Month	7:00	9:00	11:00	13:00	15:00	17:00
Male bellbird	April	149	350	118	173.50 (\pm 1.50)	36.33 (\pm 30.94)	21.75 (\pm 9.21)
	June	31.75 (\pm 19.15)	112.33 (\pm 104.33)	79.00 (\pm 58.73)	8.00 (\pm 3.81)	88.60 (\pm 77.41)	1.20 (\pm 0.97)
	September		100.25 (\pm 15.21)	196.60 (\pm 9.80)	228.80 (\pm 22.07)	264.20 (\pm 47.44)	323.20 (\pm 26.75)
Female bellbird	April	5	15	9	14 (\pm 6)	2 (\pm 2)	3 (\pm 1.78)
	June	1.50 (\pm 1.50)	2.33 (\pm 2.33)	2.50 (\pm 1.50)	0.25 (\pm 0.25)	2.00 (\pm 2.00)	0.80 (\pm 0.58)
	September	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)	0.40 (\pm 0.40)
Male hihi	April	66	92	24	80 (\pm 15)	9.67 (\pm 9.17)	48.75 (\pm 21.93)
	June	49.75 (\pm 26.03)	46.00 (\pm 45.50)	38.50 (\pm 22.04)	0 (\pm 0)	11.00 (\pm 10.00)	5.60 (\pm 2.09)
	September		74.50 (\pm 4.87)	78.20 (\pm 7.25)	83.20 (\pm 4.68)	102.00 (\pm 16.00)	145.60 (\pm 16.37)
Female hihi	April	58	75 (\pm 0)	38	60 (\pm 12)	8.67 (\pm 8.67)	31.25 (\pm 13.48)
	June	11.50 (\pm 3.88)	18.33 (\pm 18.33)	17.00 (\pm 7.69)	2.00 (\pm 1.68)	4.20 (\pm 3.71)	6.40 (\pm 2.16)
	September		8.00 (\pm 2.04)	7.20 (\pm 2.52)	5.40 (\pm 1.21)	7.20 (\pm 1.43)	22.20 (\pm 6.8)

Appendix 4.6 Daily visitation rates at the ‘Dupont’ feeder

Table 1. Mean (\pm SE) number of visits per hour throughout the day for each species and sex over the months of May, July and September at the ‘Dupont’ feeder.

		Time of day					
	Month	7:00	9:00	11:00	13:00	15:00	17:00
Male bellbird	May	1 (± 0)	11.75 (± 2.02)	13.5 (± 1.5)	6.5 (± 2.5)	6.2 (± 1.59)	0.4 (± 0.24)
	July		4	11 (± 3.26)	11.8 (± 1.93)	94 (± 71.75)	7.17 (± 4.64)
	September	20	65.75 (± 41.51)	18.4 (± 2.06)	20.2 (± 2.58)	22.2 (± 2.56)	34.6 (± 13.50)
Female bellbird	May	0 (± 0)	0 (± 0)	0 (± 0)	0 (± 0)	0 (± 0)	0 (± 0)
	July		0	0 (± 0)	0.2 (± 0.2)	0.17 (± 0.17)	0 (± 0)
	September	0	0.25 (± 0.25)	0 (± 0)	0.6 (± 0.4)	0.4 (± 0.24)	0 (± 0)
Male hihi	May	0 (± 0)	0 (± 0)	0 (± 0)	0 (± 0)	0 (± 0)	1.4 (± 1.4)
	July		2	0 (± 0)	0.2 (± 0.2)	4 (± 2.54)	5.67 (± 4.42)
	September	2	2 (± 2)	1.2 (± 0.8)	0.6 (± 0.6)	1 (± 0.63)	6.2 (± 1.85)
Female hihi	May	0 (± 0)	0 (± 0)	0.5 (± 0.5)	0 (± 0)	0 (± 0)	1 (± 0.63)
	July		0	0 (± 0)	0 (± 0)	10.67 (± 9.50)	6.83 (± 4.64)
	September	0	1 (± 1)	0.6 (± 0.6)	1.2 (± 0.73)	0.2 (± 0.2)	7.4 (± 2.11)

Appendix 4.7. Daily visitation rates at the ‘Wattle Valley’ feeder

Table 1. Mean (\pm SE) number of visits per hour throughout the day for each species and sex over the months of June, July and September at the ‘Wattle Valley’ feeder.

		Time of day					
	Month	7:00	9:00	11:00	13:00	15:00	17:00
Male bellbird	June	34	335.5 (\pm 13.5)	380 (\pm 15)	359 (\pm 26)	213 (\pm 74.08)	4.67 (\pm 2.73)
	July	95	232.5 (\pm 85.5)	361.5 (\pm 101.5)	325 (\pm 9)	267 (\pm 81)	71 (\pm 5)
	September	208 (\pm 0)	167.2 (\pm 32.35)	158.4 (\pm 13.12)	161 (\pm 39.91)	151.6 (\pm 13.70)	145.2 (\pm 20.32)
Female bellbird	June	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)
	July	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)
	September	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)	0 (\pm 0)
Male hihi	June	97	110.5 (\pm 27.5)	135.5 (\pm 10.5)	88 (\pm 18)	100.33 (\pm 14.38)	12.67 (\pm 5.78)
	July	75	66.5 (\pm 1.5)	70 (\pm 15)	100 (\pm 9)	66 (\pm 2)	34 (\pm 15)
	September	130 (\pm 66)	78 (\pm 15.27)	75.2 (\pm 13.69)	74.8 (\pm 7.14)	70.2 (\pm 16.29)	64.4 (\pm 13.37)
Female hihi	June	55	107 (\pm 12)	141.5 (\pm 5.5)	113.5 (\pm 5.5)	75.67 (\pm 5.78)	20 (\pm 11.14)
	July	51	55 (\pm 6)	52.5 (\pm 5.5)	84.5 (\pm 27.5)	58.5 (\pm 19.5)	34 (\pm 11)
	September	90 (\pm 42)	45.6 (\pm 11.43)	39.4 (\pm 13.28)	34.8 (\pm 10.2)	35.6 (\pm 12.73)	38.4 (\pm 11.86)

Appendix 4.8. Figures of resource availability against mean visitation rates to the feeders over months observed.

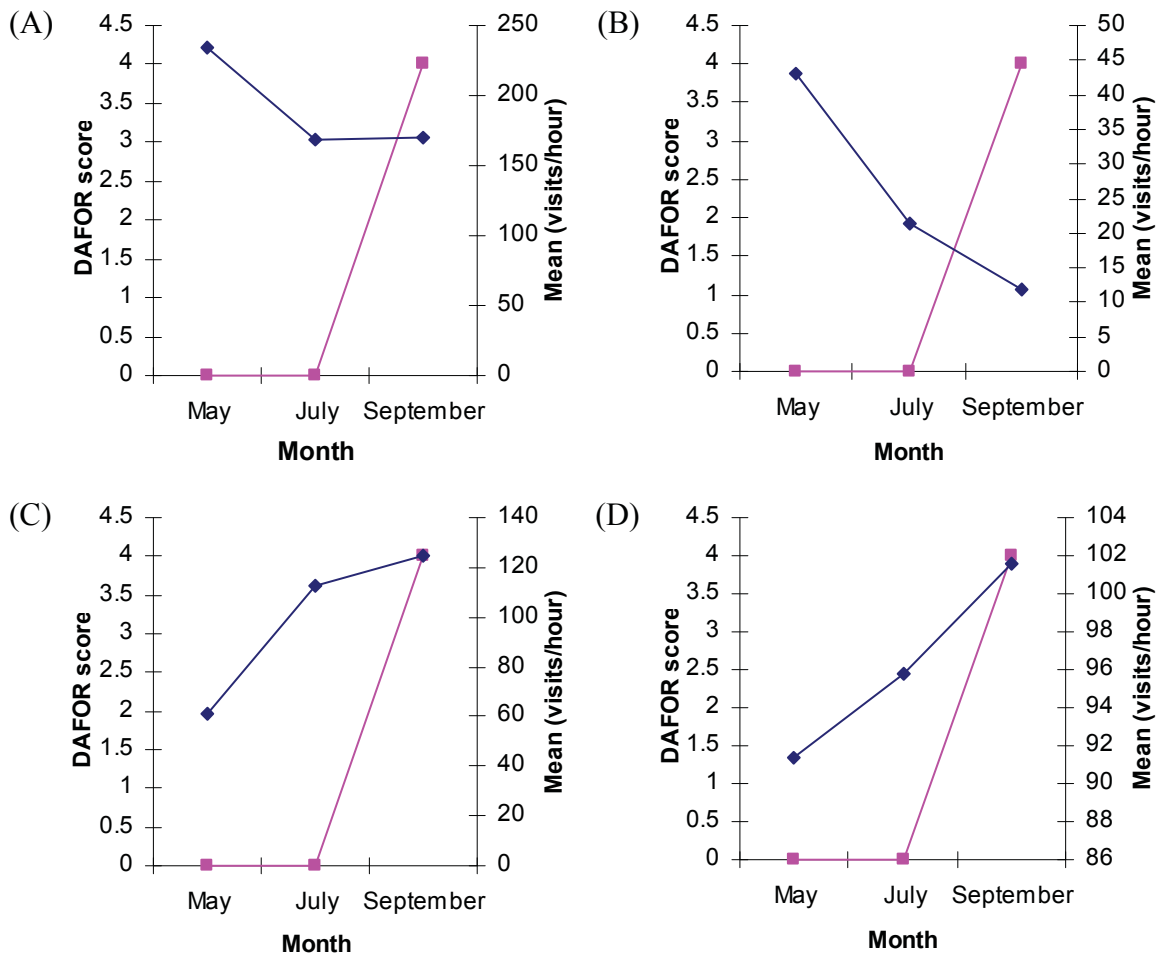


Figure 1. Plot of resource availability (cumulative DAFOR score of plants flowering; square ■) and mean number of visits per hour (diamond ◆) to the ‘Bush 1 Lower’ feeder for male bellbirds (A), female bellbirds (B), male hihi (C) and female hihi (D) each month.

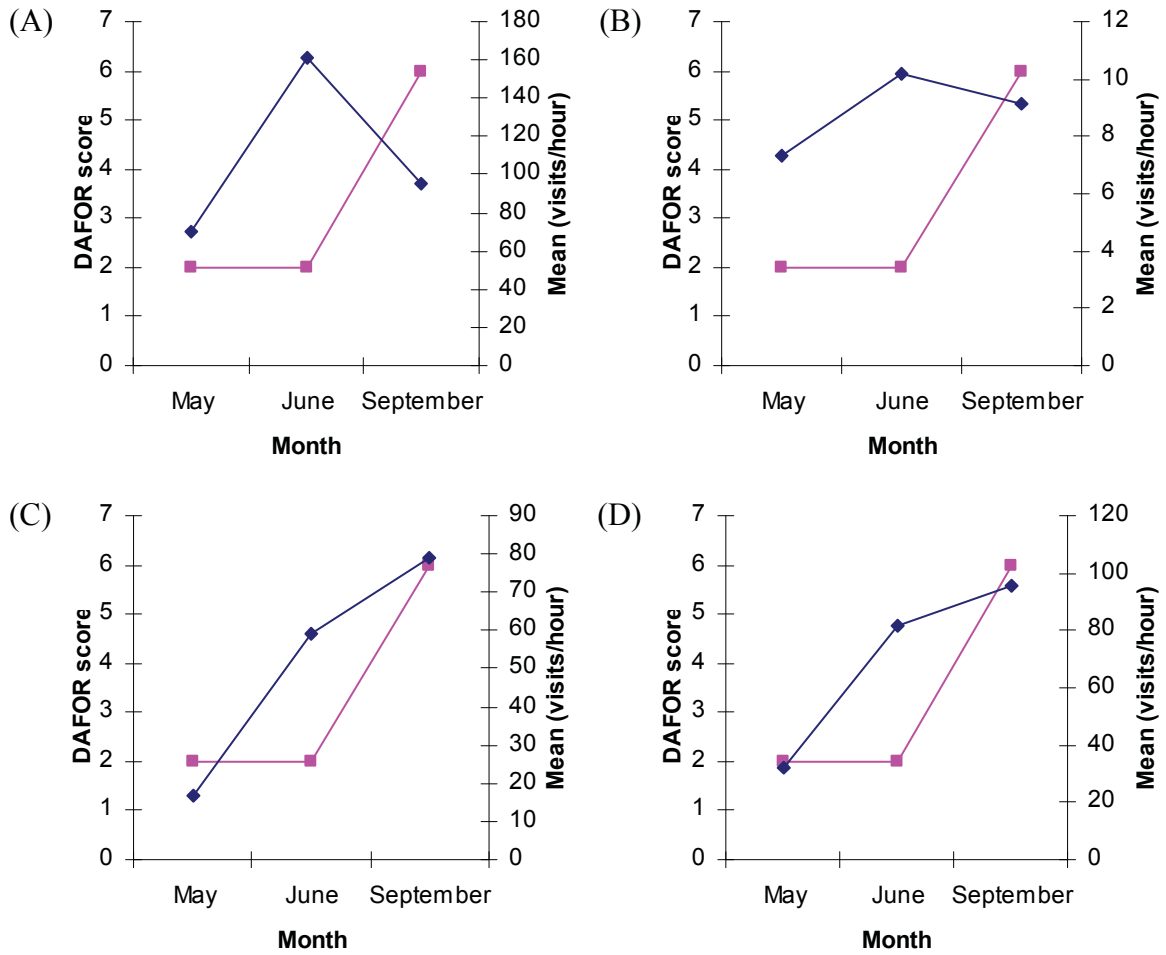


Figure 2. Plot of resource availability (cumulative DAFOR score of plants flowering; square ■) and mean number of visits per hour (diamond ♦) to the ‘Bush 1 Upper’ feeder for male bellbirds (A), female bellbirds (B), male hihi (C) and female hihi (D) each month.

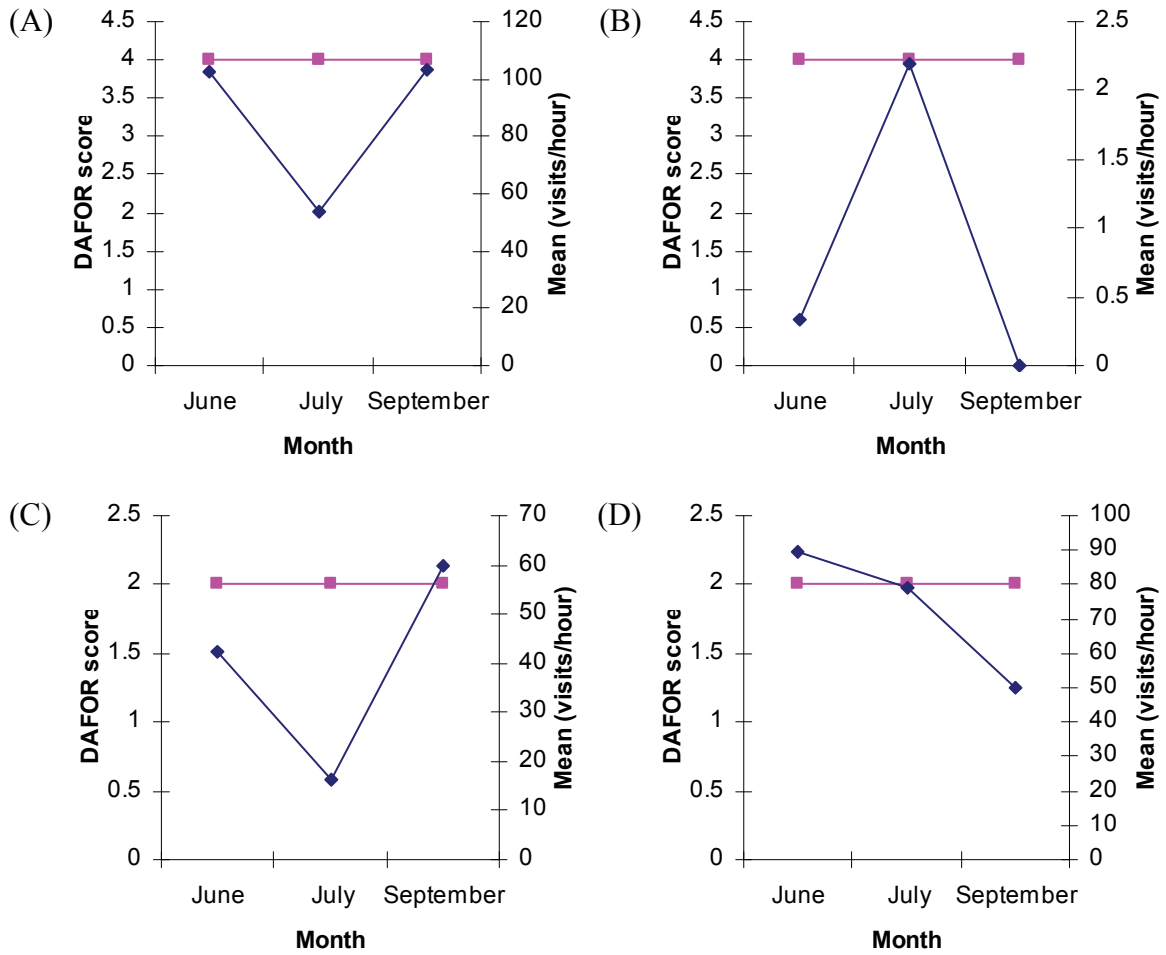


Figure 3. Plot of resource availability (cumulative DAFOR score of plants flowering; square ■) and mean number of visits per hour (diamond ◆) to the 'Bush 2' feeder for male bellbirds (A), female bellbirds (B), male hihi (C) and female hihi (D) each month.

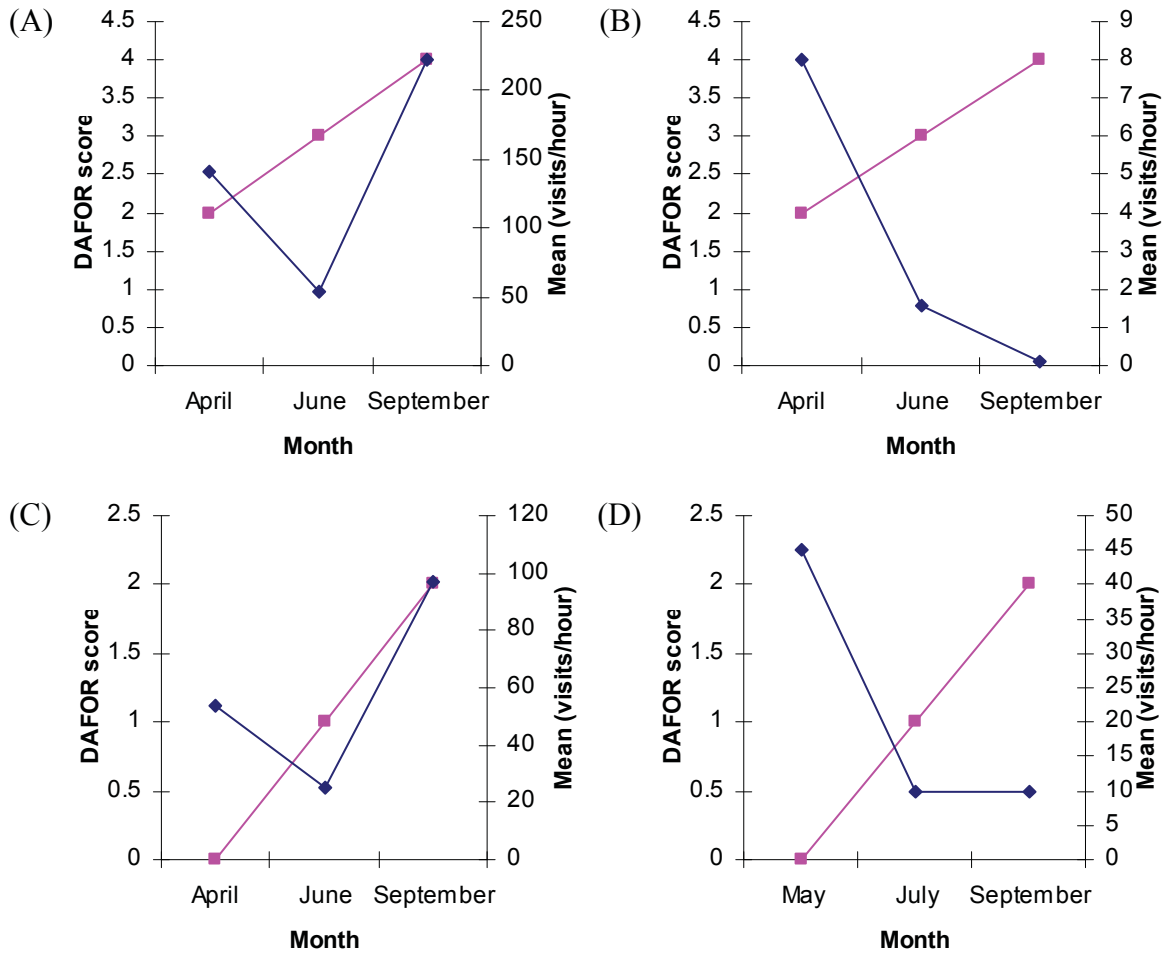


Figure 4. Plot of resource availability (cumulative DAFOR score of plants flowering; square ■) and mean number of visits per hour (diamond ♦) to the ‘Bush 22’ feeder for male bellbirds (A), female bellbirds (B), male hihi (C) and female hihi (D) each month.

