Industrious Native Bees: A Case Study in Whangarei

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Industrious Native Bees:

A Case Study in Whangarei

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Abstract

Communities of New Zealand native bees were located and observed over multiple seasons in an effort to increase baseline data on biology and behaviour of several species. Several aggregations of nesting native bees were located within a regenerative native forest on Mt. Parihaka (Whangarei, New Zealand). These communities formed the focus for multi-season analysis. Monitoring of nest sites, insect collections, and observational records were gathered over three seasons (2004-2007) on fine days and continued until bees were no longer active in each season.

In total, 1025 insects were handled and eight species of native bees were found in the Northland region from the genus *Leioproctus, Lasioglossum* and *Hylaeus.* For several species of bees data was collected on: foraging duration, floral preferences, pollen load composition analysis, nest provisioning duration, nest architecture, nest site density, maximum load lifting capacity and typical pollen loads carried.

The results of the study indicate native bees could be contributing much to New Zealand pollination systems, especially in regenerative forests such as Mt. Parihaka. Up to four species of native bees were found nesting along side each other in thriving communities. Large nest aggregations indicated bees return to the same location to nest generation after generation. Primary resources required by native bees included suitable nest sites and local forage.

Results also indicate there are possible variations in nest provisioning requirements, forage preferences or foraging strategies between species found in different local habitats. Community floral analyses show that for most species foraging range is limited (less than 100 m). Foraging duration results showed a significant difference in foraging times between three species; two species, at one location with the remaining species observed at another location. In contradiction to some studies, foraging duration and community floral analysis results did not support a relationship between foraging duration and foraging range. There was no relationship between the body length of native bees and foraging range.

He Mihi

Tena koe, tena koutou, tena tatou katoa.

Ko Te Whakapapa Tenei Mo Nga
Taonga Tuku Iho
A To Matua Kore
Ka Moe A Papatuanuku Ia Ranginui
Ka Puta Ko Tanemai-Iuta
Ko Tangaroa, Ko Tawhirimatea, Ko Tumatauenga,
Ko Haumie Tike, Me Rongomaitane.
Ko Enei Nga Taonga Tuku Iho 0 Ratou Ma
Ko Matou Nga Kai Ti Aki Mo Enei Taonga

Genealogy Recites For Us Our Divine Inheritance
Through The Union Of Mother Earth And Sky Father
Who Gave Birth To Our Resources
And Entrusted Their Care Into Our Hands
The Land And The Sea

I extend my gratitude to the special insects that allowed me insight into their lives.
For sharing with me their humble and gracious ways of being in the environment.
For their qualities of perseverance and endurance in an ever changing world.
And finally for showing me the true meaning of whanaungatanga, kaitiakitanga and manawhenua.

No reira, ka nui te mihi ki a koutou katoa. Kia ora ra.

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I owe a special thanks to friends and family who have been constant supporters throughout my research. To my Husband Wayne Haigh who spent many hours discussing native bees, editing writing, collecting samples, digging into banks and who creatively designed and constructed some of the equipment used in this study. Thanks to my children, Wyatt and Aaron for their enduring curiosity and delight in all things natural. Thanks to Demerits Vivian for the many hours he spent watching native bees (and children). A special thank-you to the Drummond family for opening their home to me and my family on our many trips to Auckland and especially Taini Drummond who has been my mentor throughout this process.

Preface

The study evolved into an investigation of the natural history of native bees providing baseline data on which to found further research.

Chapter One serves as a general introduction to New Zealand native bees, their taxonomy and biology, their role in pollination and conservation issues. Included in this chapter is an overview of traditional and current tracking methods used to assess the foraging and home range of flying insects.

Chapter Two presents the results of a community study of native bees on Mt. Parihaka (Whangarei). General abundance levels, species and sex composition counts, nesting, foraging and behavioural interactions with associated organisms were investigated.

Chapter Three examines the body metrics and load-lifting capacity of several species New Zealand native bees. Pollen loads carried in a typical foraging trip, artificial load lifting capability, flight muscle mass, body mass and length combined to indicate typical and maximum loads carried. The outcome is used to assess the suitability of employing current tracking methods for New Zealand native bees.

Chapter Four investigates native bees community structures, nest density, nesting behaviours and unique nest architecture. Habitat preferences for nest location were investigated.

Chapter Five explores the floral preferences, pollen load composition and foraging duration of several species of native bees. The foraging range of native bees on Mt. Parihaka (Whangarei) was assessed in respect to the local floral community structure.

Report "**Recommendations for the Conservation of Native Bees in Whangarei**" summarises the findings of this thesis and outlines recommendations for the future management of native bees in Whangarei.

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Chapter One New Zealand's Gentle Pollinators

1.1 Bees of the World and New Zealand

1.1.1 Introduction

There are up to 30,000 different species of bees in the world (Michener 2000). About 17,000 species have been described, of which 16,000 are categorized into genus and subgenus. Seven families of bees are classified under the Superfamily Apoidea (along with spheciod wasps) and are commonly presented in order of the most primitive to the most advanced as follows: Stenotritidae, Colletidae, Andrenidae, Halictidae, Melittidae, Megachilidae and Apidae (Michener 2000). It is thought that bees evolved from sphecoid wasps and some primitive bee species look similar to wasps although there are morphological and behavioural differences (Michener 2000). Some primitive bee species are slender and sparsely haired like wasps but most bees are more hairy and robust. Also, sphecoid wasps, unlike bees, have at least a few branched, silver coloured hairs on their body (Michener 2000). Finally, while wasps rely on spiders and insects for food, bees collect pollen and nectar to feed themselves and their larvae.

Bees pollinate natural and cultivated plants and their importance in this role has been recognised worldwide (Kearns et al. 1998; O'Toole 2002). They are regarded as keystone species. Bees are vital to the ecosystems in which they live as they help to pollinate plants, they also support otherwise separated food webs (Kevan 1991; LaSalle & Gauld 1993). Their absence would have more far-reaching effects than their abundance would indicate (McIntyre & Hostetler 2001). A loss of insect pollination, of which bees are the most important contributor, would result in extinction cascades and a total collapse of ecosystems (Buchmann & Nabhan 1996; LeBuhn et al. 2006, Michener 2000). This highlights the dependency of native plants on bees for reproduction. The continued conservation of natural habitats depended on the preservation of bee populations. Non-*Apis* native bees play an especially important role in many natural ecosystems because they are among the most critical and effective pollinators of native plants (LeBuhn et al. 2006).

Many commercial crops including: fruits, flowers, vegetables, flaxes, alfalfa and clover, are also bee-pollinated. One out of every four mouthfuls of the world food resource depends on insect pollination. The commercial value of bee pollination in the United States has been conservatively estimated to be worth between 20-40 billion US dollars per year (Michener 2000; The Xerces Society 2007b). The common honeybee, which is native to Europe and Africa, and as far east as Western Iran, is the most widely recognised bee. Honeybees have been exported around the world. They produce honey, pollinates crops, are highly social and have their own means of communication (von Frisch 1967). Although the honeybee has been the focus for much research in the past there is a growing worldwide interest in native bees, the majority of which are not social and do not produce honey. Native bees do pollinate plants (Kearns et al. 1998; Roubik & Wolda 2001; O'Toole 2002) and in some instances, their efficacy as pollinators of agricultural crops surpasses honeybees (Parker et al. 1987; O'Toole 1993; Richards 1993). Moreover, the invasive varroa mite (*Varroa destructor*) and the acarine mite (*Acarapis woodi*) continue to damage honeybee colonies around the world adding to the importance of non-*Apis* bees, which are not affected by the mites.

There are 41 different species of bees In New Zealand. When grouped according to their origin, there are 28 native (27 endemic and 1 indigenous) and 12 introduced species (see Table 1.1). Of the 27 endemic species of bees, most are from the primitive Colletidae family, 18 belonging to the genus *Leioproctus* and 6 to the genus *Hylaeus.* The remaining three, from the genus *Lasioglossum,* belong to the Halictidae family. Donovan (2007) lists at least three rare native species: *Leioproctus (Leioproctus) otautahi, Leioproctus (Nesocolletes) nunui* and *Hylaeus (Prosopisteron) murihiku*.

Table 1.1 Native and Introduced Bee Species of New Zealand

NATIVE (28 SPECIES)	
Endemic: Occur only in New Zealand	Indigenous: Also in Australia but arrived in New Zealand unaided (i.e. air dispersal)
18 *Leioproctus spp.* 6 *Hylaeus spp.* 3 *Lasioglossum spp.*	1 *Lasioglossum sp.*
INTRODUCED (12 SPECIES)	
Adventive: Also in Australia or Europe originally but have arrived unintentionally aided (i.e. in ships or aircraft)	Imported: Deliberately imported from the Northern Hemisphere for economic reasons
2 *Hylaeus spp.* 1 *Hyleoides sp.* 1 *Euryglossina sp.* 1 *Anthidium* sp.	1 *Nomia sp.* 1 *Osmia sp.* 1 *Megachile sp.* 4 *Bombus spp.* 1 *Apis sp.*

When compared to similar geographical regions of the world the diversity of native bee species in New Zealand is depauperate. According to Michener (2000) an absence of archaic bees in New Zealand indicates the original species arrived via overwater dispersal from Australia. Five species of New Zealand's native bees are also common to Australia. In comparison to New Zealand, Australia has a diverse and abundant fauna with over 1,500 native bees species. It is therefore likely, and generally accepted that most, if not all, New Zealand species of native bees are descendents from those in Australia (Michener 2000; Donovan 2007). This study focuses on native endemic bees.

1.1.2 History of research on New Zealand's native bees

The following sections review some history of the study of New Zealand's bees. Early studies were taxonomic and included the description and reclassification of some species (White & Butler 1874; Smith 1876, 1878; Cockerell 1905, 1925; Michener 1965). Aspects of general biology (Meyer 1931; Rayment 1935; Donovan 1967) and pollination biology of native bees have been investigated (Primack 1978, 1979; Lloyd 1985; Kelly 1997; Robertson et al. 2005) but there is a paucity of more recent studies (Donovan 1980, 2007).

Taxonomy

Taxonomic studies of insects in New Zealand were conducted by White (1874) and Smith (1876; 1878) and identification keys to some species of bees were published by various authors (Cameron 1898; Alfken 1903). Cockerell (1925) focused on endemic bees of New Zealand and described 7 new species of *Paracolletes,* four of which have valid species names to date including: *P. boltoni, P. monticola, P. hudsoni* and *P. maritimus* (Cockerell). Reclassification by Michener (Michener 1965) saw the new assignment of species to genus and subgenus of New Zealand bees as follows:

1) Those assigned to the genus *Paracolletes* redefined to *Leioproctus* and assigned some species to the subgenus *Leioproctus*, and others to a newly described subgenus *Nesocolletes* (restricted to New Zealand).
2) Species previously assigned to *Prosopis* placed in *Hylaeus*, and assigned to the subgenus *Prosopisteron.*
3) Species previously placed in the genus *Halictus,* and assigned to the genus *Lasioglossum*, and subgenus *Austrevylaeus.*

Cockerell (1936) was the last author to publish descriptions of New Zealand's bees until recent times (Donovan 2007). Native bee taxa are listed in Table 1.2 and show that 14 out the 28 native species have recently been described. For further information on taxonomic status of native bees refer to Chapter Two.

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Table 1.2 New Zealand Native Bee Taxa (Donovan 2007)

Superfamily **APOIDEA**
Family **Colletidae**
Subfamily **Colletinae**
Genus ***Leioproctus*** Smith, 1853
Subgenus *Leioproctus* Smith, 1853
boltoni Cockerell, 1904
huakiwi (Donovan, 2007)
imitatus Smith, 1853
maorium Cockerell, 1913
viridibasis Cockerell, 1936
kanapuu (Donovan, 2007)
keehua (Donovan, 2007)
metallicus (Smith, 1853)
Andrena trichopus "White", Butler, 1874
otautahi (Donovan, 2007)
pango (Donovan, 2007)
purpureus (Smith, 1853)
vestitus (Smith 1876)
waipounamu (Donovan, 2007)
Subgenus *Nesocolletes* Michener, 1965
fulvescens (Smith 1876)
hirtipes (Smith 1878)
opacior (Cockerell, 1936)
hudsoni (Cockerell 1925)
maritimus (Cockerell, 1936)
monticola (Cockerell 1925)
nunui (Donovan, 2007)
paahaumaa (Donovan, 2007)
pekanui (Donovan, 2007)

Subfamily **Hylaeinae**
Genus ***Hylaeus***
Subgenus *Prosopisteron* Cockerell, 1906
agilis (Smith 1876)
laevigata (Smith, 1854)
laevigatulus Michener, 1965
laevigatus (Hutton, 1904)
maoriana (Cockerell, 1909)
maorica (Kirkaldy, 1909)
ssp. *laevigata* (Cockerell, 1916)

Continued -
Subfamily **Hylaeinae**
Genus ***Hylaeus***
Subgenus *Prosopisteron* Cockerell, 1906
capitosus (Smith 1876)
capitorus (Kirby, 1884)
capitosa (Dalla Torre, 1896)
innocens (Cameron 1898)
kermadecensis (Donovan, 2007)
matamoko (Donovan, 2007)
murihiku (Donovan, 2007)
relegatus (Smith 1876)
cameroni (Cockerell 1905)
hudsoni Cockerell, 1925
maoriana (Cockerell, 1909)
maorianus (Meade-Waldo 1923)
relegata (Dalla Torre, 1896)
sulcifrons (Cameron 1898)

Family **Halictidae**
Subfamily **Halictinae**
Tribe Halictini
Genus ***Lasioglossum*** Curtis, 1833
Subgenus *Chilalictus* Michener, 1965
cognatum (Smith, 1853)
haematostoma (Cockerell, 1914)
inclinans (Smith, 1879)
subinclinans (Cockerell, 1915)
Subgenus *Austrevylaeus* Michener, 1965
mataroa (Donovan, 2007)
maunga (Donovan, 2007)
sordidum Smith, 1853)
familiaris (Smith 1876)
huttoni (Cameron, 1900)
smithii (Dalla Torre, 1896)
smithii var. *a* (Cockerell, 1916)

Biology

There are early studies of the general biology and nests of some New Zealand bees (Meyer 1931; Rayment 1935). The first substantial publication on native bees, however, was in 1967 (Donovan 1967). In this study aspects of the bionomics of a species of bee *Leioproctus (Leioproctus) boltoni* were investigated; subsequent identifications showed more than one species of bee was studied. Following on from this work, Donovan (1980) reported that, based on flower visiting preferences, most Colletinae can be divided into three groups: those that visited flowering host families of Myrtaceae (kanuka, *Kunzea ericoides*), Fabaceae (climbing broom, *Carmichaelia kirkii*) or Asteraceae (oxeye daisy, *Leucanthemum vulgare*). In 1984 a survey of native bees was conducted in the Mackenzie Basin (Quinn 1984) and 10 species of native bees were identified. Quinn (1984) visually estimated 840,000 nests of *Leioproctus (Nesocolletes) fulvescens* at one nest site, indicating the species has a seasonally prolific population. Figure 1.1 shows images of native bees on typical ground nests.

Figure 1.1 Examples of native bees on ground nests; A, The pale - pollen free scopae of this female native bee (*Leioproctus sp.*) on a ground nest indicates she is newly emerged; B, Male native bee (*Leioproctus sp.*) entering nests to search for a mate; C, This female (*Leioproctus sp.*) has returned with a large pollen load and is searching for her nest entrance.

Role as pollinators

Native bees and native flowering plants have a long evolutionary association. While there are few studies on New Zealand's native bees (Donovan 1967, 1980, 1983; Donovan & Macfarlane 1984; Donovan 2007) a number of investigations of pollination biology make reference to the insects (Primack 1978, 1979; Lloyd 1985; Kelly 1997; Robertson et al. 2005). Dugdale (1975) reported observations of small bees *Hylaeus* (*Prosopisteron*) *agilis* prising open the lobes of Loranthaceae (*Alepis flavida*) and the unexpanded flowers of *Hebe gracillima.* Similarly, Primack (1978, 1983) reported high numbers of *Lasioglossum (Austrevylaeus) sordidum* foraging on *Discaria toumatou* flowers and an abundance of *Leioproctus spp.* and *Hylaeus spp.* on flowering kanuka (see Figure 1.2 below). Kelly et al. (1996) discovered that *H.* (*P.*) *agilis* and some species of *Leioproctus* were pollinating an endangered species of mistletoe (*Peraxilla tetrapetala:* Loranthaceae). This was a pivotal study because it was thought that only birds were able to open the 'explosive' mistletoe flowers, but native bees were observed persistently gnawing at the unopened mistletoe buds, until they finally opened. These observations challenged the notion that plants have only one guild of pollinators and raised the awareness of the role of native bees in New Zealand's pollinating systems (Kelly 1997). A greater understanding of the ecology of native bees is not only critical to New Zealand's natural plant systems but also to biodiversity conservation, ecological restoration, biosecurity protection, biosafety, sustainable agriculture and horticulture (Newstrom & Roberston 2005). A reduction in the numbers of native bees could potentially adversely impact all of these systems.

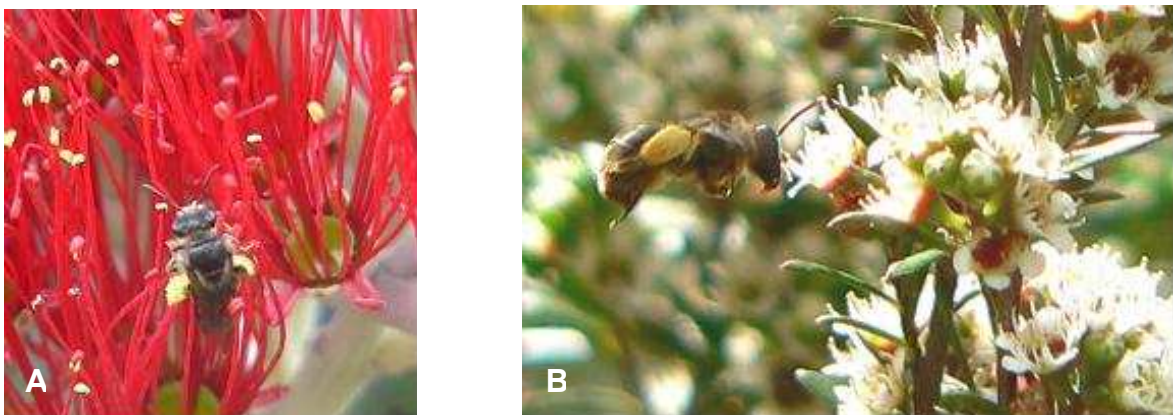

Figure 1.2 Examples of native bees and their interaction with native flora. Both images show pollen laden native bees (*Leioproctus sp.*) collecting from; A, a pohutukawa and; B, in mid flight over a kanuka.

Economic benefits

Native bees are an important part of natural systems. They are also known to forage on some crops of economic value such as kiwifruit (*Actinidia deliciosa*) but their efficacy as pollinators of these crops has not been fully investigated. Overseas authors have shown that native bees can play significant roles as pollinators of commercial crops (Parker et al. 1987; O'Toole 1993, 1994); even more so in recent times, since they are unaffected by the varroa mite. Moreover, if their habitat is protected, native bees could be easily managed (Kremen et al. 2002).

In New Zealand a survey of insect visitors to kiwifruit flowers found several native bee species were visiting the flowers including seven species of *Leioproctus* and several *Hylaeus*, and *Lasioglossum (Austrevylaeus) sordidum* (Macfarlane & Ferguson 1983). In the study of the 54 orchards between 1980-1981, native bees were present at 30% of the sites. Native bees were so numerous in some orchards that the number of honeybee hives could be reduced (Macfarlane and Ferguson 1983). Female native bees caught on the flowers carried up to half a million male pollen grains on their bodies, a number comparable to bumblebees (*Bombus spp*) and honeybees (Macfarlane & Ferguson 1983).

Conservation

Many conservation studies have focussed on the effects of resource overlaps between introduced and native bees since both are competing for similar resources (Gause 1934; Putman & Wratten 1984). Most introduced species of bees such as honeybees and bumblebees have been intentionally imported for crop pollination. Most of these species of bees are active throughout the year, are physically robust and are efficient pollinators. Native bees, on the other hand, do not forage throughout the year and they are ranked third in pollination effectiveness after honeybees and bumblebees (Macfarlane & Ferguson 1983). While there is difficulty ascertaining the abundance and diversity of native bee fauna prior to the introduction of other bees (Goulson 2003) the effects of introduced bees on native bees are thought to be minimal (Donovan 1980). In support of Donovan's (1980) findings, Paini (2004b) investigated the impacts of honeybees on Australian native bees but found the results of the study inconclusive. Thomson (2004) on the other hand, suggests honeybees do competitively suppress some species of native bees. Results from Thomson's (2004) study show some species of important native pollinators are adversely affected by the introduction of honeybee populations.

The consequences of human activities on native bees have also been investigated. Donovan (1980) mentioned both the destruction and creation of habitat; and the destruction and introductions of floral resources as possibly significant. Native bees appear to have benefited from some human activities. Road construction has created large areas of bare or semi bare soil, free from vegetation. These areas are ideal for nest sites. Introduced plants have also provided additional foraging resources. Many native bee species have been shown to forage on exotic species (i.e. *Leioproctus (Leioproctus) paahaumaa* and *Lasioglossum sordidum* foraging on *Leucanthemum vulgare*: Asteraceae, see Figure 1.3 below).

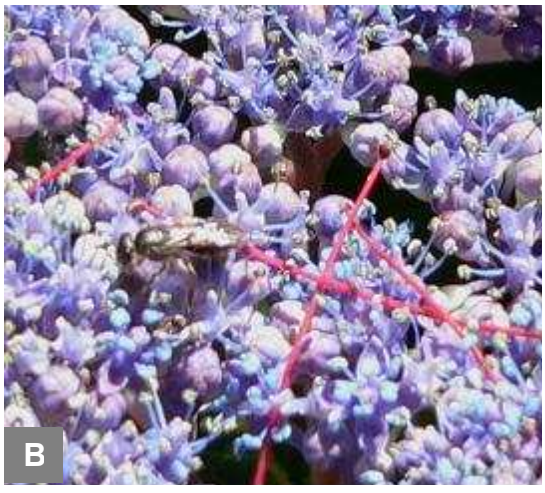

Figure 1.3 Examples of native bees foraging on introduced flora; A, A pollen laden native bee (*Leioproctus sp.*) foraging on parsley (*Petroselinum sp.*: Apiaceae); and *Lasioglossum sordidum* on two introduced flowers; B, on a *Hydrangea sp.* and; C, on an oxeye daisy (*Leucanthemum vulgare*).

1.2 Insect Movement

1.2.1 Background

All living organisms move in space and over time to varying degrees. Understanding the dynamics of individual and group movement is crucial to many ecological studies (Peck 1999); migration behaviours, foraging strategies and population dynamics, for example, all require descriptions of animal movement (Turchin 1991). Insect movement studies dominate the 'animal movement' literature (Peck 1999). Large animal movement can be easily followed using radio tracking or visual methods (Pride & Swift 1992). Tracking movements of smaller animals, such as insects, in their natural habitats is as important ,especially with respect to their biology, demography, and ethology, but the physical size of insects makes collecting information on movement difficult (Hagler & Jackson 2001). Visual tracking methods can give a good understanding of insect behaviour in a local area, but once insects disperse they become difficult to follow. Conventional radio tracking is not practical for tracking insects because most radio tags are too heavy or awkward for insects to carry (Hagler & Jackson 2001). Consequently many insect tracking methods rely on indirect analysis using any one of a variety of mark-release-recapture techniques including: tags and labels, mutilation markers, paint and inks, dust and dyes, pollen and genetic markers, radioactive-isotope and elemental markers, protein and genetically engineered markers (Hagler & Jackson 2001). Although marking insects probably started around 1920 (Geiger et al. 1919; Dudley & Searles 1923), choosing the best technique for marking insects remains essential to the success of many research projects.

1.2.2 Resource finding movements

A recent study successfully employed the use of mark-release methods to investigate the foraging range of solitary bees (Gathmann & Tscharntke 2002). Foraging strategies, described as 'vegetative' movements (e.g. the exploration of resources such as food, shelter and mates) tend to be confined to a local habitat (Woiwod et al. 2000). To aid conservation efforts Gathmann & Tscharntke (2002) gathered data on foraging strategies of solitary bees using translocation experiments. In these experiments, bees were collected at nest sites, transported in dark boxes to various locations and released. The nest sites were monitored and the time taken for bees to return to the nest was recorded. The results of the translocation study supported the hypothesis that local habitat structure is more important than large-scale landscape structure because solitary bees have a small foraging range (150 – 600 m) (Gathmann & Tscharntke 2002). Body length was

found to be the best predictor of foraging distance and duration (Gathmann & Tscharntke 2002). It was also argued that in order to ensure the long-term sustainability of solitary bee diversity and their role as pollinators all requirements for sustaining viable populations must be located within this range (Gathmann & Tscharntke 2002). While translocation methods helped to predict the foraging strategies of solitary bees there still remains an absence of suitable methods for tracking insects directly. To date, radar tracking is the only viable 'direct' method to track insects.

1.2.3 Radar entomology

Historical use of radar technology

Over the last century advances in radar technology have given new insight into insect movement (Chapman 2000). While studying radar reflections in the atmosphere, Friis (1947) observed mysterious 'dot angles'. In a similar study this phenomenon was identified as radar echoes from insects (Crawford 1949). Twenty years on, Schaefer (1969) modified a marine radar to track desert locusts, an event that is acknowledged to represent the founding discipline of Radar Entomology (Chapman 2000). Since then, conventional entomological radar has been used extensively in the study of insect migration (Drake & Farrow 1988; Reynolds 1988; Riley 1989; Reynolds & Riley 1997). Until recently, radar technology was limited to the study of high altitude movements. Current developments have seen the introduction of the harmonic direction finder (Mascanzoni & Wallin 1986) and the harmonic scanning radar (Riley et al. 1996) for studying low altitude vegetative movements associated with feeding and reproduction (Dingle 1996).

Operation, limitations and applications

Radars operate by emitting a signal and receiving a reflected signal. An acronym for Radio Detection and Range, radars give information about the range and size of a target, depending on the configuration and operating requirements. As indicated above, there are two broad categories of entomological radar, those that are used for high altitude (migratory movement) and low altitude (vegetative movement) studies. This study is concerned with the latter so a complete review of conventional radar will not be included.

Harmonic direction finder

The harmonic direction finder consists of the portable transceiver held by the operator, headphones, and the tag antenna attached to the insect. As the operator sweeps an area,

the radar will register a tagged insect as a strong tone heard through the headphones. The main advantage of this system is the design of the tag antennas, which are passive devices (i.e. they are not battery powered). Because the antenna carries no batteries it can be made lightweight and small and is suitable for an insect to lift.

The harmonic direction finder, originally developed to locate skiers caught in the snow, was adapted for entomological purposes (Mascanzoni & Wallin 1986). Since then the harmonic direction finder has been used extensively including studies of pedestrian movements of carabid beetles (Mascanzoni & Wallin 1986; Wallin & Ekbom 1988; Hockmann et al. 1989), relocation of aquatic insects (Gee et al. 2001), movements of kauri snails (*Paryphanta busbyi watti*) and ground beetles (*Plocamosthetus planiusculus*) (Lovei et al. 1997), and movements of butterflies (*Parnassius bremeri*) (Caldwell 1997).

Harmonic scanning radar

The harmonic scanning radar is a modification of the direction finder that can track and record the movements of a low flying insect. Information such as direction, altitude, and speed of the target insects is recorded periodically and presented as a plan-position display. The harmonic scanning radar consists of the base transceiver antennas - the gain transmitter/ receiver and the tag antenna attached to the insect. The base (transmitting) antenna transmits a signal at a specific frequency. This signal is reflected by the tag antenna, at double the original frequency, and captured by the receiving base antenna. The reflected signal from the tag antenna is easily identified above other electromagnetic reflections from the environment caused by objects, such as trees or buildings.

An insect in flight can be tracked and recorded while there is a direct line of sight between the tag antenna attached to the insect and base antennas. Although the cost and technical expertise required to develop and operate this system limits it's accessibility it has been widely used in various studies (Carreck 1996; Riley et al. 1996; Osborne et al. 1997; Osborne et al. 1999). The scanning radar has been particularly beneficial in understanding the foraging movements of honeybees (*Apis mellifera*). Recent literature demonstrates the continued application of scanning radar in a range of studies including: the honeybees' waggle dance (Riley 2005; Riley et al. 2005), honeybee spatial memory (Menzel et al. 2005) and investigations of butterfly movements(Cant et al. 2005).

Both the scanning radar and the direction finder are commonly referred to as harmonic radar, but the harmonic direction finder indicates the direction of a target only. The scanning radar is significantly more costly (in excess of $US 10,000-50,000 , Drake 2004)

and includes a radar display of insect movement. The harmonic direction finder requires the operator to search for the insect and listen for a signal in a similar manner to radio tracking.

1.2.4 Harmonic radar: applications in New Zealand?

A number of authors have reviewed aspects of the harmonic radar (Riley 1989; Chapman 2000; Chapman et al. 2004). Others have analysed the design of harmonic radar (Colpitts et al. 1999; Colpitts et al. 2000; Riley & Smith 2002; Colpitts 2004). Some authors have demonstrated the effectiveness of the radar in studies of insect movement (Osborne et al. 1997; Riley et al. 1998; Osborne et al. 1999; Riley & Smith 2002). The benefits of the harmonic radar have been recognised overseas. Chapman (2000), for example, includes radar as "one of the landmark events in applied entomology". The benefits have also been recognised in New Zealand and a few studies have employed the use of harmonic direction finders (Devine 1997; Stringer et al. 2003). Lovei et al. (1997) studied the movements of ground beetles (*P. planiusculus*) and kauri snails (*P. b. watti*) using a direction finder and modified the tag antenna for optimum performance. In a similar study, the Department of Conservation (DOC) employed the use of a direction finder to investigate the status of translocated land snails (*Placostylus hongii*) on Matakohe Island (DOC 2003).

1.2.5 History, current advances: interdisciplinary research?

Chapman (2000) reports that "in large part advances in our understanding of insects have depended on technological advances". From the earliest beginnings it has been those studying insects, entomologists such as Schaefer (1969) for example, that have modified radar for insect studies. Much of the literature on harmonic radar is written by entomologists for entomologists (Drake 2004). There have been a few dedicated radio engineering studies focusing on the design of tag antennas (Colpitts et al. 1999; Colpitts et al. 2000; Colpitts 2004) and even less published collaborative studies by engineers and entomologists (Riley & Smith 2002; O'Neal et al. 2004). Much of the 'engineering' of the tag antenna has relied on 'empirical trimming' of the antenna in the field (Riley & Smith 2002).

While there is limited evidence of interdisciplinary collaborations, much progress has been made in the field of radio design with the miniaturisation of antennas (Hart 2001; Skrivervik et al. 2001; Gianvittorio & Samii 2002; Morishita et al. 2002). Antenna design is

a mature field of research so it is not often that a new approach to traditional design methods arises. The combination of fractal geometry with electromagnetic theory however, has led to innovative antenna designs such as the Sierpinski Gasket (Baliarda et al. 2000; Hart 2001; Werner & Gangul 2003) (Figure 1.4) . Miniature antennas could be used to track even the smallest insects. An integrated design approach involving engineers and entomologists could make this a reality.

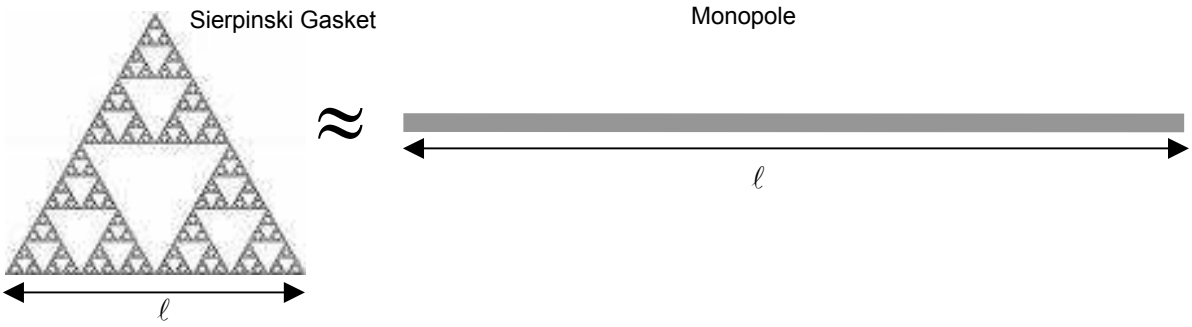

Figure 1.4 Sierpinski Gasket is an example of a fractal antenna; the self-similar design maximises the effective radiating length by 'scrunching' up the radiator into a fractal shape.

1.3 Study Aim

1.3.1 Purpose

Conservation strategies to preserve native bees and their ecosystems depend on some understanding of the role they perform and the impacts of a changing environment. Yet baseline data on New Zealand's native bee fauna is lacking or absent. Long-term data on the distribution, population, and diversity of New Zealand's native bees is also scarce and knowledge of the behaviour and biology of many is species limited. The primary purpose of this study is to gain an understanding of the behaviour of native bees in New Zealand's ecosystems to aid conservation strategies.

It is generally accepted that most species of native bees rely on a local habitat, gathering all they need to sustain them from this area. However, several questions remain unanswered; how far do they travel and what is their 'home range? How often do they embark on a foraging trip? What are their floral preferences and how much pollen can they carry? This study attempts to answer some of these questions by employing the use of indirect methods and further investigates the practicalities of employing direct tracking methods such as the harmonic radar.

The purpose of this study is to:

A. Identify important baseline data and gain an understanding of the behaviour of native bees to aid in the development of conservation strategies.
B. Investigate native bee biology to assess the feasibility of using the harmonic radar to track native bees.