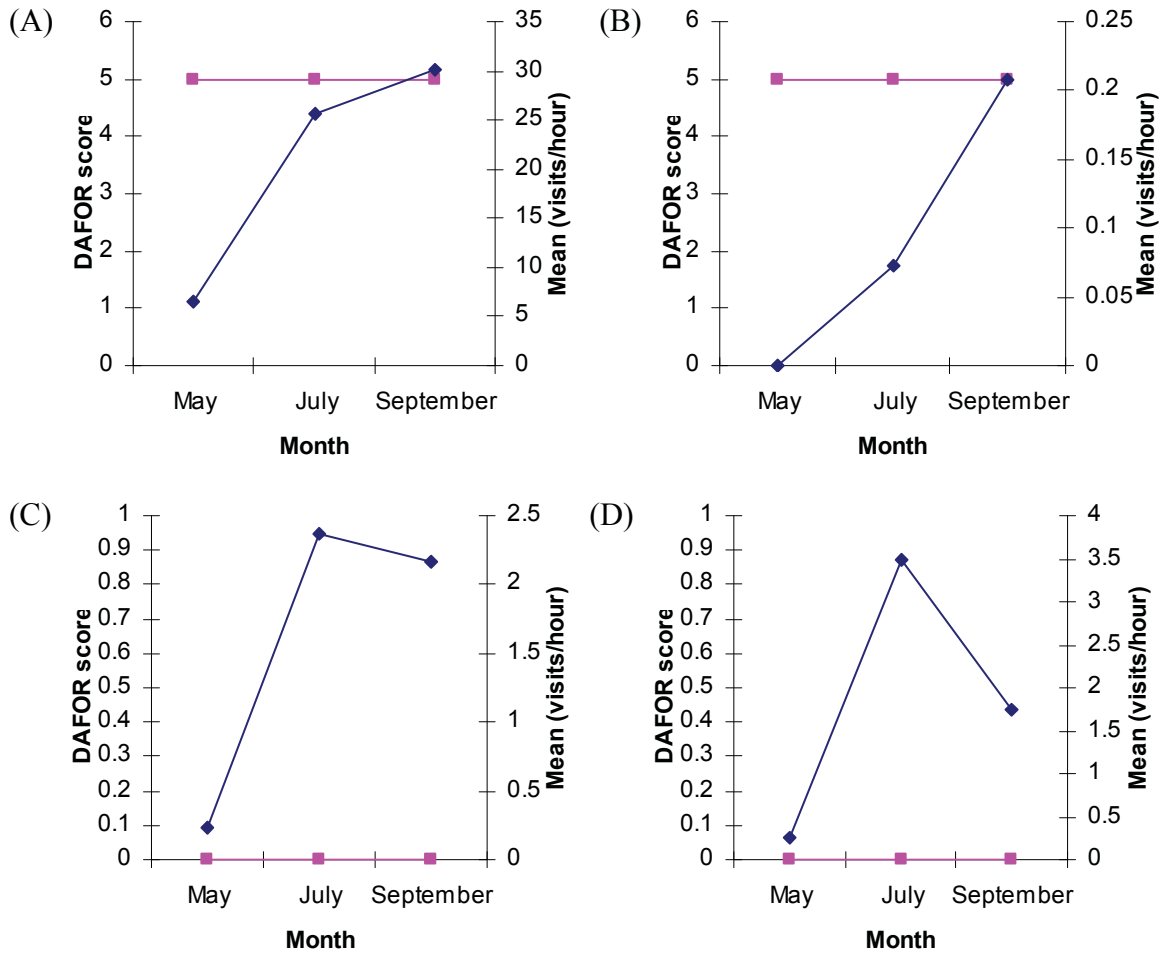


Figure 5. Plot of resource availability (cumulative DAFOR score of plants flowering; square ■) and mean number of visits per hour (diamond ◆) to the 'Dupont' feeder for male bellbirds (A), female bellbirds (B), male hihi (C) and female hihi (D) each month.

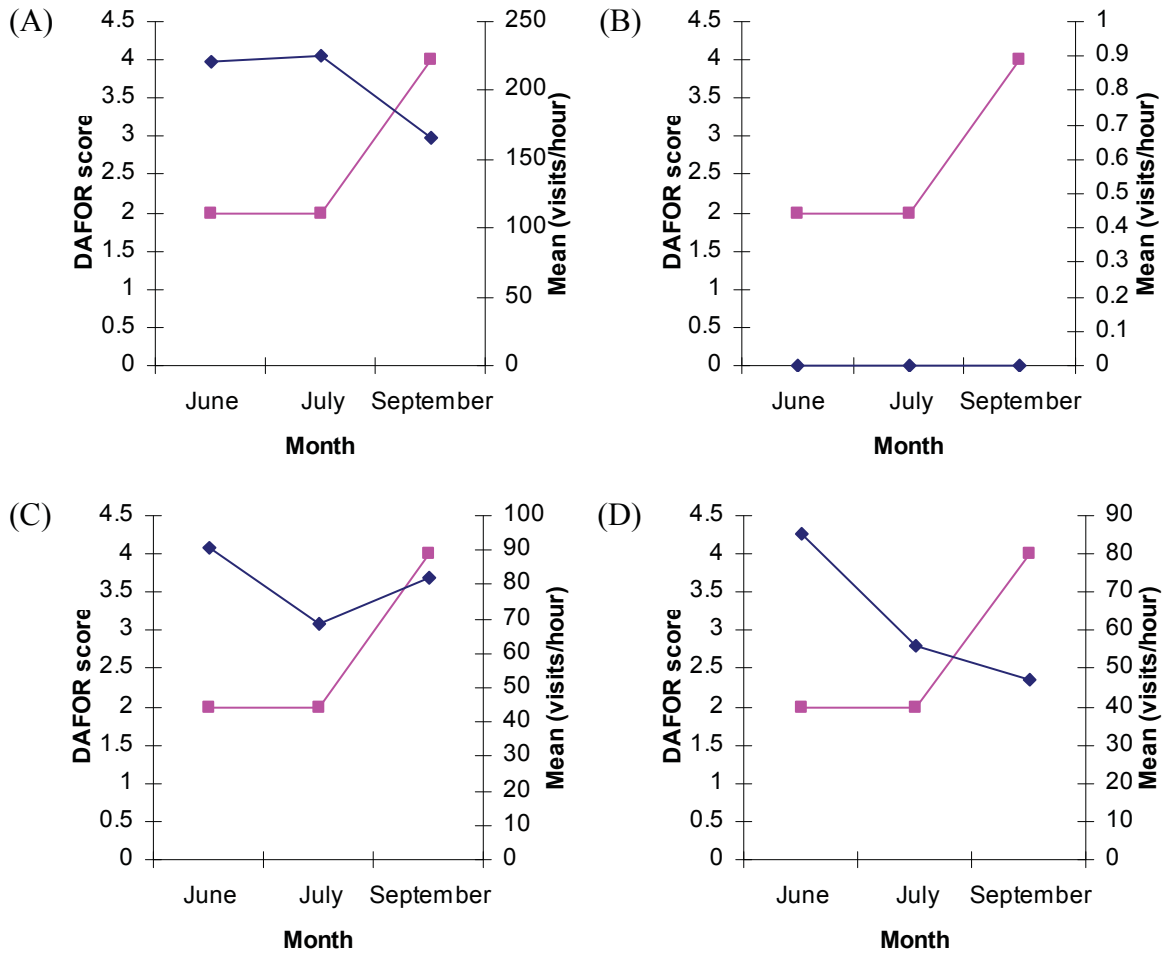


Figure 6. Plot of resource availability (cumulative DAFOR score of plants flowering; square ■) and mean number of visits per hour (diamond ♦) to the ‘Wattle Valley’ feeder for male bellbirds (A), female bellbirds (B), male hihi (C) and female hihi (D) each month.

Chapter 5:

Abundance and density distribution patterns



An example of the mature forest habitat on Tiritiri Matangi Island.

Photo: Michelle Roper, 2010.

5.1 Abstract

To understand the level of resource partitioning and competition between hihi and bellbirds, it is necessary to quantify each species habitat preferences and distribution across various habitat types. Several density estimate methods were found to be biased for a number of reasons: for hihi, inclusion of 'heard only' birds in counts resulted in an overestimate, for bellbirds and hihi transects close to feeders gave inflated density estimates. Transects greater than 85 m from feeders gave consistent results: 218 (\pm 53) hihi per 100 Ha of habitat and 1223 (\pm 409) bellbirds per 195 Ha. Their distribution differed between habitat types with hihi consistently found at highest densities in 'mature forest' with a high of 30 hihi per Ha whereas bellbirds were at highest densities in 'kanuka abundant regenerating forest' at a high of 91.5 bellbirds per Ha. Hihi distribution was relatively consistent throughout the year and influenced by the artificial feeders with highest densities (average 6.4 per ha) found at transects closest to feeders, although this relationship was strongest in spring. Bellbird distribution changed throughout the year with the distribution becoming even across habitat types by the start of the breeding season. Bellbird distribution appeared to be influenced by natural resource availability more than hihi distribution but a more accurate measure of natural resource availability may be needed. Bellbird distribution was also influenced by the artificial feeders with highest densities (average 15.0 per ha) found at transects closest to feeders, although unlike hihi this effect was stronger in autumn/winter than spring. The progressively more even bellbird distribution observed as spring approached was likely related to breeding territory establishment. In contrast, hihi breeding distribution was influenced by the placement of artificial nest boxes which they use exclusively. Both species used artificial feeders and sugar water consumption at these feeders correlated positively with hihi density at transects close to feeders but negatively with bellbird density. This difference is somewhat paradoxical but may be due to bellbirds either staying very close to a feeder (high density range not extending to closest transect) when it is in high demand or travelling longer distances from limited natural available resources to the feeders and not remaining in the surrounding area. A positive correlation was also found between density at close transects and the number of visits per hour to the feeders for both species. Overall, within each habitat type sampled there were positive correlations between hihi

and bellbird densities outside of the breeding season suggesting that hihi distribution between the habitat types is not affected by competitive exclusion from bellbirds.

5.2 Aims

- To obtain the best measures of hihi and bellbird abundance on Tiritiri Matangi Island and assess factors that influence abundance estimates.
- To assess the distribution of bellbirds, hihi and the sexes over all months of the research period.
- To obtain information on each species preferred habitat and assess the level overlap between the species.
- To assess the influence of natural resource availability and the supplementary sugar water feeders on the distribution of hihi and bellbirds across the island.

5.3 Overall abundance

5.3.1 Species

Using observations of both ‘seen and heard’ birds (the standard bird count approach) and including transects both close and far from feeders, the average calculated densities (Table 5.1) gave an estimated abundance of 871 (± 96) hihi and 2019 (± 195) bellbirds on Tiritiri Matangi Island in 2010. Both abundances are overestimates: for hihi the known population size was 176 individuals, for bellbirds previous estimates based on mark recapture are ~1500 individuals (Brunton unpubl data). Abundance estimates were then calculated to remove the potential bias of inclusion of heard only birds. Including only seen birds produced significantly lower estimates (paired t-test; hihi: $t = 13.04$, $n = 8$, $P = 0.000$; bellbird: $t = 4.43$, $n = 8$, $P = 0.000$) and the bellbird abundance was close to previous estimates. However, hihi abundance was still overestimated (Table 5.1).

Table 5.1. Estimated density and abundance of hihi and bellbirds on Tiritiri Matangi Island in 2010 with results for ‘seen and heard’ and ‘seen only’ detections.

	Detection	Area (ha)	Density (birds ha ⁻¹)	Abundance (N ± SE)	Known abundance
Hihi	Seen and heard	100	8.7	871 (± 96)	176
	Seen only	100	4.4	445 (± 206)	176
Bellbird	Seen and heard	195	10.4	2019 (± 195)	
	Seen only	195	7.3	1431 (± 178)	

Estimated hihi densities were then calculated separately from transects categorised by feeder presence as ‘non-feeder areas’ ($\geq 85\text{m}$ from feeder) and ‘feeder areas’ ($< 85\text{m}$ from feeder) and by habitat, ‘tracks/regenerating patches’ and ‘established forest’ (Table 5.2). Significant differences were found between the areas with and without feeders (seen and heard: $t = 11.07$, $n = 8$, $P = 0.00$; seen only: $t = 7.98$, $n = 8$, $P = 0.00$) and different habitat type (seen and heard: $t = 11.40$, $n = 8$, $P = 0.00$; seen only: $t = 11.62$, $n = 8$, $P = 0.00$). Significant differences were also found within each category for most months of the study period (Figure 5.1). Significant differences were also found between ‘seen and heard’ and ‘seen only’ estimated abundances for the two factors within each category (Table 5.2), with ‘seen only’ producing the lowest estimates.

Table 5.2. Estimated hihi abundance over all months calculated from densities within the categories of feeder presence (A) and habitat type (B) with test results from paired t-tests comparing ‘seen and heard’ and ‘seen only’ detections for the two factors within each category.

		Detection	Sample size	Density (birds/ha)	Abundance (N ± S.E.)	t	n	P
A)	Non-feeder areas	Seen and heard	403	5.0	497 (± 100)	8.33	8	0.00
		Seen only	403	2.2	218 (± 53)			
	Feeder areas	Seen and heard	385	12.5	1245 (± 136)	12.25	8	0.00
		Seen only	385	6.4	638 (± 88)			
B)	Tracks	Seen and heard	405	4.0	398 (± 119)	9.12	8	0.00
		Seen only	405	1.3	130 (± 69)			
	Forest	Seen and heard	383	13.4	1344 (± 138)	9.68	8	0.00
		Seen only	383	7.3	726 (± 84)			

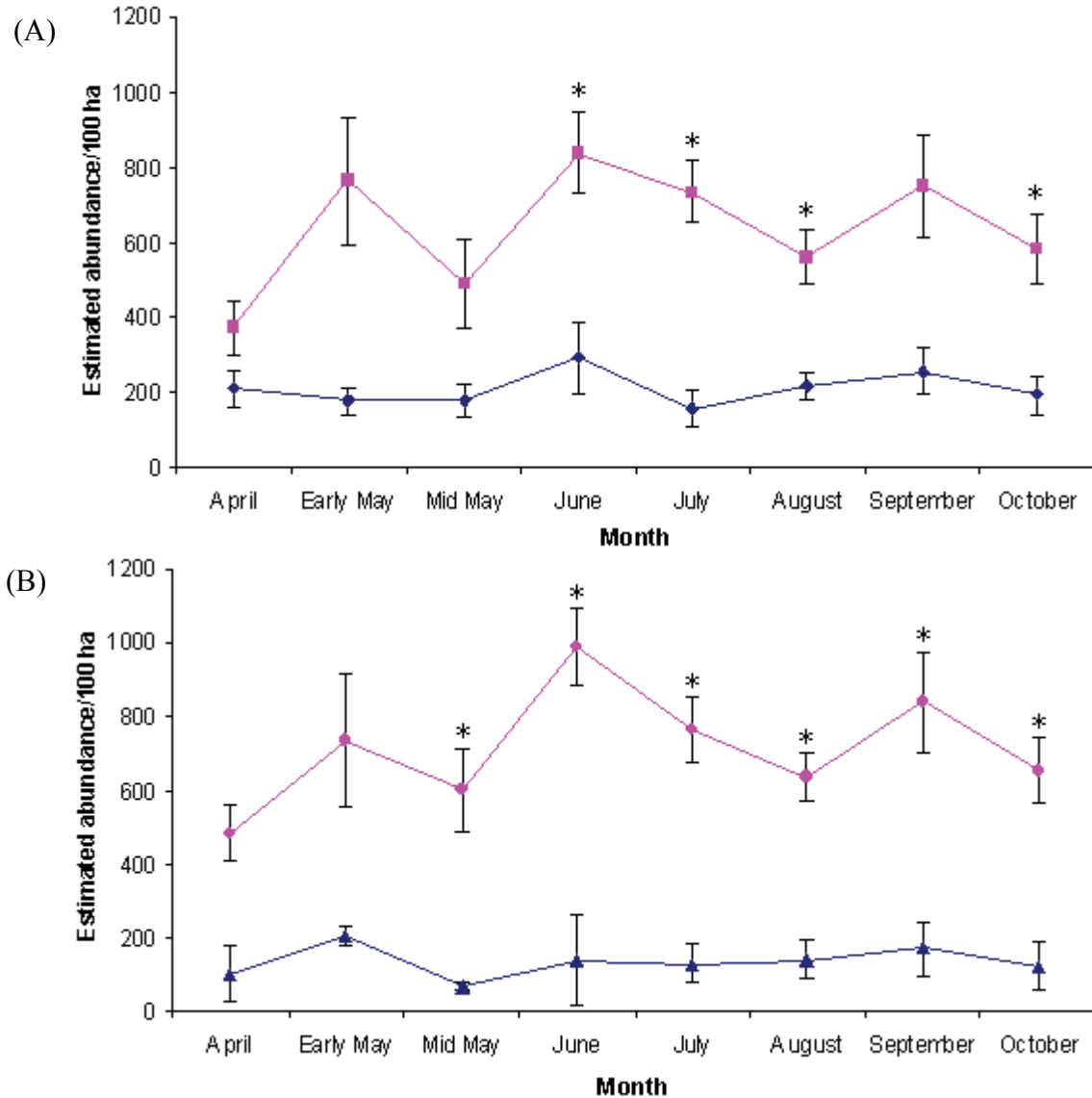


Figure 5.1. Estimated abundance of hihi for ‘seen only’ counts on Tiritiri Matangi Island using densities from ‘non-feeder areas’ (diamond ♦) and ‘feeder areas’ (square ■) (A) and ‘tracks’ (triangle ▲) and ‘forest areas’ (circle ●) (B). * = significant difference ($P < 0.05$) between ‘non-feeder areas’ and ‘feeder areas’ for the month from a Mann-Whitney U-test. Error bars represent standard error values.

These estimates were compared to the known hihi population of 176 individuals (Table 5.3). Only the ‘non-feeder areas’ ‘seen only’ estimate at $218 (\pm 53)$ individuals was not significantly different from the known abundance. Figure 5.1 shows the differences in estimated abundance between ‘feeder areas’ and ‘non-feeder areas’ over the months of observation for the ‘seen only’ counts. These results suggest that the presence of feeders and different habitat had a large impact on the estimations of hihi

densities observed in different locations on the island. The best estimator of abundance with the lowest standard error (Table 5.2) used counts from transects in ‘non-feeder areas’ gave the most consistent estimates throughout the study (Figure 5.1). This suggests that using transects at least 85 m away from feeders could provide a more reliable estimate of hihi abundance. It also suggests that hihi density varies with proximity to feeder.

Table 5.3. Test results from a paired t-test comparing known approximate hihi abundance and my estimated abundance for all transects (total) and within each feeder and habitat category.

	Detection	t	n	P
Total	Seen and heard	11.71	8	0.000
	Seen only	7.22	8	0.000
Non-feeder areas	Seen and heard	9.25	8	0.000
	Seen only	2.16	8	0.067
Feeder areas	Seen and heard	11.85	8	0.000
	Seen only	8.11	8	0.000
Tracks	Seen and heard	5.46	8	0.001
	Seen only	2.84	8	0.025
Forest	Seen and heard	12.36	8	0.000
	Seen only	9.69	8	0.000

Another potential factor affecting the density estimates is habitat. Hihi are most commonly found in mature forest (Angher, 1985) and the feeders are also predominately located in mature forest (personal observation). The density was therefore also calculated based on the counts in mature forest and regenerating forest (Table 5.4). The estimated densities from both ‘seen and heard’ and ‘seen only’ densities however were in total higher than those obtained from the overall estimates in Table 5.1 and hence would give a higher abundance than the known population of 176. Therefore, the closest and most reliable estimate of hihi density and abundance was calculated from transects in areas furthest (≥ 85 m) from the sugar water feeders suggesting that the feeders have a greater influence than habitat type on hihi density.

Table 5.4. Estimated hihi densities at different habitat types on Tiritiri Matangi Island, 2010.

Detection	Forest type	Area (ha)	Density (birds ha ⁻¹ ± SE)
Seen and heard	Mature remnant	45	16.6 ± 1.65
	Replanted	55	6.1 ± 1.72
	Open	0	0
	Grassland	0	0
	Total	100	10.8
Seen only	Mature remnant	45	10.0 ± 1.32
	Replanted	55	2.6 ± 0.97
	Open	0	0
	Grassland	0	0
	Total	100	5.9

As bellbirds also use the sugar water feeders, it is likely that the feeders could be causing bias in bellbird counts at transects near the feeders. Hence, transects were categorised into ‘non-feeder areas’ and ‘feeder areas’ as for hihi (Table 5.5). As for hihi, there were significant differences between ‘seen and heard’ and ‘seen only’ estimates (non-feeder areas: $t = 4.65$, $n = 8$, $P = 0.002$; feeder areas: $t = 3.82$, $n = 8$, $P = 0.007$) as well as between the two areas (seen and heard: $t = 2.58$, $n = 8$, $P = 0.037$; seen only: $t = 2.48$, $n = 8$, $P = 0.042$). Unlike hihi, the closest result to previous estimates on bellbird abundance is for the ‘seen and heard’ ‘non-feeder areas’ estimate at 1223 (± 409) bellbirds. Although this estimate has considerable margin of error it was relatively stable throughout the year (Figure 5.2). However, I cannot completely discount the ‘seen only’ estimate as it also has a large margin of error and was relatively consistent throughout the year. ‘Feeder area’ estimates were very high in April then gradually decreased to levels similar to ‘non-feeder areas’ by September suggesting that feeder use and therefore bias on counts occurs throughout the autumn and winter but declines at the start of the breeding season (Figure 5.2; see Appendix 5.1 for full monthly results).

Table 5.5. Estimated bellbird abundance over all months calculated from densities at ‘non-feeder areas’ and ‘feeder areas’.

	Detection	Sample size	Density (birds ha ⁻¹)	Abundance (N ± S.E.)
Non-feeder areas	Seen and heard	403	6.3	1223 (± 409)
	Seen only		4.0	781 (± 548)
Feeder areas	Seen and heard	385	15.0	2929 (± 287)
	Seen only		13.0	2529 (± 283)

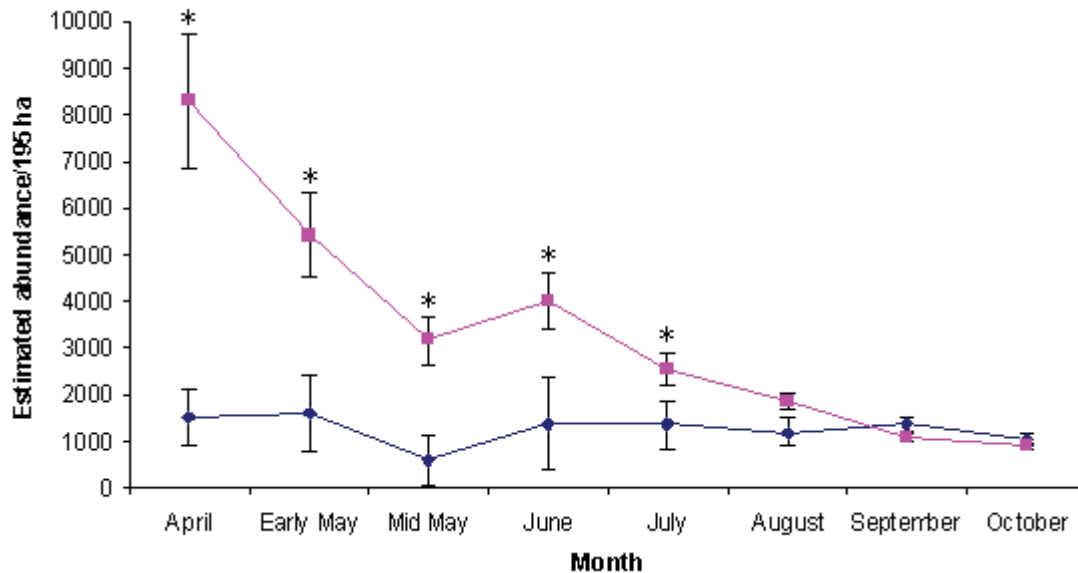


Figure 5.2. Estimated abundance of bellbirds on Tiritiri Matangi Island using densities from ‘seen and heard’ counts for ‘non-feeder areas’ (diamond ♦) and ‘feeder areas’ (square ■). * = significant difference ($P < 0.05$) between ‘non-feeder areas’ and ‘feeder areas’ for each month from a Mann-Whitney U-test. Error bars represent standard error values.

5.3.2 Sexes

The estimated density and abundance of the sexes for both species were also calculated from ‘non-feeder areas’ (Table 5.6) and compared with the estimated abundance at ‘feeder areas’ (Figures 5.3 & 5.4). The ‘seen only’ estimates for hihi were similar for both sexes unlike ‘seen and heard’ which overestimated the number of males (although both were not significantly different; seen and heard: $t = 1.89$, $n = 8$, $P = 0.101$; seen only: $t = 0.38$, $n = 8$, $P = 0.713$). This suggests that either there were more males or males were heard more frequently than females. In the September 2010 survey 102 males and 74 females were found (Ewen, J. pers. comm.) showing that there were more males than females. Both estimates calculated in this study concurred and found more males than females. The monthly estimated abundance for male and female hihi showed similar trends to those for overall hihi abundance (Figures 5.3 and 5.1). Likewise the abundance from ‘non-feeder areas’ were the better estimates of hihi abundance which were more consistent throughout the study period. Therefore, the results for the sexes support the ‘seen only’ counts from the ‘non-feeder area’ transects as the best method for estimating hihi density on a small offshore island with the presence of artificial feeders.

Table 5.6. Estimated density and abundance of male and female hihi and bellbirds on Tiritiri Matangi Island using densities from ‘non-feeder areas’ for ‘seen and heard’ and ‘seen only’ counts with test results from a paired t-test comparing the estimated abundance of each sex for hihi with the known abundance from the September 2010 survey results.

		Detection	Sample size	Density (birds/ha)	Abundance (N ± S.E.)	Known abundance	t	n	P
Hihi	Male	Seen and heard	403	2.67	267 (± 90)	102	2.57	8	0.037
		Seen only	403	1.16	116 (± 51)		0.52	8	0.621
	Female	Seen and heard	403	1.37	137 (± 53)	74	5.55	8	0.001
		Seen only	403	0.99	99 (± 33)		4.49	8	0.003
Bellbird	Male	Seen and heard	403	3.07	598 (± 166)				
		Seen only	403	2.25	438 (± 130)				
	Female	Seen and heard	403	2.29	446 (± 55)				
		Seen only	403	1.27	248 (± 43)				

Table 5.7. Test results from a paired t-test comparing estimated abundances of ‘non-feeder areas’ and ‘feeder areas’ for hihi and bellbird males and females.

		Detection	t	n	P
Hihi	Male	Seen and heard	7.09	8	0.000
		Seen only	8.38	8	0.000
	Female	Seen and heard	5.65	8	0.001
		Seen only	6.18	8	0.000
Bellbird	Male	Seen and heard	3.67	8	0.008
		Seen only	3.50	8	0.010
	Female	Seen and heard	2.62	8	0.034
		Seen only	2.46	8	0.043

For bellbirds, the estimated abundances of males were higher than females (Table 5.6). ‘Seen and heard’ versus ‘seen only’ gave higher estimates for males but lower for females suggesting that female bellbirds were more often heard than seen compared to males (seen and heard: $t = 1.36$, $n = 8$, $P = 0.216$; seen only: $t = 1$, $n = 8$, $P = 0.021$). Monthly variation in estimated bellbird abundances at ‘non-feeder areas’ and ‘feeder areas’ for both sexes showed similar trends as for the overall bellbird abundances (Figure 5.4) but the decrease in female abundance at the ‘feeder areas’ in spring was much more prominent. ‘Feeder area’ abundance was significantly higher than the ‘non-feeder area’ abundance for males and females (Table 5.7). Therefore, using ‘seen only’ counts likely underestimates female bellbird density and the best bellbird abundance estimator for this

small offshore island with the presence of artificial feeders appears to be ‘seen and heard’ counts from the ‘non-feeder area’ transects.

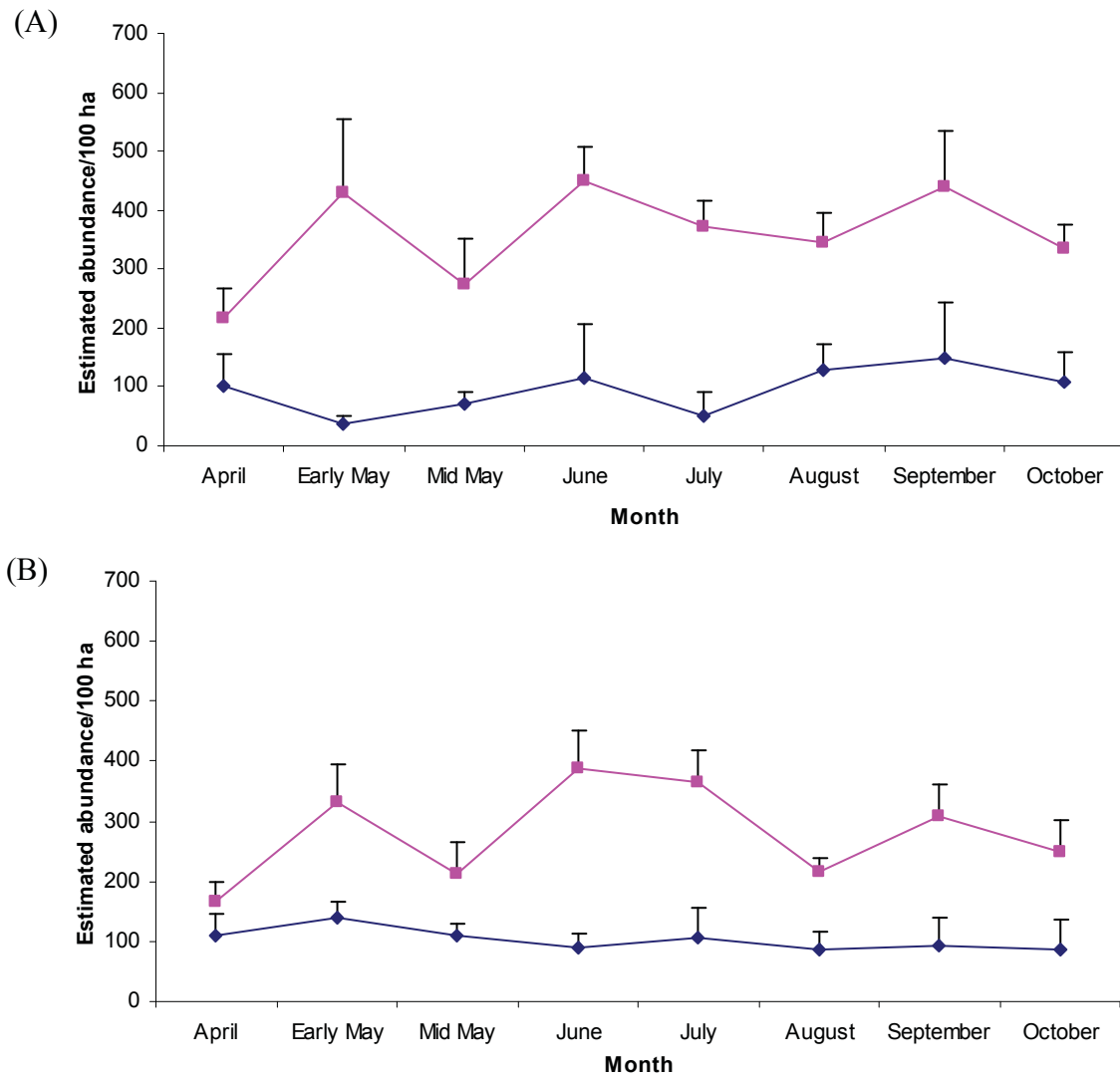


Figure 5.3. Male (A) and female (B) hihi estimated abundances (‘seen only’) on Tiritiri Matangi Island from April to October 2010 using densities from ‘non-feeder areas’ (diamond ♦) and ‘feeder areas’ (square ■). Error bars represent standard error values.

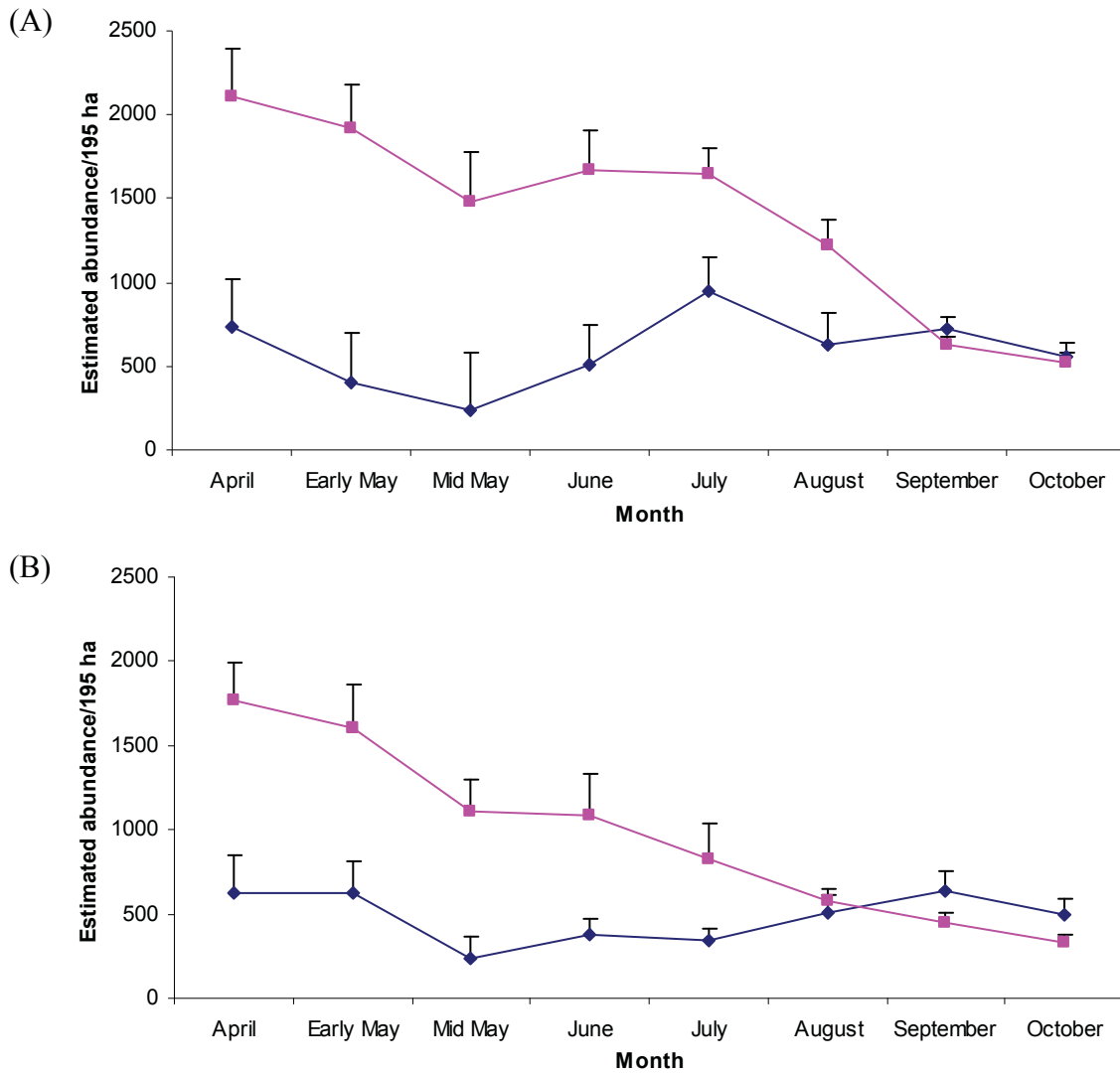


Figure 5.4. Male (A) and female (B) bellbird estimated abundances (‘seen and heard’) on Tiritiri Matangi Island from April to October 2010 using densities from ‘non-feeder areas’ (diamond ♦) and ‘feeder areas’ (square ■). Error bars represent standard error values.

5.4 Distribution

5.4.1 Habitat

The density of hihi and bellbirds (using the best estimator for each species) varied by transect and month (Figures 5.5 & 5.6). Hihi density was relatively low across most transects except for transects 7, 9 and 11 (Figure 5.6). There was some monthly variation in hihi density with for example, prominent peaks in June at transects 8 and 9 (Figures 5.5 & 5.6). For bellbirds, some transects showed much higher densities than others, particularly in autumn, for example, transects 5, 6 and 7 (Figure 5.6). Most transects also displayed prominent monthly variation with bellbirds also showing the same peaks in density in June as hihi at transects 8 and 9 (Figures 5.5 & 5.6). Transects which showed high bellbird densities in April fell to very low densities by October. These data showed that hihi and bellbird distributions varied greatly between different areas of the island and time of year.

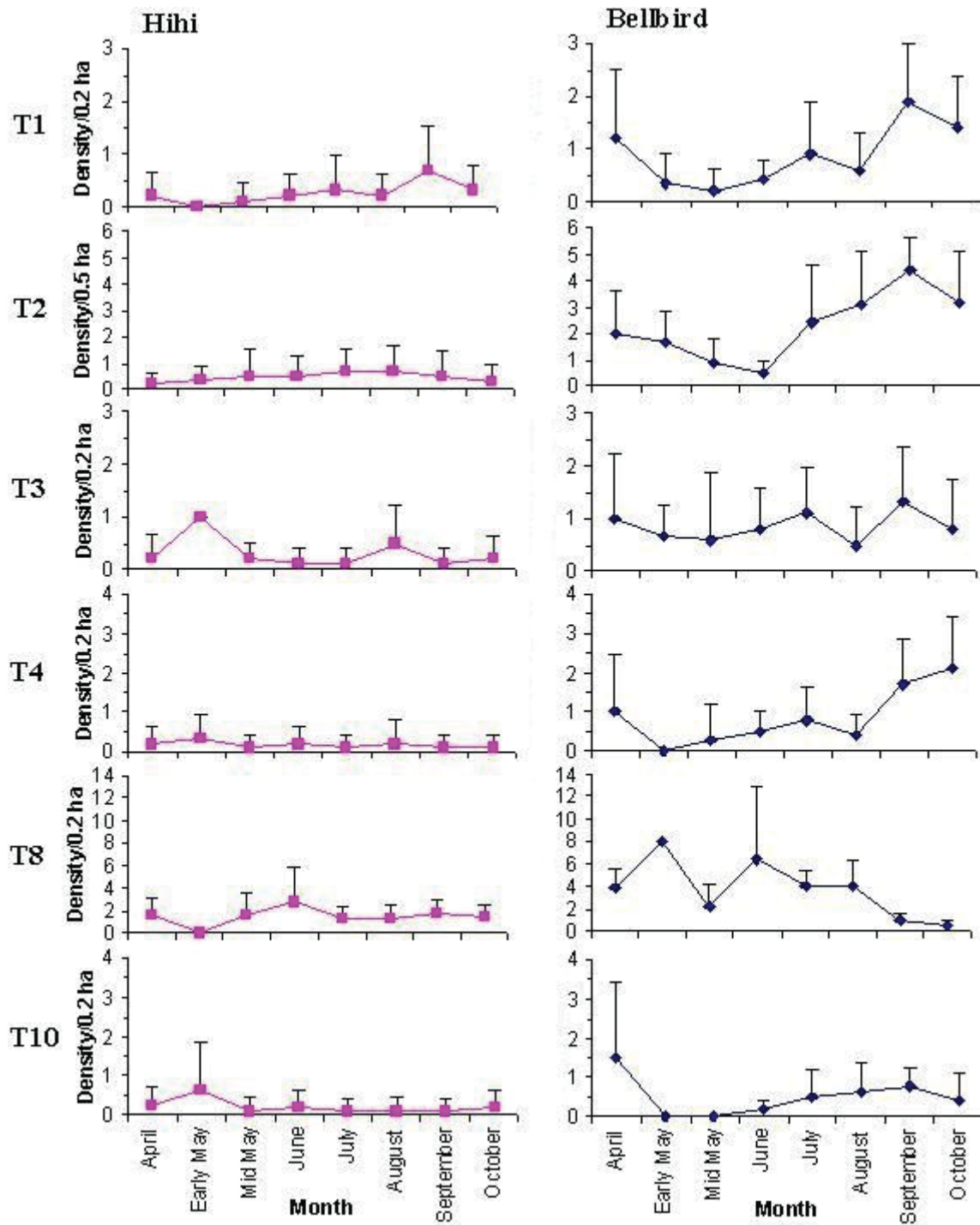


Figure 5.5. Density of hihi ('seen only') and bellbirds ('seen ad heard') from April to October 2010 at each 'non-feeder area' transect. Error bars represent standard error values.