There are four main areas of native bee biology that are considered in this study:

1. The foraging range of several species of New Zealand native bees.
2. The floral preferences of New Zealand native bees.
3. The foraging duration and nest-provisioning behaviours of two species of New Zealand native bees.
4. The load-lifting capacity of several species of New Zealand native bees.

1.3.2 Objectives

The main research goals of this study are outlined as follows.

1. To determine the population status of native bees in the Whangarei district by:
    - Locating and observing native bee communities in the district over several seasons.
    - Collecting and identifying native bee species found in the district.

2. To determine the load-lifting capacity of a species of native bee by*:*
    - Measuring the quantity of pollen lifted per bee in an average foraging trip, and the corresponding flight muscle mass.
    - Estimating the maximum artificial load a native bee can carry.

3. To determine the foraging range of a species of native bee by*:*
    - Evaluating the distance travelled from the nest site while foraging using body length relationships and floral preferences as indirect indicators of a 'home range'.
    - Evaluating the time taken to return to the nest site after leaving to forage

4. To determine nest provisioning behaviours of a species of native bee by:
    - Determining the visitation frequency to the nest.
    - Determining duration of time spent in a nest and time spent outside the nest.

5. To identify the physical aspects of the nest sites of a species of native bee by:
    - Measuring the nest metrics including width of nest entrances, depth of cells, and number of branches, number of cells and circumference (volume) of cells.

1.3.3 Limitations

There were difficulties associated with studying bees over multiple seasons. A variety of issues such as: the seasonal activity and emergence times of bees, the whereabouts of nest sites and the possibility of public tampering with equipment or study site experiments were expected complications. Poor weather prevented many days work and on several occasions washed away nest sites under observation. There were difficulties watching bees for hours particularly when collecting nest visitation frequency data; native bees are very small and move quickly. It was impossible to visually follow a single bee from her nest to a flower despite repeated attempts to do so. Native bees would actively dislodge any additional weight attached to them and could not be fitted with tracking devices.

When the research commenced there were no published keys to New Zealand bees. Identification required the use of a microscope to determine subtle differences between species. Several of the collected insects were not native bees and were later identified as sphecoid wasps. When available the keys where difficult to use and required a high degree of taxonomic proficiency; consequently bee identifications were made by comparison with a study reference collection in conjunction with advice from Dr Donovan.

First Season, October 2004 – February 2005

In the first season a search for native bee nesting sites focused on areas around Whangarei. Suitable nesting sites were investigated for evidence of the emergence of native bees. Native trees (manuka, kanuka, pohutukawa, flaxes) were monitored, especially at flowering times and checked for native bee foraging activity. Nest sites that appeared active were observed throughout the summer period. Representative specimens of native bees were collected, pinned and sent away for formal identifications by Dr. Donovan. Load-lifting experiments, flight muscle mass analysis, and nest visitation frequency / duration experiments were conducted.

Second Season, October 2005 – February 2006:

Several sites found in the previous season were monitored for activity in the second season. Once it was clear that native bees were emerging from their nests regular observations resumed. Representative specimens were collected, pinned and sent away for formal identification. Dr. Donovan undertook a two-day survey of native bee diversity on Mount Parihaka and provided training on the identification of species and general entomological methods including the collection of insects, pinning, labelling and storing. Pollen load measurements, nest visitation frequency and duration and nest metrics experiments were conducted.

Third Season, October 2006 – February 2007:

All sites monitored in the previous two seasons were observed in the final season. A wider search was made at various sites around Northland and some additional collections were made. Subtle differences in emergence times of bees were observed. Unlike the previous seasons male bees were still forming mating swarms well into December. There were also differences in the flowering times of manuka, kanuka and pohutukawa which flowered earlier than in the previous seasons. Pollen identification of native bee loads was made and artificial nest boxes were analysed. Observations on nest site preferences, distribution and densities were recorded.

Chapter Two A Community Study of Native Bees

Abstract

A search was conducted in Whangarei, New Zealand, to determine locations of active communities of native bees to study as part of a larger investigation to aid native bee conservation in the region. Five different locations were chosen for observations of native bees. One active community of bees was found on Mt. Parihaka (Whangarei) and this community became the focus for a study over three seasons (December 2004 - March 2005, October 2005 - March 2006 and November 2006 - January 2007). Monitoring of nest sites, insect collections, and observational records were gathered throughout the first two seasons on fine days and continued until bees were no longer active. Further collections and observations were conducted in the final season.

Observations of bees were made, either at nest sites, or while foraging. Nest construction, exit and entry behaviours, interactions with associated organisms, foraging behaviours and community seasonal activities were recorded in a log book and captured on a digital camera and video recorder. Insects were collected by hand using a bug vacuum (Summit ^{TM}) or sweep net as they entered or exited nests, or while they were foraging. Representative specimens were pinned and identified by Dr. Barry Donovan (Donovan Scientific Insect Research Ltd, Christchurch) and formed a study reference collection.

A total of 1025 insects were handled in this study. Eight species of native bees were found in the local Whangarei region; six species were found on Mt. Parihaka, five from the genus *Leioproctus* and one species from the genus *Lasioglossum* as follows*: Leioproctus (Leioproctus) boltoni* (Cockerell), *L. (L.) huakiwi* (Donovan), *L. (L.) imitatus* (Smith)*, L. (N.) paahaumaa* (Donovan)*, L. (L.) pango* (Donovan) (Hymenoptera: Colletidae) and *Lasioglossum (Austrevylaeus) sordidum* (Smith) (Hymenoptera: Halictidae). *Leioproctus boltoni* was also collected from Ngaiotonga Valley and *L. imitatus* was collected from Mair Park. From the Morningside subdivision, another species from the genus *Lasioglossum, Lasioglossum (Chilalictus) cognatum* (Smith) was collected. Finally, one species from the

genus *Hylaeus, Hylaeus* (*Prosopisteron*) *relegates* (Smith) (Hymenoptera: Colletidae), was collected from Raumanga Valley.

2.1 Introduction

2.1.1 Bees and the environment

Bees are keystone mutualists. They help to pollinate plants, which in turn support otherwise separate food webs (Kevan 1991; LaSalle & Gauld 1993). As pollinators, they are vital to the ecosystems in which they live. A change in their population could have far-reaching effects altering these complex food webs (Mclntyre & Hostetler 2001). Without insect pollination many flowering plants would not reproduce sexually and humans would lose an estimated 15 - 30 % of world food resources (Buchmann & Nabhan 1996; Kearns et al. 1998; The Xerces Society 2007b). Bees exhibit some of highest floral visitation rates in the insect world. This makes them the single most important group of pollinators (Neff and Simpson 1993). Non-*Apis* native bees play an especially important role in many natural ecosystems because they are among the most critical and effective pollinators of native plants (LeBuhn et al. 2006).

Concerns have been raised about the decline of native bees around the world and conservation efforts are gaining momentum (O'Toole 1993, 1994; Buchmann & Nabhan 1996; Roubik 2001; O'Toole 2002; Committee on the Status of Pollinators in North America 2006). Before conservation strategies can be implemented however, baseline data on the population, diversity and ecology of native bee species is required (Powell & Romey 2003; Committee on the Status of Pollinators in North America 2006).

New Zealand has a paucity of native bees with only 28 native species. Likewise, studies on New Zealand's native bees are few (Donovan 1967, 1980, 1983; Quinn 1984). There is a prevailing view that relatively few specialised pollinator-plant relationships exist in New Zealand (Lloyd 1985; Newstrom & Roberston 2005). Despite this view, there is evidence of the important role native bees play in New Zealand's native ecosystems. For example, native bees have been observed pollinating plants in sub alpine and alpine grasslands, beech forests and temperate rainforests (Primack 1978, 1979; Quinn 1984; Kelly 1997; Murphy & Kelly 2003). Native bees have also been observed pollinating the endangered mistletoe (*Peraxilla tetrapetala:* Loranthaceae) highlighting the complex link between plants and native bees (Kelly 1997).

A number of countries have conducted large-scale systematic surveys of native bees (Quaranta et al. 2004), but for most nations survey data on native bees are limited. Until recently (Donovan 2007) this was also the case for New Zealand native bees (Macfarlane & Ferguson 1983; Quinn 1984; Powell & Romey 2003; LeBuhn et al. 2006). To fully understand population trends monitoring across multiple years to ascertain the abundance and population of native bees is typically required (Roubik 2001) but this is an intensive process.

This study presents the results of a species survey of native bees around Whangarei, across multiple seasons. The status of several communities located on Mt. Parihaka is highlighted. It is anticipated that knowledge of bee composition on Mt. Parihaka will provide baseline data that will be useful for future conservation and management strategies aimed at maintaining pollinator diversity and maximizing pollination rates in a regenerating ecosystem. In this study, attention was given to bee identification and collection and storage of specimens. Observations of the seasonal rhythms influencing the bees' emergence patterns, mating, nesting and foraging behaviours were also recorded. These data combine to form the foundation of a wider investigation into New Zealand native bee biology.

2.1.2 Families of Colletidae and Halictidae

Colletidae is regarded as one of the most primitive families of bees (Michener 2000). There are 24 native species of Colletidae in New Zealand and they can be divided into two subfamilies, the Colletinae and the Hylaeinae. The subfamily Colletinae is made up of 18 species from the genus *Leioproctus.* Typically robust, hairy, black bees *Leioproctus* range in length from 5 –13.4 mm and females carry pollen externally on scopae (Donovan 1980, 2007). In the subfamily Hylaeinae, there are six species from the genus *Hylaeus.* Commonly known as masked bees, *Hylaeus* have distinctive yellow or white markings on their face. *Hylaeus* are slender, mainly black bees with sparse hairs. Females lack pollen scopa so they swallow pollen and carry it in their crop. They range in length from 2.5-9 mm (Donovan 1980; O'Toole & Raw 1991).

Most colletids provision their nests with a liquid pollen – nectar mixture that sits in the base of the waterproof cell. New Zealand colletids sculpt pollen into a ball upon which they lay an egg. Almost all members of this family have a short bilobed tongue. Females of the species use the specialised tongue to 'paint' glandular secretions to the walls of their cells (O'Toole & Raw 1991). The secretion is a mixture of chemicals (macrocyclic

lactones) that inhibit fungal growth. When the secretion dries it forms a waterproof cellophane membrane; the membrane remains in the nest intact over many seasons.

Halictidae is a large family found in all parts of the world. New Zealand has only four native species belonging to the subfamily Halictinae and genus *Lasioglossum.* They are commonly called sweat bees because they are attracted to human perspiration. All bees in this family are moderately to sparsely hairy, black or greenish and range in length from 4-8 mm. Females carry pollen externally on scopae, laterally on the thorax, and ventrally on the abdomen (Donovan 1980). Although the nest of *Lasioglossum* is founded by a single female the species are primitively eusocial (Michener 2000). After mating in autumn a fertilised female will hibernate in her nest and emerge in spring to found a new nest, which she mass provisions for her offspring. A generation of males and females emerge from the nest. The males leave and the female daughters remain to help build more cells, and collect pollen for their mother (Donovan 1967; O'Toole & Raw 1991). Female Halictidae, also line the walls of their cells with a macrocyclic lactone mixture (the polymer secreted by the Dufour's gland which has antibacterial/fungi properties), but unlike that of colletids, this mixture impregnates the soil like vanish (O'Toole & Raw 1991).

2.1.3 Biology of solitary miners

Introduction

There are around 17,000 described bees of the world (Michener 2000) and the majority of these are solitary (O'Toole & Raw 1991). Female solitary bees work alone to build and provision their nests. Most solitary bees have a similar life cycle, as shown in Figure 2.5 below.

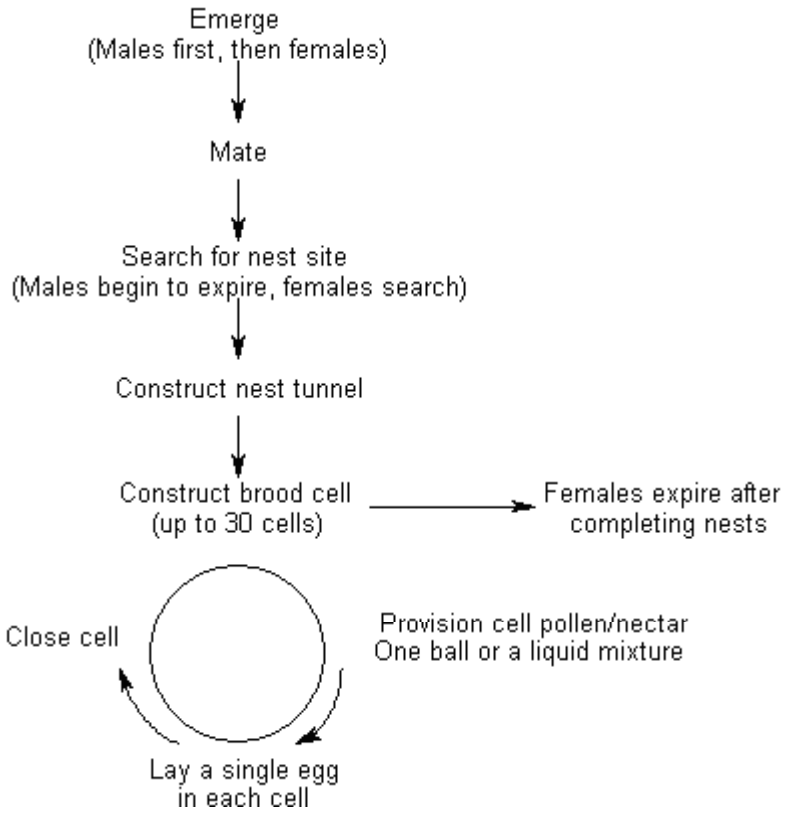

Figure 2.5 The life cycle common to all solitary bees.

Solitary bees can be classified into two groups; those that construct nests using secretions from their glands (ground burrowing or mining bees) and those that construct nests using resources they have collected from outside of the nest (O'Toole & Raw 1991). Most of New Zealand's endemic bees are solitary mining bees, including 24 species from Colletidae (18 from the genus *Leioproctus* and 6 from the genus *Hylaeus*) and three from Halictidae (all from the genus *Lasioglossum*). *Lasioglossum sordidum* exhibits some level of social organisation because several females will work from the same nest, this species is therefore considered partly social (Donovan 1980). The following sections will focus on solitary mining bees, so *Lasioglossum sordidum* will not be covered in further detail.

Reproduction and seasonal rhythms

Most solitary bees live for around one year. Colletidae overwinter as diapausing prepupae in nest cells and in spring prepupae develop into adults and start to emerge (September – December) (Donovan 1980). Females are thought to mate once, storing sperm to release as required. They have the capacity to lay up to approximately 30 eggs and construct up

to 30 cells(Donovan 1980; O'Toole & Raw 1991). When poor weather prevents foraging and nest construction it has been suggested that females have the ability to reabsorb mature eggs as standby food (O'Toole & Raw 1991). When a cell is provisioned with a pollen nectar ball, the female lays one egg and then closes the cell. After around three days the egg hatches into a larval. Within a few weeks the larval consumes all the food becoming a prepupal which diapauses until the following spring (Donovan 1980). Although emergence timing is not fully understood, it is proposed that solitary bees can predict cues such as increases in soil temperature/ moisture. They use these cues to time their emergence to coincide with the flowering of their preferred plants (O'Toole & Raw 1991; The Xerces Society 2007a).

Bee Villages and nest architecture

Many species of mining bee nest in dense aggregations (O'Toole & Raw 1991). They are shown to have a particular preference for the type of substrate they use (Petanidou & Ellis 1996). An extraordinary example of such a community was recorded in Russia, where it was estimated that nesting bees spanned an area of 7 km. At densities of up to 21 nests per km^2 it was possible that there were over 12 million nests (O'Toole & Raw 1991). Equally intriguing, Quinn (1984) estimated some 840,000 bee nests along a 7.5 km road in the McKenzie Basin, Canterbury (New Zealand). Solitary mining bees show a strong preference to form large nesting communities where many species co-exist. In these aggregations, a tumulus forms around nest entrances indicating bees at work. Without knowing the architecture of the nest it is virtually impossible to determine species from the entrance alone. In contrast, internal nest architecture is characteristic to a given species and so can explain much about a bees' biology (O'Toole & Raw 1991).

Flower relationships and foraging habits

Most native bees can be grouped according to their foraging habits. Some are generalists, gathering food from a wide range of flowers, others are specialists relying on a single plant species or a closely related group of plants for food (The Xerces Society 2007a). Myrtaceae is thought to be the primary flowering host family for Colletinae. Female Colletinae forage primarily on native Myrtaceae, Fabaceae or Asteraceae (Donovan 1980). Some species of Colletinae are restricted to a few plants within these families for example; *Leioproctus imitatus* visits manuka (*Leptospermum scoparium*), kanuka (*Kunzea ericoides*) and pohutukawa (*Metrosideros excelsa*). Some Colletinae therefore, would be considered specialists (Donovan 1980). Other species of Colletinae such as *Leioproctus huakiwi*, have adapted to forage on introduced plants such as kiwifruit (Actinidiaceae

Actinidia) and onions (Liliaceae *Allium*). Hylaeinae like Colletinae, forage on both native and introduced flowers (e.g. manuka and kiwifruit) and some species specialise on plants within a single host plant family. In contrast to Colletidae, most Halictinae are generalist foragers, visiting a wide range of introduced and native plants (Donovan 1980). A longer nesting period means there is demand for pollen through spring, summer and autumn.

2.2 Study Site and aims

2.2.1 Mount Parihaka

Mt. Parihaka, the summit of which was originally a Pa complex, is a significant heritage site in Whangarei, particularly to local iwi (Te Ihi Tito, 2005). It is located a few minutes away from central Whangarei by vehicle, via Memorial Drive. The Parihaka War Memorial car park is located near the top and pedestrian access to the War Memorial at the peak. Parihaka forest is located a little east of Parihaka War Memorial and is bordered to the west by Memorial Drive and to the north and east by private land, backing onto Whareora Road and Abbey Caves road. Parihaka forest is currently managed as pine plantation; gates into the area located to the east of the War Memorial parking area, allow pedestrian access but vehicular access is restricted to forest management activities. The forest is currently Whangarei District Councils (WDC's) largest production plantation with over 118 ha of *Pinus radiata* cover. Harvesting of the area commenced in 2005 and continued throughout 2006; 42 ha have already been logged. The areas logged will be allowed to revert back to native forest under the management of the WDC (Parks Division: Parihaka and Hatea River Reserves Management Plan).

Pine forest is the predominant cover but there are many native plant species regenerating. Pockets of wetlands at the base of the forest are dominated by cutty grass (*Gahnia setifolia*) and towai (*Weinmannia silvicola*). Other areas around the forest are dominated by introduced gorse (*Ulex europaeus:* Fabaceae), pampas (*Cortaderia spp*.), manuka and kanuka (*Leptospermum scoparium and Leptospermum ericoides:* Myrtaceae), sedges (*Carex spp.*) pate and pigeonwood (*Hedycara arborea*). In a survey the WDC (WDC 2000) found several native species to overtop gorse including: pate, hangehange (*Geniostoma rupestre*), mahoe (*Melicytus ramiflorus*), mapou (*Myrsine australis*) and towai. Also, on the open clay banks along the upper end of Memorial Drive at least 15 species of native orchids were recorded in a survey by Manning (2001). Several bird species including the harrier hawk, shinning cuckoo, morepork, tui, and kukupa can be observed in the forest. It

is also believed that North Island brown kiwi are present (DOC, 1993). The Auckland green gecko and banded kokopu, inanga, long-finned eel and koura have been observed in streams around Parihaka.

Communities of native bees were found in the Parihaka forest, shown on Figure 2.6. The first three communities were found at the gated entrance of the pine forest, to the left of Parihaka Memorial car park (Sites: 1, 2 and 3). A fourth was found at the gated entry to the reserve water tower, half way up Memorial Drive (Site 4).

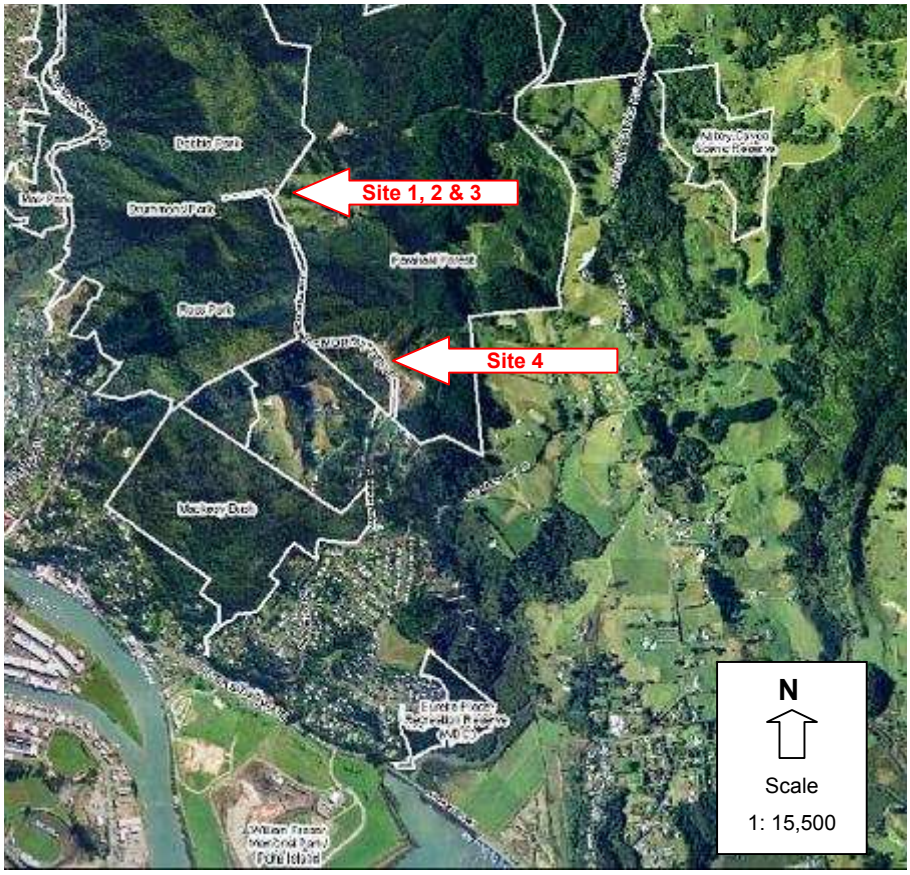

Figure 2.6 GIS Photo of Parihaka Reserve and Forest (WDC 2007).

2.2.2 Study aim

This study forms the foundation of an investigation into the biology of native bees. The purpose of this component of the research, which is largely explorative and observational, is to gain some understanding of the abundance and diversity of native bees in the Whangarei region by:

A. Finding and observing native bee communities in the district.
B. Observing the communities over several seasons.
C. Collecting and identifying native bee species found.

The study aims to answer the following questions:

1. Where are communities of native bees located?
2. What species are present in these communities?
3. How are native bees identified?
4. How abundant are native bees in these communities?
5. Are these communities easily accessible and safe?
6. Are these communities suitable for conducting multi seasonal studies on?
7. Are these communities suitably protected from public should study equipment be left in the field?
8. What difficulties are associated with a study of native bees?
9. How are these difficulties managed or avoided?

2.3 Methods

2.3.1 Search for nest sites

Active nest sites were discovered during a search conducted in season one, December 2004 - March 2005. Single one-off searches were conducted on fine days and included five areas: Ngaiotonga Valley (Whangaruru, Northland), Raumanga Valley Reserve (Otaika, Whangarei), Mair Park (Kensington, Whangarei), Morningside Subdivision (Morningside, Whangarei) and Mt. Parihaka (Riverside, Whangarei) (see Table 2.3 and Figures 2.6 and 2.7 for locations and map images).

Table 2.3 Study sites in the Whangarei district included in the initial search for native New Zealand bees. Specific site descriptions, latitude & longitude and general ecology of all areas where native bees were observed or collected from during three summer seasons (2004 – 2005, 2005 – 2006, 2006 – 2007).

Area	Location Code & Site	Location	General Ecology	Survey dates
Ngaiotonga Valley, Whangaruru. Bay of Islands	**Site 5**: Clay bank on the right-hand side, at the entrance to McGee farm.	**S -** **E -** **HAE -**	Rural. Coastal area and native bush.	Three surveys; 2004-05, 2005-06 2006-07
Raumanga Valley Reserve, Otaika. Whangarei.	**Site 6**: Garden in the back yard of property at 124 Raumanga Valley Road.	**S** 35^{O} 44' 25.23 " **E** 174^{O} 18' 06.14" **HAE** 51 m	Urban, bush reserve with river	Three surveys; 2004-05, 2005-06 2006-07
Mair Park, Kensington. Whangarei.	**Site 7**: Forest banks in public walkway area near river.	**S** 35^{O} 42' 46.33 " **E** 174^{O} 19' 40.79 " **HAE** 75 m	Urban, bush reserve with river	Two surveys; 2004-05, 2005-06
Morningside Subdivision, Morningside. Whangarei.	**Site 8**: Cleared ground areas.	**S** 35^{O} 44' 17.69 " **E** 174^{O} 19' 24.50 " **HAE** 94 m	Urban, cleared area, new subdivision. Some gorse.	Two surveys; 2004-05, 2005-06
Opposite the Warehouse	**Site 9**: On single large (50 m high) Pohutukawa tree	**S** 35^{O} 43' 21.73 " **E** 174^{O} 19' 23.21 " **HAE** 41m	Urban, unused area by stream / drain, at the side of a main road	Three surveys; 2006-07
Whangarei Marina	**Site 10**: On a single small (4 m high) Pohutukawa tree	**S** 35^{O} 43' 57.36 " **E** 174^{O} 19' 36.88 " **HAE** 43 m	Urban, at the edge of the water – mangrove ecology.	One survey; 2006-07
Mount Tiger	**Site 11**: On roadside edge, down from Home stay.	**S** 35^{O} 42' 42.99 " **E** 174^{O} 26' 08.27 " **HAE** 242 m	Rural, native bush and farmland	Three surveys; 2006-07

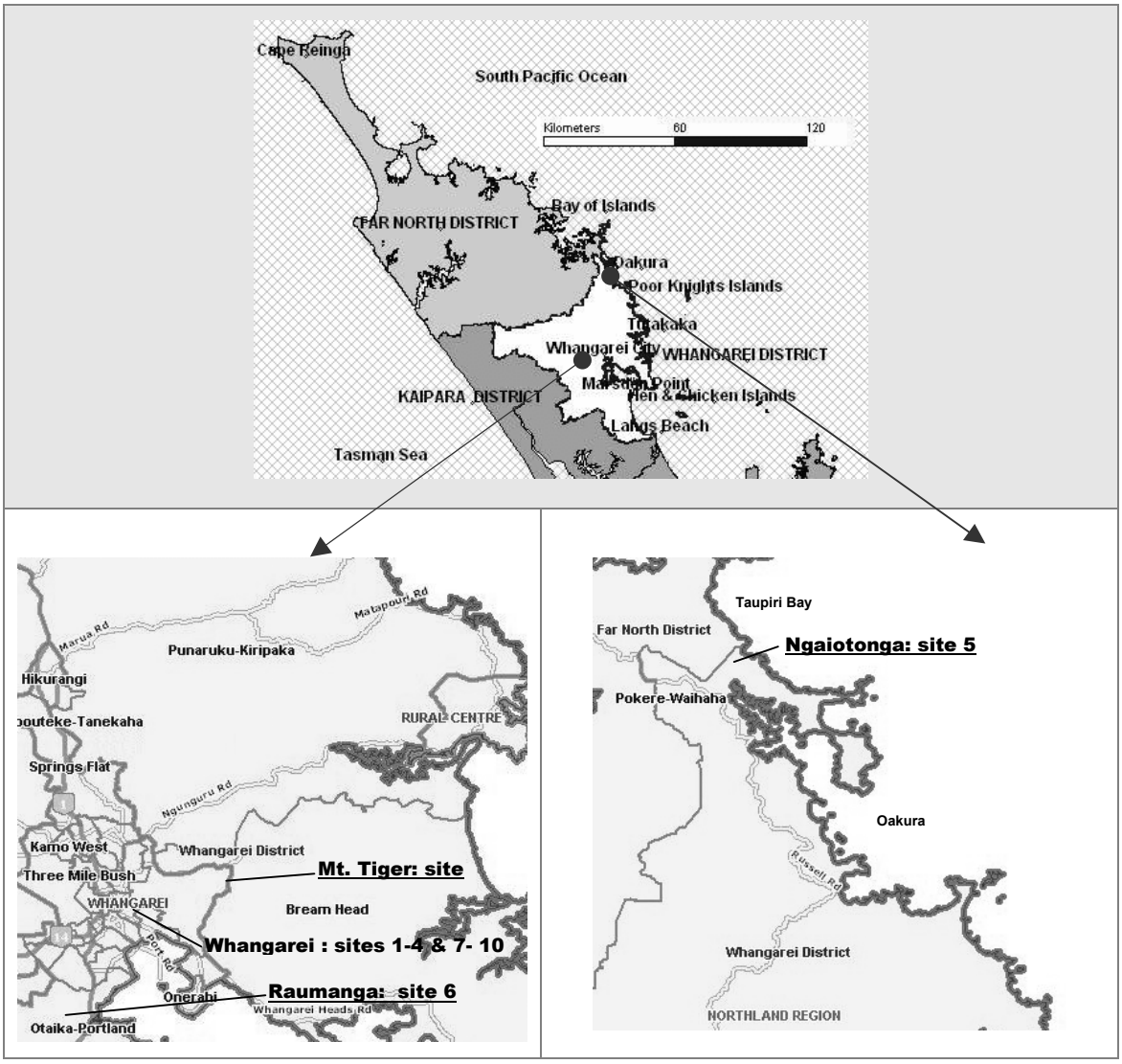

Figure 2.7 Site Locations marked of maps of: A, Upper Northland; B, Central Whangarei District; and; C, Whangaruru (Statistics NZ 1998; WDC 2007).

Large aggregations of nests and thousands of foraging native bees were found on Mt. Parihaka (sites 1 - 4) and at Ngaiotonga Valley (site 5). For logistical reasons, ease of access and safety it was decided that Mt. Parihaka would be the primary focus for the community study. Insects collected from all sites have been included in the data however. Four large communities of native bees were found on Mt. Parihaka. Three located through the gated entry to the pine plantation area (sites 1, 2 and 3) and another two in the vicinity of a water tower on Mt. Parihaka (sites 4A and 4B) (see Table 2.4 below). Abundant foraging bees were observed on one kanuka tree, near one nest site in particular (site 1A).

Table 2.4 Areas located on Mt. Parihaka that were the focus for repeat collections and observations of native New Zealand bees. Specific site descriptions, locations, latitude & longitude and general ecology of areas where bees were observed or collected from during two summer seasons (2004 – 2005 & 2005 – 2006).

Area	Location Code & Site	Location	General Ecology	Monitoring Frequency
Mt. Parihaka, Riverside. Whangarei. Main entrance at the very end of memorial drive. Car park leading to walking access war memorial on the right hand side and gated forestry area (restricted access) on the left hand side.	**Site 1A**: By gate, at the entry to forestry area. First bank on right-hand side.	**S** 35^{O} 42' 43.04 " **E** 174^{O} 20' 18.62" **HAE** 261 m	Pine forest plantation. First generation regenerative forest. Some gorse, pampas and cutty grass. Some cleared areas.	Daily peak season
	Site 1B: By gate, at the entry to the forestry area. First grassy bank on left hand side.	**S** 35^{O} 42' 42.68" **E** 174^{O} 20' 19.16" **HAE** 262 m		Daily peak season
	Site 1C: Opposite telecom transmission tower, next to water tower on left-hand side	**S** 35 ^{O} 42' 42.73" **E** 174^{O} 20' 20.18" **HAE** 261 m		Daily peak season
	Site 1D: Second bank under transmission tower.	**S** 35^{O} 42' 42.97" **E** 174^{O} 20' 20.18" **HAE** 260 m		Daily peak season
	Site 1E: Grassy knoll by telecom transmission tower.	**S** 35^{O} 42' 43.49" **E** 174^{O} 20' 19.82" **HAE** 264 m		Weekly peak season
	Site 1F: South – west side of bank on Memorial drive.	**S** 35^{O} 42 43.12 **E** 174^{O} 20 17.86 **HAE** 258 m		Daily peak season
	Site 1G: Very east side of bank on a small south east facing bank	**S** 34^{O} 41' 40.18" **E** 174^{O} 20' 16.86" **HAE** 258 m		Weekly peak season
	Site 2A: Down from gate entry. Third major bank in forestry area, on the right hand side.	**S** 32^{O} 46' 43.03" **E** 174^{O} 20' 22.01" **HAE** 258 m		Weekly peak season
	Site 3A: Down from gate. Small bank on left hand side in the forestry area	**S** 32^{O} 46' 43.03" **E** 180^{O} 20' 21.01" **HAE** 242 m		Weekly peak season
Mt. Parihaka, Riverside. Whangarei. Before memorial car park, half way up memorial drive. On the right hand side gated entrance into water tower reservoir area	**Site 4A**: Water tower entrance, over mound on the left hand side	**S** 35^{O} 43' 01.96" **E** 174^{O} 20' 37.34" **HAE** 192 m		Daily peak season
	Site 4B: Five m down from mound, on steep bank.	**S** 35^{O} 43' 01.34" **E** 174^{O} 20' 37.35" **HAE** 192 m		Daily peak season
	Site 4C: Opposite water tower entrance on the main road. Pohutukawa on left hand side travelling up Memorial drive	**S** 35^{O} 43' 03.01" **E** 174^{O} 20' 36.44" **HAE** 191m		Weekly peak season

2.3.2 Monitoring native bees activity

Daily monitoring in season one (December 2004 - March 2005) continued on fine days, until bees were no longer observed foraging and there was no longer evidence of fresh tumuli at nest sites (indicators that bees are no longer active). In total three moths monitoring data was collected. Weekly monitoring resumed in season two (October 2005 – March 2006) and continued until fresh tumuli at nest entrances were seen (an indication that new bees are emerging). Floral resources in the area were also observed for the first sign of foraging bees. Care was taken to check flowering plants that bees had been observed foraging on in the first season such as kanuka and manuka. When signs indicated the emergence of new bees, daily monitoring of the nest sites was started. Visiting entomologist, Dr. Donovan (Donovan SIR Ltd) provided advice and training in native bee taxonomy and behaviour during part of the survey (19 – 22nd November 2005). Collections made during this period formed a reference collection (Donovan SIR Ltd) that were later used to identify insects. Daily monitoring continued throughout season two on fine days, until bees were no longer as active. Weekly monitoring was then started until there was no sign of activity. Ecological data were collected (ambient temperature, humidity, wind speed, luminosity). Observational records of insect behaviour and associated organisms were also detailed. Insects were collected for load lifting experiments, muscle mass and pollen mass measurements, pollen analysis, DNA analysis and species identification (see Appendix A2 for collection records).