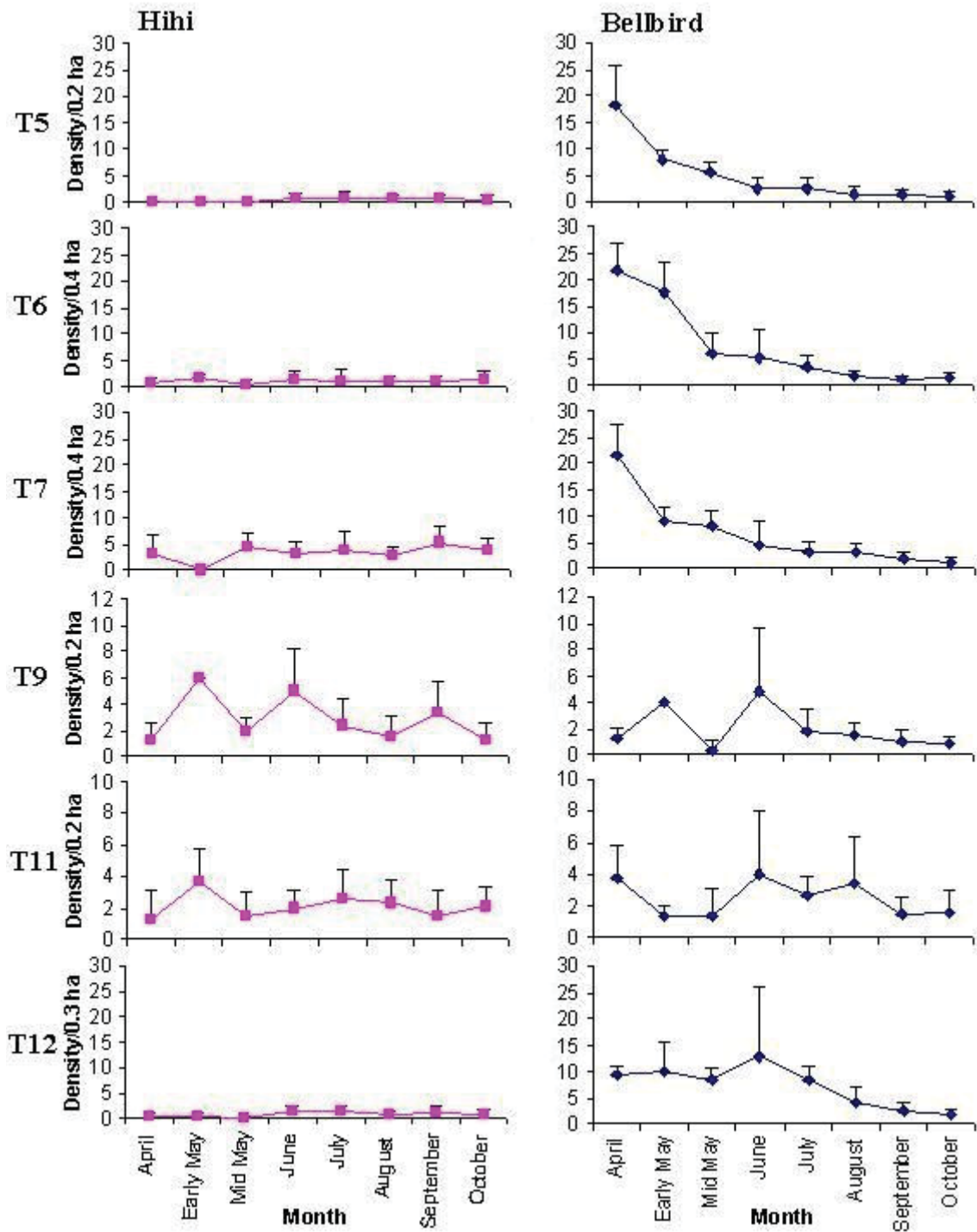


Figure 5.6. Density of hihi ('seen only') and bellbirds ('seen ad heard') from April to October 2010 at each 'feeder area' transect. Error bars represent standard error values.

The average monthly trend in hihi and bellbird density varied across transects. To establish how the distribution of hihi and bellbirds relate to each other, the number of hihi and bellbirds counted at each transect were compared on a daily basis. The test results of a Spearman rank correlation showed significant positive correlations from May to August which corresponds to the seasons of autumn and winter (Table 5.8). April, September and October showed no significant correlation. When September and October were combined as spring there was also no significant correlation (Table 5.8). See Appendix 5.2 for full details on temporal correlation at each transect as some transects showed more positive correlation than others. In autumn and winter there were areas of high densities, particularly bellbirds, but in spring the numbers were much lower and more even. In summary, there was more daily variation in autumn and winter with the distribution of hihi and bellbirds changing in a similar pattern whereas later in the year in spring, there was less daily variation and there were differences in the distribution of hihi compared to bellbirds.

Table 5.8. Test results from a Spearman rank correlation between the number of hihi ('seen only') and bellbirds ('seen and heard') each day of each month, season and overall during 2010 on Tiritiri Matangi Island.

		r_s	n	P
Month	April	0.13	62	0.333
	May	0.18	132	0.0398
	June	0.53	120	<0.0001
	July	0.44	120	<0.0001
	August	0.34	118	<0.0001
	September	-0.03	117	0.738
	October	-0.04	120	0.692
Season	Autumn	0.14	194	0.047
	Winter	0.45	358	<0.0001
	Spring	-0.03	237	0.631
Overall		0.23	789	<0.0001

Hihi densities varied with habitat (vegetation) type (Figure 5.7). The highest densities of hihi were in the 'mature forest (remnant/regenerated)' and 'exotic and native regenerating forest' habitats (Figure 5.7). The mature forest showed very prominent peaks at certain times of the year which suggest this may be the most favourable habitat for hihi. The 'open tracks through mature and regenerating forest' and 'kanuka abundant

regenerating forest' habitats had a relatively consistent but moderate density throughout the period of the study. The lowest densities were found in the 'open tracks through regenerating forest' and 'pohutukawa abundant regenerating forest' habitats but hihi were found in these habitats throughout the year suggesting it was able to sustain a few birds on a long-term temporal basis (although they may still move to other areas for resources i.e. the sugar water feeders; see Appendix 5.3 for values).

The overall distribution of bellbirds was quite different from hihi and there was a substantial change in distribution throughout the year (Figure 5.8). The highest bellbird densities were found in the 'kanuka abundant regenerating forest,' 'mature forest (remnant/regenerated)' and 'open tracks through mature and regenerating forest' habitat types. These high densities however only occurred earlier in the study period and the densities in these habitats steadily declined from April to October. The densities in the remaining habitats showed less variation and more stable bellbird densities throughout the year. By October, the densities at each transect and habitat type were very similar, but with the 'mature forest (remnant/regenerated)' showing lower densities (see Appendix 5.3 for density values).

No significant correlation was found between hihi and bellbird monthly densities for all but two transects; transect one showed a positive correlation ($r_s = 0.90$, $n = 8$, $P = 0.005 < P < 0.001$) and transect 3 showed a negative correlation ($r_s = -0.78$, $n = 8$, $P = 0.025$). Comparing the densities at transects for each month showed a significant difference between densities of hihi and bellbirds from April to August but no difference in September and October (Table 5.9). Therefore, while hihi used habitats consistently from April to October, the habitat preferences of bellbirds varied. In autumn and early winter, bellbirds have a strong preference for certain habitats but by spring they are almost evenly distributed through the entire surveyed range of different forest habitats.

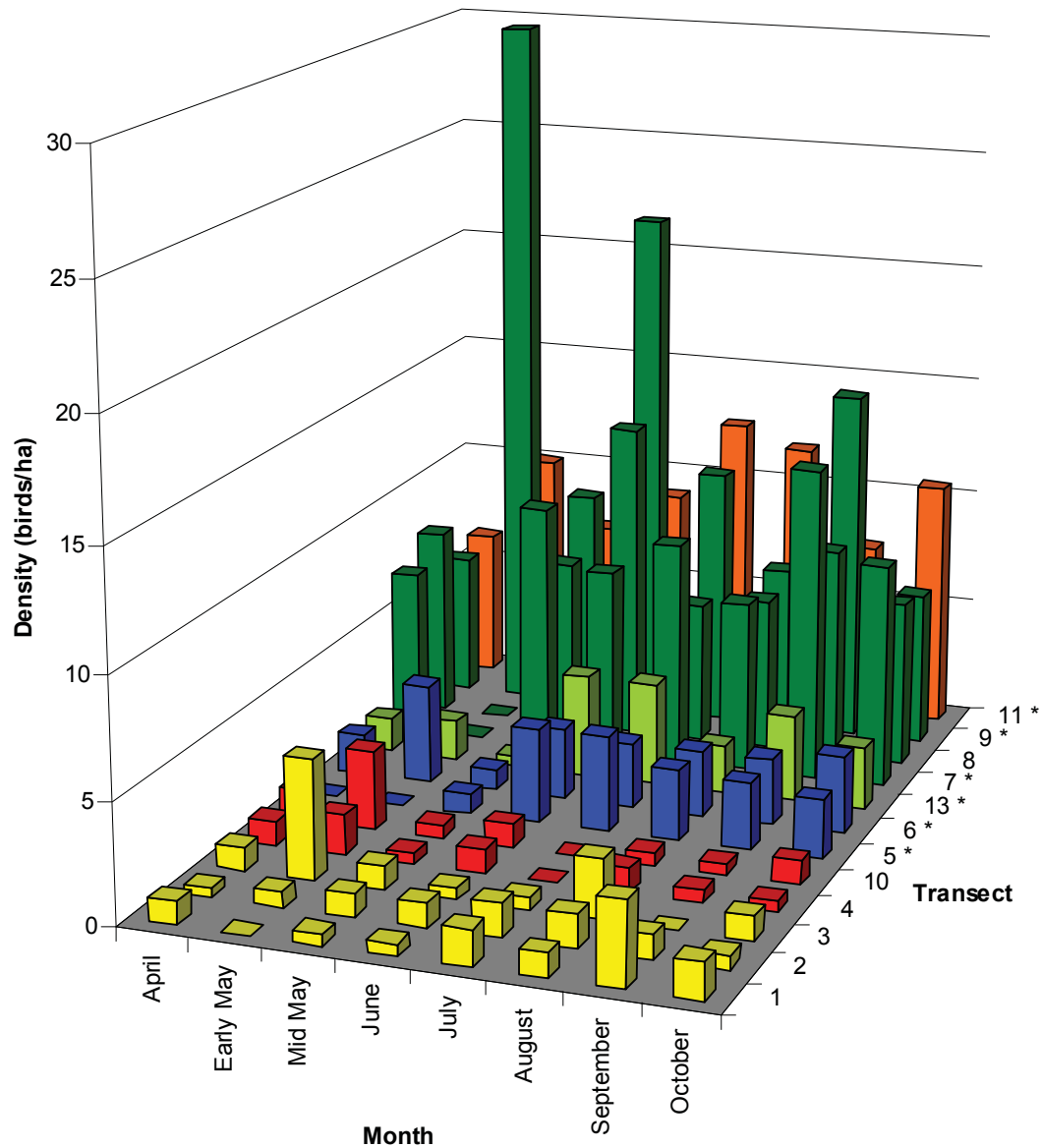


Figure 5.7. Hihi distribution ('seen only' counts) over each month and transect which are categorised into the different habitat types. Key: Yellow = open tracks through regenerating forest; Red = Pohutukawa abundant regenerating forest; Blue = Kanuka abundant regenerating forest; Light green = Open track through mature and regenerating forest; Dark green = mature remnant and regenerating forest; Orange = exotic and native regenerating forest. (Transects in 'feeder areas' labelled with *.)

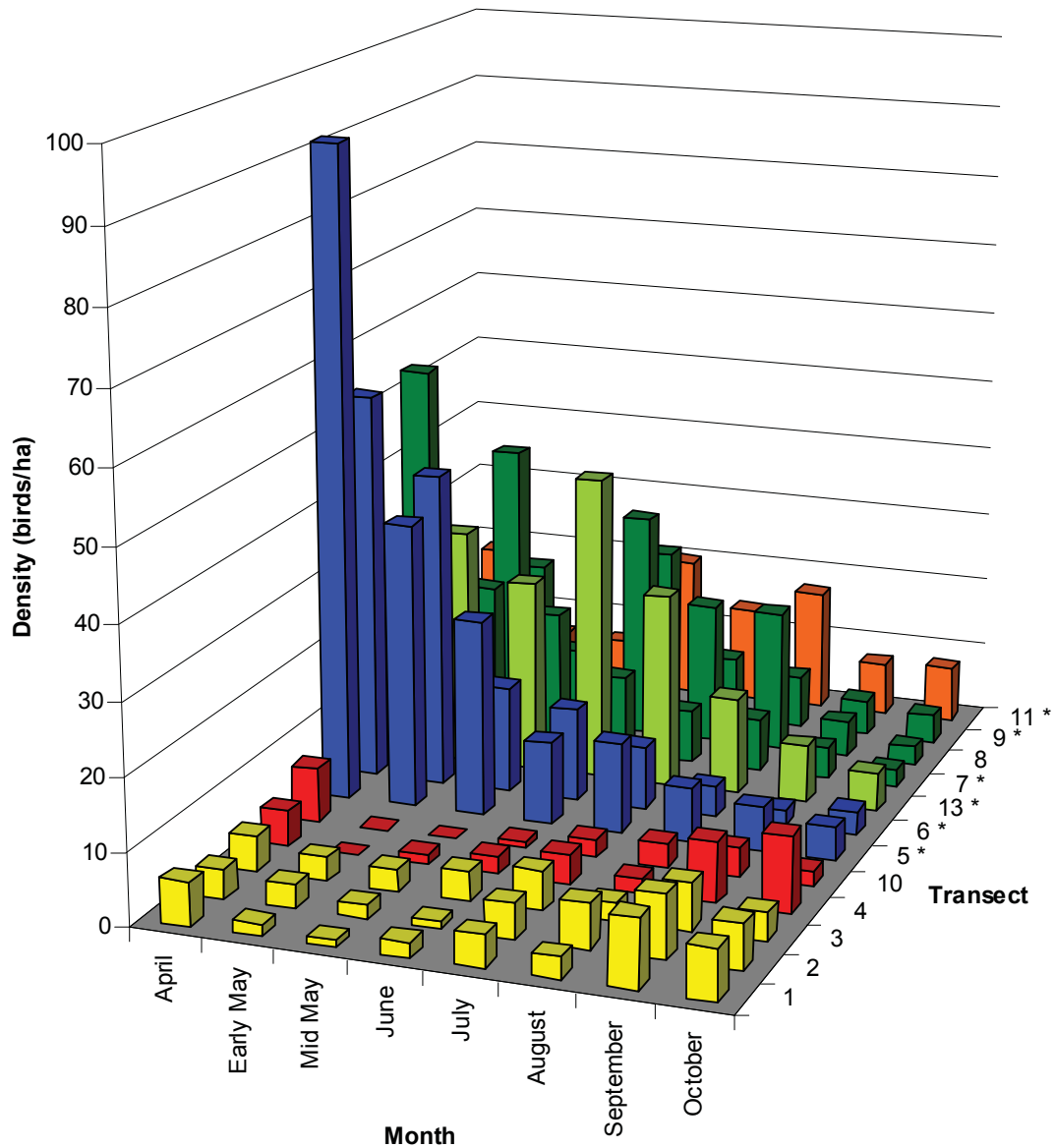


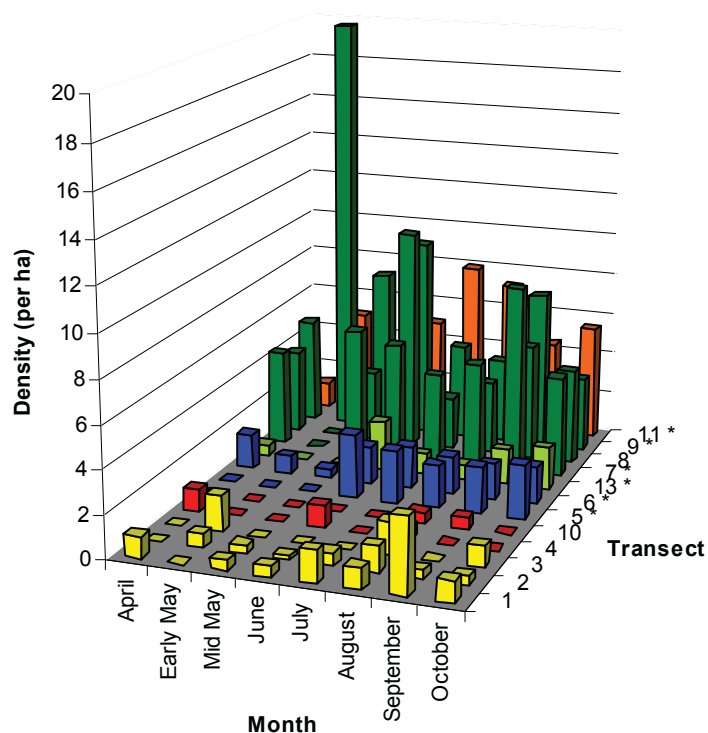
Figure 5.8. Bellbird distribution ('seen and heard' counts) over each month and transect which are categorised into the different habitat types. Key: Yellow = open tracks through regenerating forest; Red = Pohutukawa abundant regenerating forest; Blue = Kanuka abundant regenerating forest; Light green = Open track through mature and regenerating forest; Dark green = mature remnant and regenerating forest; Orange = exotic and native regenerating forest. (Transects in 'feeder areas' labelled with *.)

Table 5.9. Test results from a Wilcoxon signed-rank test comparing estimated hihi and bellbird densities (per ha) at each transect from April to October 2010.

Month	W	n	P
April	0	11	< 0.001
Early May	22.5	12	> 0.2
Mid May	13	12	0.02 < P < 0.05
June	0	10	< 0.001
July	5	12	0.001 < P < 0.005
August	0	11	< 0.001
September	26	11	> 0.2
October	24	11	> 0.2

The sexes of both species typically followed the same trend as for the overall results above (Figures 5.9 & 5.10). Male and female hihi both had highest densities in the ‘mature forest (remnant/regenerated)’ and ‘exotic and native regenerating forest’ habitats. In ‘kanuka abundant regenerating forest’, males tended to have higher densities than females, particularly in late winter and spring. In contrast, females tended to have higher densities in the ‘open track through mature and regenerating forest’ habitat than males, particularly in winter. There was no significant correlation in densities over the months at each transect except for one transect which showed significant negative correlation (Table 5.10), but this could potentially be from the very low number of birds that were seen in this area. Comparing the densities for each month over all transects (Table 5.11) showed no significant difference in densities between male and female hihi from April to July. The significant difference between the sexes in August and September could potentially be due to more males than females being observed in the ‘open tracks through regenerating forest’ habitat, particularly transect 1 in September (see Figure 5.9), as the density of males in this habitat reduces in October where there was no longer any significant difference between the sexes.

(A)



(B)

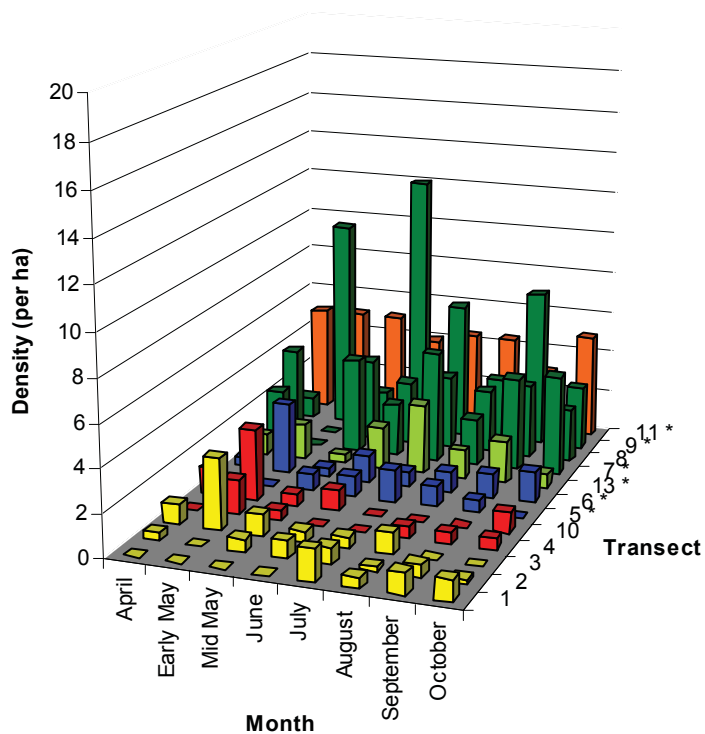
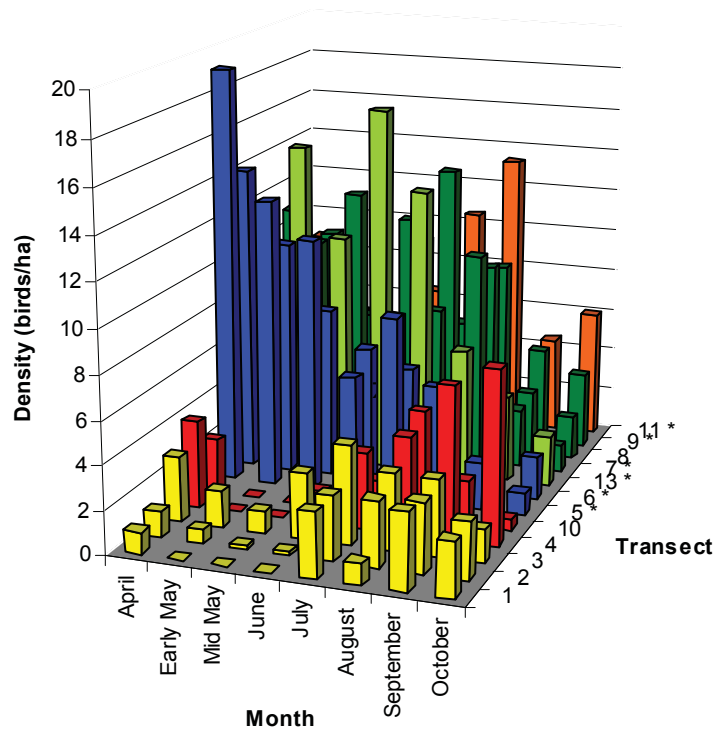


Figure 5.9. Male (A) and female (B) hihi distribution ('seen only' counts). Key: Yellow = open tracks through regenerating forest; Red = Pohutukawa abundant regenerating forest; Blue = Kanuka abundant regenerating forest; Light green = Open track through mature and regenerating forest; Dark green = mature remnant and regenerating forest; Orange = exotic and native regenerating forest. (Transects in 'feeder areas' labelled with *.)

(A)



(B)

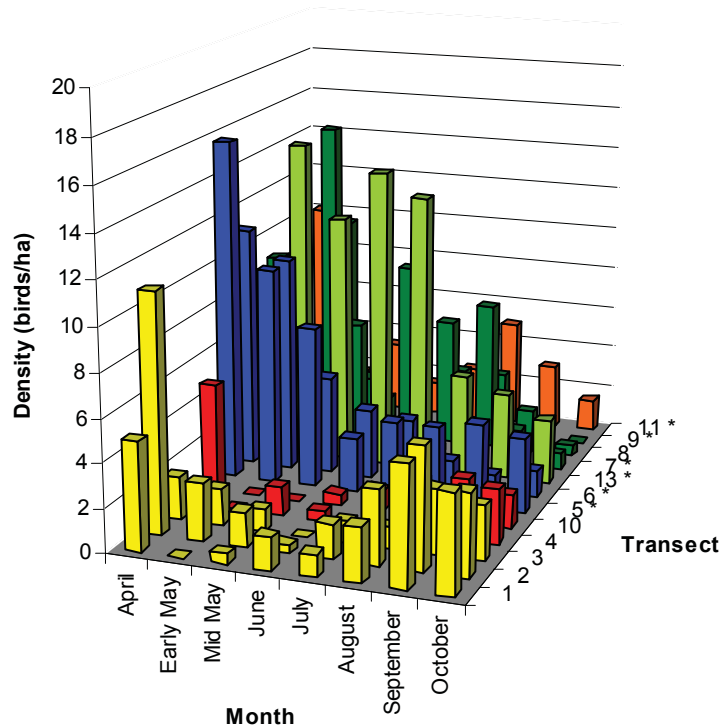


Figure 5.10. Male (A) and female (B) bellbird distribution ('seen and heard' counts). Key: Yellow = open tracks through regenerating forest; Red = Pohutukawa abundant regenerating forest; Blue = Kanuka abundant regenerating forest; Light green = Open track through mature and regenerating forest; Dark green = mature remnant and regenerating forest; Orange = exotic and native regenerating forest. (Transects in 'feeder areas' labelled with *.)

Table 5.10. Test results of a Spearman rank correlation between male and female densities per ha for hihi and bellbird at each transect from April to October 2010.

Transect	Hihi			Bellbird		
	r_s	n	P	r_s	n	P
1	-0.07	8	>0.10	0.66	8	0.05>P>0.025
2	-0.42	8	>0.10	0.53	8	0.1>P>0.05
3	0.41	8	>0.10	-0.07	8	>0.10
4	-0.52	8	>0.10	0.41	8	>0.10
5	0.48	8	>0.10	0.71	8	0.05>P>0.025
6r	0.10	8	>0.10	0.99	8	<0.001
6o	0.41	8	>0.10	0.98	8	<0.001
7	0.16	8	>0.10	0.28	8	>0.10
8	0.08	8	>0.10	0.66	8	0.05>P>0.025
9	0.51	8	>0.10	0.73	8	0.05>P>0.025
10	-0.65	8	0.05>P>0.025	0.88	8	0.005>P>0.001
11	-0.24	8	>0.10	0.20	8	>0.10

Table 5.11. Test results from a Wilcoxon signed-rank test comparing estimated male and female densities (per ha) for hihi and bellbirds each month from April to October 2010 over all transects.

Month	Hihi			Bellbird		
	W	n	P	W	n	P
April	22.5	10	> 0.2	29.5	12	> 0.2
Early May	8	7	> 0.2	13	7	> 0.2
Mid May	24	11	> 0.2	21	10	> 0.2
June	25.5	12	> 0.2	12	12	0.02 < P < 0.05
July	20	10	> 0.2	0	12	< 0.001
August	4	10	0.01 < P < 0.02	4	12	0.001 < P < 0.005
September	6.5	10	0.02 < P < 0.05	21	10	> 0.2
October	16.5	11	0.10 < P < 0.20	34	12	> 0.2

Male and female bellbirds exhibited similar patterns with the highest densities in the ‘kanuka abundant regenerating forest,’ ‘mature forest (remnant/regenerated)’ and ‘open tracks through mature and regenerating forest’ habitats in autumn and early winter (Figure 5.10). However, for some transects/habitats there were distinguishable differences between male and female densities throughout the year. For example, males tended to have higher densities in the ‘pohutukawa abundant regenerating forest’ habitat in spring and females had higher densities in the ‘open tracks through regenerating forest’ in autumn and spring. However, overall positive correlations (5 out of 13 transects) were found over the months and habitat types (Table 5.10). Comparing the densities for each month over all transects showed no significant difference in densities between males and

female bellbirds from April to mid May was found but significant differences were found from June to August (Table 5.11). The densities of females at some transects, especially in the ‘kanuka abundant regenerating forest,’ ‘open tracks through regenerating forest’ and ‘exotic and native regenerating forest’ habitats, declined earlier compared to males (Figure 5.10). Male densities then declined further in September and October where there was no longer any significant difference between males and females (Table 5.11). Therefore, female bellbirds appear to more rapidly disperse from the high density areas into all habitats compared to males.

Food resources and their patterns of availability are likely to influence the distribution of hihi and bellbirds. In general, the levels of resources available at most transects increased from April to October (Figures 5.11 & 5.12). The density of hihi at each transect had little temporal variation and hence did not generally correlate with resource availability (Table 5.12). Only one transect (12; Figure 5.12) showed a significant positive correlation. The trends for Bellbirds were strikingly different (Figures 5.11 & 5.12). Some transects showed significant positive correlations (2 and 8; Figure 5.11), significant negative correlations (5, 6 & 7; Figure 5.12) and no correlation (1, 3, 4, 9, 10, 11, 12; Figures 5.11 & 5.12). Combining all transects, bellbird densities showed a significant positive correlation with resource scores but hihi did not (Table 5.12). The transects that showed positive correlations between bellbird density and the DAFOR score were mainly in the ‘non-feeder areas’ and those with negative correlation were in the ‘feeder areas’. Combining all transects in each area showed significant positive correlation for bellbirds in ‘non-feeder areas’ but not for the ‘feeder areas’ (Table 5.12). No correlation in these areas was found for hihi (Table 5.12).

Despite few significant results, there were some positive correlations between densities and resource levels provided by particular plant species. For example, at transects 8 and 9 (Figures 5.11 & 5.12 respectively) there was a peak in both resource availability and densities of hihi and bellbirds in June which correlated with the onset of kohekohe (*Dysoxylum spectabile*) flowering which is found at either ‘occasional’ or ‘dominant’ levels based on the DAFOR method (Chapter 3).

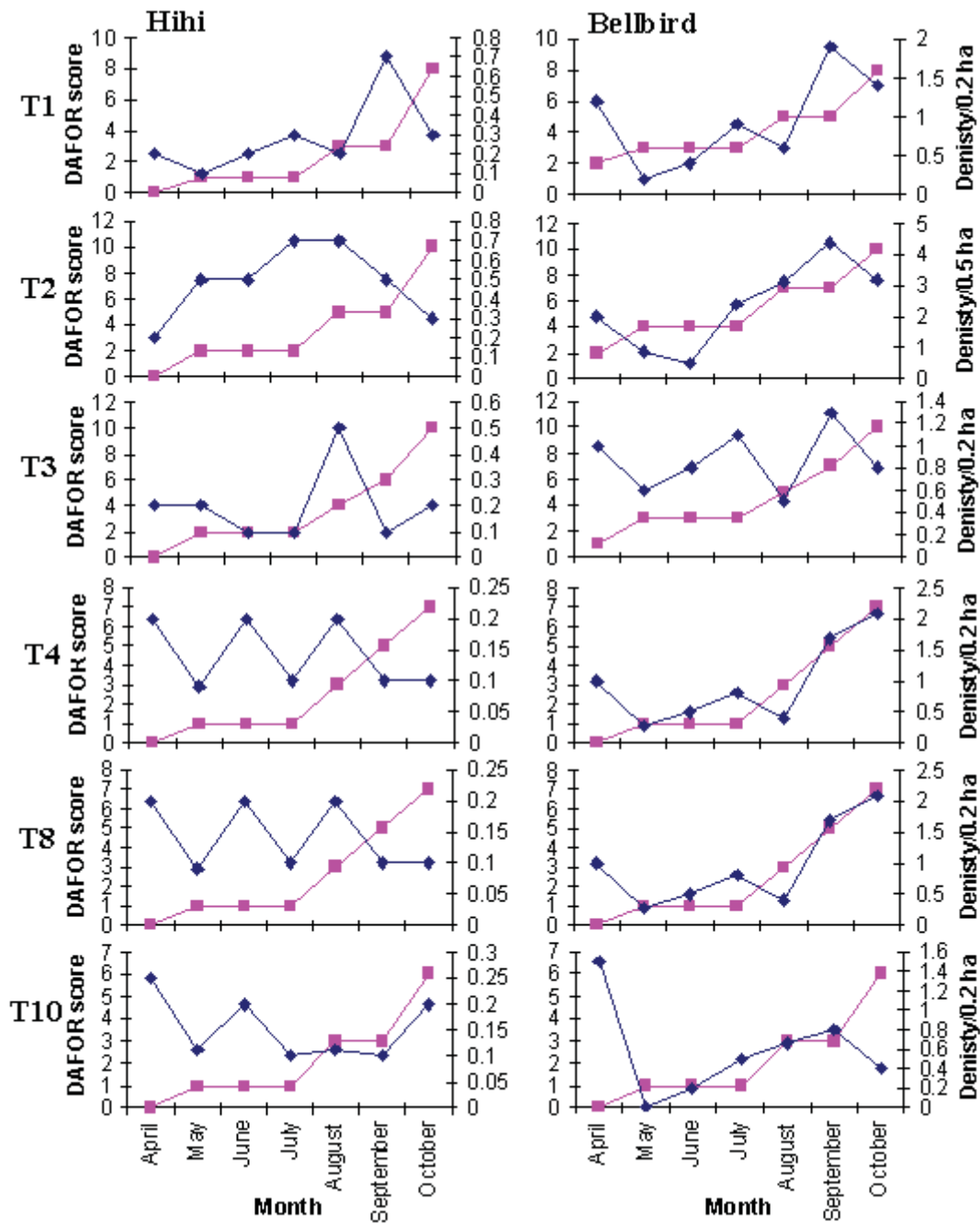


Figure 5.11. Cumulative DAFOR score (*food resources level*; square ■) versus the estimated density (diamond ♦) of hihi ('seen only') and bellbirds ('seen and heard') at the 'non-feeder area' transects.

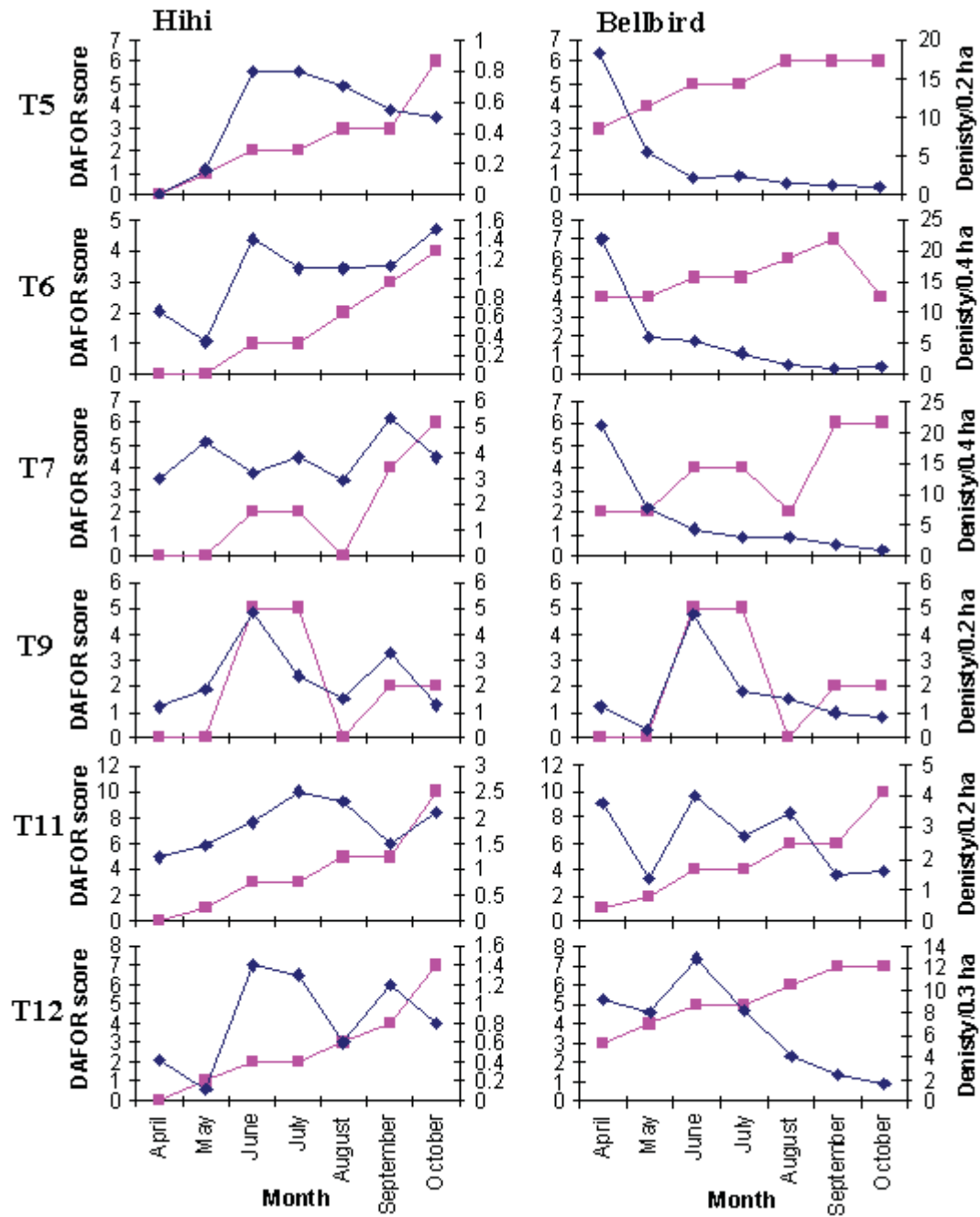


Figure 5.12. Cumulative DAFOR score (*food resources level*; square ■) versus the estimated density (diamond ♦) of hihi ('seen only') and bellbirds ('seen and heard') at the 'feeder area' transects.

Table 5.12. Test results from a Spearman rank correlation between the cumulative DAFOR score (*food resources level*) and the estimated densities of hihi ('seen only') and bellbirds ('seen and heard') at each transect, 'non-feeder areas', 'feeder areas' and overall. NS = not significant.

Transect	Hihi			Bellbird		
	r_s	n	P	r_s	n	P
1	0.51	7	NS	0.41	7	NS
2	0.17	7	NS	0.75	7	0.05>P>0.025
3	0.08	7	NS	-0.04	7	NS
4	-0.28	7	NS	0.44	7	NS
5	0.33	7	NS	-0.95	7	0.005>P>0.001
6	0.38	7	NS	-0.78	7	0.05>P>0.025
7	0.50	7	NS	-0.81	7	0.025>P>0.01
8	0.03	7	NS	0.72	7	0.05>P>0.025
9	0.68	7	NS	0.57	7	NS
10	-0.29	7	NS	-0.09	7	NS
11	0.58	7	NS	-0.22	7	NS
12	0.82	7	0.025>P>0.01	-0.62	7	NS
Non-feeder areas	0.13	40	NS	0.50	40	0.000784
Feeder areas	0.22	40	NS	-0.16	40	NS
All	0.10	84	NS	0.30	84	0.00622

5.4.2 Density distribution and feeders

5.4.2.1 Distance from transects to feeders

Distribution of hihi and bellbirds was also influenced by the proximity of sugar water feeders to transects. The average density and distance to the nearest feeder in the 'non-feeder areas' and 'feeder areas' varied considerably for both hihi and bellbirds (Figure 5.13) showing that in general the nearer a transect was to a feeder, the higher the density of hihi and bellbirds. The presence of feeders near transects resulted in higher densities at certain times of the year dependent on species.(Figure 5.14). The density of hihi was similar at all distances from the feeders in autumn and winter, but as spring approached, the density at the majority of the 'feeder areas' increased. The opposite was seen with bellbirds where the majority of transects in 'feeder areas' had much higher densities in autumn and winter but as spring approached the densities in 'feeder areas' decreased to levels similar in 'non-feeder areas'. Significant negative correlations between the minimum distance from a feeder and density occurred from June to October (except September was marginally significant) for hihi and significant negative correlations from April to August (except early May) for bellbirds (Table 5.13).

Significant differences were found between densities in the two areas from June to October (September not quite significant) for hihi (Figure 5.1) and from April to July (August not quite significant) for bellbirds (Figure 5.2). Therefore, the relationship between density and distance to nearest feeder changed with month/season and opposite trends were observed for hihi and bellbirds.