2.3.3 Recording observational data

Daily ecological data were collected (ambient temperature, humidity, wind speed, luminosity) over the active period when observations and collections of bees were made. Nest construction, exit and entry behaviours, interactions with associated organisms, foraging behaviours, and community seasonal activities were recorded in a log book, captured on video, and digital camera. Detailed observations were made at two communities (site 1 and 4) for data on foraging duration and nesting provisioning duration times as part of the larger study on native bee biology (Chapters Three and Four). Video recordings of nest activity were made (12 hours) and used to verify foraging duration and nesting provisioning duration times. When possible, nest exit and entry behaviours were also captured on shorter length videos (several minutes).

2.3.4 Collecting insects

Collections were made only when there was a high level of activity at the nest site, or at least 30 bees were observed actively foraging. Insects were caught while they were foraging around nest sites or from 'mating swarms' around shrubs, using either a sweep net or a bug vacuum (Summit ^{TM}). The sweep net was used to collect groups of foraging bees and mating swarms. Five sweeps was sufficient in most instances to collect many hundreds of bees for identification purposes and to gather estimates of sex ratios. Male and female insects for sex ratios were counted and then released. The vacuum method was used to collect bees in close proximity to nest sites where sweep netting was difficult and could potentially destroy nest integrity. The trigger activated vacuum allowed for a controlled collection of individual insects and some insects were collected from single flower heads using this method.

Once insects were collected they were placed into an ethyl acetate killing jar until they expired. Some insects that were collected for Donovan SIR Ltd were placed in a cyanide-killing jar. Individual insects were placed in individual containers labelled with date, time, location (and/or plant collected from) and collector name. For sweep netted insects, the entire collection was placed in a jar. Individuals from the collection were then transferred to separate containers labelled with date, time, location (and/or plant collected from) and collector name.

2.3.5 Preparation and storage of insects

Insects collected were either pinned or frozen at -20°C. Pinned insects were included in the study reference collection. Complete frozen insects were stored for flight muscle measurements. Body parts of insects were frozen after flight muscle mass measurements. All insects collected for the study reference collection were mounted on pins and labelled the day of collection then stored in an insect box. Representative insects were pinned, packaged and posted to Dr. Donovan for identification. These were later returned identified and labelled to include in the study reference collection. Additional native bee specimens (stored in alcohol with identification labels) were supplied by Landcare Research Ltd. and were included in the study reference collection. These were removed from the alcohol room dried and pinned along with labels, to include in the study reference collection. Bees stored for flight muscle mass and measurements were identified on the day of collection before they were frozen. The body parts of insects already analysed for flight muscle mass from season one, were identified from the faces and back legs after

the study reference collection was compiled when keys for New Zealand native bees became available and after taxonomic training was received (2006). The body parts were glued to cardboard, pinned and labelled to include in the study reference collection. Other insects included in this survey were based on records supplied from Dr. Donovan who collected, identified and stored insects from Whangarei during the three-day survey in November 2006 (19^{th} – 22^{nd}). Dr. Donovan supplied a species list compiled from this collection. The insects collected by Dr. Donovan for the survey, formed part of another reference collection and DNA analysis, as part of another research project (Donovan SIR Ltd).

2.3.6 Identification of insects

At the end of the study collection period (March 2006) all stored insects were systematically re-checked using the study reference collection, the Donovan SIR Ltd reference collection, the Landcare reference collection, expert advice, and follow-up verification where necessary from Dr. Donovan. A list of morphological similarities and differences of species found on Mt. Parihaka (Table 2.5 below) was primarily relied on for identifications (Donovan pers. comm.). All insects were viewed with a Leica Zoom 2000 dissecting microscope using a combination of 12x and 25x magnification. Care was taken with older male specimens of *L. boltoni, L. huakiwi, L. imitatus* and *L. pango* that had worn facial hairs (vestiture) because they appeared similar. Frozen insects were dried so vestiture could be easily identified and then re-frozen. Identification guides and keys were not the primary method used for identification because they required a high degree of taxonomic proficiency. Comparison of unidentified insects with the reference collection was the preferred technique.

Table 2.5 The morphological similarities and differences between species used as a guide to identify bees during the study (Donovan pers. comm.).

L. boltoni	
Female	Male
Supraclypeus is rounded almost protruding and has very few or no punctures centrally. The hairs on the dorsal half of the scopa are always black.	Broad central part of the clypeus almost flat with many punctures Often an impunctate central longitudinal line on the supraclypeus
L. imitatus	
Female	Male
Supraclypeus has small close punctures throughout. Most have the scopal hairs pale throughout. Some have the upper half of the scopal hairs dark.	Hairs on the supraclypeus and the adjacent paraocular areas are short and tightly packed. Hairs on young males are orange - as they age the hairs fade to almost white. Supraclypeus is nearly flat, except for a point between the antennal sockets. Supraclypeus is densely and closely punctured throughout. Most have pale hairs dorsally on the end of the abdomen. Some can have black hairs dorsally on the end of the abdomen
L. pango	
Female	Male
The vestiture of some entirely black; the only native bees with this character Smaller, shorter face than *L. boltoni.* Supraclypeus is different to *L. boltoni* - in side view it slopes upwards and outwards from below.	
L. huakiwi	
Female	Male
Supraclypeus with a longitudinal impunctate ridge, readily seen in lateral view. Clypeus often shows almost a slightly similar ridge-like appearance.	Hairs on supraclypeus very short. Hairs longer beside the supraclypeus. The clypeus is evenly rounded from side-to-side. No flattened central area like *L. boltoni.*

2.4 Results

2.4.1 Species identified

Eight species of native New Zealand bees were recorded from the Whangarei region (Table 2.6), three newly described (Donovan 2007) and five previously described. Six species were found on Parihaka, three newly described and three previously described. Colletidae was represented by six species and Halictidae by two. The greatest diversity was seen Colletidae (subfamily Colletinae). The genus *Leioproctus* was represented by five species in total, four from the subgenus *L. (Leioproctus)* and one from the subgenus *L.* (*Nesocolletes*). *Hylaeus* (subfamily Hylaeinae) was represented by one species belonging to the subgenus *H.* (*Prosopisteron*). Two species of *Lasioglossum* (subfamily Halictinae, Family Halictidae) were recorded, one from each of the two subgenera: *Lasioglossum (Chilalictus)* and *Lasioglossum (Austrevylaeus).*

Table 2.6 Native bee taxa found in the Whangarei region.

Family **Colletidae**
Subfamily **Colletinae**
Genus ***Leioproctus*** Smith, 1853
Subgenus *Leioproctus* Smith, 1853
boltoni (Cockerell, 1904)
huakiwi (Donovan, 2007)
imitatus (Smith, 1853)
pango (Donovan, 2007)
Subgenus *Nesocolletes* Michener, 1965
paahaumaa (Donovan 2007)
Subfamily **Hylaeinae**
Genus ***Hylaeus***
Subgenus *Prosopisteron* Cockerell, 1906
relegatus (Smith 1876)
Family **Halictidae**
Subfamily **Halictinae**
Tribe Halictini
Genus ***Lasioglossum*** Curtis, 1833
Subgenus *Chilalictus* Michener, 1965
cognatum (Smith, 1853)
Subgenus *Austrevylaeus* Michener, 1965
sordidum (Smith, 1853)

2.4.2 Collection records

General

One thousand and twenty five bees were handled in this study and 782 were collected for further study. A total of 50 bees, representing six species, were collected from eight areas in season one (December 2004 – March 2005). In season two (October 2005 – February 2006) a further 629 insects were handled. Three hundred and eighty six were collected for analysis and 243 were collected and released. In total eight species were represented in collections from season two. Over a two-day period in season two (20th – 21st of November 2005) 61% of all insects were collected from Mt. Parihaka. In total 23% of these insects were used for DNA analysis and 38% for a reference collection. A further 346 insects were collected from seven different sites in the third season (December 2006). A summary of all collections, species and sex compositions are presented in the following sections. For detailed collection records refer to Appendix A2.

The summary of collections, the number of individuals collected, species, sex and the location the insect was collected from is shown in Table 2.7. Only one female insect was collected from the species *Hylaeus relegatus. Lasioglossum cognatum* (*4* ♀♀) and *Lasioglossum sordidum* (*9* ♀♀) were also collected in low numbers; there were no males collected.

Table 2.7 Collection records of native New Zealand bees from all seasons (2004-05, 2005-06 & December 2006).

Species	Sex	Number of individuals collected at each location								Totals	% Sex	
		Site 1-4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10	Site 11		F	M
Hylaeus relegatus	♀			1						1	100%	0%
	♂									0		
L. boltoni	♀	37	37	2			1		23	100	31%	69%
	♂	220							4	224		
L. huakiwi	♀	3	1						29	33	23%	90%
	♂	34	78							112		
L. imitatus	♀	79	3	2	2					86	40%	60%
	♂	124	4							128		
L. paahaumaa	♀	22								22	79%	21%
	♂	6								6		
L. pango	♀	8		1			2			11	19%	81%
	♂	38					8			46		
Lasioglossum cognatum	♀	2				2				4	100%	0%
	♂									0		
Lasioglossum sordidum	♀	4		5						9	100%	0%
	♂									0		

Collections from nest sites, foraging and mating

Of the 782 insects collected, around 4% were caught while foraging on introduced plants and 21% on native plants. A further 20 % were collected as they formed mating swarms around shrubs, gorse and pine with the remaining 55% collected from ground and bank nest sites (Table 2.8 below).

Although *L. boltoni* was the most abundant species caught at nest sites (201 individuals were collected) *L. huakiwi* as a species, was mostly limited to nest site collections with nearly 87% of all *L. huakiwi* collected from around ground and bank nests. In total 84% of

L. huakiwi collected were male bees. In contrast to this male and female *L. imitatus* were collected from nest sites in similar proportions. Nest site collections formed around 39% of all individuals collected for this particular species. Collections of *L. paahaumaa* were made at nest sites and from plants around nest sites (1 - 10 m); 78% of all *L. paahaumaa* collected were female. Only two female *Lasioglossum cognatum* were collected, both at nest site locations. A single *Lasioglossum sordidum* was collected from a nest site the remaining 8 were collected while foraging.

Table 2.8 Quantity of insects collected from nest site areas, while foraging (on introduced or native plants) or while forming mating swarms around shrubs in Whangarei.

Bee species	Total collected	Nest sites (55%)	Introduced plants (4%)	Native plants (21%)	Mating swarms (20%)
L. boltoni	324	201	4	50	69
L. imitatus	214	83	3	66	62
L. paahaumaa	28	13	15		
L. pango	59	4	1	43	11
L. huakiwi	145	126		6	13
Lasioglossum sordidum	9	1	8		
Lasioglossum cognatum	2	2			
Hylaeus relegatus	1		1		

Table 2.8 above shows some bees were collected as they foraged on flowers (introduced and native) while others were collected as they formed mating swarms around shrubs like kamahi (Cunoniaceae *Weinmannia racemosa*) and pine. *Lasioglossum sordidum, Hylaeus relegatus* and *Leioproctus paahaumaa* were collected while foraging on introduced plants and were not caught foraging on native species. A single female *L. pango* was collected from mandarin (Rutaceae *Citrus reticulata*) and many more individuals were observed foraging on *Citrus*. For more results on the foraging preferences refer to Chapter Five.

Species composition

Leioproctus boltoni was the most abundant species collected from sites around Whangarei followed by *L. imitatus* and *L. huakiwi* (Figure 2.8). These three species combined represent 87% of all insects collected. *Leioproctus pango* and *L. paahaumaa* represent 11% followed by *Lasioglossum sordidum*, *Lasioglossum cognatum* and *Hylaeus relegatus* (~2%).

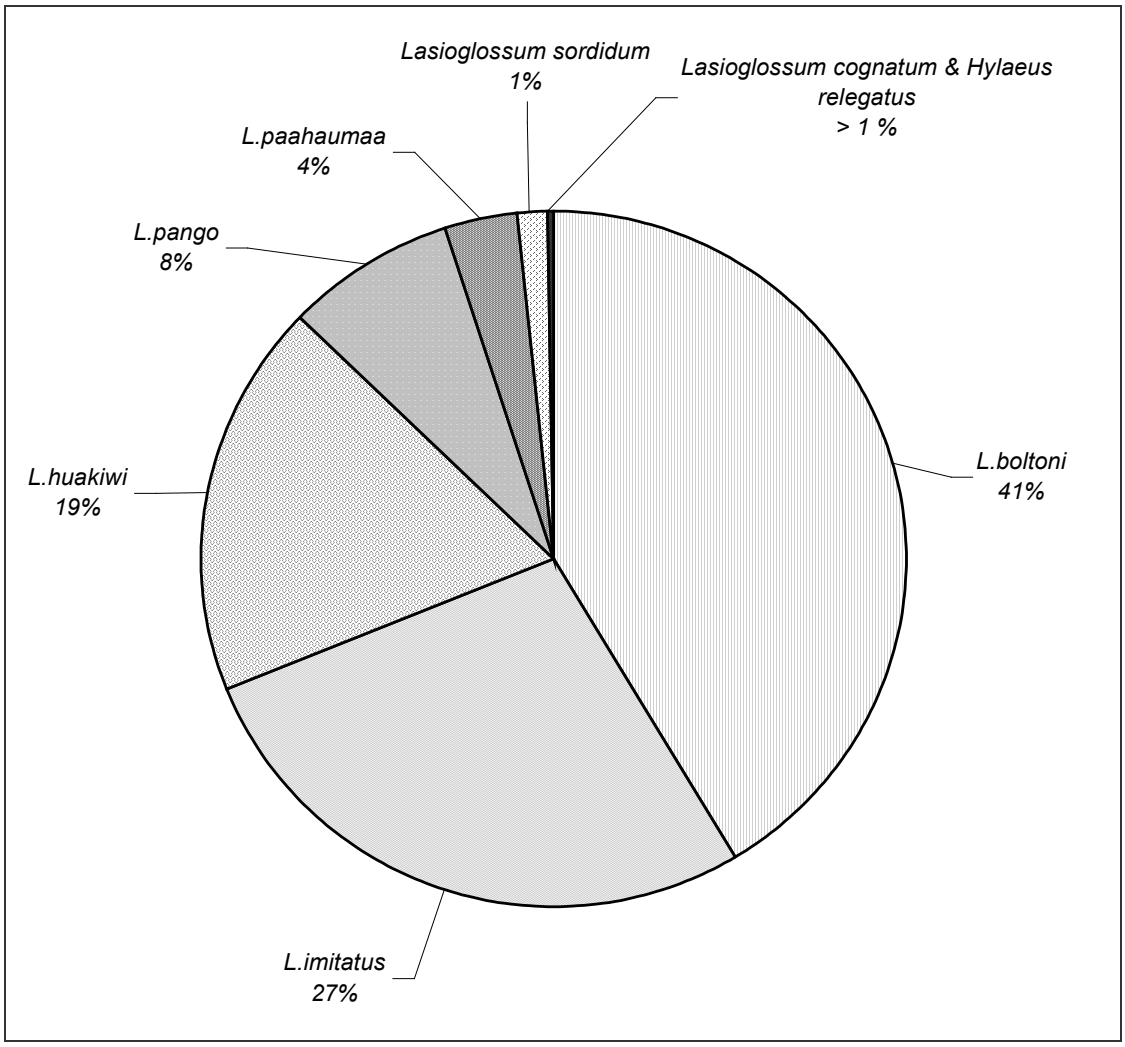

Figure 2.8 Percentage composition of species of native New Zealand bees collected over three seasons (2004- 05, 2005- 06, & December 2006)

Sex composition of species

Approximately 44% more male bees were collected from all collection sites. Twenty to seventy percent more males than females were collected from the species, *L. boltoni, L. imitatus and L. pango*. In contrast, female *L. paahaumaa* were collected in higher

numbers than males. Only one female *Hylaeus relegatus, Lasioglossum cognatum* and *Lasioglossum sordidum* was collected (Figure 2.9).

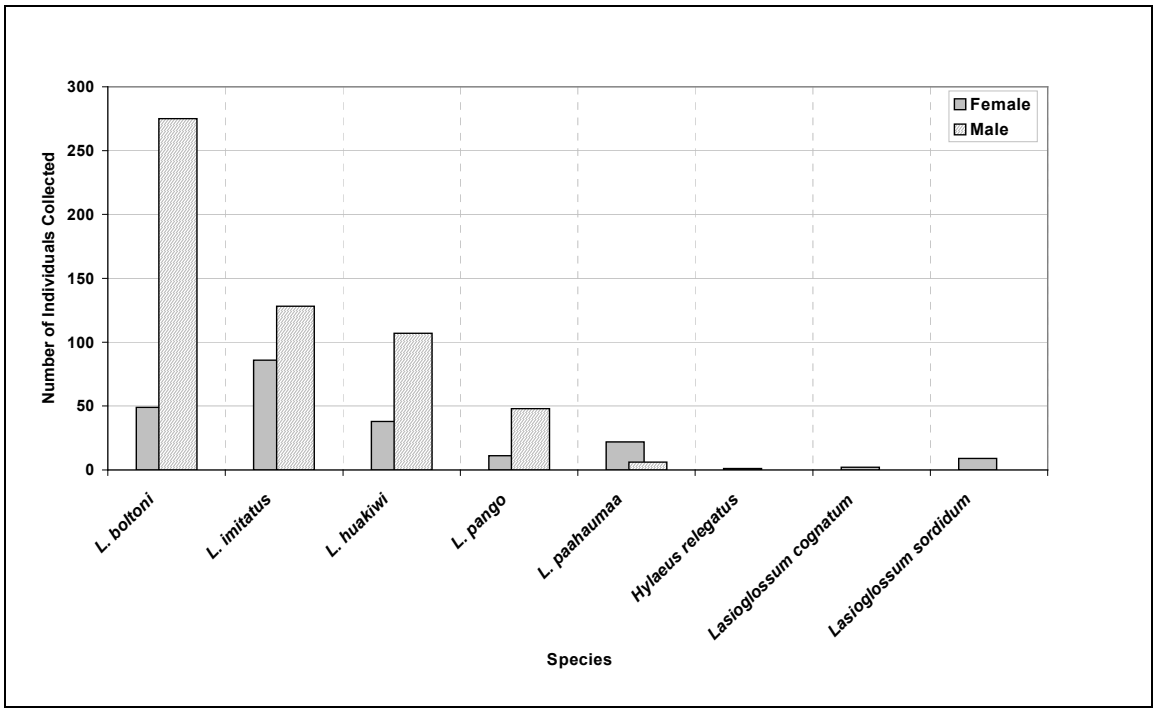

Figure 2.9 Sex composition of species of native New Zealand bees collected from all sites over three seasons (2004-05, 2005-06, & December 2006).

Species diversity at various sites

Of the 782 insects collected *L. boltoni* (41 %) was the most prominent species, followed by *L. imitatus* (27%), *L. huakiwi* (19%), *L. pango* (8%) and *L. paahaumaa* (4%). *Lasioglossum sordidum*, *Lasioglossum cognatum* and *Hylaeus relegatus* were not well represented in collections (~1%). These species were observed in large numbers along side other nesting bees on Mt. Parihaka (Site 4A), foraging on citrus trees at Raumanga Valley and nesting in banks beside Raumanga Valley Reserve creek however.

Approximately 74% of insects were collected during this study were from Mt. Parihaka. The remaining 26% were collected from various areas in Whangarei. Sites 1 – 4 represent areas on Mt. Parihaka and are highlighted on Figure 2.10. Five different species were collected from sites 1A and 1D, 4 from 2A, 3 from 1C, 1E, 1F, 4B, 4C and 5. *Leioproctus boltoni* was the only species collected from site 1G (Table 2.9).

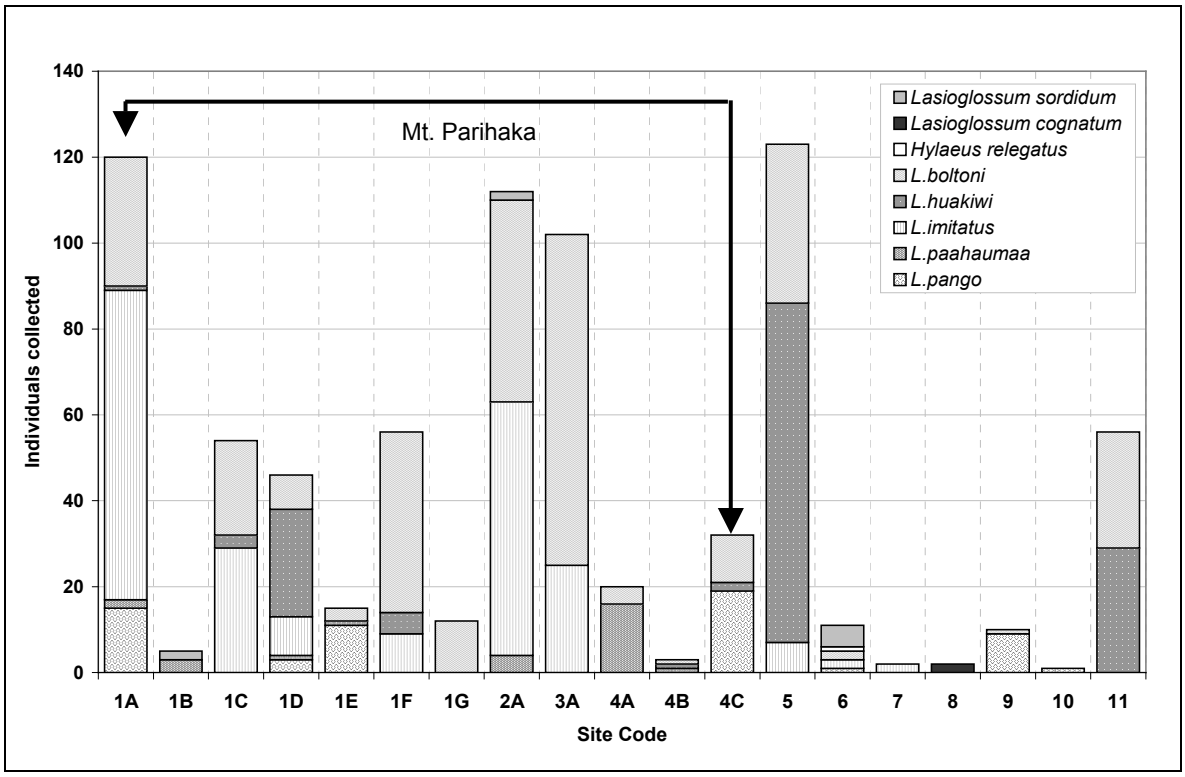

Figure 2.10 Diversity of species of native New Zealand bees collected at different locations. Sites 1 – 4 were located on Mt. Parihaka and sites 5 – 11 were other locations in the Whangarei region. Site codes as listed in Tables 2.3 and 2.4.

Table 2.9 Diversity of species of native New Zealand bees collected at different locations around the Whangarei region. Site codes as listed in Tables 2.3 and 2.4.

Number of Species	Site Code
1	1G, 7, 8, 10
2	1B, 3A, 4A, 9, 11
3	1C, 1E, 1F, 4B, 4C, 5
4	2A
5	1A, 1D, 6

2.4.3 Behavioural observations

Seasonal activity and collections

Observations on Mt. Parihaka indicated the activity of bees fluctuated slightly from season to season. Especially the emergence times seemed to vary by several weeks over the seasons. There was a general pattern to the increase in activity at certain sites. In all seasons site 1 was earliest to become active and site 4A the latest. Different species dominated respective areas. Site 1 was dominated by: *L. imitatus L. boltoni* and *L. huakiwi* and site 4 was dominated by *L. paahaumaa* and *L. boltoni*. Peak flight periods for the three species shown in Figure 2.11 below, show *L. boltoni*, *L. huakiwi* and *L. paahaumaa* peak in November, December and January respectively (Donovan 2007). First collection, and last collection dates also indicate this trend (Table 2.10). *Leioproctus paahaumaa* was not collected from site 4 in January 2007 though this species was observed nesting at site 4.

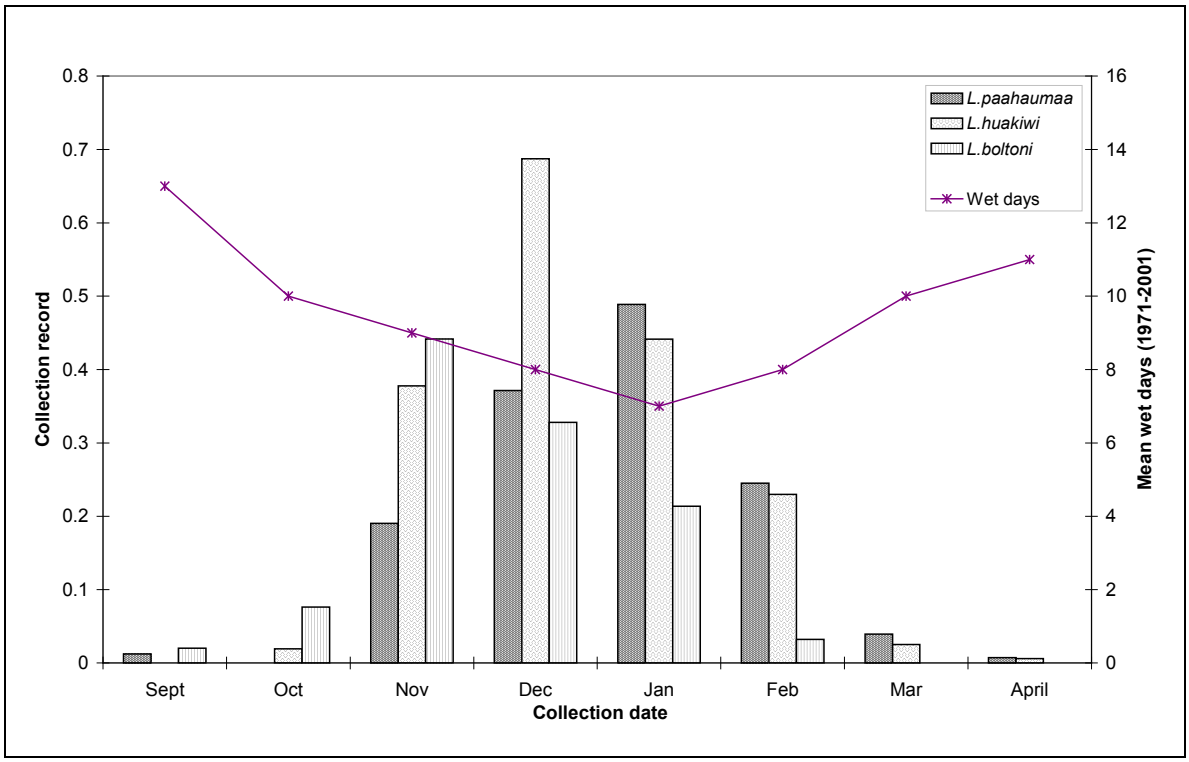

Figure 2.11 Flight period of 3 species of native bee *L. paahaumaa*, *L. huakiwi* and *L. boltoni*. Relative data are taken from existing records of 'collections' for each species (Donovan 2007). Mean wet days (at least 1.0 mm of rain) for the years 1971 – 2001 (NIWA 2007).

Table 2.10 First and last collection dates for three species of native bees, *L. paahaumaa, L. huakiwi* and *L. boltoni* on Mt. Parihaka sites 1 and 4.

First Collection	Last Collection
21 December 2004: 1D, *L. huakiwi*, 5 ♂♂	17 January 2005: 4A, *L. paahaumaa*, 2 ♀♀
17 October 2005: 1D, *L. boltoni*, 3 ♂♂	31 January 2006: 4A, *L. paahaumaa*, 7 ♀♀
8 December 2006: 1A, *L. boltoni*, 1♂	12 January 2007:1E, *L. boltoni*, 1 ♂♂

There were no standardised collection methods for population trends in this study. The collection records therefore reflect the impulse of the collector and collection method rather than true trends. Collection method also influenced the ratio of male to female bees caught. Sweep netting collected the majority of all insects (83%) and the remainder were collected using the bug vacuum (17%). Since male bees often formed large mating swarms hundreds of individuals were easily caught with a sweep net; 83% of all bees caught in these swarms using a sweep net were males. Female collection was generally labour intensive because it was nearly always of an individual insect returning to her nest, using the bug vacuum; 82% of all insects collected using the bug vacuum were female bees. In total 429 insects were collected from various nest sites around Whangarei. One hundred and fifty five insects were collected from mating swarms and the remainder were collections of foraging insects. Thirty two insects were collected from introduced plants and 165 were collected from native plants

Daily activity and collections

Daily fluctuations in weather were often experienced and while native bees were seen to be active on mild slightly wet days poor weather often prevented the bees from foraging. On cold wet days bees were observed resting at nest entrances and would not emerge until the ambient temperature had increased and the rain had stopped. Similarly, bees would not emerge from nests even on fine days, until the ambient temperature increased to at least 15^{o} C. This was usually when the bank they were nesting in was exposed to full sunlight. On several occasions the rain washed away nest sites under observation. These sites would become active again when the weather cleared so long as the nests within the banks retained integrity and did not completely slip away. Mean monthly wet days for Whangarei, shown in Figure 2.11 above indicates that up to one third of the total days in the bees' active cycle could be influenced by rain. Primack (1978) found similar results in

a study recording the number of insect visitors to montane flowers (December 1976 and January 1977). In the study, three out of the 6 observation days were cold and cloudy. While rainfall was not recorded in the study, Primack (1978) states that "in cold, cloudy conditions, solitary bees were seldom seen" and indicates ambient temperature rather than rainfall was influencing the activity of bees. Bees foraged so long as the ambient temperature was above 15 ^{o} C, regardless of rainfall. Observations of bees on Mt. Parihaka supports Primack's (1978) theory because bees were seen foraging on wet warm days.

The weather affected the quantity of data collected during the active season, but there were also other practical difficulties associated with data gathering. Observing bees for any length of time required intense concentration. All New Zealand native bees are small and move quickly. Males are even smaller than females and move faster still. While male bees were difficult to spot in mid flight, it was virtually impossible to visually follow a single female bee from her nest to a flower, despite repeated attempts to do so.

The rapid movements of native bees along with a small body size also made identification of species with the naked eye nearly impossible. Further more, when the research commenced there were no published keys to New Zealand bees. When keys did become available they were difficult to use and required a degree of taxonomic proficiency. All bees were therefore identified in the second season when comparisons could be made with the study reference collection after taxonomic support and training was received. The importance of taxonomic support in ecological and biodiversity research has been raised by authors such as O´Toole (2004) and some solutions to existing problems have been proposed. For studies such as this, insect identification is pivotal non-trivial and time consuming. A prior commitment from a taxonomist to provide identification services should be given due consideration from the outset. For those non-specialists undertaking ecological studies requiring insect identification there are new visual software tools such as the Lucid® software package, that can help identify insects (Polaszek 2005).

Nest aggregations

For three seasons native bees were located and observed in many locations from sites around the Whangarei district to Whangaruru. Native bees were found nesting in vertical banks, horizontal areas of land, grassy banks beside rivers, in fine shifting sand and heavier shelly sands beside the sea (Figure 2.12). Nest aggregations were often visible from a moving car because the mounds of tumuli in drains on roadside edges appeared

like small slips in the bank as shown in Figure 2.13. Density of aggregations varied at different locations. At high density sites, for example the horizontal nest aggregation at the road edge of Memorial Drive, nest distribution appeared to be evenly distributed (Figure 2.12 – B). While other nests, such as nests under heavy vegetation at Raumanga Valley reserves were found to be sparse and randomly distributed (Figure 2.12 – C). These examples highlight the theory that in dense aggregations, female bees will construct nests a certain distance from their neighbours and reduce the length of lateral tunnels to maintain nest integrity and avoid collapsing another's nest (Potts & Willmer 1997; Potts 2005).