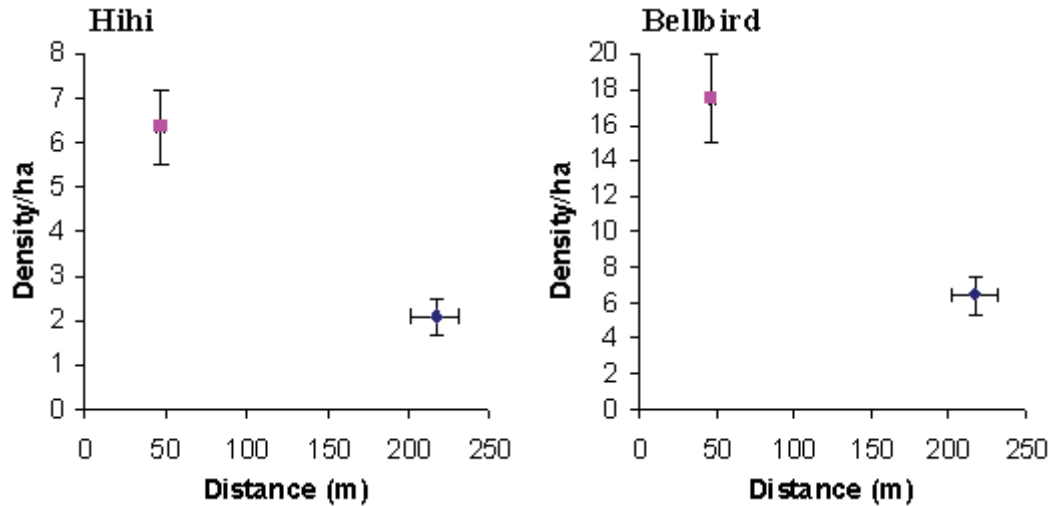


Figure 5.13. The average density per ha (\pm SE bars) and average distance from nearest feeder (\pm SE bars) at ‘non-feeder areas’ (● circle) and ‘feeder areas’ (■ square) for hihi (‘seen only’) and bellbirds (‘seen and heard’).

Table 5.13. Test results from a Spearman rank correlation between the minimum distance from a feeder and density (per ha) at transects for hihi and bellbirds each month.

Month	Hihi			Bellbird		
	r_s	n	P	r_s	n	P
April	-0.39	12	0.214	-0.67	12	0.017
Early May	-0.29	12	0.363	-0.49	12	0.105
Mid May	-0.26	12	0.421	-0.53	12	0.075
June	-0.72	12	0.008	-0.65	12	0.023
July	-0.71	12	0.010	-0.64	12	0.026
August	-0.67	12	0.018	-0.62	12	0.032
September	-0.53	12	0.074	0.40	12	0.194
October	-0.68	12	0.014	0.08	12	0.812

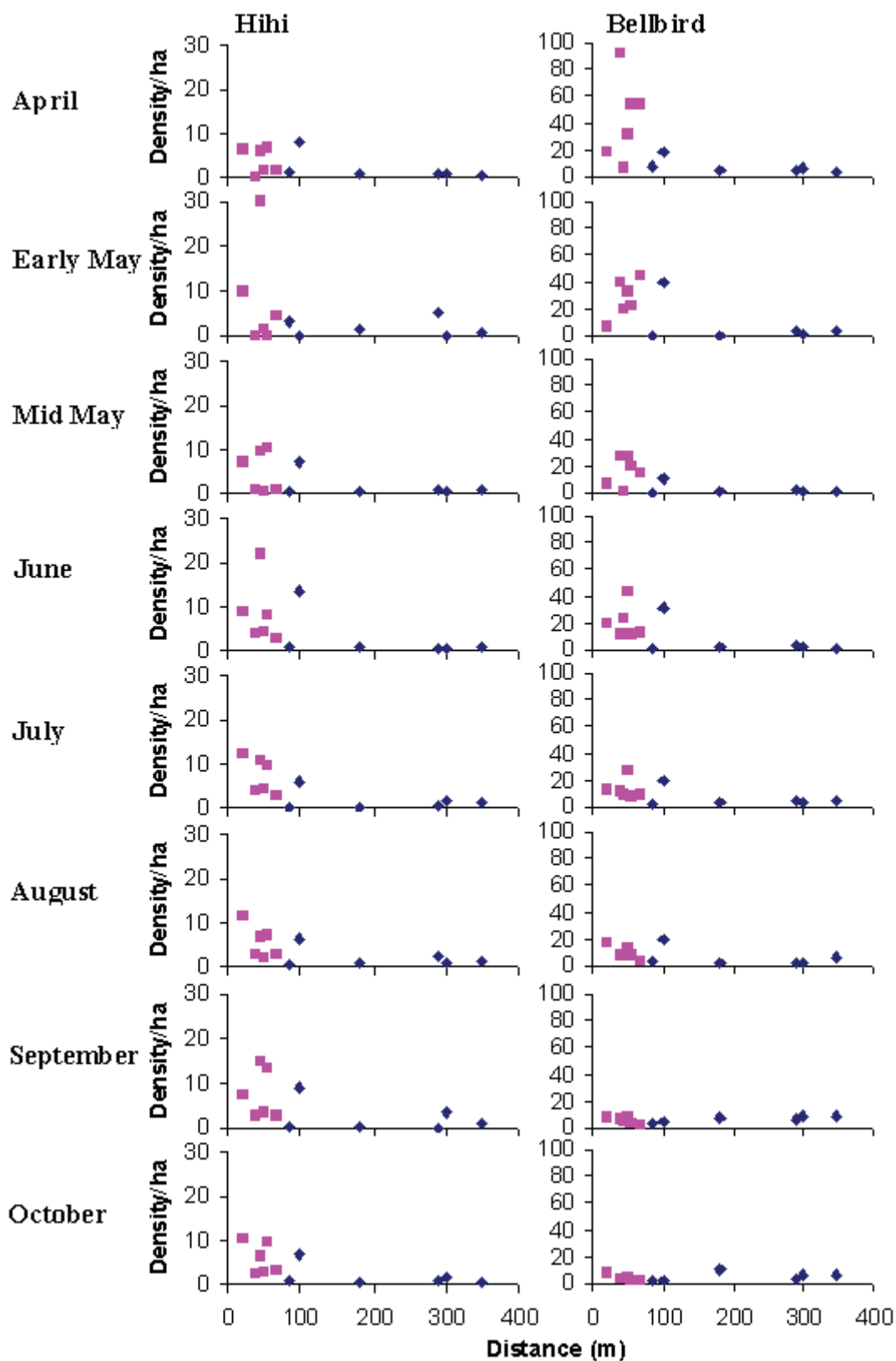


Figure 5.14. Comparisons between the minimum distance to a feeder and estimated density (per ha) of hihi ('seen only') and bellbirds ('seen and heard') for 'non-feeder areas' (■ square) and 'feeder areas' (◆ diamond) each month.

5.4.2.2 Sugar water consumption

To further test the impact of feeders on bird density, I correlated transect densities with the amount of sugar water consumed at the nearest feeder for the ‘feeder areas’. The sugar water consumption records were incomplete for some periods when bird counts were carried out therefore the measurements (litres) were standardised into a percentage for each feeder and each sampling period (Table 5.14). Sugar water consumption was categorised as low (0-10 %), medium (11-20 %) and high (>21 %) sugar water consumption. Densities for transects nearest to feeders in each of these categories (during the sampling period) were compared. The average density (\pm SE) was calculated for each category giving the overall result (Figure 5.15). Hihi showed a positive correlation between density and sugar water consumption with the highest densities of hihi found at transects near feeders with the highest sugar water consumption ($H = 7.64$, $df = 2$, $P = 0.022$). Bellbirds showed the opposite trend with the lowest densities of bellbirds found at transects near feeders with the highest sugar water consumption ($H = 6.83$, $df = 2$, $P = 0.033$).

Table 5.14. Number of litres of sugar water consumed at each feeder per month for the bird count sampling period converted to percentage of litres consumed.

Month	n (days)	Unit	Bush 1 Lower	Bush 1 Upper	Bush 2	Bush 22	Dupont	Wattle Valley
April	6	Litres	28	21	15.75	16.5	4.5	30.75
		Percent	24.0	18.0	13.5	14.2	3.9	26.4
Early May	4	Litres	12.75	8.8	9	10.5	0.7	14.8
		Percent	22.5	15.6	15.9	18.6	1.2	26.2
Mid May	5	Litres	12.7	3	8.8	1.2	1.5	14.9
		Percent	30.2	7.1	20.9	2.9	3.6	35.4
June	4	Litres	12	10.5	6.75	9	0	10.5
		Percent	24.6	21.5	13.8	18.5	0.0	21.5
July	3	Litres	7.5	4.5	3.75	4.5	3	10.5
		Percent	22.2	13.3	11.1	13.3	8.9	31.1
August	6	Litres	15	9	5.5	11	0	12.75
		Percent	28.2	16.9	10.3	20.7	0.0	23.9
September	8	Litres	0.5	10.6	15.75	1.5	20.55	20.25
		Percent	0.7	15.3	22.8	2.2	29.7	29.3
October	8	Litres	11	22.1	16.5	12	28.5	10.8
		Percent	10.9	21.9	16.4	11.9	28.2	10.7

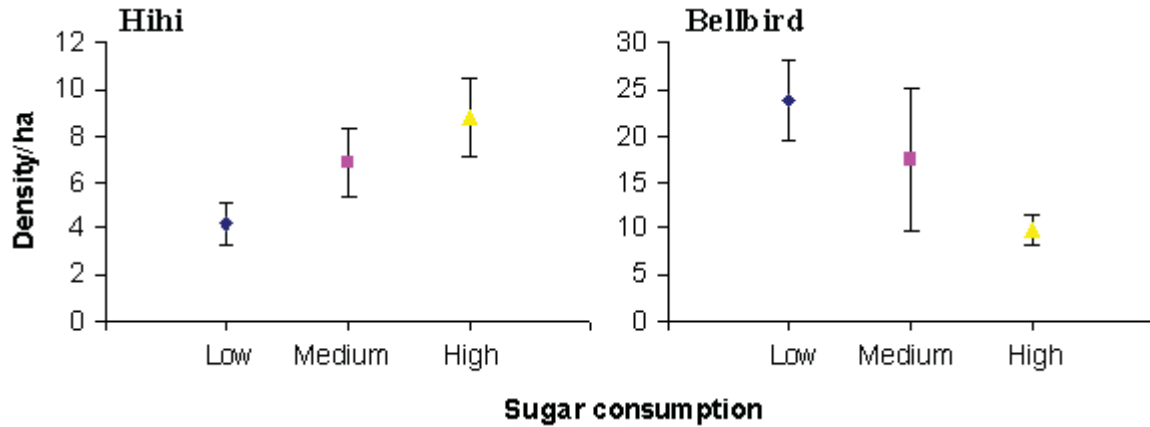


Figure 5.15. Comparison between density per ha at transects in the ‘feeder areas’ with low, medium and high sugar water consumption for hihi (‘seen only’) and bellbirds (‘seen and heard’). Error bars represent standard error values.

5.4.2.3 Feeder visits

The number of birds visiting the feeders was also a potential factor affecting the densities at each transect. Plots of average density per ha against the average number of visits per hour at the nearest feeder show some slight positive correlations for both hihi and bellbirds, particularly in July and September (Figure 5.16). For the sexes of both hihi and bellbirds, no significant correlation was found between density and number of feeder visits per hour each month (Table 5.15). However, pooling data across months did show a positive correlation between density and visits for male and female hihi but not bellbirds except when the sexes were pooled together (Table 5.15). In general, the number of visits to the nearest feeder appears to be positively correlated with density in the surrounding area although this is more so for hihi than bellbirds.

Table 5.15. Test results from a Spearman rank correlation comparing average density per ha with the average number of visits per hour at the nearest feeder for males, females and both sexes of both species during the months of video recording where sufficient data was available. n/a = not available.

		Hihi			Bellbird		
		r_s	n	P	r_s	n	P
Male	May	0.71	4	0.293	-0.45	4	0.553
	June	n/a	2	n/a	n/a	2	n/a
	July	0.32	5	>0.10	0.49	5	>0.10
	September	0.50	6	>0.10	0.49	6	>0.10
	Overall	0.64	17	0.0053	-0.15	17	0.541
Female	May	0.89	4	0.106	0.00	4	1
	June	n/a	2	n/a	n/a	2	n/a
	July	0.81	5	0.1>P>0.05	0.65	5	>0.10
	September	0.68	6	0.1>P>0.05	-0.03	6	P>0.10
	Overall	0.69	17	0.002	0.07	17	0.783
Total	May	0.75	8	0.025>P>0.01	-0.07	8	>0.10
	June	0.40	4	0.6	0.60	4	0.4
	July	0.33	10	>0.10	0.73	10	0.025>P>0.01
	September	0.58	12	0.049	0.40	12	0.196
	Overall	0.59	34	0.0002	0.32	34	0.041

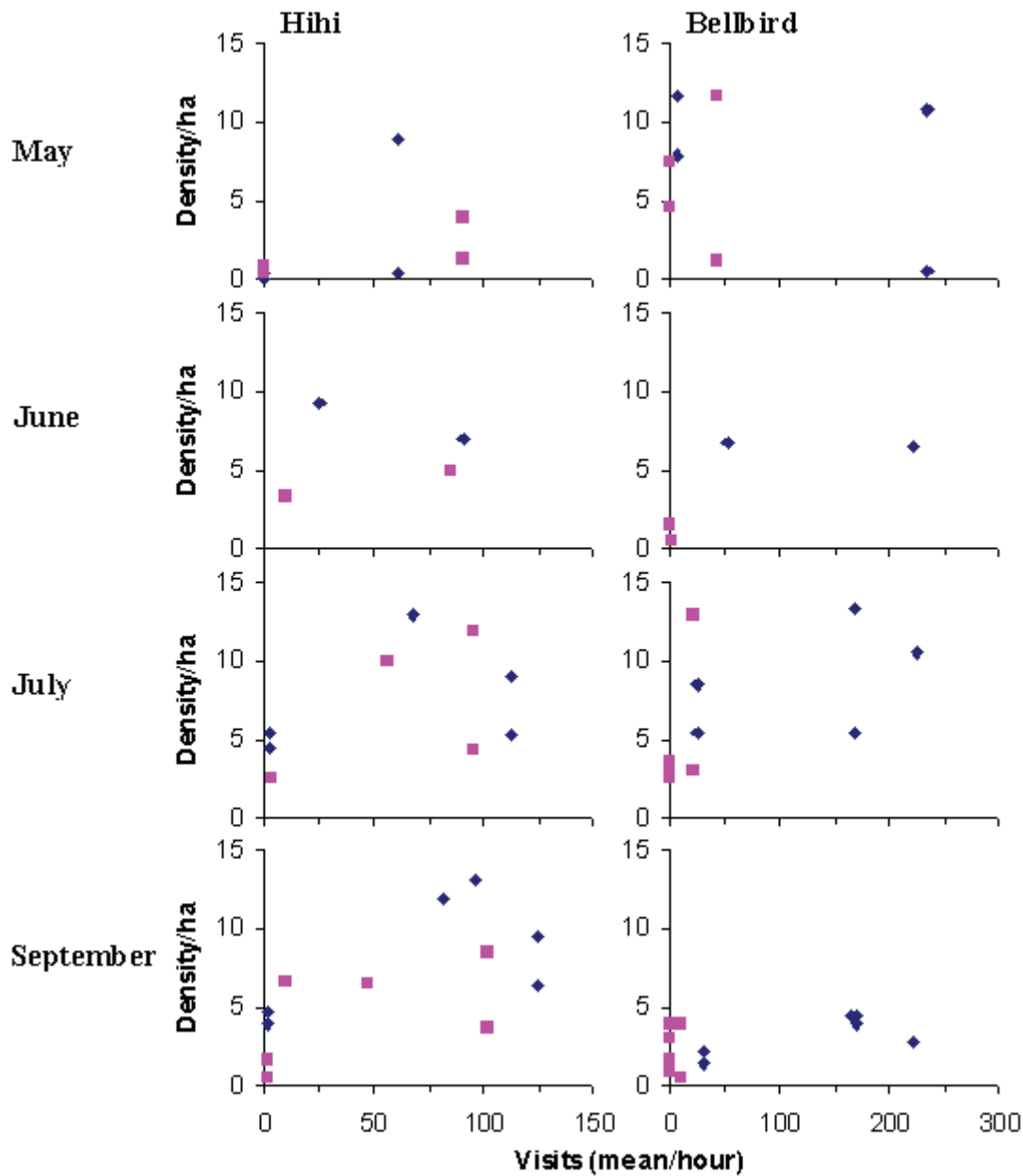


Figure 5.16. Comparisons between the estimated densities per ha and the mean number of visits per hour at nearest feeder for male (♦ diamond) and female (■ square) hihi ('seen only') and bellbirds ('seen and heard') during May (mid-May sampling period), June, July and September 2010.

Because of the contrasting results found from the impacts of the feeders, a comparison was then made between sugar water consumption and visitation to feeders. In general the feeders with the highest sugar water consumption had the highest number of visits per hour (Figure 5.17). However, considerable variation in visitation rates within each consumption category meant that visits in each sugar water consumption category

were not significantly different for both hihi ($H = 1.08$, $df = 2$, $P = 0.582$) and bellbirds ($H = 0.41$, $df = 2$, $P = 0.815$). Likewise for comparisons between sexes of both hihi (male: $H = 0.59$, $df = 2$, $P = 0.746$; female: $H = 0.72$, $df = 2$, $P = 0.696$) and bellbirds (male: $H = 1.47$, $df = 2$, $P = 0.479$; $H = 0.17$, $df = 2$, $P = 0.916$).

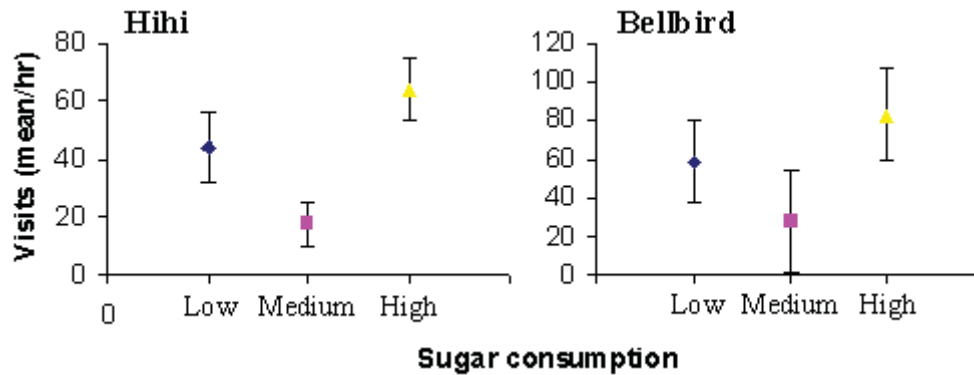


Figure 5.17. Comparison between the average number of visits per hour and the level of sugar water consumption for feeders closest to transects in ‘feeder areas.’ Data for May (mid-May sampling period), June, July and September 2010. Error bars represent standard error values.

5.5 Discussion

5.5.1 Overall abundance

The density and distribution of hihi and bellbirds varied throughout the year under the influence of multiple factors. Standard procedures for calculating density based on fixed-width transects greatly overestimated the density of both species, particularly for hihi. Modifications of these methods were possible as the population size of hihi was known. Best hihi abundance estimates were based on ‘seen only’ counts in areas ≥ 85 m from feeders. Hihi have a wide range of high-pitched vocalisations, males can often call louder than females and there are a number of different calls that each sex can use in different situations (Castro *et al.*, 1996; Higgins *et al.*, 2001). This made it much harder to distinguish between the sexes and it was not easy to identify whether calls were being repeatedly produced by one bird moving around the area or produced by one and then responded to by others. Hihi also increase calling rates at the start of the breeding season in September with intensity being greatest by males before females lay their eggs (Castro *et al.*, 1996) with calling observed to be less common during mid-winter (Angehr, 1984

cited in Higgins *et al.*, 2001). The ‘seen and heard’ counts were highest in August and September which correlates well with the start of the breeding season as in August hihi start to investigate cavities for nest sites and in September males begin calling at the nest sites (Castro *et al.*, 1996; Higgins *et al.*, 2001). However, ‘seen and heard’ counts were lowest in autumn and gradually increased from June to August. Males can sing all year and sing more than females outside of the breeding season (Higgins *et al.*, 2001) which may be why the ‘seen and heard’ counts gave a much higher abundance of males than females and why our ‘seen and heard’ counts were higher than the ‘seen only’ counts. A study by Nijman (2007) on the Great Argus pheasant (*Argusianus argus*) showed that at times when these birds are more highly vocal the abundance estimates are higher. Although the estimated abundance is not significantly different between high and low vocal activity for line transects, it is for point counts and there is no fixed pattern in their calling rates giving the general conclusion that behaviour can affect census methods (Nijman, 2007). Gibb (1996) collected bird counts from a variety of New Zealand bird species and showed that using either ‘first seen’ or ‘first heard’ counts can affect the overall counts for some species but not others showing that there is some discrepancy between using ‘seen’ and ‘heard’ counts (although not for bellbirds) but perhaps only for certain species.

There were other factors that could have biased the estimate of density and abundance. Although including only seen birds produced the closest estimates to the known population size, the main contributing factor to the overestimation of hihi density was the presence of feeders near transects. Feeders are an important food source for hihi survival, condition and reproductive success (Armstrong & Ewen, 2001; Castro *et al.*, 2003) resulting in the attraction of hihi to areas containing feeders. Hihi are known to most commonly inhabit mature and regenerating forested areas on Tiritiri Matangi Island (Ewen *et al.*, 2011) and in my study the highest densities of hihi were in the mature forested areas. Calculating the abundance of hihi based on the size of different habitats and the densities in these habitats however still largely overestimated the abundance indicating that the feeders still may be an integral part in causing this overestimation rather than habitat preference. Calculating the estimated abundance of each sex from ‘non-feeder areas’ and ‘seen only’ counts also gave the best estimate, one similar to the

true population size (102 males and 74 females in September 2010), although slightly more overestimated for females.

Previous surveys of the bellbird population on Tiritiri Matangi Island have been only carried out on single occasions rather than across extended time periods. The current study surveyed over several months and provided a good indication of how the population density in the different habitat types changes over time. Overall monthly densities showed that the estimated abundance of bellbirds dramatically decreased from April to October, possibly due to juvenile mortality, but the margin of error showed that the densities at each transect varied greatly showing differences in their distribution at this time (e.g. flocking in kanuka trees) and potentially indicating there are numerous factors influencing density (Verner, 1981 cited in Moffat & Minot, 1994). Due to bellbirds also being such frequent visitors to the sugar water feeders (Chapter 4), it was assumed that the method for calculating hihi abundance could also be applied. The abundance estimates however were relatively low with a high margin of error and the lowest value within this range was less than a quarter of a previous one-off mark-recapture estimate of 1500. Unlike hihi, bellbirds have vocalisations that are very distinct between the sexes (Brunton & Li, 2006) and female and male song types are easily distinguished in the field. It is also known that bellbirds commonly sing to defend breeding territories and resources and often when a bellbird sings another will reply if it is nearby (Brunton & Li, 2006). So when only one bird was heard signing it could be assumed there was only one bird present in the area (Brunton, *et al.*, 2008) but we would check for other bellbirds if they were in kanuka where they were most commonly observed flocking (personal observation). ‘Seen only’ counts underestimated females compared to males unlike the ‘seen and heard’ counts suggesting that females were more visually inconspicuous and hence heard counts may provide a more reliable detection method for females. A study on bird counts by Gibb (1996) found that using either ‘first seen’ or ‘first heard’ did not affect the overall counts for bellbirds giving further support that using both counts may be appropriate for estimating bellbirds densities. The best abundance estimator for bellbirds was determined to be ‘seen and heard’ counts at the ‘non-feeder areas’. This provided an estimate of 1223 bellbirds for the island in 2010. A

declining trend in bellbird density (for both sexes) over the months was only found in the ‘feeder areas’ showing the strong influence of feeder presence.

One limitation of the fixed-width transect method is the placement of transects. Most transects were located along tracks and in areas with easy access so that regenerating vegetation was not disturbed. This meant that our samples were not random and transects on more exposed tracks could have been subjected to edge effects (Cassey, Craig, McArdle & Barraclough, 2007). Tracks often do not represent particular habitat features and species may avoid the tracks (Buckland, 1985 cited in Cassey *et al.*, 2007). Cassey *et al.* (2007) found that saddleback (*Philesturnus carunculatus rufusater*) density is underestimated by using counts from tracks although this is not significantly different from random transect counts. My best estimates from using transects in ‘non-feeder areas’ contained 3 relatively open tracks however the average estimate was still a slight overestimate for hihi. Our transects covered a range of habitat types that both hihi and bellbirds most commonly occupy therefore our samples were representative despite not being randomly predetermined. Some areas of regenerating forest on the island are not very wide hence if we ran transects through the forest furthest away from the tracks, they may have still been affected by edge effects. Another problem with tracks is that they were not always straight but contain curves (Hiby & Krishna, 2001). Walking pace could also vary and increase the chances of birds being double-counted (Reynolds *et al.*, 1980, Scott and Ramsey, 1981, Fuller and Langslow, 1984, Verner, 1985 cited in Lee & Marsden, 2008) which could have contributed to our overestimates. However, the time it took to sample each transects was fairly consistent and care was taken to avoid errors in methodology.

5.5.2 Distribution

5.5.2.1 Habitat

The density and distribution of both hihi and bellbirds within different habitat types varied throughout the course of this study. Average monthly densities for hihi showed subtle variation with some areas showing higher densities than others. Average monthly bellbird densities however showed much greater variation especially in some

areas where densities dramatically decreased from autumn to spring. Despite the differences in monthly trends between hihi and bellbirds, these species showed positive correlation in their temporal distribution in autumn and winter showing that there were similar factors influencing their preference for particular habitats. Not unsurprisingly, the habitat with relatively high densities of both hihi and bellbirds was the mature (remnant/regenerating) forest. Nonetheless, densities of hihi in each habitat remained more consistent throughout the study compared to bellbird densities

One of the likely causes for such a change in distribution outside of the breeding season is the availability of food resources. The highest densities of bellbirds were found in the 'kanuka abundant regenerating forest' where they were observed feeding on honeydew. These high densities in autumn and early winter relate to the high consumption of honeydew found from the 'first food eaten' data (Chapter 3). The relationship between density and resource availability however was not highly significant for hihi where as bellbirds showed both positive and negative correlations. This likely meant that the method for calculating the resource availability was potentially not sufficiently precise. Considering both hihi and bellbirds showed positive correlation in their numbers at particular areas but hihi habitat preference did not change much throughout the year, it is likely that hihi were responding to resource availability within their preferred habitats whereas bellbirds may be more flexible in their habitat choices and hence were able to move to where the best resources were available regardless of where it was located. A potential reason for the lack of significant correlation between density and resource level was that the method for calculating the resource availability did not take into account the size and productivity of the plants and hence the amount of resources each plant was producing. For example, at transects 8 and 9 there was an increase in both density and resource availability in June with the onset of kohekohe flowering but in July there was a large decrease in density but the resource score remained the same as it did not take into account that the kohekohe flowering and nectar production had also reduced (personal observation). Therefore, although this method did provide some positive correlation between density and resource availability, there were many insignificant results and some negative correlation for bellbirds which will be explained next by other behavioural traits.

These preferences and changes in hihi and bellbird distribution also relate to the onset of the breeding season and territoriality. Hihi are cavity nesters (Rasch, 1985) and therefore require large mature trees to provide such cavities. Tiritiri Matangi Island has very few trees that are large and old enough to provide such cavities therefore artificial nest boxes are provided and used successfully. These nest boxes are predominantly placed in the mature habitat as they would naturally exist, although they are also placed in various areas of regenerating forest habitat (Low, 2005; Ewen, Thorogood, Brekke, Cassey, Karadas & Armstrong, 2009). Therefore, hihi could be favouring the mature forest where the majority of nest boxes were available, hence giving the highest densities in the mature forest (primary habitat) and lower densities in the regenerating forest (secondary habitat; Newton, 1998). Bellbirds are less specific, do not use artificial nest boxes and will nest in a range of trees (Anderson & Craig, 2003) but predominantly cabbage trees on Tiritiri Matangi Island (Cope, 2007). Whilst they are known to highly defend resources throughout the year (Craig & Douglas, 1986) they defend a territory around their nesting site during the breeding season (Brunton & Li, 2006). This change from only defending selected food resources to defending a territory with nesting site and food resources may help explain why bellbird densities change from high densities in selected habitats to a more even spread through all habitats as they must spread to establish (or re-establish) their own territory. This spread may also explain why there were some negative correlations between resource availability and density as only a few pairs of bellbirds may be able to defend territories in some areas even if significant food resources were available. Flocking behaviour, particularly juveniles (Anderson & Craig, 2003), and use of concentrations of food resources (Craig & Douglas, 1986; Higgins *et al.*, 2001) may also have contributed to large densities of bellbirds in autumn and early winter.

5.5.2.2 Distance from transects to feeders

The presence of the feeders had a large impact on hihi and bellbird distribution and this was confirmed by comparing the distances from transects to nearest feeder: the closer a feeder was to a transect, the greater the density of hihi and bellbirds. However, this only occurred during certain times of the year, with opposing trends for hihi and

bellbirds. The correlation was most commonly found in spring for hihi and in autumn/winter for bellbirds. Since hihi have been shown to increase their condition and breed more successfully with the provision of sugar water (Armstrong & Ewen, 2001; Castro *et al.*, 2003), perhaps the significant correlation relates to more hihi using the feeders to improve their condition for the oncoming breeding season and defending nest boxes. The strong correlation with 'feeder areas' for bellbird densities in autumn/winter may relate to the flocking behaviour mentioned above as the 'feeder areas' contained many kanuka trees. However, it is likely that the bellbirds would be intermittently travelling between the kanuka and feeders as the *food resources level* showed how little resources were available in autumn and winter. The decline in correlation between bellbird densities and feeders in spring was likely due to the need for bellbirds to move away from these areas to setup their territories for the breeding season and from increased territorial defence around the feeders. Resource availability increased towards the breeding season which could support them and they would still be able to travel to the feeders when in need. Therefore, these changes in breeding season behaviour have a great impact on where hihi and bellbirds are distributed which makes it more difficult to distinguish a consistent relationship between the densities of birds and relative closeness of a feeder.

5.5.2.3 Sugar water consumption

Directly comparing the average usage of the feeders with density showed some distinguishable results between hihi and bellbirds. Comparing density with sugar water consumption at the nearest feeder showed opposite trends for hihi and bellbirds. Highest hihi densities were near feeders with the highest sugar water consumption whereas highest bellbird densities were near feeders with the lowest sugar water consumption. The results for hihi are logical because the more the sugar water feeders are being used the more birds we expect in the surrounding area. The result for bellbirds was unexpected but could be explained by their long distance movements between resources as bellbirds are known to be able to travel further than hihi (Higgins *et al.*, 2001). Although Tiritiri Matangi is not a very large island, hihi may still tend to be more sedentary and remain closer to feeder sites. Bellbird distribution was variable throughout the year and hence

most likely due to changes in resource availability around the island. An alternative explanation is that at the high sugar water consumption feeders, the bellbirds were condensed around the feeder and were not venturing out into the surrounding area. However given that female bellbirds do not use feeders to the same extent as male bellbirds this is probably not the full explanation. Hence, further research on their movements between feeders and natural resources (e.g. with radio tags) is needed to further understand why these different trends between hihi and bellbirds occurred.

5.5.2.4 Feeder visits

The average number of visits per hour showed some similar results between hihi and bellbirds. When the results were combined for both sexes there was positive correlation between density and visits to the nearest feeder for some months. For hihi this relationship was strong. However, there was considerable variation in the visits to feeders within each sugar water consumption category such that visitation rates did not statistically vary between low, medium and high consumption feeders. This finding was not expected because when observing the feeder footage (Chapter 4) there appeared to be a high level of sugar water consumption when there were a high number of visits. A factor potentially affecting these results is that when a sugar water feeder became blocked, little sugar water could be obtained which meant the birds had to visit more often to acquire a substantial amount of sugar water. Bellbirds only showed slight significant positive correlation when the sexes and months were combined indicating that there may be a weaker relationship between density and number of visits for bellbirds unlike hihi which showed a slightly stronger relationship. Therefore, both high visitation rates and level of sugar water consumption are predictors for high densities of hihi in the surrounding area but only high visitation rates may be a predictor for high bellbird densities in the area surrounding the feeder not high levels of sugar water consumption. Further research on this should include more accurately measuring and keeping track of how many litres of sugar water is being consumed at each feeder and directly comparing the number of litres consumed with the number of visits to the feeder, also taking into account whether a feeder was blocked.

5.6 Conclusion

Estimates of abundance of hihi and bellbirds on Tiritiri Matangi were influenced by their behaviour, seasonal changes in behaviour, resource availability and the presence of artificial sugar water feeders. Conducting counts on transects at least 85 m from a feeder produced the most consistent estimates of abundance for both hihi and bellbirds. Hihi abundance was also most accurate when ‘seen only’ counts were used. For bellbirds avoiding feeders is also recommended but best estimates of abundance can be achieved using ‘seen and heard’ counts. Replication of many transects is essential to give low standard error and increase precision. Hihi had a strong preference for mature forest which was consistent throughout the year compared to bellbirds where there was preference for some habitat types such as ‘kanuka abundant regenerating forest’ but by the breeding season there was an even distribution across all habitat types sampled. Within these habitats there was positive correlation between hihi and bellbirds outside of the breeding season suggesting that hihi distribution between habitat types is not affected by competitive exclusion from bellbirds.

Appendix 5.1. Monthly abundance estimates for bellbirds

Table 1. Estimated density and abundance of bellbirds on Tiritiri Matangi Island each month from April to October 2010.

Month	Detection	Sample size	Density (birds ha ⁻¹)	Abundance (± S.E.)
April	Seen and heard	62	25.15	4903 (± 832)
	Seen only		16.60	3237 (± 694)
Early May	Seen and heard	30	17.92	3494 (± 550)
	Seen only		14.87	2899 (± 547)
Mid May	Seen and heard	102	9.64	1880 (± 313)
	Seen only		7.45	1452 (± 245)
June	Seen and heard	120	13.77	2685 (± 412)
	Seen only		10.27	2002 (± 385)
July	Seen and heard	120	9.99	1948 (± 223)
	Seen only		8.00	1560 (± 229)
August	Seen and heard	118	7.89	1538 (± 147)
	Seen only		4.95	965 (± 121)
September	Seen and heard	117	6.30	1228 (± 85)
	Seen only		3.65	711 (± 56)
October	Seen and heard	120	5.00	975 (± 72)
	Seen only		2.88	561 (± 47)

Appendix 5.2. Statistical outputs for the comparison of daily variation between the number of hihi and bellbirds

Table 1. Temporal comparisons between the number of hihi (seen only) and bellbirds (seen and heard) counted at each transect from April to October 2010 on Tiritiri Matangi Island.

		Transect											
		1	2	3	4	5	6r	6o	7	8	9	10	11
April	r _s	0.00	0.36	-0.56	0.79	-	0.02	-0.69	0.21	0.08	0.46	-0.54	0.50
	n	5	5	5	5	6	6	7	7	5	5	4	4
	P	P>0.10	P>0.10	P>0.10	P>0.10	-	P>0.10	0.1>P>0.05	P>0.10	P>0.10	P>0.10	P>0.10	0.466
May	r _s	-0.16	-0.19	0.27	-0.11	0.15	0.73	-0.53	-0.05	-0.11	0.55	-	-
	n	13	13	13	14	9	9	10	7	10	10	12	12
	P	0.606	0.530	0.373	0.700	P>0.10	0.025>P>0.01	0.1>P>0.05	P>0.10	P>0.10	0.1>P>0.05	-	-
June	r _s	-0.22	0.04	-0.38	0.25	0.12	0.61	-0.12	0.46	0.48	0.41	-0.25	0.24
	n	10	10	10	10	10	10	10	10	10	10	10	10
	P	P>0.10	P>0.10	P>0.10	P>0.10	P>0.10	0.05>P>0.025	P>0.10	0.1>P>0.05	0.1>P>0.05	P>0.10	P>0.10	P>0.10
July	r _s	0.48	-0.05	0.46	-	-0.08	0.61	0.19	0.96	-0.11	0.61	-	-0.20
	n	10	10	10	10	10	10	10	10	10	10	10	10
	P	0.1>P>0.05	P>0.10	0.1>P>0.05	-	P>0.10	0.05>P>0.025	P>0.10	P<0.001	P>0.10	0.05>P>0.025	-	P>0.10
August	r _s	-0.48	-0.04	-0.17	0.41	0.04	-0.03	0.52	-0.42	0.75	-0.24	0.23	-0.18
	n	10	10	10	10	10	10	10	10	10	10	9	9
	P	0.1>P>0.05	P>0.10	P>0.10	P>0.10	P>0.10	P>0.10	0.1>P>0.05	P>0.10	0.01>P>0.005	P>0.10	P>0.10	P>0.10
September	r _s	-0.31	0.24	-	0.55	0.11	0.01	0.13	0.68	0.00	0.16	-0.67	-0.18
	n	10	10	10	10	9	9	10	9	10	10	10	10
	P	P>0.10	P>0.10	-	0.1>P>0.05	P>0.10	P>0.10	P>0.10	0.05>P>0.025	P>0.10	P>0.10	0.025>P>0.01	P>0.10
October	r _s	-0.08	-0.02	0.09	0.06	-0.27	0.03	0.11	0.48	0.36	0.07	0.65	0.02
	n	10	10	10	10	10	10	10	10	10	10	10	10
	P	P>0.10	P>0.10	P>0.10	P>0.10	P>0.10	P>0.10	P>0.10	0.1>P>0.05	P>0.10	P>0.10	0.05>P>0.025	P>0.10

Appendix 5.3. Estimated monthly densities of hihi and bellbirds at each transect

Table 1. Estimated hihi densities (per ha; ‘seen only’ counts) on Tiritiri Matangi Island at each transect from April to October 2010.

	Transect	Month							
		April	Early May	Mid May	June	July	August	September	October
Non-feeder areas	1	1.00	0.00	0.50	0.50	1.50	1.00	3.50	1.50
	2	0.40	0.67	1.00	1.00	1.40	1.40	1.00	0.60
	3	1.00	5.00	1.00	0.50	0.50	2.50	0.00	1.00
	4	1.00	1.67	0.45	1.00	0.00	1.00	0.50	0.50
	8	8.00	0.00	7.22	13.50	6.00	6.50	9.00	7.00
	10	1.25	3.33	0.56	1.00	0.00	0.56	0.50	1.00
Feeder areas	5	0.00	0.00	0.83	4.00	4.00	3.00	2.78	2.50
	6	1.67	4.17	0.83	3.00	2.75	2.75	2.78	3.25
	7	7.00	0.00	10.50	8.00	9.50	7.25	13.33	9.50
	9	6.00	30.00	9.44	22.00	11.00	7.00	15.00	6.50
	11	6.25	10.00	7.22	9.00	12.50	11.67	7.50	10.50
	12	1.43	1.67	0.42	4.33	4.33	2.00	3.67	2.67

Table 2. Estimated bellbird densities (per ha; ‘seen and heard’ counts) on Tiritiri Matangi Island at each transect from April to October 2010.

	Transect	Month							
		April	Early May	Mid May	June	July	August	September	October
Non-feeder areas	1	6.00	1.67	1.00	2.00	4.50	3.00	9.50	7.00
	2	4.00	3.33	1.80	1.00	4.80	6.20	8.80	6.40
	3	5.00	3.33	3.00	4.00	5.50	2.50	6.50	4.00
	4	5.00	0.00	1.36	2.50	4.00	2.00	8.50	10.50
	8	19.00	40.00	11.11	32.00	20.00	20.00	5.00	2.50
	10	7.50	0.00	0.00	1.00	2.50	3.33	4.00	2.00
Feeder areas	5	91.50	40.00	27.50	11.50	12.50	7.50	6.11	4.50
	6	54.50	44.17	15.00	13.00	8.75	4.25	2.22	3.25
	7	53.50	22.50	19.50	11.25	7.50	7.50	4.44	2.50
	9	6.00	20.00	1.67	24.00	9.00	7.50	5.00	4.00
	11	18.75	6.67	6.67	20.00	13.50	17.22	7.50	8.00
	12	31.00	33.33	27.08	43.00	27.33	13.67	8.00	5.33

Chapter 6:

Impact of the removal of bellbirds on hihi distribution



Male bellbird at a water trough on Tiritiri Matangi Island.

Photo: Michelle Roper, 2010.