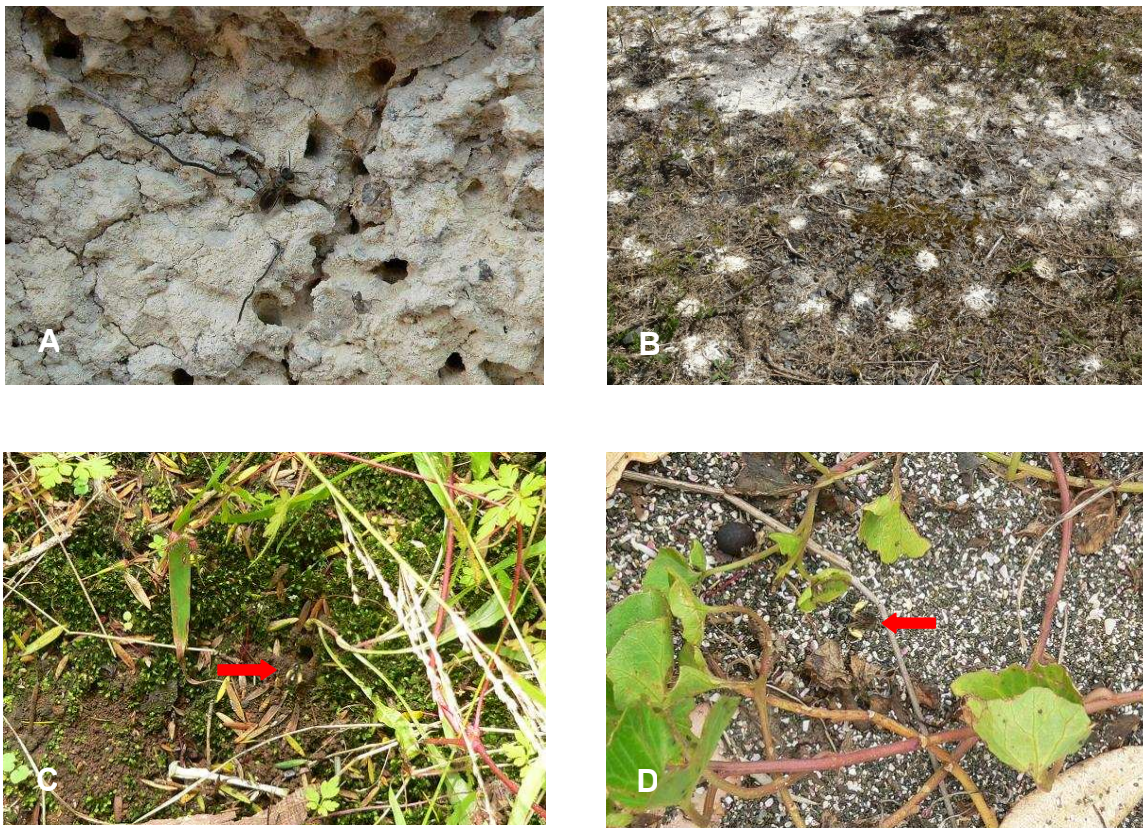

Figure 2.12 Examples of native bee nest sites around Whangarei; A, Captures an image of a native bee, on a vertical bank located at Mt. Parihaka; B, Shows an example of a horizontal nest aggregation at the road edge of Memorial Drive; C, Shows a native bee arriving back to a nest in amongst heavy vegetation at Raumanga Valley reserve; D, Is a example of a native bee returning to her nest in the sand above the high tide mark at Taupiri Bay, Whangaruru.

Figure 2.13 Large quantities of tumuli accumulating in the roadside drains on Mt. Tiger.

Of the several large nest sites found on Mt. Parihaka site 1 was the largest. At an estimated 100 m in length and 5 m in height there were around 15 thousand nests at this location (Figure 2.13 above). Bees generally formed nests over the entire bank. The substrate was highly suitable because it was easy to excavate and the bank was north facing, warm and sheltered. Even though forage rewards have generally been accepted as the primary determinants of pollinator community structure, this nesting trend lends evidence to the concept that population success is largely dependent on the availability on suitable nesting substrate (Donovan 1967; O'Toole & Raw 1991; Petanidou & Ellis 1996).

Nesting substrate suitability is identified as an important factor determining the number and species of bees found in a particular habitat. For example, on Mt. Parihaka female bees from the species: *L. imitatus, L. boltoni, L. pango* and *L. huakiwi* were collected from nests at site 1A and 1D and were found to be nesting beside each other in vertical and horizontal nests. A much smaller localised aggregation was found at site 4 and at an estimated area of 25 m^2 there were approximately 750 nests. Female bees from the species *L. paahaumaa* and *L. boltoni* were collected from nest site 4 and *Lasioglossum spp.* were also observed nesting at this location.

Nesting behaviour

Approximately 77 hours were spent watching 388 individual bees making 259 complete foraging trips (See Chapter Five for details). Bees were observed for at least 130 hours as they prepared to exit on their first foraging trip, when they returned to their nests with pollen loads, while they searched for mates and as they interacted with other closely associated organisms.

Female bees would not emerge from their nests until the ambient temperature had increased. In most instances, this was when the bank they were nesting in was exposed to full sun light. Insects nesting in Northeast facing banks (e.g. site 1) were always the first to emerge for the day. A female bee would wait at her nest entrance until the temperature increased. Once the temperature was right the female would tentatively exit, walking the entire nest opening three or four times. She would then conduct an increasing figure eight flight pattern around her nest before leaving the area. These observations provide some circumstantial evidence for scent marking of nest entrances and sun-compass orientation (O'Toole & Raw 1991).

Foraging behaviours

Native bees were collected and observed foraging on introduced and native pants (see Chapter five for details). When high numbers of insects were gathered on the same plant observations became difficult in the confusion of activity. On Mt. Parihaka, one kanuka tree in particular seemed to be the plant of choice for many species nesting in the area. In all three seasons hundreds and thousands of foraging bees enveloped the tree. The activity of the bees foraging on the tree created an audible hum (Figure 2.14 below).

Male bee movements were generally much harder to follow by eye than females, because they are physically smaller and move faster. Occasionally however, male bees could be watched as they foraged. For example, at the Whangarei town basin, male bees were observed foraging on a pohutukawa as they stopped to feed on nectar at the base of the flower. In contrast to this, female bees were never seen feeding on nectar at the base of the pohutukawa, even though their pollen balls are a mixture of nectar and pollen. They were often seen delicately balancing on the very tips of the pohutukawa stamen as they collected pollen.

Figure 2.14 Gated entry to forestry area on Mt. Parihaka on the left and Memorial Drive on the right. In the centre a single kanuka tree that was a popular source of food for many native bees nesting on both sides of the bank.

Associated organisms

On Mt. Parihaka, several insects were seen to co-exist at nests sites along side native bees including the golden hunting wasp (*Cryptocheilus australis*, Hymenoptera: Pompilidae), the black cockroach hunter (*Tachysphex nigerrimus*, Hymenoptera: Sphecidae) and the mason wasp (*Pison spinolae*, Hymenoptera: Sphecidae). Kotare (*Halcyon sancta vagans*, Coraciiformes: Alcedinidae) were often seen hunting on Mt. Parihaka and nests were in the same banks where the native bees resided.

Other species were closely associated and included the parasitic wasp (*Pseudofoenus pedunculatus* (Schletterer), Clistogastra: Evaniidae) and the tiger beetle (*Cincindela tuberculata*, Coleoptera: Carabidea). Parasitic wasps were observed as they searched for vacant bees nests in which to lay their eggs. Very high numbers of wasps were observed in the native bees' peak flight season (i.e. December). At site 1, in an area of one m^2 there was a recorded 30 wasps. Across the entire area there may have been up to 15 thousand

wasps so their population appears to mirror that of the bees. The wasps were still observed in high numbers even after the bees' population seasonally declined in late January.

While still prominent there were fewer tiger beetles at nest sites. At site 1 there was at least one tiger beetle patrolling a 1 m^2 area. Across the entire area there may have been up to 500 beetles during the bees' peak flight season. The larvae of the tiger beetle live in narrow tunnels alongside native bees. There is no tumulus at the entrance to their tunnels, which start as pinholes and increase to around 3 mm in diameter as the larvae grow. While the larvae were often seen snapping aggressively at movement around the tunnel entrance there was no evidence that native bees were preyed upon. On the other hand, adult tiger beetles were observed tackling female bees as they returned with pollen loads. In one encounter, a tiger beetle removed a clump of pollen from the scopae of a bee and consumed it. The bee recovered from the encounter and later returned with another full pollen load; she was again tackled by the tiger beetle but quickly recovered to find her nest. On four separate occasions several tiger beetles were observed fighting over a native bee carcass (see Figure 2.15 below). In all instances the carcass was quickly dismantled and consumed by the tiger beetles. While it seems certain that tiger beetles are opportunistic scavengers they were not seen preying on live native bees. This observation confirms that of previous studies (Donovan 1967).

Figure 2.15 Tiger beetles; A, consuming the carcass of a native bee (in the bug vacuum container) at site 4 and; B, patrolling the nest face at site 1.

2.5 Conclusions

In the wider Whangarei district, native bees can be located in a variety of ecosystems from regenerative forests such as Mt. Parihaka, to existing native forests such as Raumanga Valley Reserve. Large nest aggregations on roadside banks are commonly seen particularly in rural areas. Smaller communities can be found on closer observation. For example, native bees were found nesting in forest undergrowth and beneath grass, in moving sands, and shelly beaches. Native bees were collected from a variety of plants both introduced and native, in rural, agricultural and urban environments.

Most species handled in this study were seasonally abundant. In their peak flight season observations of native bees out numbered those of honeybees (*Apis mellifera*) and bumblebees (*Bombus spp*). The community study on Mt. Parihaka showed that several insects co-exist with native bees including the golden hunting wasp, the black cockroach hunter and the mason wasp. Other species have a close association with native bees including the parasitic wasp and tiger beetle. Kotare were present, nesting in banks along side native bees.

The large nest areas and variety of species found on Mt. Parihaka were ideal for a medium term case study especially in terms of easy access to the site and limited public disturbance. A plan in 2005 to restore the pine plantation on Mt. Parihaka to natural forest was not anticipated at the start of this study. These developments however, created a unique opportunity to understand native bee pollinators in the ecosystem especially in terms of conservation restoration of a native forest.

Six species of native bees were found on Mt. Parihaka, five from the genus *Leioproctus* and one species from the genus *Lasioglossum* as follows*: L. boltoni, L. huakiwi, L. imitatus, L. paahaumaa, L. pango* and *Lasioglossum sordidum*. Eight species overall were found in Whangarei, so Mt. Parihaka has proved to be representative of Whangarei native bees. Understanding the native bee community organization on Mt. Parihaka is the first step towards the management of pollinator biodiversity and conservation in a rejuvenating native ecosystem.

Chapter Three Load-lifting Capacity of Native Bees

Abstract

The load lifting capacity was measured for five species of New Zealand native bees: *Leioproctus (Leioproctus) boltoni* (Cockerell), *L. (L.) huakiwi* (Donovan), *L. (L.) imitatus* (Smith), *L.* (*Nesocolletes*) *paahaumaa* (Donovan) and *L. (Leioproctus) pango* (Donovan) (Hymenoptera: Colletidae). Of the 88 insects collected for analysis, 40 carried pollen, 21 were not carrying pollen, 13 carried artificial loads and 14 would not carry artificial loads and were released during experiments. Mean pollen mass collected in a typical foraging trip was measured. Maximum lift force was determined using load lifting experiments. Measurements of body length and flight muscle mass were taken on 74 insects. These were used to estimate foraging range and assess the constraints associated with attaching tag antennas to the thorax of native bees for harmonic radar tracking.

The results showed male *L. pango, L. huakiwi* and *L. boltoni* were significantly shorter than females (1.4 – 5 mm) and both sexes of *L. imitatus* and *L. paahaumaa* were similar in length. The mean pollen mass collected in a complete foraging trip showed that none of the species carried pollen loads greater than 23 % their body mass. *Leioproctus imitatus* carried the greatest pollen loads up to 23 % their body mass, *L. boltoni* up to 19 %, and *L. paahaumaa* up to 15 % their body mass. Artificial load lifting capacity experiments showed that *L. boltoni* carried the greatest loads up to 52 % their body mass and *L. huakiwi* up to 41 %. A wide range of flight muscle ratios (0.088 - 0.336) and marginal flight muscle ratios (0.036 - 0.312) was found for native bee taxa. Mean flight muscle ratio ± standard error (SE) for native bee taxa was 20.3 ± 0.7 mg (*n* = 74) and is lower than the reported value for hymenoptera of 0.306 (Marden 1987).

For harmonic radar applications tag antennas range in weight from 0.4 – 80 mg. *Leioproctus boltoni* and *L. paahaumaa* could carry the additional mass of the smaller tag antennas (0.4 -1 mg) based on load-lifting capacity results. *Leioproctus imitatus* carried mean loads significantly less than expected although based on a mean flight muscle mass (± SE) of 21.0 ± 1.07 mg (*n* = 42) the species should be able to carry loads of 0.4 mg.

Leioproctus huakiwi and *L. pango* lifted little additional weight (pollen or artificial) so it is unlikely these species could carry even the smaller tag antennas. Both species had the lowest mean flight muscle ratios: 0.166 ± 0.0251 and 0.159 ± 0.0246 respectively.

Harmonic radar tag antennas used in current applications could be suitable for New Zealand native bees. Three out of the five species investigated in this study could carry the weight in addition to their normal pollen load and body mass. While the results are positive in this respect many individual bees tested with artificial loads simply refused to fly. Behavioural aspects of flight were not considered at the onset of this investigation but have much influence on the outcomes of this research. Future harmonic radar applications will be limited by the behaviour of native bees, which actively attempt to dislodge additional loads.

3.1 Introduction

3.1.1 Tracking insects to assess foraging range

Understanding the foraging range of native bees is a crucial step towards developing conservation management strategies of pollinator communities. Studies have shown that in order to ensure the long-term sustainability of solitary bee diversity all the requirements for sustaining viable populations must be within the insects' home range (Gathmann & Tscharntke 2002). However, difficulties arise when trying to quantify the foraging range of native bees and the floral requirements required to sustain a population. Most techniques used to gather this information rely on indirect analysis of floral community structure or translocation of insects using mark-release-recapture methods. While the home range of other animals can be easily monitored using radio tracking methods, native bees and smaller insects cannot carry radio tags because they are too heavy (Pride & Swift 1992). To date, tracking insects using the harmonic scanning radar, which has a very light weight tag antenna, is the only viable direct method.

The scanning harmonic radar has been used in a variety of studies including the foraging movements of honeybees (*Apis mellifera*) (Carreck 1996; Riley et al. 1996; Osborne et al. 1997; Osborne et al. 1999). Recent literature demonstrates continued application of scanning radar in a range of insect studies such as the honeybees' waggle dance (Riley 2005; Riley et al. 2005), honeybee spatial memory (Menzel et al. 2005) and investigations of butterfly movements (Cant et al. 2005). For many investigations however, the ability of the insect to carry even a lightweight tag antenna limits the success of the study. Tag antennas can weigh anywhere between 80 to 0.4 mg and range in length from 8 to 120 mm (for exact specifications refer to Appendix A3, Table A3.11). Most insects can lift between 0.5 to 3 times their own body mass (Dudley 2002) but there is a wide variation in body mass between species. Some can easily carry a tag antenna while others cannot.

Without exact data on an insects load-lifting capacity, many harmonic radar studies rely on trial and error attachment of loads to insects. Most studies also indicate the extra weight of the tag antenna has little effect on the flight performance (Riley & Smith 2002). One study in particular has assessed the suitability of using the harmonic radar to track an insect by first evaluating the effect of artificial weights on the insects' flight performance (Boiteau & Colpitts 2001; Boiteau & Colpitts 2004). In the study, Boiteau & Colpitts (2001) used wing loading as a descriptor of flight ability of the Colorado potato beetle

(*Leptinotarsa decemlineata* (Say) , Coleoptera: Chrysomelidae). Although wing loading was used in the study, flight muscle mass is recognised as the strongest predictor of the capacity of an insect to generate vertical lift (Marden 1987, 2000; Dudley 2002).

3.1.2 Load-lifting capacity of insects

There are extraordinary examples of the load lifting capacity of insects. Load lifting can help illustrate unique aspects of insect biology. For example, some species of wasps, can carry prey 88% heavier than their body weight and certain species of flies copulate in mid air as they consume prey (Berwaerts et al. 2002). Load-lifting ability can also help to describe foraging capacity and strategies in some insects. For example, in the genus Ammophila (Hymenoptera: Sphecidae) the smaller the prey the greater the home range (Coelho & Ladage 1999). While other insects, such as the great golden digger wasp (*Sphex ichneuoneus,* Hymenoptera: Sphecidae) will choose smaller prey if their flying capacity has been impaired (Coelho & Ladage 1999). Load-lifting capacity has also been used to describe foraging strategies of some species of yellowjackets (*Vespula spp.*, Hymenoptera: Vespidae) (Coelho & Hoagland 1995).

Early studies of insect flight date to the nineteenth century when researchers fixed small amounts of wax to the thorax of various insects to determine their load-lifting capacity (Dudley 2002). Like these early studies, Marden (1987) also attached weights to the thorax of insects to determine their maximum lift capacity. As a comparative study, he found that for a wide variety of insects the maximum lift per unit flight muscle mass was similar across species. Marden (2000) also reports flight muscle mass as the strongest predictor of the capacity of an insect to generate vertical lift (Marden 1987; Dudley 2002). Coelho & Hoagland (1995) used empirically derived formula from Mardens' (1987) work to predict the maximum load mass of three species of yellowjackets: *Vespula germanica* (Fabricius), *V. squamosa* (Drury), *V. maculifrons* (Buysson) (Hymenoptera: Vespidae). The predictions were compared with the actual load carrying capacity in field studies. It was shown that there was very good correlation between the predicted and actual loads (Coelho & Hoagland 1995; Coelho & Ladage 1999).

3.1.3 New Zealand native bees

Baseline data on New Zealand's native bee fauna is lacking and knowledge of the behaviour and biology of many is species limited. It is generally accepted that most species of native bee rely on a local habitat, gathering all they need to sustain themselves

from this area (Gathmann & Tscharntke 2002; Potts 2005). But, how far do they travel and what is their home range? How much pollen do they carry and how do they contribute to pollination systems in New Zealand? An intention of this study is to investigate the load-lifting capacity of several species of native bees so that the feasibility of using the harmonic radar to track native bees can be assessed.

Four species of *Leioproctus* are investigated in this study: *L. boltoni, L. imitatus, L. huakiwi, L. paahaumaa*, and *L. pango*. All belong to the primitive bee family Colletidae. Collectively known as plasterer bees. New Zealand colletids provision their nests with a mixture of pollen and nectar shaped into a ball that sits in the base of the waterproof cell (Donovan 1967). All the species belonging to the genus *Leioproctus* are typically robust, hairy, black bees and range in length from 5 –13.4 mm; females carry pollen externally on scopae (Donovan 2007) (Figure 3.16 below). It is anticipated that by understanding the role native bees perform in the ecosystem, practical conservation strategies can be implemented to help sustain their population and diversity in an ever-changing landscape.

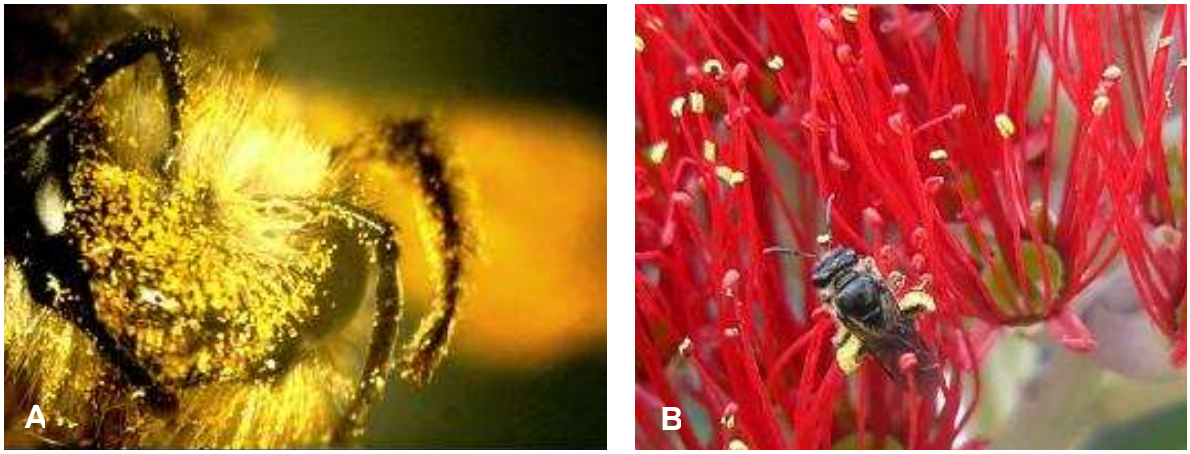

Figure 3.16 *Leioproctus spp.* A, Close-up microscopic photo of female native bee, *L. paahaumaa* showing pollen grains on hairy facial vestiture in the foreground; and on her scopae in the background. B, Photo of a female *Leioproctus sp.* foraging on a Pohutukawa, in the Whangarei town basin, with pollen-laden scopae.

3.2 Study Aim

The aim of this investigation is to determine the load-lifting capacity of five species of native bees: *L. boltoni, L. imitatus, L. huakiwi, L. paahaumaa*, and *L. pango.* Pollen mass measurements of average loads are recorded and artificial loads are attached to native bees to determine their maximum lift capacity. As part of a wider investigation into the biology of native bees, the main purpose of this study is to gain insight into the types of loads (typical and artificial) native bees can carry by:

A. Measuring the quantity of pollen lifted per bee in an average foraging trip, and the corresponding flight muscle mass of a species of native bee.
B. Measuring the load lifting capacity and the corresponding flight muscle mass of a species of native bee.

For each species the study aims to answer the following questions:

1. What is the average pollen load collected in a typical foraging trip?
2. What is the maximum (estimated or actual) artificial load the insect is able to carry?
3. What is the load-lifting capacity of the species?

3.3 Methods

3.3.1 Collections and nest sites

Bees used in the study were collected over two seasons (December 2004 – March 2005 and October 2005 – February 2006) from four areas on Mt. Parihaka. Specific site locations are described in Table 3.11 below.

Table 3.11 Areas located on Mt. Parihaka where New Zealand native bees were collected for load capacity analysis. Specific site descriptions, locations, latitude & longitude and general ecology of areas where bees were observed or collected from during two seasons (2004 – 2005 & 2005 – 2006).

Area	Location Code & Site	Location	General Ecology
Mt. Parihaka, Riverside. Whangarei. Main entrance at the very end of memorial drive. Car park leading to walking access war memorial on the right hand side and gated forestry area (restricted access) on the left hand side.	**Site 1A**: By gate, at the entry to forestry area. First bank on right-hand side.	**S** 35^{O} 42' 43.04 " **E** 174^{O} 20' 18.62" **HAE** 261 m	Pine forest plantation. First generation regenerative forest. Some gorse (*Ulex europaeus*), pampas and cutty grass.
	Site 1D: Second bank under transmission tower.	**S** 35^{O} 42' 42.97" **E** 174^{O} 20' 20.18" **HAE** 260 m	
	Site 2A: Down from gate entry. Third major bank in forestry area, on the right hand side.	**S** 32^{O} 46' 43.03" **E** 174^{O} 20' 22.01" **HAE** 258 m	
Mt. Parihaka, Riverside. Whangarei. Before memorial car park, half way up memorial drive. On the right hand side gated entrance into water tower reservoir area	**Site 4A**: Water tower entrance, over mound on the left hand side	**S** 35^{O} 43' 01.96" **E** 174^{O} 20' 37.34" **HAE** 192 m	Pine forest plantation. First generation regenerative forest. But mainly gorse, pampas and cutty grass in the immediate vicinity of nest site. Some cleared areas.

3.3.2 Mass measurements

Insects were collected from various locations while they were foraging as they returned to nest sites or as they formed 'mating swarms' around shrubs. Insects were collected using either a sweep net or a bug vacuum (Summit ^{TM}). Once collected they were placed into an ethyl acetate killing jar until they expired. They were then removed from the jar and placed in individual containers and labelled with date, time and location. When possible, insects were identified the day of collection, their body length measured using vernier callipers and pollen and body mass measurements were taken immediately. When this was not practical insects were identified, body length measured and they were frozen for later analyses.

All mass measurements were performed on a Mettler Toledo Balance (B204 – S) in triplicate for each specimen. Fresh mass measurements were taken on 15 specimens. These specimens were then frozen and re-measured frozen, within 1 hour of removal from fridge and after bench drying for 2, 24, 48 and 72 hours. There was no measurable mass difference between specimens bench dried for 48 and 72 hours. These specimens had a mean body mass loss ± standard error (SE) of 36.8 ± 1.52 % for n = 15. All remaining frozen samples were bench dried for 48 hours to a constant mass prior to measurements. The body and thorax mass of frozen specimens was adjusted for losses by a factor of 1.596 in all analysis.

3.3.3 Pollen mass measurements

When the insect collected was carrying pollen (visible on its scopae), the laden body mass measurement was recorded. The pollen was removed from the scopae of the bee using a scalpel and the pollen mass measured. The insects unladen body mass was then re-weighed. The pollen mass was recorded as the total (laden) body mass minus the unladen body mass and the value was checked against pollen mass measured. Pollen removed from these insects was prepared for further analysis (refer to Chapter Five: Foraging Behaviours of Native Bees).

3.3.4 Load lifting capacity experiments

Individual insects used for load-lifting experiments were freshly collected (between the hours of 0900 – 1200) using the bug vacuum ™. Care was taken to collect new female bees, characterised by having a clean scopae. Each individual was placed into a separate labelled container. To sedate the bees they were refrigerated immediately on return from the field.

All load-lifting experiments were conducted in doors, in still air, between the hours of 1300 – 1500. The ambient temperature and humidity data was collected. Load weights were made of tin foil moulded into small oval shapes. The weights were attached to the thorax of the bee, using gum. The insect was then placed on the floor and stimulated through prodding to take flight towards the window. Each bee was given three attempts at take-off with rest periods and sugar water in between an increased load. Once flight was achieved a consecutively heavier weight was added and the procedure repeated. When the insect could not lift a weight it was killed and frozen for body and flight muscle mass analysis. The mass of the artificial tin foil weights was measured. The maximum load was

estimated as the load halfway between the maximum load the insect could lift, and the minimum load where the insect could no longer take off.

3.3.5 Flight muscle mass measurements

Flight muscle mass measurements were performed in one continuous session. Frozen samples were bench dried for 48 hours before measurements were taken in triplicate. For each sample the total unladen body mass was measured. The head, abdomen, and legs were then removed and the thorax mass measured. The thorax, sectioned in half, was placed in a solution of NaOH (0.35 mol l^{-1}) for 24 hours. After 24 hours, the remaining muscle was washed away with water and the exoskeleton was dried at room temperature for another 48 hours before being weighed. The body (and thorax) mass of frozen specimens was adjusted for losses by a factor of 1.596. In summary six mass measurements were made, along with the body length (from head to end of abdomen) and are shown below in Table 3.12

Table 3.12 A summary of all measurements (abbreviations included).

Definition	Abbreviations
Body length [mm]	Lb
Unladen body mass [g]	Mb
Laden body mass [g]	Mbl
Pollen mass [g]	Mp
Artificial load mass [g]	Ma
Thorax mass [g]	Mth
Exoskeleton mass [g]	Mex

From these measured data the flight muscle mass, estimated as the difference between the thorax and exoskeleton mass, can be derived. Other parameters including the flight muscle ratio, marginal flight muscle ratio, lift force production, total lifted mass, load mass and maximum load mass are also derived as described in the following section (Table 3.13).

Table 3.13 A summary of data derived from measured parameters (abbreviations included).

Definition	Abbreviations
Flight Muscle Mass [g]	Mf
Flight muscle ratio (Mf / Mb)	FMR
Marginal Flight muscle ratio (Mf / Mbl)	MFMR
Lift force production [N or N/kg or N*10^2]	LFP
Total lifted mass [g or kg]	MT
Load mass [g or mg]	ML
Maximum load mass to be carried [g]	Max ML

Flight muscle ratio

The flight muscle ratio is the ratio of flight muscle to total body mass and is a measure of manoeuvrability in flight. According to Marden (1987) there are two important values: the mean unladen and mean marginal flight muscle ratio. The marginal flight muscle ratio is the value that represents a marginal take off ability and represents the lowest proportion of flight muscle to body mass that is required for actual lift off. For Hymenoptera, Marden (1987) reported a mean marginal flight muscle ratio of 0.179, and predicted an unladen flight muscle ratio for Hymenoptera within the range 0.209 to 0.401.

Lift force production and maximum load

The force required to propel an object into the air is described as the lift force. Marden (1987) demonstrates the strong correlation between flight muscle mass and maximum lift force where:

$$\text{LFP } [\text{Nx}10^2] = (1.01\text{x Mf [kg]}) + 1.76,\ r^2 = 0.99,\ n = 33,\ P < 0.001.$$

The maximum load an insect can carry is a function of the maximum lift force production where:

Lift force production [N] = Total Mass [*kg*] *x* Acceleration [*m/s/s*]

Total mass [*kg*] = Body Mass [*kg*] + Load Mass [*kg*]

Acceleration (of Gravity) [*m/s/s*] = 9.81

Given the values of flight muscle mass and lift force production the estimated maximum load mass can be calculated.
Where:

$$\text{Total lifted mass } [kg] = \frac{\text{Lift Force Production [N]}}{\text{Acceleration [m/s/s]}}$$

$$\text{Load mass } [kg] = \text{Total Mass } [kg] - \text{Body Mass } [kg]$$

3.3.6 Statistics

Statistical analyses were performed using Microsoft Excel 2000 Statistical Toolbox. All analysis utilised the data from individual animals (for raw measurement data see Appendix A3, Table A3.15). Data was tested for normality and transformed where possible. Satterthtwaite's corrected *t*-test was used for data when population variances were different (if one sample had 4 or more times the population variance than the other). For those data compared using ANOVA, Gabriel comparison interval is plotted with mean (not SE) (Mcardle 1987; Sokal & Rohlf 1995). For all other data the arithmetic means are given ± standard errors (SE).

3.4 Results

3.4.1 Collection records

A total of 88 insects were collected for mass measurements. Twenty one insects were not carrying pollen (12 new female and 9 male bees). Forty female insects were collected carrying pollen. Thirteen insects carried artificial loads in load-lifting experiments; 14 individuals would not fly with artificial loads and were released during load-lifting experiments. Body length and flight muscle mass measurements were taken on 74 insects.

3.4.2 Measurements

Body length

There is a strong significant difference in mean body length between species (ANOVA: df = 4, *n* = 73, F = 10.83, P = 7.08×10^{-7}). Figure 3.17 below shows the Gabriel comparison interval (vertical bars) and means; those intervals that do not overlap indicate mean body length of species that are significantly different from each other. Body lengths of *L. boltoni, L. imitatus* and *L. paahaumaa* are similar but vary significantly to body lengths of *L. huakiwi* and *L. pango*.

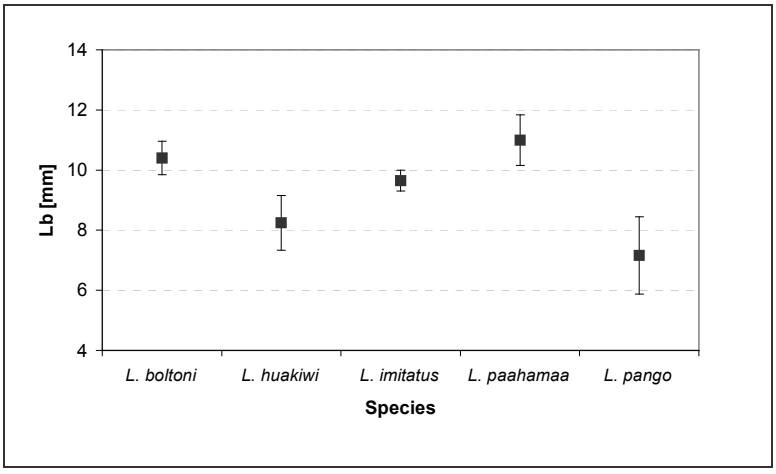

Figure 3.17 Gabriel's comparison interval (GI) of mean body length (Lb, ■) (mm) shown for four New Zealand native bee species: *L. boltoni n = 16, L. huakiwi n = 6, L. imitatus n = 42, L. paahaumaa n = 7 and L. pango n = 3*. Black vertical bars show the GI not SE. Species intervals that do not overlap are significantly different to each other.

In the comparisons above male and female insects within species were not separately tested. Existing published data (Donovan 2007) shows males of *L. boltoni, L. huakiwi* and *L. pango* are shorter in length than females (Figure 3.18). The greatest difference was observed in the species *L. boltoni* where females are up to 5 mm longer than males. Student's *t* – test shows a very highly significant difference in means for male and female *L. boltoni* (*df* = 6, *t* = 38, *p* > 0.001) and significant differences for male and female *L. huakiwi* and *L. pango* (*df* = 38, *t* = 2, *p* > 0.05). Male and female *L. imitatus* and *L. paahaumaa* do not vary significantly.

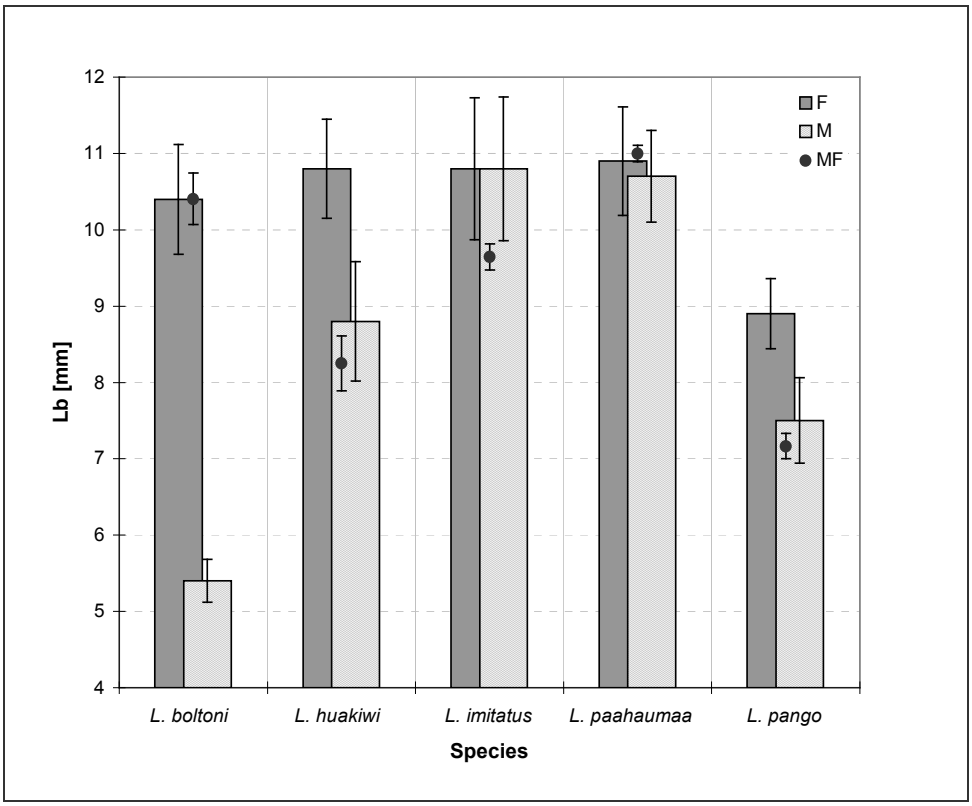

Figure 3.18 Mean body length (Lb) ± SE (mm) of five species of male (M, light grey) and female (F, dark grey) native bees (*n* = 20 individuals per species) from published data (Donovan 2007) compared to mean body length of mixted male and female individuals (MF, ●) from New Zealand native bee study: *L. boltoni n* = 16, *L. huakiwi n* = *6*, *L. imitatus n* = 42, *L. paahaumaa n* = 7, and *L. pango n* = 3.

Pollen load mass

Of the 40 female insects that were collected carrying pollen, none were from the species *L. huakiwi*. In the species *L. huakiwi* five new females and two males were caught. One female *L. pango* was collected with a pollen mass of 3.0 mg. There were 27 female *L. imitatus* caught; 13 were collected while foraging on a kanuka (*Leptospermum ericoides*)

and 14 were collected as they returned from a foraging trip (Figure 3.19). The mean pollen mass for all *L. imitatus* collected was 3.4 ± 0.37 mg, (*n* = 28). For individuals returning from a foraging trip was 5.1 ± 0.89 mg (*n* = 14) and for those collected while foraging was 1.7 ± 0.25 mg (*n* = 13). A significant difference in mean pollen load was observed between insects collected while foraging and those collected returning to nest sites; Satterthtwaite's corrected *t*-test: *df* = 15, *t* = 4.07, *P* [T<=t, two-tail] = 0.0025.

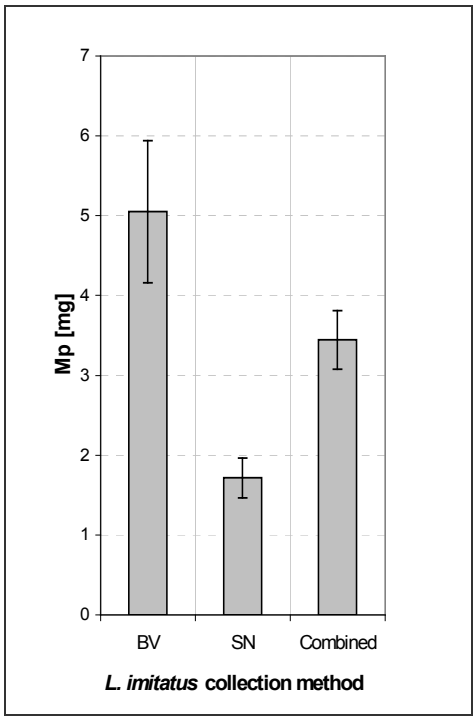

Figure 3.19 Mean pollen load (Mp, grey) ± SE (mg) for *L. imitatus* collected at nest sites (using the bug vacuum), and while foraging (sweep net). A total of 27 insects carried pollen loads; 14 were captured at their nest entrances when they returned from a foraging trip (BV), and 13 were captured using a sweep net as they foraged on kanuka (SN).

A further 11 insects were collected carrying pollen from two species, *L. boltoni* and *L. paahaumaa*; all were caught at their nest sites as they returned from a foraging trip. Figure 3.20 compares the mean body mass with the pollen mass carried. *Leioproctus. boltoni* carried the greatest load with a mean pollen mass of 5.5 ± 0.72 mg (*n* = 7) followed by *L. imitatus* 3.40 ± 0.37 mg (*n* = 27) and *L. paahaumaa* 4.1 ± 0.37 mg (*n* = 5). No significant difference in mean pollen load (ANOVA: *df* = 2, *n* = 38, *F* = 1.7, *P* = 0.196) or mean body mass was observed between species (ANOVA: *df* = 2, *n* = 38, *F* = 0.65, *P* = 0.52). Mean percentage pollen mass to body mass for three species described in Table 3.14 shows *L. boltoni* carried the greatest mean percentage pollen to body mass of 14 ± 1.9 % (*n* = 7); followed by *L. paahaumaa* and *L. imitatus.* No strong significant difference

in mean percentage pollen to body mass was observed between the three species (ANOVA: *df* = 2, *n* = 39, *F* = 1.7, *P* = 0.1).

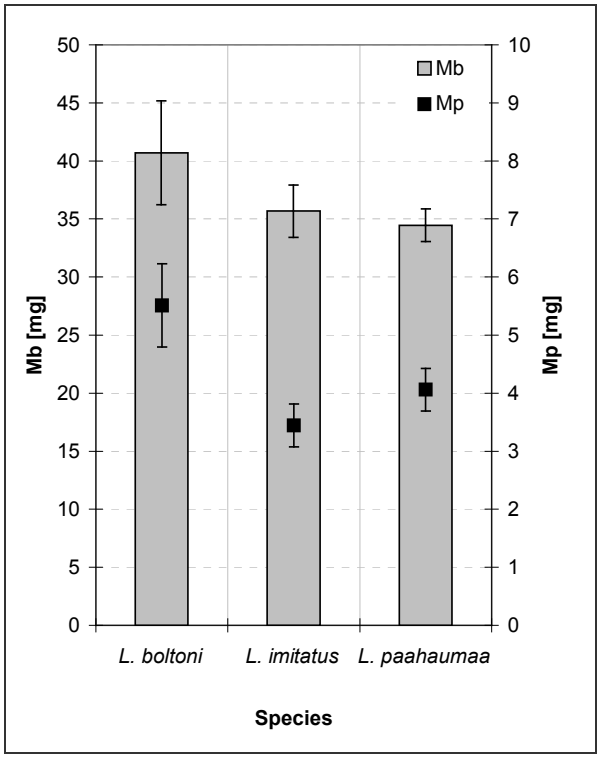

Figure 3.20 Mean body mass (Mb, grey) ± SE (mg) and mean pollen mass (Mp, ■) ± SE (mg) for four species of New Zealand native bees: *L. boltoni n* = 7, *L. imitatus n* = 27, *L. paahaumaa n* = 5.

Table 3.14 Mean pollen to body mass ± SE (%) and maximum pollen mass to body mass ± SE (%) for four species of New Zealand native bees: *L. boltoni n* = 7, *L. imitatus n* = 27 and *L. paahaumaa n* = 5.

Species	Mean Mp: Mb [%]	Maximum Mp: Mb [%]
L. boltoni	14 ± 1.9%	19%
L. imitatus	9 ± 1.0%	23%
L. paahaumaa	12 ± 1.1%	15%

Artificial load mass

Figure 3.21 and Table 3.15 compares the mean body mass with artificial load mass for two species. Mean percentage artificial mass to body mass for *L. boltoni* was 26 ± 4% (*n* = 8), and for *L. huakiwi* was 20 ± 6% (*n* = 5). *Leioproctus boltoni* carried an artificial load up to 52% and *L. huakiwi* up to 41% their body mass. A significant difference in mean artificial load carried was observed between the two species (*t*-test: *df* = 11, *t* = 2.6, *P* [T<=t, two-tail] = 0.02). Mean percentage artificial mass to body mass was similar between both species (*t*-test: *df* = 11, *t* = 0.7, *P* [T<=t, two-tail] = 0.46) although mean body mass has a very strong significant difference between the two species (*t*-test: *df* = 11, *t* = 6.52, *P* [T<=t, two-tail] = 4.3×10^{-5}).

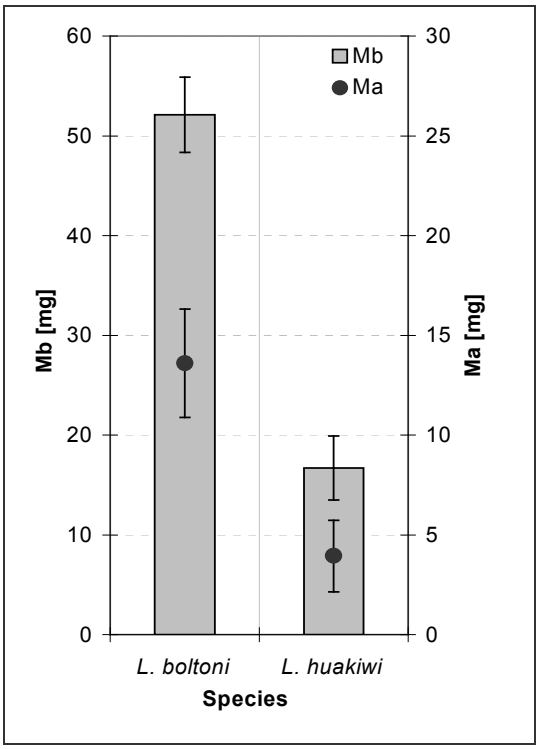

Figure 3.21 Mean body mass (Mb, grey) ± SE (mg) and mean artificial load mass (Ma, ●) ± SE (mg) for *L. boltoni n* = 8 and *L. huakiwi n* = 5.

Table 3.15 Mean artificial load to body mass ± SE (%) and maximum artificial load mass to mean body mass (%) for *L. boltoni n* = 8 and *L. huakiwi n* = 5.

Species	Mean Ma: Mb [%]	Maximum Ma: Mb [%]
L. boltoni	26 ± 4.2 %	52%
L. huakiwi	20 ± 6.3 %	41%

Flight muscle mass and ratio

The results of this study showed a wide range of flight muscle ratios (0.088-0.336) and marginal flight muscle ratios (0.036-0.312) (see Table 3.16 below). The mean flight muscle ratio for all New Zealand native bee taxa tested in this study is 0.203 ± 0.007 (*n* = 74). This value is lower than the reported value for hymenoptera of 0.306 (Marden 1987). The mean marginal flight muscle ratio for New Zealand native bee taxa tested in this study is 0.185 ± 0.0067 (*n* = 74). This is slightly higher than the reported value for hymenoptera of 0.179 (Marden 1987). Figure 3.22 below shows the flight muscle and body mass compared to the corresponding flight muscle ratio for five species of native bees. *Leioproctus paahaumaa* had the highest mean flight muscle ratio with approximately 24 ± 1 % (*n* = 7) total body mass composed of flight muscle, followed by *L. imitatus* (21 ± 1 %, *n* = 42), *L. boltoni* (19 ± 1 %, *n* = 16), *L. huakiwi* (17 ± 3 %, *n* = 6) and *L. pango* (16 ± 2 %, *n* = 3). A slight difference in mean flight muscle ratio between tested species is observed (ANOVA: *df* = 4, *n* = 74, *F* = 2.5, *P* = 0.07). Mean body mass (ANOVA: *df* = 4, *n* = 74, *F* = 9.0, *P* = 6.63 x 10^{-6}) and mean flight muscle mass (ANOVA: *df* = 4, *n* = 74, *F* = 15.9, *P* = 2.70 x 10^{-9}) shows a very strong significant difference between the five species.

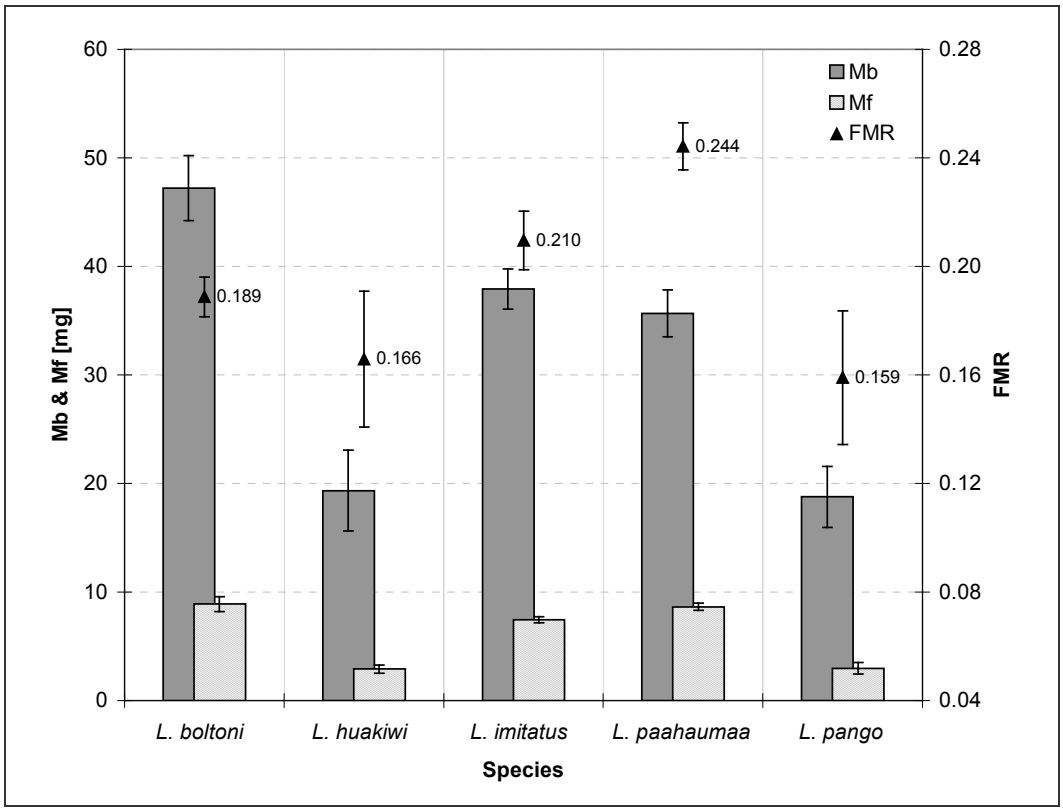

Figure 3.22 Mean flight muscle (Mf, light grey) and body mass (Mb, dark grey) ± SE (mg) compared to flight muscle ratio (FMR, ▲) ± SE for five species: *L. boltoni n* = 16, *L. huakiwi n* = 6, *L. imitatus n* = 42, *L. paahaumaa n* = 7, and *L. pango n* = 3.

Gabriel's comparison interval of mean body mass, flight muscle mass and FMR for five species of native bees is shown below (Figure 3.23). Mean body length, body mass and flight muscle mass measurements for *L. boltoni, L. imitatus* and *L. paahaumaa* were not significantly different. Similarly, mean measurements for *L. huakiwi* and *L. pango* were not significantly different. Mean body length, body mass and flight muscle mass for *L. boltoni, L. imitatus* and *L. paahaumaa* was shown to be significantly different to the mean body length body mass and flight muscle mass of *L. huakiwi* and *L. pango* however. A slight difference in mean flight muscle ratio was observed between the four species but overlapping comparison intervals indicate that this difference is not highly significant (ANOVA: $df = 4$, $n = 74$, $F = 2.5$, $P = 0.07$).

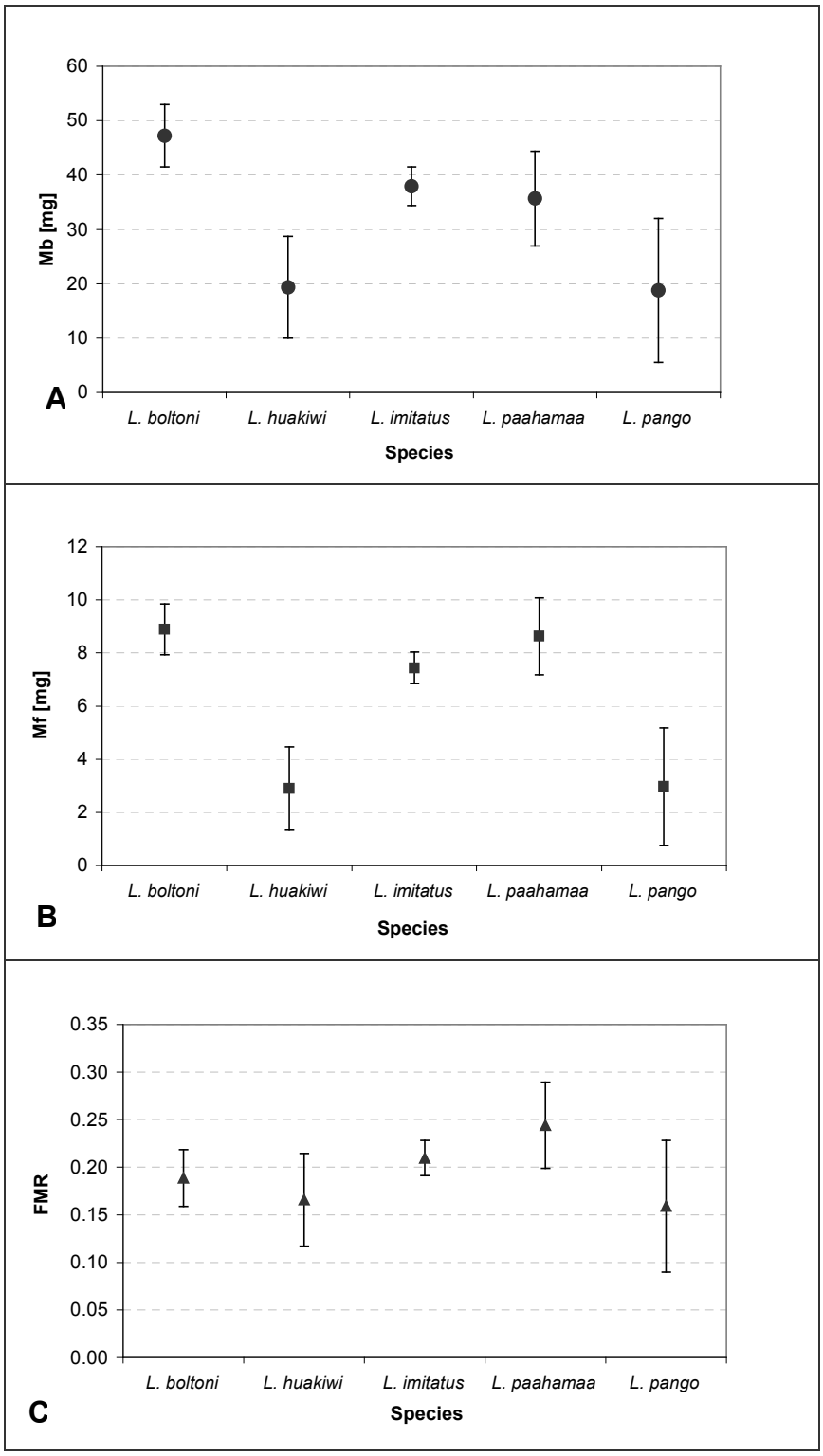

Figure 3.23 Gabriel's comparison interval (GI) is shown for four New Zealand native bee species: *L. boltoni n = 16, L. huakiwi n = 6, L. imitatus n = 42, L. paahaumaa n = 7 and L. pango n = 3*. Vertical bars show the GI and not SE. Intervals that do not overlap are significantly different to each other. A, Mean body mass (Mb, ●) ± (GI); B. Mean flight muscle mass (Mf, ■) ± (GI); and C, Flight muscle ratio (FMR, ▲) ± (GI).

The marginal flight muscle ratio shown in Table 3.16 lists the minimal flight muscle required when a maximum load is attached. Mean marginal flight muscle ratio was shown to be significantly different between the five species (ANOVA: *df* = 4, *n* = 74, *F* = 3.9, *P* = 0.007). Gabriel's comparison interval of mean marginal flight muscle ratio (Figure 3.24) for *L. boltoni* and *L. huakiwi* was significantly different to both *L. imitatus* and *L. paahaumaa;* intervals do not overlap. *Leioproctus pango* was not significantly different to *L. boltoni*, *L. huakiwi*, *L. imitatus* or *L. paahaumaa*.

Table 3.16 Range of unladen flight muscle ratios, mean flight muscle ratio (FMR) ± SE and mean marginal flight muscle ratio (MFMR) ± SE for five species of New Zealand native bee: *L. boltoni n* = 16, *L. huakiwi n* = 6, *L. imitatus n* = 42, *L. paahaumaa n* = 7, and *L. pango n* = 3.

Species	Range FMR	Mean FMR	Mean MFMR
L. boltoni	0.143 - 0.241	0.189 ± 0.0073	0.160 ± 0.0068
L. huakiwi	0.089 - 0.265	0.166 ± 0.0251	0.133 ± 0.0308
L. imitatus	0.114 - 0.336	0.210 ± 0.0107	0.198 ± 0.0098
L. paahaumaa	0.212 - 0.281	0.244 ± 0.0087	0.226 ± 0.0104
L. pango	0.126 - 0.207	0.159 ± 0.0246	0.153 ± 0.0271

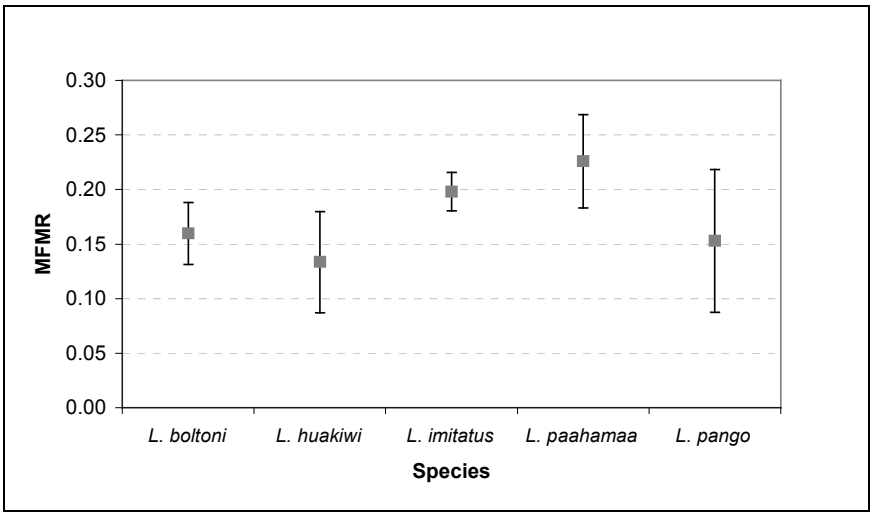

Figure 3.24 Gabriel's comparison interval is shown for four species of New Zealand native bees: *L. boltoni n = 16, L. huakiwi n = 6, L. imitatus n = 42, L. paahaumaa n = 7 and L. pango n = 3*. Mean marginal flight muscle ratio (MFMR, ■) ± (GI) is shown. Intervals that do not overlap are significantly different to each other.

Load-lifting capacity

Figure 3.25 illustrates maximum lift force production versus flight muscle mass for insects used in load-lifting experiments. Results for *L. boltoni* and *L. huakiwi* are compared to maximum lift force production for hymenoptera. For all individuals the maximum lift force was lower than published data for hymenoptera (Marden 1987). Data followed a similar correlation line only when one outlier for *L. huakiwi* (XY: -5.886, -3.451) is omitted from analysis. Difficulties experienced during load-lifting capacity experiments, such as attachment of weights to insects, could account for differences in measurements, which resulted in the outlier data (see Discussion of Methodology).

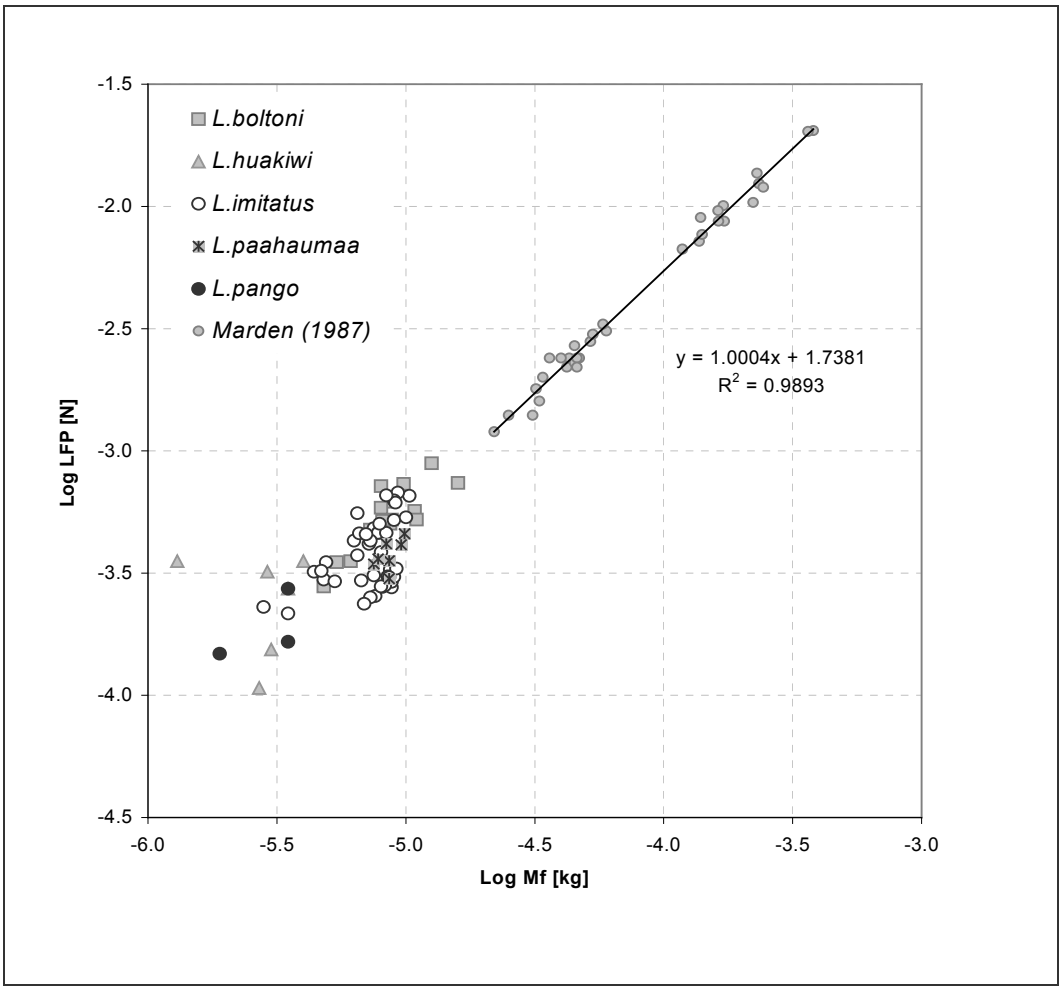

Figure 3.25 Scatter plot of log - log transformed lift force (LFP) (N) versus flight muscle mass (Mf)(Kg) for individual bees (*L. boltoni n* = 8 and *L. huakiwi n* = 5) tested for maximum lift compared to raw data points of individual insects (correlation line, rectilinear equation and coefficient of determination, R^2) on maximum lift for hymenoptera (Marden 1987).

Summary of load bearing capacity

Mean pollen mass measurements were taken on 40 individuals from four species. The mean pollen mass collected in a complete foraging trip showed that none of the species examined carried pollen loads greater than 23 % their body mass. *Leioproctus imitatus* carried the greatest pollen loads up to 23 % their body mass, *L. boltoni* up to 19 %, and *L. paahaumaa* up to 15 % their body mass. Artificial load lifting capacity experiments were conducted on 14 individuals from two species. *Leioproctus boltoni* carried the greatest artificial loads up to 52 % their body mass and *L. huakiwi* up to 41 %. Data on typical pollen loads (n = 7) and artificial loads (n = 8) were collected for *Leioproctus boltoni* only; a very significant difference is observed in mean artificial load and pollen load carried by *L. boltoni* (t-test: df = 13, t = 2.7, P [T<=t, two-tail] = 0.01). Table 3.17 below lists data on mean load mass ± SE g for five species of New Zealand native bees. Mean loads for each species includes individuals collected with pollen loads, no measurable load and for those tested with artificial loads. Gabriel's comparison intervals shows a very significant difference in mean loads of *L. boltoni* compared to *L. huakiwi*, *L. imitatus*, *L. paahaumaa* and *L. pango* (ANOVA: df = 4, n = 74, F = 8.3, P = 1.22 x 10^{-5}) (Figure 3.26).

Table 3.17 Mean load (ML) ± SE (g) and mean total load to mean body mass (ML: Mb) ± SE (%) for five species of New Zealand native bees: *L. boltoni n* = 16, *L. huakiwi n = 6*, *L. imitatus n* = 42, *L. paahaumaa n* = 7, and *L. pango n* = 3.

Species	ML± SE [mg]	ML: Mb ± SE [%]
L. boltoni	9.0 ± 0.18	19 ± 2.9%
L. huakiwi	3.0 ± 0.16	17± 0.9%
L. imitatus	2.0 ± 0.04	6 ± 0.9%
L. paahaumaa	3.0 ± 0.08	8 ± 2.3%
L. pango	1.0 ± 0.12	5 ± 4.9%

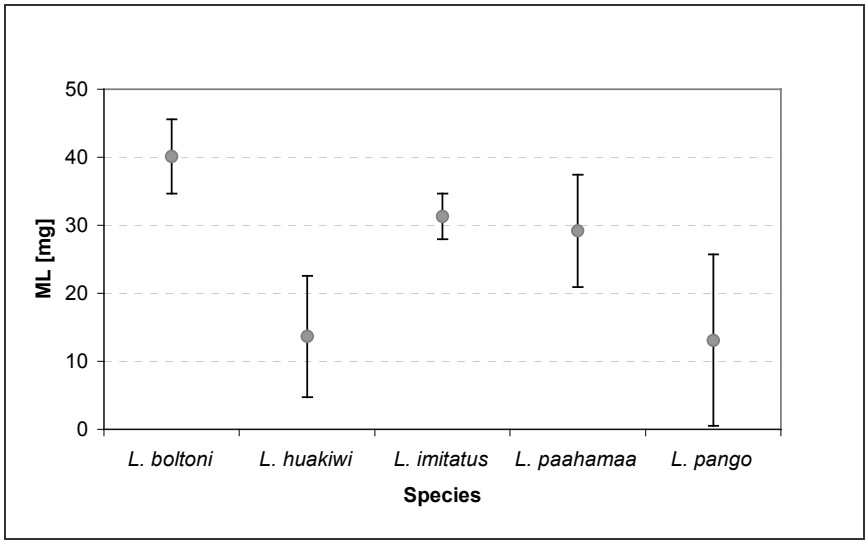

Figure 3.26 Gabriel's comparison interval is shown for four species of New Zealand native bees: *L. boltoni n = 16, L. huakiwi n = 6, L. imitatus n = 42, L. paahaumaa n = 7 and L. pango n = 3*. Mean load (ML, ●) (mg) ± (GI) is shown. Intervals that do not overlap are significantly different to each other.

Harmonic radar applications

For most harmonic radar applications tag antennas have ranged in weight from 0.4 – 80 mg. Body masses for various taxa tagged in tracking studies ranges from 45 – 350 mg (Appendix A3). Bearing in mind the mean pollen mass each species actually lifted, *L. boltoni, L. huakiwi* and *L. paahaumaa* could carry the additional mass of the smaller tag antennas (0.4 -1 mg) in addition to their typical pollen loads. *Leioproctus imitatus* carried mean loads significantly less than expected. Thirteen *L. imitatus* individuals however, were collected while foraging with a sweep net and carried less than full loads (Satterthtwaite's corrected *t*-test between insects collected while foraging and returning to nest sites: *df* = 15, *t* = 4.07, *P* [T<=t, two-tail] = 0.0025). Based on the mean flight muscle mass of the species (Mf = 21.0 ± 1.07 mg, *n* = 42) *L. imitatus* should be capable of carrying loads of 0.4 mg. For four species: *L. boltoni, L. huakiwi, L. imitatus,* and *L. paahaumaa* tag antennas within the range of 0.4 – 1 mg represent 1 – 5 % total lifted mass (body mass and pollen or artificial load mass) or total body mass (Table 3.18). Results show that *Leioproctus pango* lifted little additional weight and it is unlikely this species could carry even the smallest tag antenna (refer to Table 3.17 above). Maximum vertical lift for individuals was examined and not the insects' endurance capacity, or capacity to carry loads in addition to normal pollen loads.

Table 3.18 Harmonic radar tag antenna weights of 0.4 and 1 mg as a percentage of total mean mass lifted (body and pollen / or artificial load) (±SE), and mean body mass (±SE), for five species of New Zealand native bees: *L. boltoni n* = 16, *L. huakiwi n* = *6*, *L. imitatus n* = 42, *L. paahaumaa n* = 7, and *L. pango n* = 3.

Species	Mt [mg]	0.4: Mb [%]	1: Mb [%]	Mb [mg]	0.4: Mb [%]	1: Mb [%]
L. boltoni	63 ± 5.0	1%	2%	47 ± 3.0	1%	2%
L. huakiwi	27 ± 4.5	1%	4%	19 ± 3.7	3%	5%
L. imitatus	52 ± 2.4	1%	2%	38 ± 1.9	1%	3%
L. paahaumaa	42 ± 2.4	1%	2%	36 ± 2.2	1%	3%
L. pango	19 ± 2.7	2%	5%	19 ± 2.8	2%	5%

3.4.3 Discussion of methodology

Load-lifting methods

There were practical problems encountered attaching weights to native bees although data from load-lifting experiments provides an indication of their ability to lift loads in vertical take-off. Dudley (2002) notes several methodological features of Mardens (1987) research on which this study was based. Firstly, from a biological mechanical perspective the experiments do not address the capacity for maximum acceleration, but rather the ability for an animal to lift loads vertically. Since this study is concerned with the loads that native bees can carry, data on the maximum acceleration of flight, or descriptions of mechanical flight performance is not considered necessary. Secondly, Dudley (2002) points out the potential for fatigue to influence the animals capacity to fly, highlighting the difficulties associated with discriminating between an animals behavioural motivation to fly and biomechanical ability to lift off.