6.1 Abstract

Bellbirds are a more dominant species than hihi hence there is the potential for hihi to be competitively excluded from areas where bellbirds are abundant. Areas where bellbird numbers have been reduced or are low may be attractive to hihi and allow occupation that otherwise would not be possible (Grant, 1972 cited in Ford & Paton, 1976a). The aim of this chapter was to test the hypothesis that the removal of 100 bellbirds from various sites on Tiritiri Matangi Island would impact on the immediate density and distribution of hihi and bellbirds. Immediately following the removal of bellbirds, hihi density did not consistently increase at all bellbird capture sites and bellbird density decreased at all transects including non-capture sites. One month after the bellbird removal, hihi density increased at capture sites, but so did bellbird density. Therefore, there was no consistent evidence that the removal of 100 bellbirds had any impact on either hihi or bellbird distribution. It appears that temporal and spatial changes in habitat (food availability) and aggregation behaviour, independent of bellbird removal, had more influence on density. Nonetheless, bellbirds and hihi use different strata of the same forest (Chapter 3), and there could have been a change in the vertical habitat which was not measured in this study.

6.2 Aims

- To assess whether the removal of 100 bellbirds had any detectable effect on the distribution of hihi in the areas of bellbird removal

6.3 Results

Hihi and bellbird distribution changed throughout the year (Chapter 5). One of my initial aims was test whether hihi distribution would change after the removal of 100 bellbirds for a planned translocation. From the data obtained, the simplest method to test this was by comparing the densities of hihi and bellbirds at each transect before, after and one month after the translocation as 7 transects were at or near bellbird capture sites and 5 transects were not. For bellbirds the best method for estimating density was using 'seen and heard' counts and for hihi the best estimates come from 'seen only' counts (Chapter 5). Figure 6.1 displays these respective density estimates for hihi and bellbirds before

(April), after (May) and one month after (June) the translocation and shows changes in their distribution over the months.

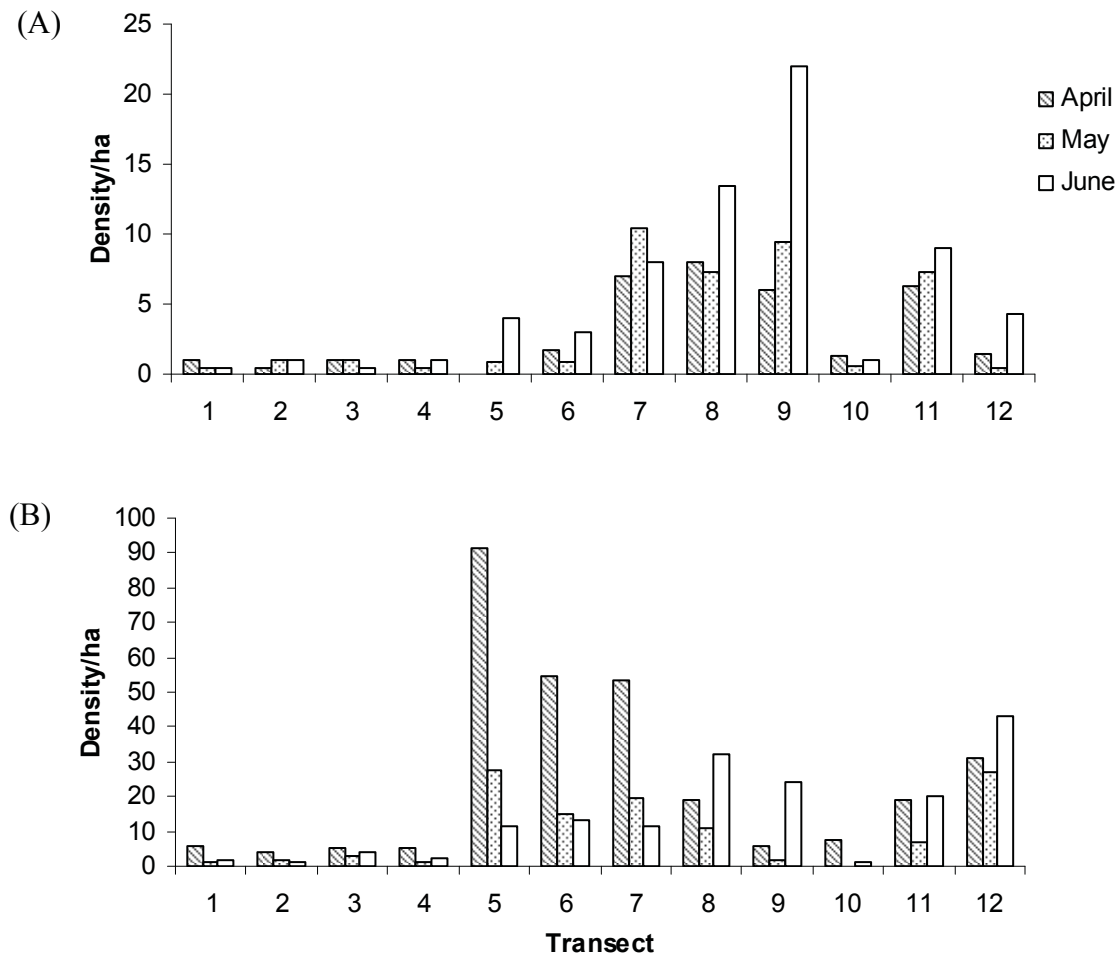


Figure 6.1. Estimated hihi (A) and bellbird (B) densities at each transect before (April), after (May) and one month after (June) the removal of 100 bellbirds from Tiritiri Matangi Island 2010.

Immediately following the translocation there was a decrease in bellbird density at all transects and most transects for hihi (Table 6.1). One month later the densities of bellbirds at the majority of transects had decreased compared to before the translocation whereas the majority of transects had higher hihi densities. However, at 4 of the 7 capture sites bellbird densities had also increased compared to before the translocation with the same 4 sites also having increased hihi densities.

Table 6.1. Description of the change in bellbird ('seen and heard') and hihi ('seen only') densities immediately following (after) and one month after the removal of 100 bellbirds at or near certain transects, including areas of no removal for comparison. Key: + = density increased; 0 = no change in density; — = density decreased.

Transect	Capture site	After		One month after	
		Bellbird	Hihi	Bellbird	Hihi
1	N	—	—	—	—
2	N	—	+	—	+
3	N	—	0	—	+
4	N	—	—	—	0
5	Y	—	+	—	+
6	Y	—	—	—	+
7	Y	—	+	—	+
8	Y	—	—	+	+
9	Y	—	+	+	+
10	N	—	—	—	—
11	Y	—	+	+	+
12	Y (nearby)	—	—	+	+

To account for any potential spatial differences during the day, the counts were divided into morning and afternoon to recalculate the densities for these two periods of the day. Some differences in the changes in densities were found between morning and afternoon, but overall no consistent relationships between densities of bellbirds and hihi were found at the bellbird capture sites (Tables 6.2 & 6.3). Therefore, the data does not provide any clear evidence that the removal of 100 bellbirds caused a significant change in the density of hihi at transects where the bellbirds were removed.

Table 6.2. Description of the change in bellbird ('seen and heard') and hihi ('seen only') densities in the morning (AM) and afternoon (PM) immediately following (after) and one month after the removal of 100 bellbirds at or near certain transects, including areas of no removal for comparison. Key: + = density increased; 0 = no change in density; – = density decreased. N/A = not available.

	Transect	Capture site	After		One month after	
			Bellbird	Hihi	Bellbird	Hihi
AM	1	N	–	–	–	–
	2	N	–	–	–	–
	3	N	–	–	–	–
	4	N	–	–	–	–
	5	Y	–	–	–	+
	6	Y	–	–	–	–
	7	Y	–	+	–	+
	8	Y	–	–	+	+
	9	Y	–	0	+	+
	10	N	–	+	–	+
	11	Y	–	+	–	+
	12	Y (nearby)	–	–	+	+
PM	1	N	–	–	–	–
	2	N	–	0	–	+
	3	N	–	0	–	+
	4	N	–	0	0	+
	5	Y	–	–	–	+
	6	Y	–	–	–	+
	7	Y	–	–	–	–
	8	Y	–	–	+	–
	9	Y	–	–	+	+
	10	N	N/A	N/A	+	+
	11	Y	N/A	N/A	+	–
	12	Y (nearby)	–	–	+	+

Table 6.3. Test results from a Wilcoxon signed-rank test comparing densities of bellbirds ('seen and heard') and hihi ('seen only') before the removal of 100 bellbirds (April) with densities straight after (mid May) and one month after (June) in 2010 on Tiritiri Matangi Island.

		After		One month after	
		Bellbird	Hihi	Bellbird	Hihi
Total	W	0	27.5	26	6
	n	12	11	12	11
	P	P < 0.001	P > 0.2	P > 0.2	0.01 < P < 0.02
AM	W	1	24	23	14
	n	12	10	12	11
	P	P < 0.001	P > 0.2	P > 0.2	0.10 < P < 0.20
PM	W	5.5	4.5	27	21
	n	10	7	11	11
	P	0.02 < P < 0.05	0.10 < P < 0.20	P > 0.2	P > 0.2

6.4 Discussion

The removal of bellbirds had little if any effect on the distribution of hihi suggesting that competitive exclusion does not restrict hihi numbers in these locations or that insufficient bellbirds were removed to reveal competitive exclusion. Additionally competition among bellbirds may be very high and bellbirds may also quickly disperse into the capture areas. Bellbirds use song to defend their resources and territories (Brunton & Li, 2006) hence other bellbirds may re-inhabit the area quicker than hihi due to the absence of song protecting the areas where resident bellbirds were removed. Hihi numbers either increased, had no change or decreased at various transects and this appeared to be independent of whether transects were a capture site or not. Interestingly, bellbird densities had both increased and decreased one month after the removal but hihi densities had increased at all capture sites. In fact for bellbirds the densities of birds at many of the capture sites decreased after the translocation suggesting causes of decline other than the removal of 100 birds. Therefore, it is concluded that too few birds were removed to observe changes in density and that bellbird and hihi distribution is highly variable on a local scale.

Where bellbird densities increased, hihi densities also tended to increase showing there may not be a high level of competitive exclusion between areas of the island but rather that they are attracted to similar resource concentrations. Gravatt, (1971) found both species coexist in the same habitats but utilise different strata i.e. the vertical plane rather in the horizontal plane. On Tiritiri Matangi Island bellbirds most commonly foraged higher in the vegetation than hihi (Chapter 3). Therefore, the removal of a small number of bellbirds is more likely to affect the vertical distribution of local hihi rather than attract more hihi into an area. A more appropriate test of competitive exclusion in such circumstances would be a finer scale study to assess the resources surrounding the bellbird capture site and monitor the number of each species using these resources immediately before and after the removal of the dominant bellbirds.

6.5 Conclusion

There was little evidence suggesting that the removal of 100 bellbirds had any impact on the distribution of hihi. Hihi patterns of change in density and distribution followed those of the control sites and the trends in distribution over the entire study period from April to October, 2010. This does not mean that competitive exclusion was not occurring. Hihi and bellbirds may be distributing themselves within resources in the vertical plane and the removal of bellbirds may result in local vertical use changes. Also nearby bellbirds may have quickly changed their distribution in relation to bellbird removal giving hihi no opportunity to taken advantage of the removal of competitors. A more effective approach would be to assess hihi and bellbird distribution within resources near the bellbird capture sites to see whether hihi move into the higher vegetation layers where bellbirds are usually most commonly found foraging.

Chapter 7: Conclusions

Overview of resource partitioning between hihi and bellbird on Tiritiri Matangi Island with research and management recommendations



Sugar water feeder station on Tiritiri Matangi Island
Video capture photo: Michelle Roper, 2011

7.1 Outline of this chapter

This chapter will explore the outcomes of this thesis in relation to the planned goals. At the outset of this study the main goal was to understand the level of competition and resource partitioning between two ecologically similar species: the hihi and bellbird. To achieve this, I collected data on bellbird and hihi foraging ecology on Tiritiri Matangi Island, a site where these two species coexist and where their foraging ecology is predicted to differ on a local scale and with season. Supplementary sugar water feeders are supplied for hihi to enhance their reproductive output but bellbirds also use these feeders and appear to benefit directly by access to this food supply. How much, when and how these two species interact at these feeders is a reoccurring question for conservation managers but also of theoretical value for assessing interspecific competition for resources. Bellbird and hihi density and distribution were also estimated to compare spatial and temporal patterns and determine the degree and nature of resource partitioning by these two species across the dominant habitat types found on the island. I also give an example of resource partitioning between Australian honeyeaters (Meliphagidae). Finally given all of this information, recommendations are made for future research and the implications of this information assessed for hihi management.

7.2 Overview

Previous studies on hihi and bellbird foraging ecology found that hihi are more frugivorous and bellbirds more insectivorous (Gravatt, 1971; Gaze & Fitzgerald, 1982); hence an important means of resource partitioning between these two nectar-feeding species. However, these results are not consistent across seasons and differ between locations in New Zealand (Gravatt, 1971; Stewart, 1980 cited in Craig *et al.*, 1981b; Castro, 1995). The results from my study on Tiritiri Matangi Island showed some support for hihi being more frugivorous, although only in the autumn and winter months, but there was no evidence to support bellbirds being more insectivorous. It was concluded that the dietary components are associated with resource availability and vegetation structure and hence may only have a small contribution to their resource partitioning.

Foraging height was more consistent between studies. Bellbirds typically foraged more frequently in the higher vegetation layers whilst hihi foraged more in the middle

canopy layers. However, Gravatt (1971) on Little Barrier Island found bellbirds forage more in the upper understorey than in the canopy and sub-canopy layers as in my study suggesting this could be affected by the different densities of tui and/or the overall lower canopy (less mature) forest. This study and Gravatt's (1971) showed hihi foraging more in the middle storey, although only in spring on Tiritiri. Given the lower vegetation on Tiritiri it is also important to note that tui may be able to defend and monopolise entire food patches (trees or shrubs). This is an example of interference competition where a species excludes others from resources whereas exploitation competition is when limited resources are exploited by species that are, for example, more efficient foragers (Ford 1979), and these concepts may have a role in resource partitioning between bellbirds and hihi. Overall, previous studies and my study support the idea that bellbirds most commonly forage in the higher vegetation on higher quality resources (interference competition) and hihi forage in the layers below with potentially lower quality resources (exploitation competition); a form of resource partitioning (Shoener, 1974) where the two species coexist in the same habitat type but differ in the different vegetation strata (vertical plane). Their occurrences at each level in the strata, however, could also be affected by the presence of tui and vegetation maturity.

The distribution of hihi and bellbirds on Tiritiri suggests that there may also be some resource partitioning between different habitat types (horizontal plane). Hihi typically have a preference for mature forest and considering their dependence on cavities for nesting, they could be considered a more specialist species (Castro *et al.* 2003) than bellbirds. On Tiritiri, the highest densities of hihi were found in the mature forest suggesting that other habitats were less favourable and perhaps that patches were near (hihi) carrying capacity (Newton, 1998). Mature habitat was preferred by hihi overall. In contrast, bellbirds showed preference for certain habitat types depending on season. For example, in spring bellbirds were distributed evenly between habitats presumably due to the formation of breeding territories and their generalist nesting requirements. Hihi have more restricted nesting requirements (obligate cavity nesters) and the presence of artificial nest boxes may indeed enable hihi to occupy less preferred habitat types as the more mature forest becomes saturated. Bellbird habitat preference in the autumn and winter months was strongly correlated with food resources such as the sugar water

feeders and kanuka. I conclude that there is unlikely to be competition between the two species as negative correlations in density were not found for any transect. This suggests the distribution of food resources generally determine hihi and bellbird densities. Hence, their differences in habitat type preferences may also contribute to their resource partitioning.

Different forms of resource partitioning occur within the Australian honeyeater guild. Species often differ significantly in the proportions of different dietary components (Recher, 1971; Ford, 1979), those with similar diets have distinct habitat type preferences (Ford & Paton, 1976a) and some honeyeaters differ in foraging height and manoeuvres (Recher, 1985; Slater, 1994). For example, the uncommon black-chinned honeyeater (*Melithreptus gularis*) is potentially at risk from competition with the co-occurring and much more common fuscous honeyeater (*Lichenostomus fuscus*; Lollback, Ford & Cairns, 2008). Both species have similarities in foraging manoeuvres, tree species used and foraging height, although the black-chinned honeyeaters are found more often at higher foraging heights and fuscous honeyeaters forage more often at lower strata (Lollback *et al.*, 2008). However, the main difference in their foraging ecology was that black-chinned honeyeaters more often used a refined gleaning technique of probing between leaves that were bound together supporting that their foraging behaviour is more specialised and with the food resources associated with this foraging technique thought to be uncommon, this may be a contributor to why the black-chinned honeyeater is rare (Lollback *et al.*, 2008).

Competition at the sugar water feeders was shown to be more intraspecific than interspecific. Whilst male bellbirds were the most dominant and frequent visitors to the sugar water feeders, they were unable to defend them exclusively against the overwhelming number of competitors at the feeder; making defence uneconomical. Hihi (male and female) were the next most common visitors and often visited in comparable numbers to not being significantly lower than male bellbirds. Female bellbird visits were always low and often irregular either showing there is greater competition between bellbird sexes than between the species or female bellbirds are less dependent on the feeders. Hihi sexes often fed in similar numbers showing little intraspecific competition. There were sex-based hierarchies at feeders on Kapiti Island, except when feeder use was

high, and they did not use them in winter (Castro, 1995) unlike on Tiritiri suggesting that hihi on Tiritiri are more food-limited in the non-breeding season and that dominance of feeders may be uneconomical. Positive correlation was found at most feeders between all categories of birds with very few aggressive interactions in the non-breeding season; therefore, there is little evidence of competitive exclusion at the feeders.

7.3 Recommendations for future research

7.3.1 Foraging ecology

Studies on bellbird and hihi foraging ecology have focused on single observations and independent samples. However, Merton (1966) found that the proportion of dietary components of bellbirds differed from independent samples and the time spent foraging on each component. Future studies on individual activity budgets could be conducted along with ‘first food eaten’ independent samples to enable comparisons of these approaches. The inclusion of tui in future foraging studies would also be relevant as this study showed differences in foraging heights which could have been attributed to differences in competition with tui. Studies should also included observing foraging manoeuvres and micro-habitat differences such as branch size, to assess for any differences between the species as was found in the black-chinned honeyeater example (Lollback *et al.*, 2008).

7.3.2 Feeder visitation

Further research on feeder visitation would benefit from observing aggressive interactions and dominance hierarchies of known colour banded individuals in and around the feeders. Potentially guarding the area surrounding a feeder may give dominant individuals better control to this resource. This would also help to understand benefits to resident territory owners with a feeder. Likewise information on bird movements between different feeders would help to further understand how they use the feeders. High sugar water consumption did not positively correlate with high bellbird densities in the surrounding areas therefore tracking their movements by radio tags, for example, would help to assess whether they stay near feeders when there is high consumption or whether

they are visiting from further distances than hihi and returning after using the feeder. This study primarily examined feeder use in the non-breeding season and very early in the breeding season. Extending this approach to the full breeding period would be useful and highlight periods when resources for reproduction may be scarce.

7.3.3 Abundance and distribution

Further research is needed to assess whether our results of ‘seen only’ counts for hihi and ‘seen and heard’ counts for bellbirds apply to other populations for estimating abundance. Kapiti Island may be an ideal location to test this as there is an original population of bellbirds, hihi were reintroduced and there are sugar water feeders. Hence whether the sugar water feeders have similar high impacts on hihi and bellbird densities and distribution could also be tested.

7.4 Implications for hihi management

This research has shown that hihi (male and female) use the feeders at a constant and high rate, less than male bellbirds but much more than female bellbirds showing that bellbirds are not competitively excluding hihi. Male and female hihi visit feeders at similar rates also suggesting that males are not excluding females. Therefore, there is little evidence that hihi managers should be concerned that hihi are being excluded from the feeders. Hihi used these feeders continuously from April until October showing that at this point in time, continued supply of sugar water is an important component of hihi diet.

The ‘Wattle Valley’ feeder was one of the most frequently used feeders. There were no female bellbird visits observed at this feeder over 3 months of video recording and there was often no correlation between the numbers of male bellbirds and hihi. This suggests that there may be more competition at this feeder compared to other feeders. Therefore, it is suggested that another feeder is needed in this area. For example a feeder in neighbouring ‘Little Wattle Valley’ may help relieve the pressure. If a new feeder is added, it is recommended that monitoring of the existing ‘Wattle Valley’ and new feeder is carried out to assess what impact the new feeder has on known levels of feeder use.

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