Observations during load-lifting experiments

Behavioural motivation to fly influenced the results of this study. Difficulty was experienced during load-lifting experiments when attaching consecutive loads and

encouraging bees to fly. Several insects were damaged when attempting to attach loads and they appeared fatigued through handling. Although no bees became aggressive or tried to sting, their discomfort was obvious. Fourteen bees would not fly with artificial loads despiteencouragement. Instead these individuals tried to dislodge the artificial load by crawling into gaps or crevices around objects. Ten individuals squeezed through very small gaps around a window and dislodged the artificial load to escape (see Figure 3.27 below). Similar behaviour was observed with captive bees which would investigate gaps or vents in a container from which they could escape. On one occasion, five female bees (*Lasioglossum sp.*) were seen removing pollen from their scopae, thorax and abdomen so they could fit through small vent holes (0.1 mm wide).

Figure 3.27 Native bees; A, Turning around in a length measuring tube 0.3 mm wide, and; B, Crawling on a pair of tweezers, attempting to dislodge the artificial load which is attached to its' thorax.

Body mass measurements

Insects for this study were collected over three seasons (2004-2006). Some were frozen prior to body and flight muscle mass measurements for practical reasons. For example, it was not practical to set up analytical balance and laboratory equipment to measure two or three insects in one session. In an effort to standardise the technique, total body mass was measured on 15 bees (an hour after collection) and these were then frozen and the body mass was re-measured after bench drying for 2, 24, 48 and 78 hrs. There was no measurable difference between those insects dried for 48 and 72 hours. All other frozen specimens were dried to a constant mass after 48 hours. Body loss was calculated at 36.8 ± 1.52 % for bees bench dried for 48 hours (n = 15). All other frozen insects were adjusted

by a factor of 1.596 to account for this loss. Mean flight muscle mass for native bee taxa measured in this study indicates a lower than reported value. Mean flight muscle ratio for native bee taxa is 0.203 ± 0.007 (*n* = 74) and the reported value for hymenoptera is 0.306 (Marden 1987). A scatter plot and rectilinear equation for frozen - bench dried for 48 hrs versus fresh body mass indicates that body mass values are slight over estimates (~ + 5.0 mg). While flight muscle ratios are slight under estimates (~ - 0.5 %)(Figure 3.28).

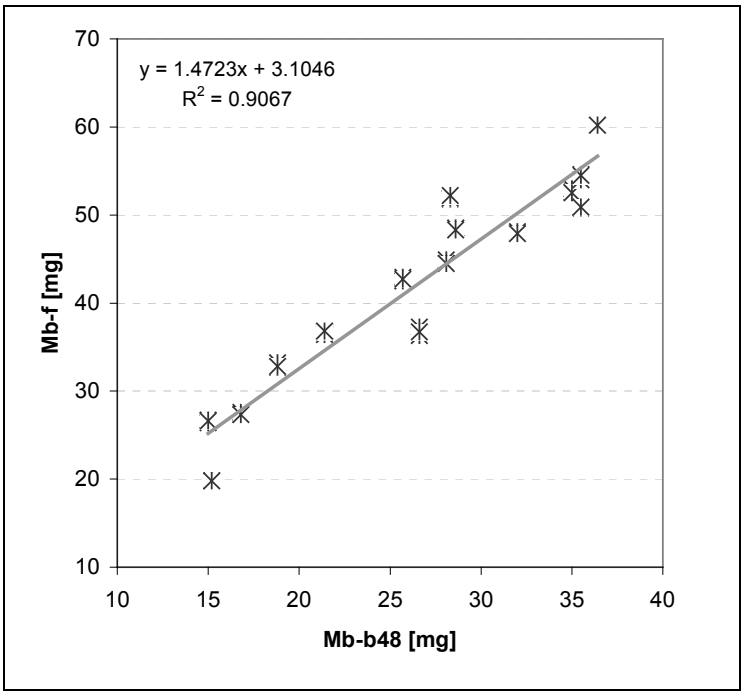

Figure 3.28 Scatter plot, rectilinear equation and coefficient of determination (R^2) frozen bench dried (48 hrs) body mass (Mb–b48) (mg) versus fresh body mass (Mb-f) (mg) for n=15 native bees.

Alternative load-lifting methods

A modified load-lifting method has been used to investigate the maximum vertical force production orchid bees (Apidae: Euglossini) (Dillon & Dudley 2004). This method addresses the difficulties described above; and has been used to investigate the relationship between lift duration and performance (Chai et al. 1997). Parameters such as flight endurance are not directly investigated in this study. While maximum loads have been determined, the capacity for an insect to carry a load for a specified duration has not been established; normal foraging behaviour with a load is an important consideration for determining the efficiency and practicality of harmonic radar methodology.

3.5 Discussion

3.5.1 Load-lifting capacity and tag antennas

Benefits of direct tracking with harmonic radar and overcoming design constraints

The benefit of directly tracking the foraging activities of native bees is that it could lend critical insights into the structure and scope of pollinator communities. To ensure the insect under observation is performing normal foraging activities, tag antennas need to be as lightweight as possible. From an engineering perspective, the size and shape of a radiator is limited by fundamental electromagnetic constraints and these parameters cannot be easily manipulated. For example, reducing the length of an antenna reduces the operating frequency. For engineers and entomologists alike these constraints require a novel solution if tracking very small insects is to become a reality.

Wing loading versus flight muscle mass

The effect of harmonic tag antennas on animal flight has not generally been assessed. While some studies conclude minimal effect, Riley et al. (1996) indicate further experiments are necessary to determine whether or not the tag antennas modify flight behaviour. Based on this premise and as an ongoing investigation into the design of the harmonic radar, Boiteau & Colpitts (2001) investigated the effect of tag antennas on the flight of the Colorado potato beetle (*Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). They specifically analysed the wing loading of the beetle and it's tolerance for extra weight (Boiteau & Colpitts 2001). Their findings indicate the Colorado potato beetle can carry a weight of 2.8 mg (2.4 % of their average body mass of 117 mg) (Boiteau & Colpitts 2001). In contrast, wing loading was not used to investigate the load lifting capacity of New Zealand native bees. Flight muscle mass is recognised as more predictive of load-lifting capacity (Dudley 2002). Further more, in other studies of insect lift capacity (Coelho & Hoagland 1995; Coelho & Ladage 1999), flight muscle mass is typically used to predict load-lifting capacity. This method, although challenging, was considered the most appropriate standardised method.

Behaviour of native bees

Analysis of the load-lifting capacity of New Zealand native bees was not intended to be a detailed study of the flight mechanics of these insects. An objective of the study was to ascertain the maximum weight tag antenna that could be attached for harmonic tracking.

Insect load-lifting capacity is not only a function of body and flight muscle mass, it also includes parameters such as metabolic rate, flight aerodynamics and behavioural motivation. The difficulties associated with load-lifting capacity experiments highlight the complexity of New Zealand native bee behaviours. Some native bees tested went to extraordinary lengths to remove unwanted loads. These observations were unexpected but are crucial to the study. They indicate that even if some species of New Zealand native bees have the capacity to lift tag antenna loads, without impeding normal foraging flight, loads could simply be rejected and the insects would persistently attempt to remove them.

Lifting capacity: artificial and pollen loads

The results of this study confirm that native bee taxa have a lower mean flight muscle ratio 0. 203 ± 0.007 (n = 74) compared to other hymenoptera (FMR = 0.306, n = 33) (Marden 1987; Coelho & Hoagland 1995; Coelho & Ladage 1999). In general New Zealand native bees carry very little additional weight. None of the species collected carrying pollen carried loads that exceeded 23% of their mean body mass (*L. imitatus*). Artificial loads did not exceed 52% body mass (*L. boltoni*). The maximum load for five species of New Zealand native bees was compared to data from harmonic radar studies. Mean body mass for native bee taxa ranged from 19 ± 2.8 mg (*L. pango*) to 47 ± 3.0 (*L. boltoni*) mg. The smallest tag antennas designed to date are within the range of 0.4 -1 mg. These antennas may be suitable to use with some New Zealand native bee species including: *L. boltoni*, *L. imitatus* and *L. paahaumaa* and represent 1-3% the body mass of the bees. But observations and the results of pollen and artificial load-lifting capacities of *L. huakiwi* and *L. pango* indicate that even the smaller antennas could not be lifted. Flight muscle mass measurements confirm that both *L. huakiwi* and *L. pango* have a minimal percentage of body mass composed of flight muscle (0.166 ± 0.0251 and 0.159 ± 0.0246 respectively). They had the lowest flight muscle mass ratio of all the species tested. Gabriel's comparison intervals of mean flight muscle mass showed *L. huakiwi* and *L. pango* as not significantly different from one another but a strong significant difference to the other species tested was observed (ANOVA: df = 4, n = 74, F = 2.5, P = 0.07) (see Figure 3.29).

3.5.2 Body length

Body length: Can it be used to predict foraging range?

The foraging range of pollinating insects is critical for many studies including; biodiversity conservation, ecological restoration, biosecurity protection, biosafety, sustainable

agriculture and horticulture (Newstrom & Roberston 2005). A prime example is determining the dispersion range of genetically modified material through insect pollination. While insect movement is fundamentally important for many studies, techniques to determine absolute ranges are often fraught with practical complications. Translocation methods have traditionally been used to estimate range; while some authors have suggested the best predictor of foraging range of solitary bees is their body length (Gathmann & Tscharntke 2002). In the absence of suitable practical methods to track the foraging range of native bees, body length data could provide a broad estimation of home range. Based on body length the home range of the species of New Zealand native bees examined in this study could range from 150 – 479 m. Body length is not generally accepted as a robust predictor of foraging range however (pers com, Donovan, Newstrom) and this is investigated further in Chapter Five: Foraging Behaviours of Native Bees.

3.5.3 Future studies

Predictions of flight muscle mass and load

Ecologically, flight with loads such as prey, mates, pollen or nectar is an important descriptor of performance but load lifting methods are time consuming and difficult to manage (Dudley 2002). The results of this study, demonstrate that future studies requiring measurements of flight muscle mass ratios need not involve complex load lifting experiments. Correlation was tested for two sets of variables: mean flight and thorax muscle mass as well as, mean total lifted and body mass. Flight muscle mass was shown to have strong correlation with thorax mass (r = 0.975, n = *74*) and total lifted mass was correlated with body mass (r = 0.941, n = *74*). These variables could used to predict flight muscle mass and total lifted mass, to determine maximum lift force and load mass (Figure 3.29).

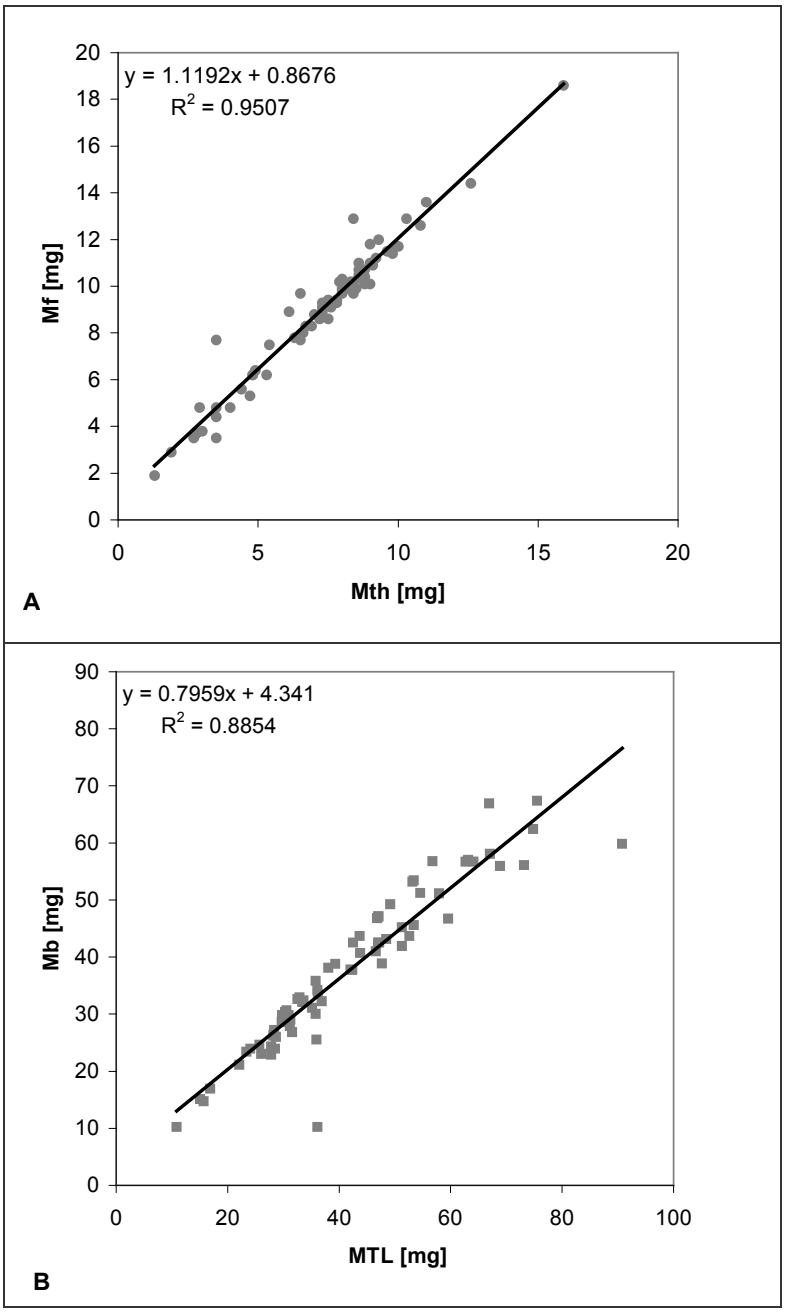

Figure 3.29 Scatter plot, rectilinear equation and coefficient of determination (R^2) of A. Flight muscle mass (Mf)(mg) versus thorax mass (Mth)(mg) and B, total lifted mass (MTL)(mg) versus body mass (Mb)(g) for native bee taxa studied.

3.6 Conclusions

This study aimed to identify the maximum load that could be carried by New Zealand native bees. Five species were examined, *L. boltoni, L. imitatus, L. huakiwi, L. paahaumaa*, and *L. pango* and of these mean pollen mass measurements were taken of three species (*L. boltoni n* = 7, *L. imitatus n* = 27 and *L. paahaumaa n* = 5). Artificial load mass was determined for two species (*L. boltoni n* = 8 and *L. huakiwi n* = 5). Based on load-lifting capacity parameters including: flight muscle mass ratio, flight muscle mass and body mass, all but two species, *L. huakiwi* and *L. pango*, are expected to be capable of lifting small tag antennas in the range of 04 –1 mg. These are tag antennas are currently used in harmonic tracking systems abroad. Harmonic radar systems can be used to directly evaluate the foraging range of insects and would provide significant benefits to the study of New Zealand native bees and their foraging range. Confirmation that native bees can carry some additional weight is clearly beneficial for any future application of the technology. Results also provide base-line data for engineers and entomologists alike. Behavioural aspects of New Zealand native bees on the other hand, indicate they simply would not carry a tag antenna. This was an unforeseen outcome and it is critically important when considering the application of any future tracking technology.

Chapter Four Nesting Behaviours of Native Bees

Abstract

New Zealand native bees were found in large nest aggregations on Mt. Parihaka (Whangarei). Nest sites were observed over three active seasons (December 2004 - March 2005, October 2005 - March 2006 and November 2006 - January 2007). Six species were found, five from the genus *Leioproctus* and one from the genus *Lasioglossum.* Nesting behaviour in aggregations was recorded. At least two species of bee were found nesting beside each other at most nest sites. Female bees showed a high degree of tolerance towards their neighbours as they constructed nests. A description of nest architectures and the time spent provisioning nests between foraging trips was recorded for three species: *Leioproctus (Leioproctus) boltoni* (Cockerell), *L. (L.) imitatus* (Smith) and *L. (N.) paahaumaa* (Donovan) (Hymenoptera: Colletidae). Data was collected from two separate locations, at the top of Mt. Parihaka (TP) and at the water reservoir half way up Memorial Drive (WR). Density of nests per m^2 was recorded at five separate nest aggregations around Mt. Parihaka.

Artificial nest boxes were placed in the ground at both locations (TP and WR) and removed after the active season was complete. Both boxes showed different nest architecture unique to one of three species, *L. boltoni, L. imitatus* or *L. paahaumaa.* This specific nest architecture varied according to local environmental conditions. Nests of *L. paahaumaa* at location WT (site 4A) were built on near horizontal sites. Observations indicate the species uses sink-traps to prevent water from entering cells in habitats vulnerable to flooding. Nests of *L. boltoni* and *L. imitatus* were in vertical banks at location TP (site1A). All nests were abandoned at around 150 mm depth as the artificial nest box walls restricted nest construction. Results indicate bees attempted to build tunnels pointing upwards and were blocked by the artificial nest box dimensions. The density of nests varied from as few as 14 nests per m^2 to 22 nests per m^2. The largest aggregation was found at site 1 with up to 12 thousand nests over the entire 500 m^2 area.

4.1 Introduction

4.1.1 Nesting in aggregations: a case study on Mt. Parihaka

Many species of mining bee nest in dense aggregations (O'Toole & Raw 1991). They have a preference for the type of substrate they use (Petanidou & Ellis 1996) and so many individuals will nest within a localised area. In New Zealand, Quinn (1984) estimated some 840 thousand bees nests, over a 7.5 km road in the McKenzie Basin. Solitary mining bees tend to form large nesting communities where many species co-exist. In these aggregations, large mounds of excavated soil (tumuli) forms around nest entrances indicating bees at work. It is virtually impossible to determine species from the nest entrance alone so knowledge of nest architecture is important. Architecture is generally unique to a species and can explain much about a bees' biology (O'Toole & Raw 1991).

In Northland, communities of native bees can be located in a variety of ecosystems from regenerative forests, such as Mt. Parihaka, to existing native forests, such as Raumanga Valley Reserve. Several large communities of native bees found in the Mt. Parihaka forest provided an ideal opportunity for a study of community structure in a regenerative forest. Six different species of New Zealand native bees were identified on Mt. Parihaka, five from the genus *Leioproctus* and one species from the genus *Lasioglossum.* This study investigates aspects of the nesting biology of three of these species in order to gain a greater understanding of their community structure and role in the environment.

4.2 Study aims

This largely explorative community investigation of New Zealand native bees in Whangarei aims to promote an understanding of their nesting behaviours.

There are two areas considered in this study:

A. To identify the physical aspects of nests of for three species of native bees, *L. imitatus, L. boltoni* and *L. paahaumaa* by:
    - Quantifying nest metrics.
    - Estimating densities of nests.

B. To document the behaviours associated with nesting of three species of native bees, *L. imitatus, L. boltoni* and *L. paahaumaa*.

For each species or nest site observed or collected the study aims to answer the following questions:

1. What are the physical aspects of nest sites including nest metrics?
2. What are the aspects of nest architecture of the species?
3. What is the density of nests at each study site?

4.3 Methods

4.3.1 Nest site locations and descriptions

Several communities of native bees were found on Mt. Parihaka. A nest aggregation was found at the gated entrance of the pine forest, to the left of Parihaka Memorial car park at the top of Mt. Parihaka nominated as location TP. Location TP includes nest sites 1, 2 and 3. Another nest aggregation was found approximately 6 km from the first, at the gated entry to the water reservoir half way up Memorial Drive nominated as location WR. Location WR includes sites 4A & 4B. These communities formed the basis of this investigation (Table 4.19).

Table 4.19 Locations on Mt. Parihaka that were the focus for repeat collections and foraging duration observations of New Zealand native bees. Specific site descriptions, locations, latitude & longitude and general ecology of areas where bees were observed or collected over two seasons (2004 – 2005 & 2005 – 2006).

Location	Nest site & code	Location	General Ecology
Top of Mt. Parihaka (TP) Mt. Parihaka, Riverside. Whangarei. Main entrance at the very end of memorial drive. Car park leading to walking access war memorial on the right hand side and gated forestry area (restricted access) on the left hand side.	**Site 1A**: By gate, at the entry to forestry area. First bank on right-hand side.	**S** 35^{O} 42' 43.04 " **E** 174^{O} 20' 18.62" **HAE** 261 m	Pine forest plantation. First generation regenerative forest. Some gorse, pampas (*Cortaderia spp*.) and cutty grass.
	Site 1D: Second bank under transmission tower.	**S** 35^{O} 42' 42.97" **E** 174^{O} 20' 20.18" **HAE** 260 m	
	Site 2A: Down from gate entry. Third major bank in forestry area, on the right hand side.	**S** 32^{O} 46' 43.03" **E** 174^{O} 20' 22.01" **HAE** 258 m	
	Site 3A: Down from gate. Small bank on left hand side in the forestry area	**S** 32^{O} 46' 43.03" **E** 180^{O} 20' 21.01" **HAE** 242 m	
Water reservoir (WR) Mt. Parihaka, Riverside. Whangarei. Before memorial car park, half way up memorial drive. On the right hand side gated entrance into water tower reservoir area	**Site 4A**: Water tower entrance, over mound on the left hand side	**S** 35^{O} 43' 01.96" **E** 174^{O} 20' 37.34" **HAE** 192 m	Pine forest plantation. First generation regenerative forest. But mainly gorse, pampas and cutty grass in the immediate vicinity of nest site. Some cleared areas.
	Site 4B: Five m down from mound, on steep bank.	**S** 35^{O} 43' 01.34" **E** 174^{O} 20' 37.35" **HAE** 192 m	

4.3.2 Nest architecture

Three artificial nest boxes were designed and constructed using plexiglass based on an original glass and wood prototype by Donovan (1967). Each box measured 150 x 250 mm wide and 400 mm deep and was designed with 10 separate 15 mm levels (Figure 4.30 below). The complete structure was held together using temporary ties and each of the 10 levels was made to slot into the box so it could be easily deconstructed to examine

nest architecture. Artificial nest boxes were filled with soil from Mt. Parihaka. Once they were tightly packed with soil the boxes were inserted into the ground at location A, nest site 1 (a vertical nest site) and location B, nest site 4 (a horizontal nest site). They were left for one complete season. The boxes were placed in the ground in December 2006 and removed in October 2007. Nest parameters were recorded including the number of nests entrances, the size of entrance, depth and number of tunnels and chambers.

Figure 4.30 Artificial nest boxes, A. Empty box ready to fill with soil from Mt. Parihaka; B. partially filled with soil and C. Inserting the completed filled box into position at Site 1.

4.3.3 Nest provisioning duration

Three separate nest sites were investigated over two seasons, sites 1, 2 and 4 (2004 - 2005 and 2005 - 2006). Observations were conducted on sunny days, between the hours of 10:00 – 16:00, over the main foraging season December through to February each year.

An 0.80 m^2 fold-up flexible grid was designed and constructed to place over nest areas, suitable for monitoring vertical and horizontal sites (Figure 4.31 below) and for estimating

nest density. Sectioned into individual grids of 0.10 m^2, a total of 64 separate areas could be checked for activity. The grid position was marked so that it could be easily placed over the same site for repeat monitoring. Once the grid was positioned data was collected on the entry and exit times of bees within the grid area as follows: As a bee entered a nest, 1) the nest was identified with numbered tag, 2) the entry time recorded, 3) a stiff cone-shaped net was placed over the entrance of the nest until the bee was ready to exit the nest, 4) the net was removed and the exit time recorded (see Figure 4.31).

Estimations of nest density were taken at all sites where nest provisioning duration data was collected; nests per 0.8 m^2 was extrapolated over the entire visually estimated active nest area.

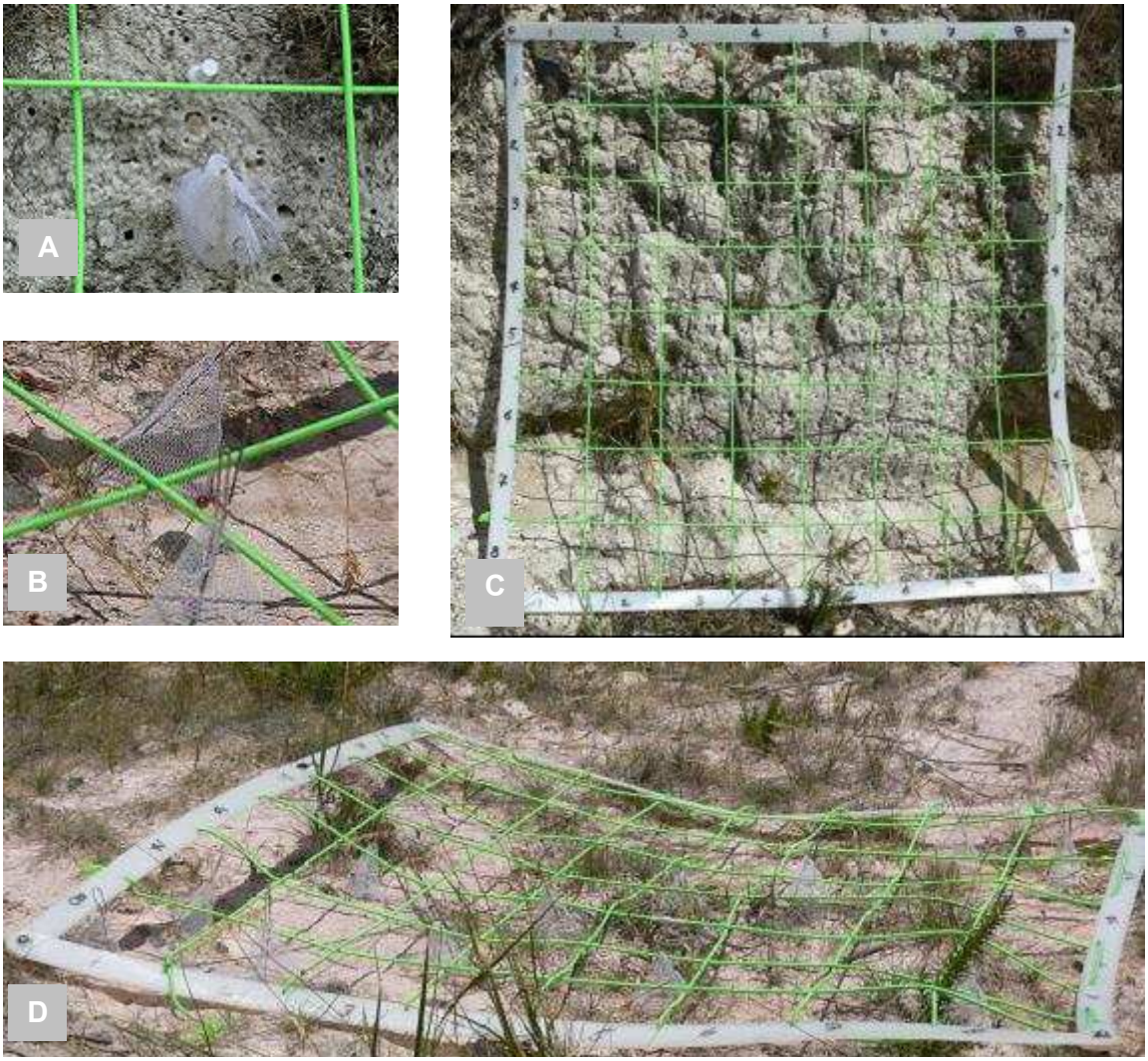

Figure 4.31 Foraging and nesting provisioning duration monitoring equipment. A, Shows a close up of a vertical nest with stiff cone net placed over the entry of a nest. B, Two cones on a horizontal nest. C, The flexible grid attached to the wall of a vertical nest (site 1) and D, on a horizontal nest (site 4).

4.3.4 Statistics

Statistical analyses were performed using Microsoft Excel 2000 Statistical Toolbox. For those data compared using ANOVA, Gabriel comparison interval is plotted with mean (not SE) (Mcardle 1987; Sokal & Rohlf 1995). For all other data, the arithmetic means are given ± standard errors (SE).

4.4 Results

4.4.1 Nest Architecture

Location TP: site 1A

There were 16 nest entrances started in the nest box inserted at location TP, site 1A (Figure 4.32). The width of nest entrances varied between 5 – 8 mm. All tunnels terminated 100 – 150 mm and no complete nests were constructed. It was not possible to identify the species involved in tunnel construction.

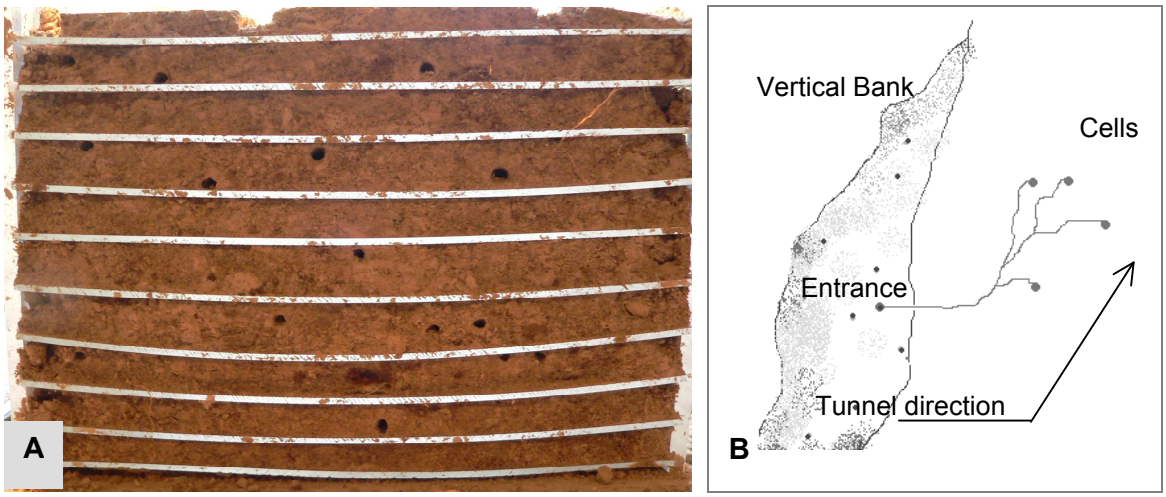

Figure 4.32 Nest architecture; A, the removed artificial nest box inserted at site 1A showing up to 16 nest entrances and; B, hypothetical nest architecture for species at site 1A showing the change in tunnel direction around 100 – 150 mm deep, branches and cell chambers.

Location WR: site 4B

From site 4B, a single nest containing three cells, one contained a prepupae, was constructed in the artificial nest box (Figure 4.33). The entrance tunnel branched at 15 mm depth into two tunnels, the first terminated in a chamber at 15 mm and the second in a chamber at 22 mm and the third at 25 mm. Cells were oval in shape and were no more than 10 mm in length, and 5 mm wide. The width of nest tunnels varied between 5 – 10 mm. *Leioproctus. (L.) paahaumaa* formed two small nest aggregations at this location so they are thought to be the primary species for the area. Two other species, *L. boltoni* and *L. imitatus*, were also collected from site 4B.

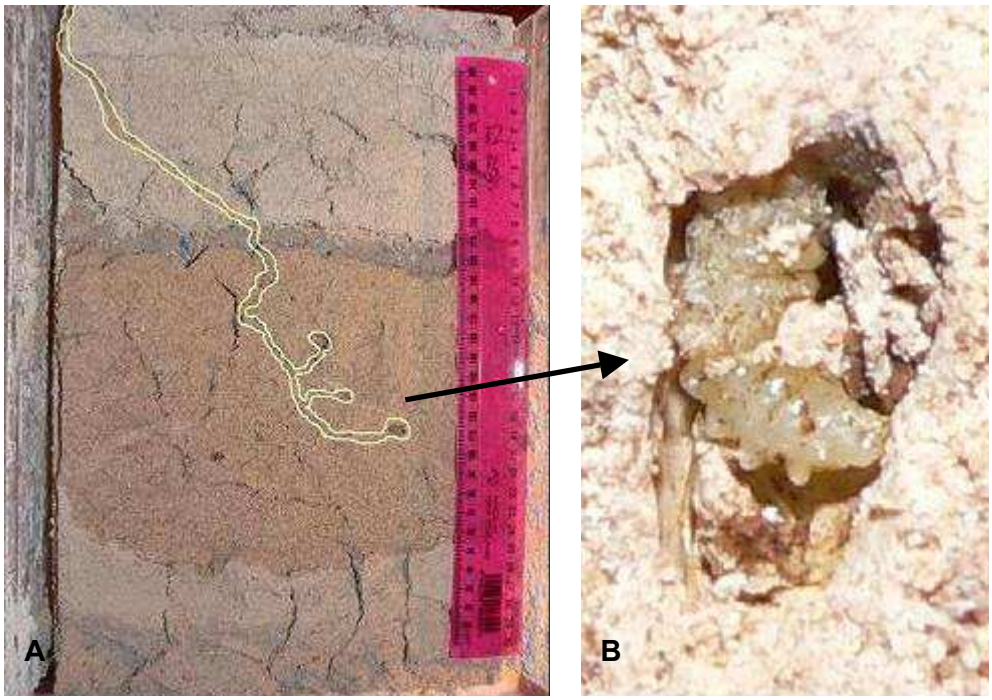

Figure 4.33 Nest Architecture; A, the removed artificial nest box inserted at site 4B showing a single three chamber nest and; B, a close up photo of prepupae in a cell of the nest.

4.1.1 Nest provisioning duration

Table 4.20 below details the results from three nest aggregations (1A, 3A and 4A) at two physically separated locations, at the top of Mt. Parihaka (TP) and the water reservoir (WR). Native bees were monitored at these sites. Data was collected on length of time native bees spent provisioning their nests in between foraging trips (as well as the frequency and duration of foraging trips – see Chapter Five: Foraging Behaviour of Native Bees for details). At location WT, site 4A the species *L. paahaumaa* was observed for 24

hrs in total, 220 individual female bees were watched as they completed 300 nest-provisioning sessions. Mean time inside the nest between foraging trips (± SE) was 0:25 ± 0:14 hrs and ranged from 0:01- 1:42 hrs for *L. paahaumaa*.

At location, TP (site 1A and 3A) it is likely that more than one species of native bee was observed; *L. boltoni* (48%) and *L. imitatus* (44%) were both found nesting at the site in high numbers and are not easily distinguishable from each other while on the wing. Foraging duration data collected from site 1A and 3A therefore includes female individuals from *L. boltoni* and *L. imitatus* in all likelihood. In total 7 complete foraging trips were recorded from sites 1A and 3A, and 131 individual female bees were observed over a period of 21 hrs. A mean time spent in the nest (± SE) of 1:06 ± 0:42 hrs was recorded and ranged from 0:02 – 3:46 hrs for *L. imitatus* and *L. boltoni.*

Table 4.20 Foraging trip data for New Zealand native bees observed at three sites (1, 3 and 4) on Mt. Parihaka, Whangarei.

Location, nest site and species	**Location A, site 4** **Species: *L. paahaumaa***	**Location B, site 1&3** **Species: *L. imitatus or boltoni***
Observation dates	17/01/2005 - 21/01/2005 10/01/2006 - 21/01/2006	11/01/2005 - 14/01/2005 14/11/2005 - 18/12/2005
Nest provisioning sessions	300	27
Individual bees observed	220	131
Total monitoring hours	24:00	21:00
Mean time in nest ± SE (hrs)	0:25 ± 0:14	1:02 ± 0:13
Range (max, min) - time in nest (hrs)	0:01 - 1:42 hrs	0:02 - 3:46

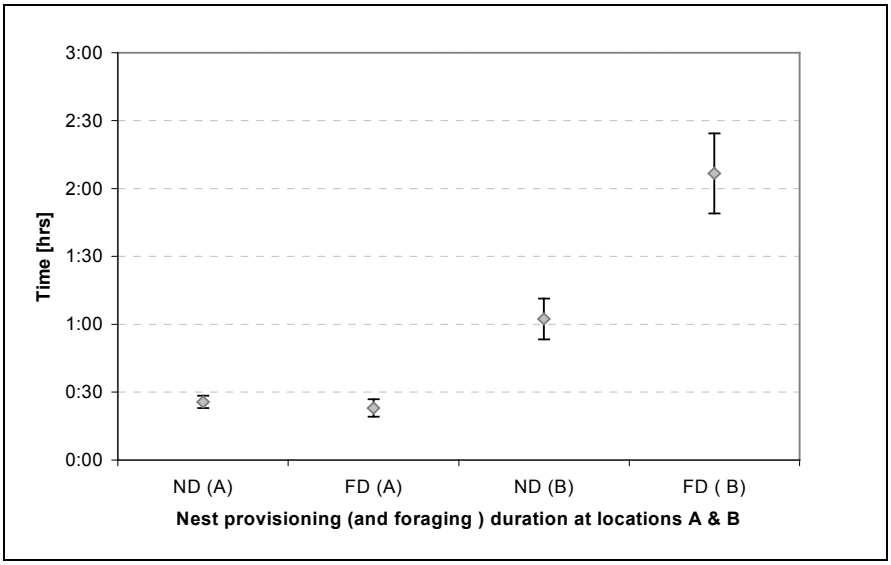

Figure 4.34 Gabriel's comparison interval (GI) of mean nest provisioning duration (ND) and foraging duration (FD) is shown for species at two different locations: A, site 4 (ND, *n* = 300 and FD, *n* = 145) & B, sites 1 & 3 (ND, *n* =27 and FD, *n* = 7). Different species of New Zealand native bees were active the locations. *Leioproctus (N.) paahaumaa* was the primary species at location WR; *L. imitatus* and *L. boltoni,* at location TP. Black vertical bars show GI and not SE. Intervals that do not overlap are significantly different to each other.

Figure 4.34 above shows the Gabriel comparison intervals of mean nest provisioning (and foraging duration) for three species of New Zealand native bees at two physically separated locations; there is a highly significant difference between locations in mean nesting provisioning and foraging duration times (ANOVA: *df* = 3, *n* = 478, *F* = 5.98, *P* = 5.27×10^{-31}). For the species *L. paahaumaa* observed at location WR, mean nest provision and foraging duration times are not significantly different (Student's *t* – test: *df* = 443, *t* = 1.33, *P* [T<=t, two-tail] = 0.184). Similarly, mean nest provision and foraging duration times are not significantly different for those species observed at location TP, (*L. imitatus* and *L. boltoni*) (Student's *t* – test: *df* = 8, *t* = 2.14, *P* [T<=t, two-tail] = 0.065).

In contrast, Student's *t* – test to compare the mean foraging duration time for species observed at location WR and TP show there is a very strong significant difference between *L. paahaumaa* observed at location WR and *L. imitatus* and *L. boltoni* observed at location TP (*df* = 150, *t* = 11.23, *P* [T<=t, two-tail] = 1.131×10^{-21}). Student's *t* – test to compare the mean nesting provisioning duration time for species observed at the two locations show there is a very strong significant difference between *L. paahaumaa* and *L. imitatus / L. boltoni* (*df* = 325, *t* = 7.14, *P* [T<=t, two-tail] = 6.04×10^{-12}).

4.4.2 Nest Density

Nest density is recorded below (Table 4.21). The greatest density was found at site 1D on vertical bank nests with up to 7,000 nests per m^2; site 4A was the least populated nest aggregation with around 500 nests per m^2. The most populated nest area at the top of Mt. Parihaka covered at least 500 m^2; up to 12 thousand native bees from five species nested at this location.

Table 4.21 Density of active nests at various nest site locations on Mt. Parihaka. Site 1 (top of Mt. Parihaka) above all other sites, supported the greatest population and highest diversity of New Zealand native bees in the study. In total over the entire area, approximately 12 thousand nests were evident. Smaller, highly localised nests were found at site 4A.

Nest site	Active area (m)	Nests per m^2	Nests per m^2 X Total Active Area
1A	3 x 10	22	660
1D - Ground	2 x 100	22	4,400
1D – Bank	5 x 100	14	7,000
3A	3 x 25	24	1,800
4A	5 x 5	20	500

4.5 Discussion

4.5.1 Artificial nest boxes

Data from artificial nest boxes was limited. At location TP several factors could have prevented female insects from completing their nests in vertical banks. Firstly, the soil in the nest box may not have been compacted to a suitable consistency and therefore bees abandoned efforts to try elsewhere. Secondly, since all tunnels terminated abruptly at 100 – 150 mm deep it is possible that upper and lower boundaries of the nest box layer prevented the female bee from changing the tunnel angle. All terminated tunnels ran horizontally into the bank; upper and lower layers prevented bees from making any vertical changes in direction. Although this cannot be confirmed tunnelling in an upward vertical direction would be of practical benefit since this would prevent water from entering deep into the nest architecture. It was not possible to identify the species involved in tunnel construction however, collection records for site 1A show that the 60% of nesting

bees from the area are *L. imitatus,* followed by 25% *L. boltoni* and 13% *L. pango* (refer to Chapter Two: Section 2.2 Collection records). Based on collected records, it is expected that the tunnels were constructed by *L. imitatus* and *L. boltoni.* At location WR, two highly localised, near horizontal nest aggregations of *L. paahaumaa* were observed. They are thought to be the dominant species in the area although two other species, *L. boltoni* and *L. imitatus*, were also collected from site 4B (refer to Chapter Two: Section 2.2 Collection records).

4.5.2 Nest Architecture

A description of the nest architecture can explain much about a bees' biology because it is often unique to a species (O'Toole & Raw 1991). For native bees on Mt. Parihaka, the high rainfall in the area suggests that some native bees have evolved to thrive in a wet environment. In this ecology nest structures incorporate specialised waterproofing techniques including a cellophane lining observed throughout remains of collapsed nests sites. The cellophane lining consists of macrocyclic lactones secreted from glands on the bees abdomen (Dufor's gland) that polymerises to form a waterproof lining of the brood cell (O'Toole & Raw 1991). But it is also likely that sink traps are used to prevent water from entering cells for species that have constructed horizontal nests such as *L. paahaumaa* (Figure 4.35 below).

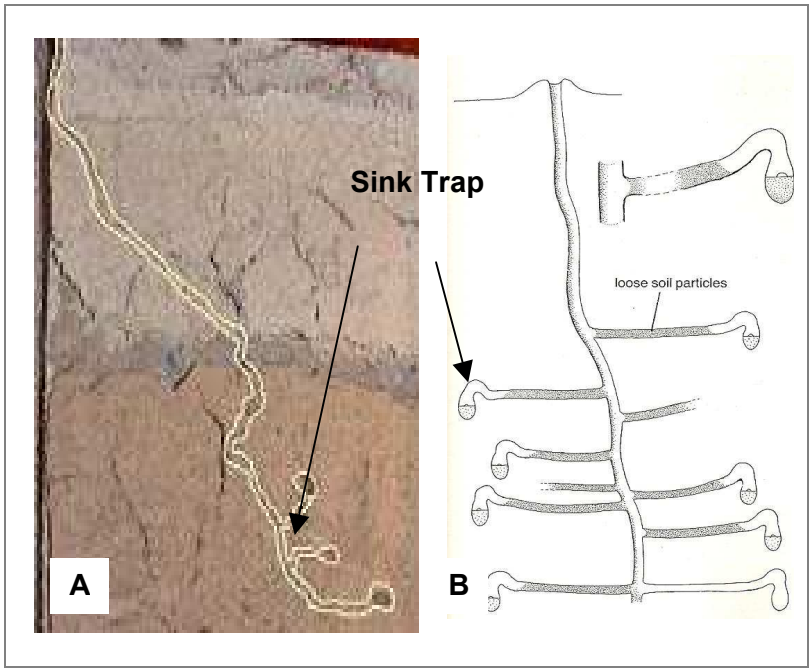

Figure 4.35 Nest architecture; A, Ground nest architecture of *L. paahaumaa* and; B, Nest architecture of *Ptiloglossa guinnae* (Colletidae) (O'Toole & Raw 1991) in cool, wet, mountain forests of Costa Rica.

Although one aim of this project was to record descriptions of nest architecture difficulties in examining natural nests prevented a detailed description for species of native bees on Mt Parihaka. At site 1, on the top of Mt. Parihaka, generations of nests resulting in thousands of entrances per m^2 made excavation of active nests virtually impossible without collapsing entire sections of bank (see Figure 4.36-B). Another confounding factor was that many species were found nesting along side each other and identification of nests to species was unlikely (unless the female was collected during nest construction). Up to five species were collected nesting at site 1 including: *L. boltoni, L. huakiwi, L. imitatus, L. paahaumaa* and *L. pango.* Similar reports show the same species nesting beside each other (and two extra species *L. kanapuu* and *Lasioglossum cognatum*) at Island Bay, Auckland (Donovan 2007). In addition to these issues, of the two artificial nest boxes that were inserted at site 1D and site 4B, only one incomplete nest was collected at site 4B (see Figure 4.35 above).

Several theories are raised from these results; firstly, artificial nest boxes actually prevented bees from constructing a natural three dimensional nest structure and secondly nest architecture is not only unique to a species but changes depending on site location nest site density and community structure (Potts & Willmer 1997). Donovan (1967) reported similar findings with artificial nest boxes when recoding the nests of *L. boltoni* and *L. imitatus* but also identified differences in nests unique to two species; reporting the diameter of the nests of *L. boltoni* are 6 mm while those of *L. imitatus* are 4.5 mm (Donovan 1967). Results also showed that bees nested in the restricted area of the artificial nest boxes with modified nest architecture to accommodate the limited space (Donovan 2007). Natural nest sites are also limited especially where substrate and aspect are at a premium (i.e. the soils are easily mined and the aspect is warm and sheltered).

4.5.3 Nest aggregations

On Mt. Parihaka, the density of aggregations varied at different locations depending on area of premium substrate and the aspect. Estimations of nest density were taken at all sites where foraging and nest building duration data was collected. Nests per 0.8 m^2 was extrapolated over the entire active nest area which was visually estimated. At high-density nest sites nest distribution appeared evenly distributed (e.g. site 2, Figure 4.36-B below), at other sites they were sparse or randomly distributed (e.g. site 4A, Figure 4.36-C). Differences in distribution of nests highlight the theory that in dense aggregations, in order to maintain nest integrity and avoid collapsing another's nest, female bees will construct nests a set distance from their neighbours and reduce the length of lateral tunnels (Potts

& Willmer 1997; Potts 2005). Donovan's (1967) findings also support this theory since *L. boltoni* and *L. imitatus* were shown to construct nests even when limited by an artificial nest box.

Of the three large nest sites found on Mt. Parihaka, site 1 was the largest with an estimated 7 x 100 m active nest area. Up to 12 thousand nests were active at this location alone (Figure 4.36). Bees formed nests over the entire bank. The vertical north facing banks were warm and sheltered and the substrate was soft and easy to excavate. Individual female bees were observed nesting in very close proximity to others and showed a high level of neighbourly tolerance. Male bees were often seen investigating new nests, moving quickly from one entrance to another and aggressively tussling with a female as they mated.

Abiotic factors such as the soil type and sun exposure are widely considered to be the main factors determining the congregation of nesting females in a particular area (Potts & Willmer 1997; Potts & Willmer 1998; Potts 2005). It has also been argued however, that biotic factors such as the presence of other nesting females and mating systems also influence aggregations (Giovanetti et al. 2005). Alternatively, forage rewards have also been accepted as the primary determinants of pollinator community structure (Petanidou & Vokou 1990; Petanidou & Ellis 1996). The nesting trends on Mt. Parihaka lends evidence to the concept that population success is also dependent on the availability of suitable nesting substrate (O'Toole & Raw 1991; Petanidou & Ellis 1996; Potts 2005; Potts et al. 2005). Observations of floral community structure on Mt. Parihaka indicate that forage rewards were no greater at large nest aggregations such as site 1, compared to smaller aggregations such as site 3. Both sites 1 and 3 had similar floral diversity and abundance but a greater area of substrate and an ideal north-facing bank provided more nesting areas at site 1 compared to the small south east facing bank at site 3.

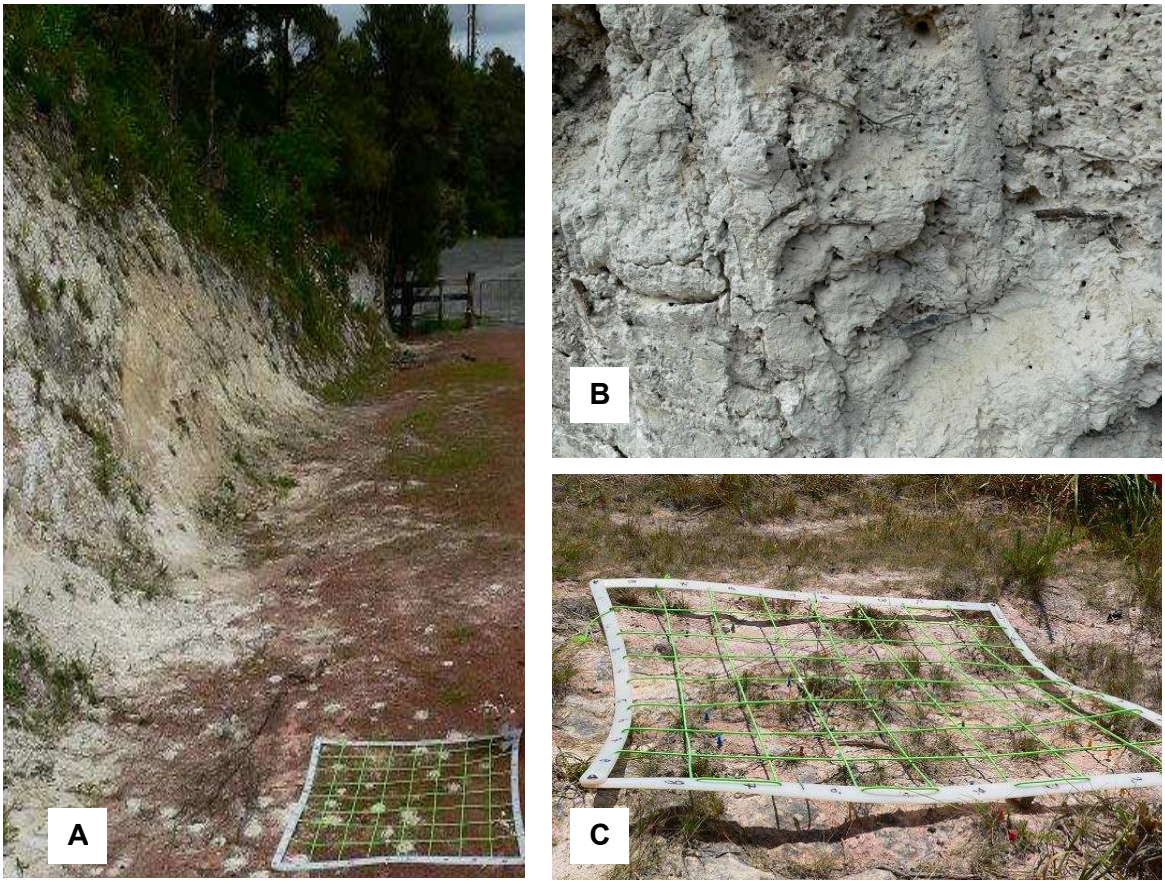

Figure 4.36 Nest sites; A, Ground nests (site 1D) beside bank at site 1 with approximately 35 visually active nests per m^2 and; B, Dense aggregations on North East facing cliff face at site 2A with approximately 1700 nest entrances per m^2 and; C, Ground nests of small localised community of *L. paahaumaa* with approximately 20 active nests per m^2 (with around 500 active nests over the entire 25 m^2 area).

4.5.4 Nesting behaviour

Some aspects of nesting behaviour have already been discussed (e.g. communities of native bees show a high tolerance towards each other and some species will adjust nest architecture if space is limited). Data recorded on nest provisioning shows a strong significant difference in the length of time species at locations TP (site 1 and 3) and WT (site 4) spend inside their nest between foraging trips.

The two species recorded at location TP were *L. boltoni* and *L. imitatus* and they spent a mean time spent in the nest (± SE) of 1:06 ± 0:42 hrs between mean foraging trips (± SE) that were 2:06 ± 0:13 hrs in duration. Donovan (1967) reported similar results for 10 individual females, showing *L. boltoni* had a mean time spent inside the nest (± SE) of 1:39 ± 0.19 (*n* = 5 nest provisioning sessions) between foraging trips (± SE) of 1:56 ±

0.11 hrs duration (*n* = 15 foraging trips). Given the duration of the foraging trips and the length of time spent provisioning cells it is likely the species only completes one cell per day (and supplies at the most two pollen loads per day per cell). The results support Donovan's (1967) observations.

Leioproctus (N.) paahaumaa was the only species observed at location WT and the mean time inside the nest (± SE) was 0:25 ± 0:14 hrs, between foraging trips (± SE) that were 0:23 ± 0:13 hrs in duration. Up to five foraging trips were made per day corresponding to four nest-provisioning sessions. When the nesting behaviour of *L. paahaumaa* is compared to that of *L. boltoni* and *L. imitatus* a significant difference in the length of time each species spends inside the nest between foraging trips is indicated (Student's *t* – test to compare the mean nesting provisioning duration for species at location TP and WT: *df* = 325, *t* = 7.14, *P* [T<=t, two-tail] = 6.04×10^{-12}). Based on the number of foraging trips made per day *L. paahaumaa* could be constructing up to five cells per day but more data on nest architecture would be required to confirm this hypothesis.

4.6 Conclusions

The nesting behaviour of three species of New Zealand native bees, *L. boltoni, L. imitatus* and *L. paahaumaa,* were closely observed at two separate locations (TP and WT). General community nesting behaviours were also recorded. The importance of suitable nesting substrate, a warm and sheltered nesting location and local access to forage is one aspect of native bee ecology highlighted by this study.

Large nest sites found on Mt. Parihaka further support the theory that native bees will form aggregations where the substrate is ideal and the physical aspects of nest sites offer warmth and shelter. Results on nest architecture data for three species of native bees was lacking; only one (probably incomplete) nest was constructed in artificial nest boxes. This belonged to the species *L. paahaumaa*. The nest design showed that the species has adapted to a wet environment by using sink-trap type tunnelling which will prevent water from entering cells. In a second artificial nest box nests belonging to *L. boltoni* and *L. imitatus* were abandoned at around 100 – 150 mm in depth. Artificial nest boxes appeared to restrict nest architecture so much that all nests started were eventually abandoned. The nest architecture of *L. boltoni* was recorded using a similar method and a near complete nest was constructed (Donovan 1967). The results from Donovan's (1967) study showed that *L. boltoni* will modify nest architecture when space is restricted. The results from this study show the species will abandon sites that are not suitable.

Nest densities at different sites varied from 14 - 22 nests per m^2. At premium sites the density of nests appeared to be evenly distributed. This observation supports a theory that females nesting in close proximity to others will modify their nest architecture to avoid collapsing another's nest. This also supports the findings of the modified architecture of *L. boltoni* outlined in Donovan's (1967) study. With this in mind nest architecture is not only unique to a species but it is also highly influenced by physical nesting resources and dimensions.

The length of time spent inside the nest for three species of native bees showed that *L. boltoni* and *L. imitatus* had significantly longer nest provisioning sessions compared to *L. paahaumaa.* The variation indicates differences in nest architecture. Since *L. boltoni* constructs up to one cell per day and makes up to two foraging trips it is hypothesised that *L. paahaumaa* constructs up to five cells per day. More data on the nest architecture of *L paahaumaa* is necessary to confirm this theory.

Chapter Five Foraging Behaviours of Native Bees

Abstract

The floral preferences, foraging duration and foraging range of New Zealand native bees are investigated. Large nest aggregations on Mt. Parihaka (Whangarei) were observed over three active seasons (December 2004 - March 2005, October 2005 - March 2006 and November 2006 - January 2007). Six species of native bees were found on Mt. Parihaka, five from the genus *Leioproctus* and one species from the genus *Lasioglossum.* Collections of native bees were made at nest sites as females returned from foraging trips with pollen loads. Pollen types were identified from loads and percentage pollen composition determined for five species: *Leioproctus (Leioproctus) boltoni* (Cockerell), *L. (L.) huakiwi* (Donovan), *L. (L.) imitatus* (Smith)*, L. (N.) paahaumaa* (Donovan)*, L. (L.) pango* (Donovan) (Hymenoptera: Colletidae). Native bees were also collected from mating swarms and associated plants. Foraging duration data was collected on three species: *L. boltoni, L. imitatus* and *L. paahaumaa*. The three species were observed at two separate locations: at the top of Mt. Parihaka (TP) and at the water reservoir half way up Memorial drive (WT).

For three species pollen composition and plant-associated collections indicate floral preferences vary depending on nest site locations and available resources. Records of host plant families for *L. boltoni* showed the species had broad foraging tendencies and will forage on introduced and native plants (Donovan 2007). This study confirmed existing records (Donovan 2007). Pollen composition analysis showed *L. boltoni* foraged on species in the Myrtaceae and Asteraceae families depending on location. *Leioproctus imitatus* displayed specialist foraging tendencies and showed an overwhelming preference for plants in the Myrtaceae family. Existing records of the foraging preferences of *L. paahaumaa* indicated the species preferred introduced plant species from the Asteraceae, Cucurbitaceae and Nymphaeacae families (Donovan 2007). Plant associated collections and pollen composition analysis showed the species had specialist foraging tendencies; they were collected from only two plant species, oxeye daisy and wild carrot, in two families, Apiaceae and Asteraceae.

Results from plant associated collections and pollen load composition showed *L. boltoni* had broad foraging tendencies visiting plants in the Myrtaceae and Asteraceae families. Preferences were largely site dependent. At site 1A, *L. boltoni* preferred pohutukawa and at site 1D preferred wild carrot. Unlike *L. boltoni*, *L. imitatus* displayed specialist foraging tendencies with an overwhelming preference for native species in the Myrtaceae family. At site 1A *L. imitatus* preferred kanuka and manuka. At site 1D *L. imitatus* preferred pohutukawa. *Leioproctus (N.) paahaumaa* also had specialist foraging tendencies, results showing a preference for introduced species in the Apiaceae (wild carrot) and Asteraceae (oxeye daisy) families.

To estimate foraging range, the floral community structure of two nest sites was used in conjunction with data recorded on the foraging duration and frequency of foraging trips for three species of New Zealand native bees (*L. boltoni, L. imitatus* and *L. paahaumaa*). Floral transects were not used in this study. General floral community structure using visually estimated distances from floral resources to nest sites and records of plant species within an estimated 100 m radius were used. Difficult terrain prevented detailed analysis and the use of standard transect methods. Foraging duration, the time between leaving and returning to a nest site, was collected. Nest sites were observed for 45 hrs in total and 152 complete foraging trips were recorded. In total 351 individual bees were monitored. The results of the study do not support a relationship between the foraging range and foraging duration of native bees. Furthermore no relationship between the body length of insects and the foraging range was established. These results contradict previous studies (Gathmann & Tscharntke 2002).

5.1 Introduction

5.1.1 Flower relationships and foraging habits

Flower preferences of native bees

Most native bees can be grouped according to their foraging habits. They are either generalists gathering food from a wide range of flowers or specialists relying on a single plant species or a closely related group of plants for food (The Xerces Society 2007a). Colletidae is classified into three distinct subfamilies: Colletinae, Hylaeinae and Euryglossinae. The flower relationships for species in subfamily Colletinae show that they will forage on Myrtaceae, Fabaceae or Asteraceae (Donovan 2007). Some species of Colletinae are restricted to a few plants in one family (Donovan 2007) and others have adapted to forage on introduced plants such as kiwifruit (Actinidiaceae) and onions

(Liliaceae). Similarly, species in the subfamily Hylaeinae are known to forage on both native and introduced flowers and in most cases will specialise on a few species. In contrast to some species of Colletidae, which have specialist foraging tendencies, some species of Halictidae appear to be broad generalist foragers (Donovan 2007). Halictidae have a longer nesting period than Colletidae so there is demand for pollen through spring, summer and autumn. Because they have a longer nesting period a wide range of native plant species and up to 80 introduced species may be visited by members of the subfamily Halictidae.

The role of native bees in the pollination systems of New Zealand is largely unexplored. Flower relationships and pollination biology aspects of native bees have not generally been recognised or is only occasionally mentioned in pollination biology research (e.g. Godley (1979), Primack (1978; 1979)). More recently however, native bees have been included in pollination studies (Primack 1983; Webb 1994) and some studies especially, highlight the specialised role of native bees (Godley 1979; Kelly et al. 1996; Kelly 1997). For example, *Hylaeus* (*Prosopisteron*) *agilis*, had been observed prising open the closed buds of *Elytranthe flavida* (Loranthaceae), *Hebe gracillima* (Scrophulariaceae) and *Peraxilla tetrapetala* (Loranthaceae) (Godley 1979; Kelly et al. 1996).

Kelly et al (1996) reported that two species of New Zealand native bees have been observed opening *P. tetrapetala* flowers: *H.* (*P.*) *agilis* and *Leioproctus (L.) tarangahape* (Figure 5.37). Kelly et al (1996) also explains that since there are now few native birds that can open the flowers native bees play an important role in pollinating the endangered mistletoe.

Figure 5.37 Small New Zealand native bees opening *P. tetrapetala* flowers; A, *Hylaeus* (*P.*) *agilis* and; B, *Leioproctus (L.) tarangahape* (Kelly 2004)

Methods used to assess the foraging range of native bees

The foraging range of pollinating insects is critical for many studies including: biodiversity conservation, ecological restoration, biosecurity protection, biosafety, sustainable agriculture and horticulture (Newstrom & Roberston 2005). An example of the importance of determining the foraging range of pollinating insects is assessing the distance insect pollinators might carry genetically altered material. In this study however, understanding the foraging range of New Zealand native bees is viewed as a crucial step towards developing conservation management strategies of pollinator communities. International studies have shown that in order to ensure the long-term sustainability of solitary bees, all the requirements for sustaining viable populations must be within the insects' home range (Gathmann & Tscharntke 2002).

Difficulties arise when trying to quantify the foraging range of native bees and the floral requirements required to sustain a population. Insect movement is a fundamentally important subject, but techniques used to determine absolute ranges are often fraught with practical complications. Most techniques used to gather this information rely on indirect analysis of floral community structure or translocation of insects using mark-release-recapture methods. While the home range of other animals can be easily monitored using radio tracking methods, native bees and smaller insects cannot carry radio tags because they are too heavy (Pride & Swift 1992). To date, tracking insects using the harmonic scanning radar, which has a very light weight tag antenna, is the only viable direct method. This technology is costly however. It is also in early development stages, especially for small insect applications and its suitability for tracking New Zealand's native bees is questionable (see Chapter Three: Load-lifting Capacity of Native Bees).

Can body length be reliably used to predict foraging range?

Translocation methods have traditionally been used to estimate the foraging range of bees. Some authors have suggested the best predictor of foraging range of solitary bees is their body length (Gathmann & Tscharntke 2002). In the absence of suitable practical methods to track the foraging range of native bees, body length data could provide a broad estimation of home range. Based on body length, and the linear regression model (where: $y = -232.28 + 54.69x$, $F = 10.13$, $r^2 = 47$ %, $n = 21$, $P < 0.001$) suggested by Gathmann & Tscharntke (2002) the home range of the species of New Zealand native bees examined in this study could range from 150 – 479 m . Body length is not generally accepted as a robust predictor of foraging range (pers com, Donovan, Newstrom). The true efficacy of this method is yet to be determined.

5.2 Study aims

This largely explorative community investigation of New Zealand native bees in Whangarei aims to promote an understanding of their foraging behaviours. There are two areas considered in this study outlined as follows:

A. To determine the foraging range of a species of native bee by*:*
    - Evaluating the distance travelled from the nest site while foraging using body length relationships and floral preferences as indirect indicators of a 'home range'.
    - Evaluating the time taken to return to the nest site after leaving to forage

B. To determine nest provisioning behaviours of a species of native bee by:
    - Determining frequency of visitation to nest.
    - Determining the time spent outside of the nest foraging.

For each species observed or collected the study aims to answer the following questions:

1. What is the distance travelled from nest to food in a typical foraging trip?
2. How long does a typical foraging trip take?
3. What food sources do the species prefer?

5.3 Methods

5.3.1 Nest site locations and descriptions

Bees used in the study were collected or observed over two seasons (December 2004 – March 2005 and October 2005 – February 2006) from several nest sites on Mt. Parihaka. Locations, specific nest sites and descriptions are listed in Table 5.22. The first communities were found at the gated entrance of the pine forest, to the left of Parihaka Memorial car park at the top of Mt. Parihaka, nominated as location TP. Location TP includes nest sites 1, 2 and 3. Another community was found approximately 6 km from the first, at the gated entry to the water reservoir half way up Memorial Drive and is nominated as location WR. Location WR includes site 4A and 4B.

Table 5.22 Locations on Mt. Parihaka that were the focus for repeat collections and foraging duration observations of New Zealand native bees. Specific site descriptions, locations, latitude & longitude and general ecology of areas where bees were observed or collected over two seasons (2004 – 2005 & 2005 – 2006).

Location	Nest site & code	Location	General Ecology
Top of Mt. Parihaka (TP) Mt. Parihaka, Riverside. Whangarei. Main entrance at the very end of memorial drive. Car park leading to walking access war memorial on the right hand side and gated forestry area (restricted access) on the left hand side.	**Site 1A**: By gate, at the entry to forestry area. First bank on right-hand side.	**S** 35^{O} 42' 43.04 " **E** 174^{O} 20' 18.62" **HAE** 261 m	Pine forest plantation. First generation regenerative forest. Some gorse (*Ulex europaeus*), pampas (*Cortaderia spp*.) and cutty grass.
	Site 1D: Second bank under transmission tower.	**S** 35^{O} 42' 42.97" **E** 174^{O} 20' 20.18" **HAE** 260 m	
	Site 2A: Down from gate entry. Third major bank in forestry area, on the right hand side.	**S** 32^{O} 46' 43.03" **E** 174^{O} 20' 22.01" **HAE** 258 m	
	Site 3A: Down from gate. Small bank on left hand side in the forestry area	**S** 32^{O} 46' 43.03" **E** 180^{O} 20' 21.01" **HAE** 242 m	
Water reservoir (WR) Mt. Parihaka, Riverside. Whangarei. Before memorial car park, half way up memorial drive. On the right hand side gated entrance into water tower reservoir area	**Site 4A**: Water tower entrance, over mound on the left hand side	**S** 35^{O} 43' 01.96" **E** 174^{O} 20' 37.34" **HAE** 192 m	Pine forest plantation. First generation regenerative forest. But mainly gorse, pampas and cutty grass in the immediate vicinity of nest site. Some cleared areas.

5.3.2 Floral preferences and pollen identification

Specimens collected for pollen and body mass investigations (Chapter Three: Load-lifting Capacity of Native Bees) were frozen and used for pollen identification. Some specimens were collected at nest sites and others while foraging. The collection was complete at the end of three seasons and the insects were then prepared for pollen analysis. The body parts of the insects were soaked in 200 mℓ of Carberla's staining solution for half an hour. Exactly 0.015 mℓ of the solution was removed and placed on a microscope slide. An 18 mm^2 cover slip was placed on top of the sample, which was immediately examined. Each sample was scanned and photographed so representative pollen images could be collated

for professional identification (Anderson pers. comm.). Photos were also compared to published records (Cranwell 1953; Moar 1993). Pollen types and frequency counts were made using a combination of 40X and 100X objectives (depending on the size of pollen grains). Slides were placed in identical positions and starting at one corner systematically scanned across all fields (Moar 1985).

Pollen was collected from all flowering plants accessible within the study area. Difficult terrain prevented the use of standard transect methods (Beattie 1971). Pollens from plants were processed in the field using standard methods with small cubes of fuschin-stained jelly> These were then fixed on slides and stored in a fridge for later analysis (Erdtman 1943; Beattie 1971; Parrish 2004). Plant vouchers were collected and stored. Each pollen sample collected from plants was photographed so representative images could be collated for professional identification. Photos were also used for comparison with published records and pollen samples from bees (Moar 1993).

5.3.3 Duration and frequency of foraging trips

An 0.8 m^2 fold-up flexible grid was designed and constructed to place over nest areas. The grid was suitable for monitoring vertical and horizontal sites (Figure 5.38 below) and was also used for estimating nest density. Sectioned into individual grids of 0.1 m^2, a total of 64 separate areas could be checked for activity. The grid position was marked so that it could be easily placed over the same site for repeat monitoring. Once positioned, data was collected on the entry and exit times of bees within the grid area as follows: As a bee entered a nest, 1) the nest was identified with numbered tag, 2) the entry time recorded, 3) a stiff cone-shaped net was placed over the entrance of the nest until the bee was ready to exit the nest, 4) the net was removed and the exit time recorded (see Figure 5.38). Three separate nest sites were investigated over two seasons, sites 1, 2 and 4 (2004-2005 and 2005-2006). Observations were conducted on sunny days, between the hours of 10:00 – 16:00, over the main foraging season December through to February.

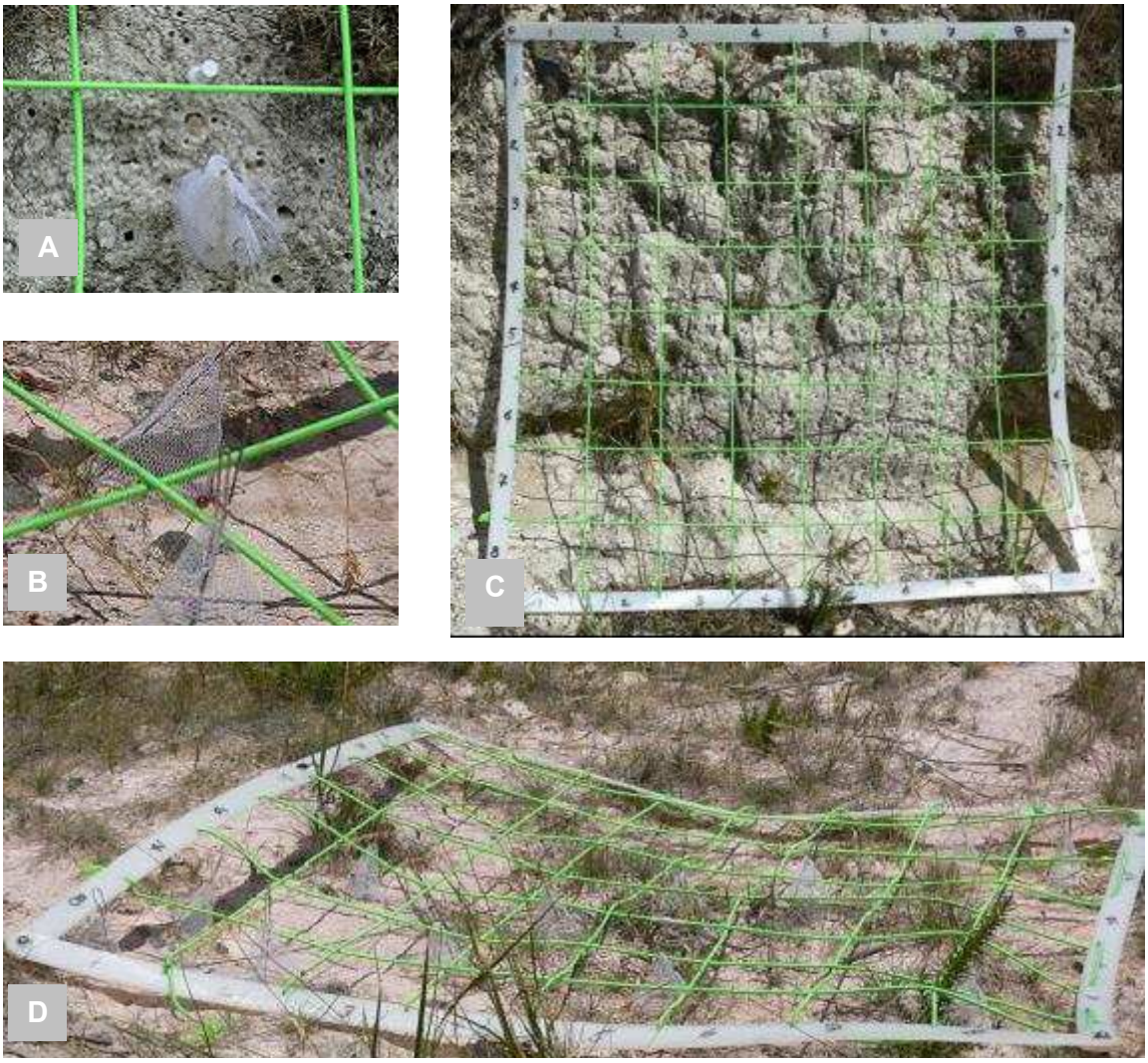

Figure 5.38 Foraging and nesting provisioning duration monitoring equipment. A, Shows a close up of a vertical nest with stiff cone net placed over the entry of a nest. B, Two cones on a horizontal nest. C, The flexible grid attached to the wall of a vertical nest (site 1) and D, on a horizontal nest (site 4).

5.3.4 Statistics

Statistical analyses were performed using Microsoft Excel 2000 Statistical Toolbox. For those data compared using ANOVA, Gabriel comparison interval is plotted with mean (not SE) (Mcardle 1987; Sokal & Rohlf 1995). For all other data, the arithmetic means are given ± standard errors (SE).

5.4 Results

5.4.1 Floral preferences

Native bee collections and associated plants

The majority of insects were collected from nest sites (55%), followed by insects foraging on native plants (21%) and mating swarms (20%). Only 4% of all insects collected were caught on introduced flora. Native plants associated with collections included: kamahi (*Weinmannia racemosa*: Cunoniaceae), kanuka, manuka and pohutukawa (*Kunzea ericoides, Leptospermum scoparium, Metrosideros excelsa*: Myrtaceae). Mating swarms formed around a variety of shrubs including small manuka, kanuka, kamahi, pine (*Pinus radiata*: Pinaceae) and gorse (*Ulex europaeus*: Fabaceae). Native bees were collected from a number of introduced plants including: wild carrot (*Daucus carota*: Apiaceae), oxeye daisy and dandelion (*Leucanthemum vulgare, Taraxacum sp.*: Asteraceae), grapefruit and mandarin (*Citrus grandis reticulata, citrus reticulata:* Rutaceae).

Table 5.23 below lists the plants male and female insects were captured on. *Lasioglossum cognatum, Lasioglossum sordidum* and *Hylaeus relegatus* were collected in very low numbers (12 in total) but nearly all were foraging on introduced plants. Similarly male and female *L. paahaumaa* were found foraging on exotic plants, representing 47 % of all insects that were collected foraging on introduced plants. A total of 145 individuals of *L. huakiwi* were caught, but no females were collected while foraging. Male *L. huakiwi* were collected from native flora only (6 individuals). Female *L. boltoni, L. imitatus* and *L. pango* were collected from native and exotic plant species. Male *L. imitatus* and *L. pango* were collected from native plants with a single male *L. boltoni* collected from an oxeye daisy.

Table 5.23 Male and female collections from native plants: kanuka, manuka, pohutukawa (Myrtaceae), kamahi (Cunoniaceae) and introduced plants: citrus (Rutaceae), dandelion and oxeye daisy (Asteraceae), wild carrot (Apiaceae), rose (Rosaceae) and pine (Pinaceae). Total collections for each plant family are given at the bottom of the table. Mating swarms collections from shrubs and collections at nest sites excluded.

Species	Native Plants				Introduced Plants					
	Kanuka	Manuka	Pohutukawa	Kamahi	Citrus	Dandelion	Oxeye daisy	Wild carrot	Rose	Pine
Male										
Leioproctus boltoni	13	21	12	1			1			
L. huakiwi	1	3	2							
L. imitatus	11	25								
L. paahaumaa							5			
L. pango	10		27							
Lasioglossum cognatum										
Lasioglossum sordidum										
Hylaeus relegatus										
Female										
Leioproctus boltoni	2	1			1		1	1		1
L. huakiwi										
L. imitatus	26	4				1	2			
L. paahaumaa							7	3		
L. pango	1		2		1					
Lasioglossum cognatum										
Lasioglossum sordidum					4		2	2		
Hylaeus relegatus									1	
Total collections for each plant family	**Myrtaceae**			**Cunoniaceae**	**Rutaceae**	**Asteraceae**		**Apiaceae**	**Rosaceae**	**Pinaceae**
All native bee species in study	64	54	43	1	6	1	18	6	1	1

Pollen identification

On Mt. Parihaka, pollen samples were collected from six species of native bees including: *L. boltoni, L. huakiwi, L. imitatus, L. paahaumaa* and *L. pango.* Collections were made from two sites, 1 and 4. In total, 61 bees were collected for pollen analysis. Thirty one of these were directly caught foraging on manuka and kanuka and 30 were collected from nest sites as they returned from a foraging trip.

Seven different types of pollen were identified and are shown in Figure 5.39 below. Native bees were observed visiting all except two plant species identified in the pollen analysis. The two plant species that bees were not observed visiting were harakeke (*Phormium tenax*: Agavaceae) and koromiko (*Hebe*: Scrophulariaceae). Harakeke and koromiko were not seen in the study area. Pollen from three native plants, kanuka, manuka and pohutukawa, and two introduced plants, wild carrot and oxeye daisy were associated with native bee collections. These plants were prominent species in the study area.

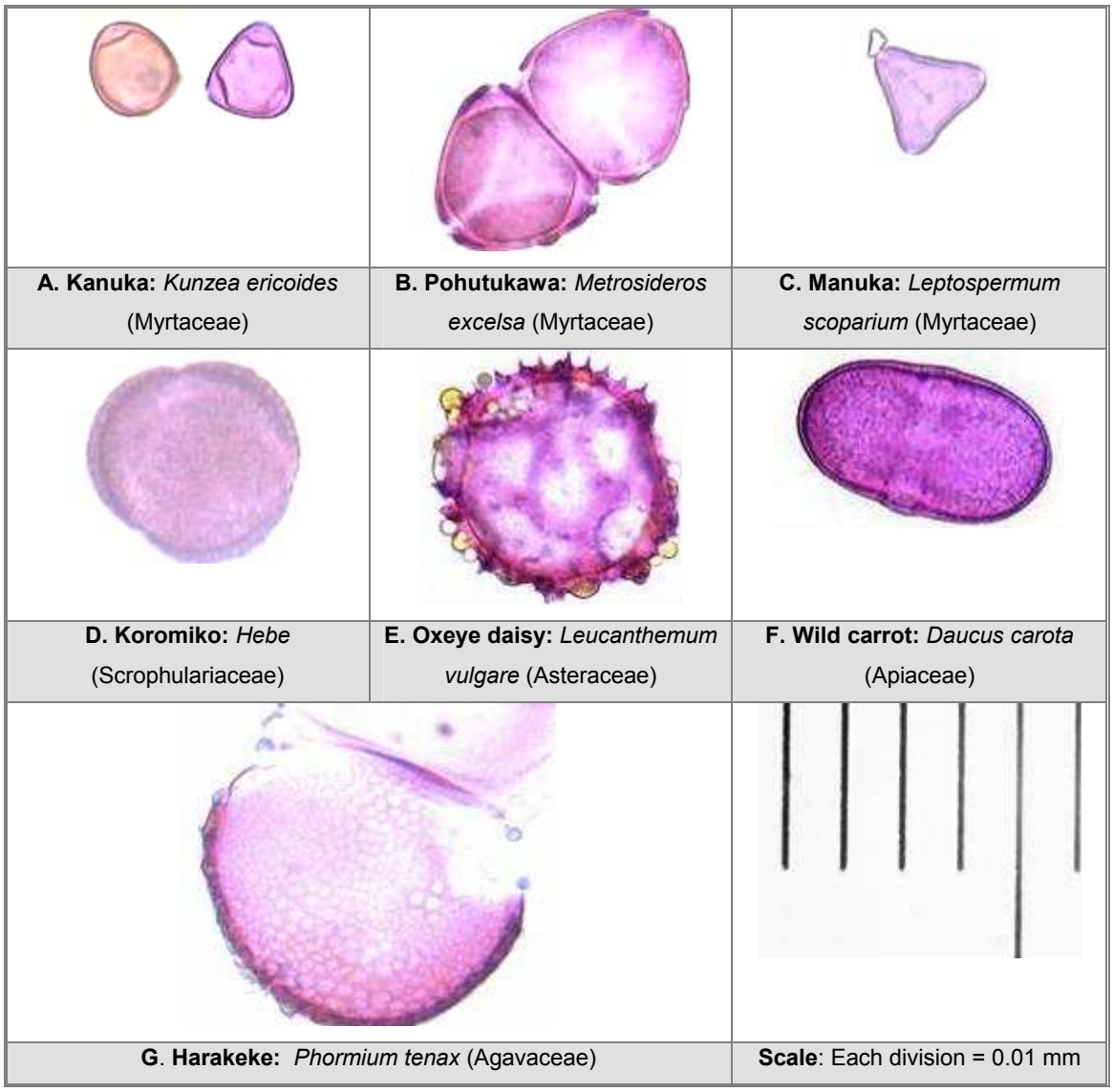

Figure 5.39 Seven distinct types of pollen were observed; pollen grains were photographed and used for identification (Moar 1993). Scale (each division = 0.01 mm) provides size reference pollens.

5.4.2 Pollen composition and frequency counts

Thirty one insects were collected from nest site 1A while they foraged on kanuka. They carried predominantly kanuka pollen. *Leioproctus boltoni* (1♀), *L. huakiwi* (1♂), *L. imitatus* (7♂, 20♀) and *L. pango* (2♂) carried 98% kanuka pollen or greater. A further 21 individuals carried only kanuka pollen (100%). Thirty female insects collected from various nest sites including: 1A, 1D and 4A, carried a range of pollens. Figure 5.40 below describes the pollen composition for *L. boltoni* (*n* = 6), *L. paahaumaa* (*n* = 7) and *L. imitatus* (*n* = 16).

Leioproctus boltoni showed a preference for pohutukawa at site 1A and wild carrot at site 1D. *L. paahaumaa* preferred oxeye daisy at site 4A. *Leioproctus imitatus* carried mainly kanuka and manuka at site 1A and pohutukawa at site 1D. One female *L. pango* was caught at nest site 1A and had a pollen composition of 73% harakeke, 19% wild carrot, and 8% kanuka.

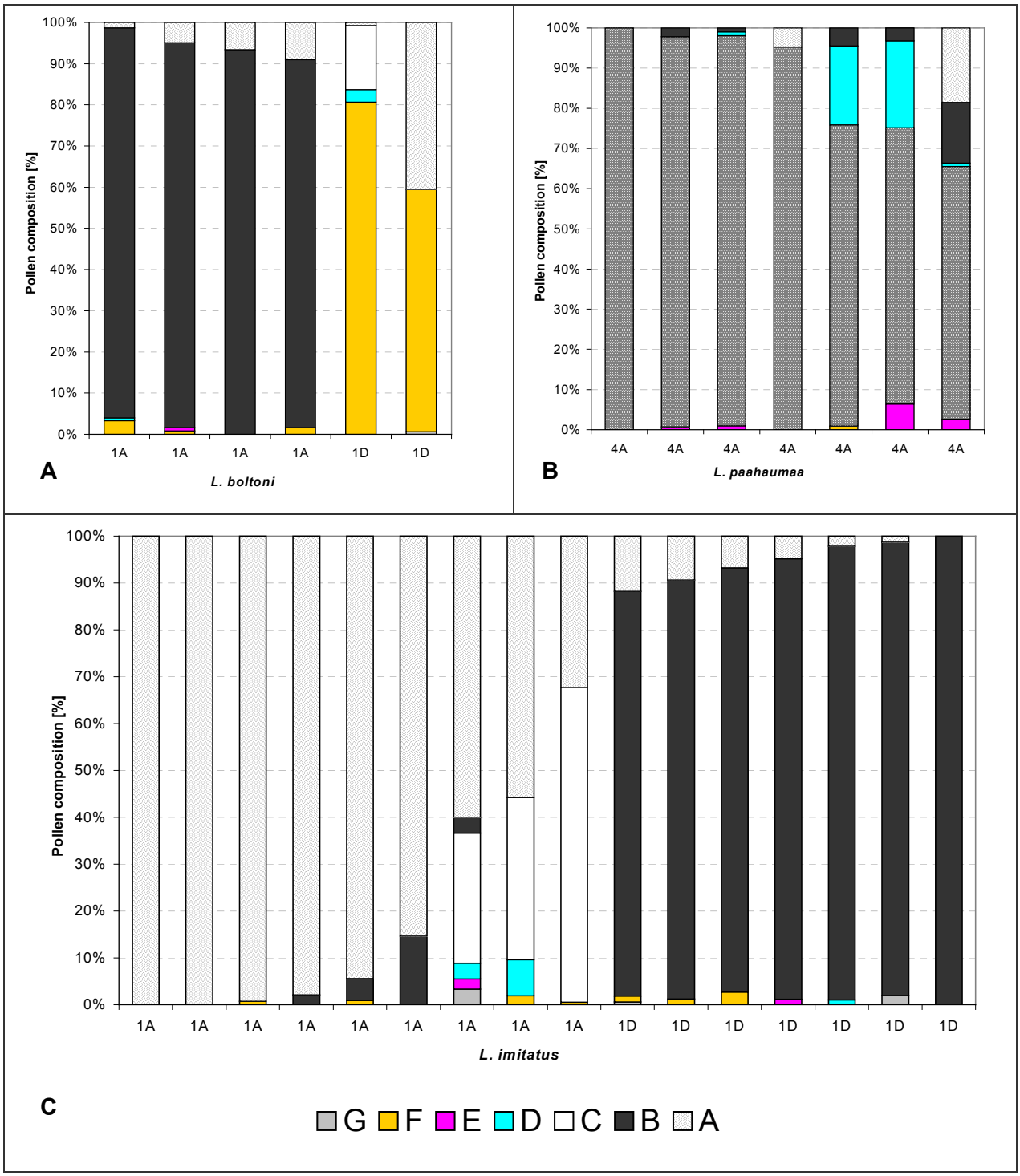

Figure 5.40 Analysis (% occurrence) of pollen type distribution from female insects collected at nest sites; A, *L. boltoni* [*n* = 6] site 1. B, *L. paahaumaa* [*n* = 7] site 4, and C, *L. imitatus* [*n* = 16] site 1. (Pollen Types: A = Kanuka, B = Pohutukawa, C = Manuka, D = Koromiko, E = Oxeye daisy, F = Wild carrot, G = Harakeke)

Pollen frequency counts and range

The mean pollen frequency counts as a percentage total (± SE) for three species of native bees is shown in Figure 5.41.

Predominant pollen counts are those greater than 45%, secondary pollen ranges from 16 - 44%, important minor pollen from 3 -15%, and minor pollen is less than 3% (Moar 1985). Predominant pollens carried by *L. boltoni* (*n* = 6) were pohutukawa (93 ± 1%) wild carrot and manuka (29 ± 1%, 6 ± 0%). Secondary pollen carried by *L. boltoni* was kanuka (11 ± 6%) and important minor pollens were koromiko and oxeye daisy. Minor pollen carried by carried by *L. boltoni* was harakeke (< 3%)

Pohutukawa, kanuka, and wild carrot (62 ± 13%, 51 ± 11%, 43 ± 12%) were predominant pollens carried by *L. imitatus* (*n* = 16). Hebe (4 ± 2%) was an important minor pollen carried by *L. imitatus* and harakeke. Oxeye daisy and wild carrot (< 3%) were minor pollens carried by the species.

The oxeye daisy (85 ± 6%) was the predominant pollen carried by *L. paahaumaa* (*n* = 7). Kanuka, koromiko and pohutukawa (12 ± 7%, 11 ± 6%, 5 ± 3%) were important minor pollens carried by *L. paahaumaa.* Harakeke and wild carrot (< 3%) were minor pollens carried by the same species.

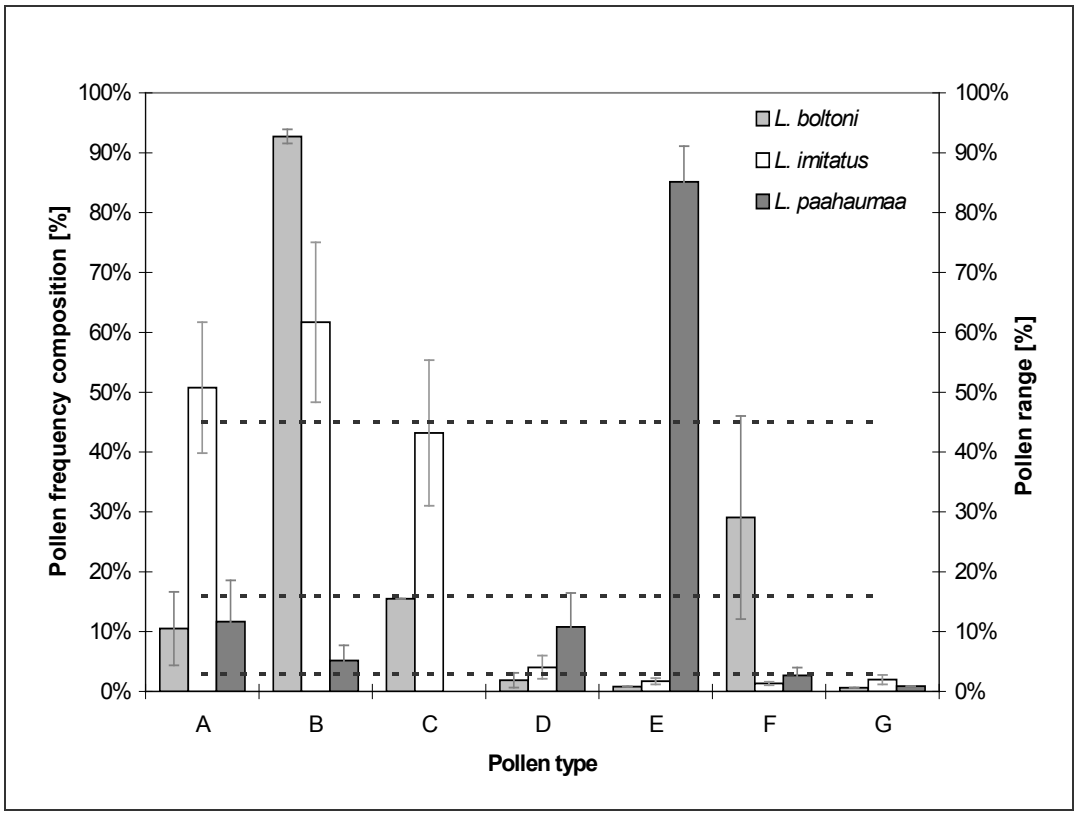

Figure 5.41 Mean pollen frequency count ± SE for three species collected at nest sites: *L. boltoni* (light grey, *n* = 6) site 1, *L. imitatus* (white, *n* = *16*) site 1 and *L. paahaumaa* (dark grey, *n* = 7) site 4. Dotted grey lines indicate the boundary for predominant, secondary and important minor pollen where: predominant pollen is > 45%, secondary pollen is 16- 44%, important minor pollen is 3-15%, and minor pollen is < 3%. (Pollen Types: A = Kanuka, B = Pohutukawa, C = Manuka, D = Koromiko, E = Oxeye daisy, F = Wild carrot, G = Harakeke).

5.4.3 Discussion of bee species and host plants

For three species, pollen composition and plant-associated collections indicate floral preferences vary depending on nest site locations and available resources. Records for host plants of *L. boltoni* indicates the species prefers plants in the Myrtaceae and Actinidiaceae families; of the 256 pollen carrying females collected from plants 44% were associated with Myrtaceae and 48% with Actinidiaceae (Donovan 2007). Only seven female *L. boltoni* were collected from plant species around the Whangarei area; five families are represented in the collections including: Myrtaceae, Rutaceae Asteraceae, Apiaceae and Pinaceae. Pollen composition analysis showed *L. boltoni* prefers Myrtaceae and Asteraceae depending on location. For *L. imitatus*, records show the species prefers plants in the Myrtaceae family; of the 457 pollen carrying females collected from plants, 97% were associated with Myrtaceae (Donovan 2007). In this study, *L. imitatus* also

showed an overall preference for Myrtaceae although they were also collected from plant species in the Asteraceae family. Records for *L. paahaumaa* indicate a strong preference for introduced plants from the Asteraceae, Cucurbitaceae, and Nymphaeacae families; of the 24 pollen carrying females collected from plants, 95% were associated with plant species in these families. *Leioproctus. N. paahaumaa* shows a similar preference in this study; collections were associated with plants in the Apiaceae and Asteraceae families and pollen composition confirms this trend.

5.4.4 Duration and frequency of foraging trips

Table 5.24 below details the results of the foraging duration from three nest aggregations (1A, 3A and 4A) at locations TP and WR. Native bees were monitored at these locations. Foraging duration time, frequency of foraging trips and nest provisioning duration data was collected.

Table 5.24 Foraging trip data for New Zealand native bees observed at three sites (1, 3 & 4) on Mt. Parihaka, Whangarei.

Location, nest site and species	**Location A, site 4** **Species: *L. paahaumaa***	**Location B, site 1&3** **Species: *L. imitatus or boltoni***
Observation dates	17/01/2005 - 21/01/2005 10/01/2006 - 21/01/2006	11/01/2005 - 14/01/2005 14/11/2005 - 18/12/2005
Complete foraging trips	145	7
Individual bees observed	220	131
Total monitoring hours	24:00	21:00
Mean foraging time ± SE (hrs)	0:23 ± 0:13	2:06 ± 0:13
Range (max, min) - foraging time (hrs)	0:01 - 1:26 hrs	0:46 - 4:28

The predominant species collected from location WR (site 4A) was *L. paahaumaa* (80%) and *L. boltoni* (20%). A smaller species of native bee, *Lasioglossum sp.* was also observed nesting at this site but was not collected. *Leioproctus. N. paahaumaa*, which is a robust hairy bee, is easily distinguishable from *Lasioglossum sp*. and *L. boltoni sp.* on the wing. It is therefore likely that all foraging duration data collected from this site was that of *L. paahaumaa.* At location WR the species *L. paahaumaa* was observed for 24 hrs. In total 220 individual female bees were watched as they completed 145 foraging trips. A

mean foraging time (±SE) of 0:23 ± 0:13 hrs for female *L. paahaumaa* was recorded. This corresponds to time inside the nest between foraging trips (± SE) of 0:25 ± 0:14 hrs. Foraging duration ranged from a minimum of 0:01 hrs to a maximum of 1:26 hrs and nesting provisioning sessions between foraging trips ranged in time from 0:01- 1:42 hrs for *L. paahaumaa*.

The predominant species at location TP (sites 1A and 3A) was *L. boltoni* (48%) and *L. imitatus* (44%). Determining the differences between species while in mid flight was difficult because both species have similar physical characteristics. Foraging duration data collected from TP probably includes females from *L. boltoni* and *L. imitatus.* In total 7 complete foraging trips were recorded from TP. One hundred and thirty one female bees were observed over a period of 21 hrs. A mean foraging trip duration (± SE) of 2.06 ± 0:13 hours was recorded for the species at these sites (*L. imitatus* and *L. boltoni*) with a corresponding time in the nest (± SE) of 1:06 ± 0:42 hrs. Foraging duration ranged from a minimum of 0:46 hrs to a maximum of 4:28 hrs and nesting provisioning between foraging trips ranged from 0:02 - 3:46 hrs for *L. imitatus* and *L. boltoni.*

Figure 5.42 below shows the Gabriel comparison intervals of mean nest provisioning and foraging duration time for three species of New Zealand native bees at two physically separated locations. There is a highly significant difference in mean nesting provisioning and foraging duration times (ANOVA: $df = 3$, $n = 478$, $F = 5.98$, $P = 5.27 \times 10^{-31}$). For the species *L. paahaumaa* observed at location WR, mean nest provision and foraging duration times were not significantly different (Student's t – test: $df = 443$, $t = 1.33$, P [T<=t, two-tail] = 0.184). Similarly, mean nest provision and foraging duration times were not significantly different for those species *L. imitatus* and *L. boltoni* observed at location TP (Student's t – test: $df = 8$, $t = 2.14$, P [T<=t, two-tail] = 0.065).

In contrast, Student's t – test to compare the mean foraging duration time for species observed at location WR and TP show there is a very strong significant difference between *L. paahaumaa* observed at location WR and *L. imitatus* and *L. boltoni* observed at location TP ($df = 150$, $t = 11.23$, P [T<=t, two-tail] = 1.131×10^{-21}). Student's t – test to compare the mean nesting provisioning duration time for species observed at the two locations show there is a very strong significant difference between *L. paahaumaa* and *L. imitatus / L. boltoni* ($df = 325$, $t = 7.14$, P [T<=t, two-tail] = 6.04×10^{-12}).

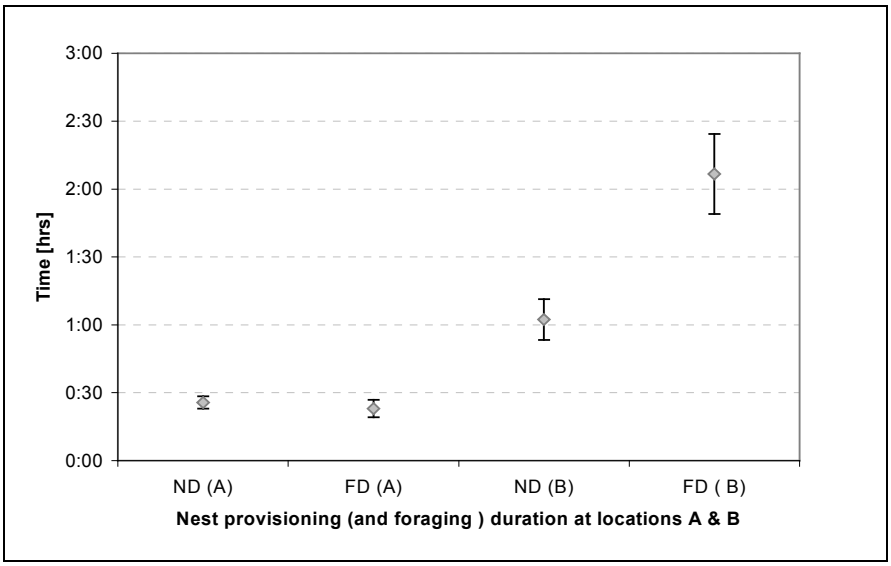

Figure 5.42 Gabriel's comparison intervals of mean nest provisioning duration (ND), foraging duration (FD) for species at two locations: A, site 4 (ND, *n* = 300 and FD, *n* = 145) and B, sites 1 & 3 (ND, *n* =27 and FD, *n* = 7). Distinct species of New Zealand native bees were active at the locations. *Leioproctus (N.) paahaumaa* was the primary species at location WR; *L. imitatus* and *L. boltoni* at location TP. Black vertical bars show the GI and not SE. Intervals that do not overlap are significantly different to each other.

Foraging duration versus body length and flight muscle mass

Mean foraging and nest provisioning duration data collected from the two locations was compared to mean body length for three species of New Zealand native bees (Figure 5.43). Mean body length ± (SE) for *L. paahaumaa* was 10.9 ± 0.71 mm (*n* = 20). This species also had the shortest mean foraging and nesting provisioning duration times ± (SE) of 0:23 ± 0:13hr (*n* = 145) and 0.25 ± 0:13 hr (*n* = 300). Mean body length ± (SE) for *L. boltoni* and *L. imitatus* was 10.9 ± 0.71 mm (*n* =20). Both species also had the longest mean foraging and nesting provisioning duration times ± (SE) of 2:06 ± 0:13 hr (*n* = 145) and 1:02 ± 0:13 hr (*n* = 300). Mean foraging and nest provisioning duration data collected from the two locations is compared to mean flight muscle mass for three species of New Zealand native bees (Figure 5.43).

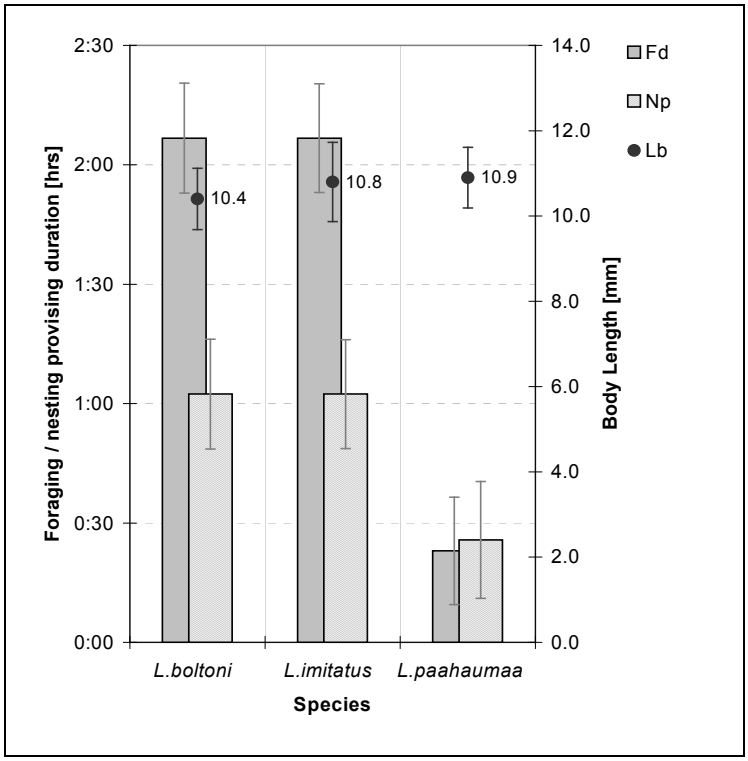

Figure 5.43 Mean foraging (Fd, dark grey) and nest provisioning session duration (Np, light grey) ± SE for three species of New Zealand native bees: *L. boltoni* and *L. imitatus* (foraging duration *n* = 7, nest provisioning sessions *n* = 131); and *L. paahaumaa* (foraging duration *n* = 145, nest provisioning sessions *n* = 300). Compared to mean body length (Lb, ●) ± SE (mm) where *n* = 20 for each species (Donovan 2007).

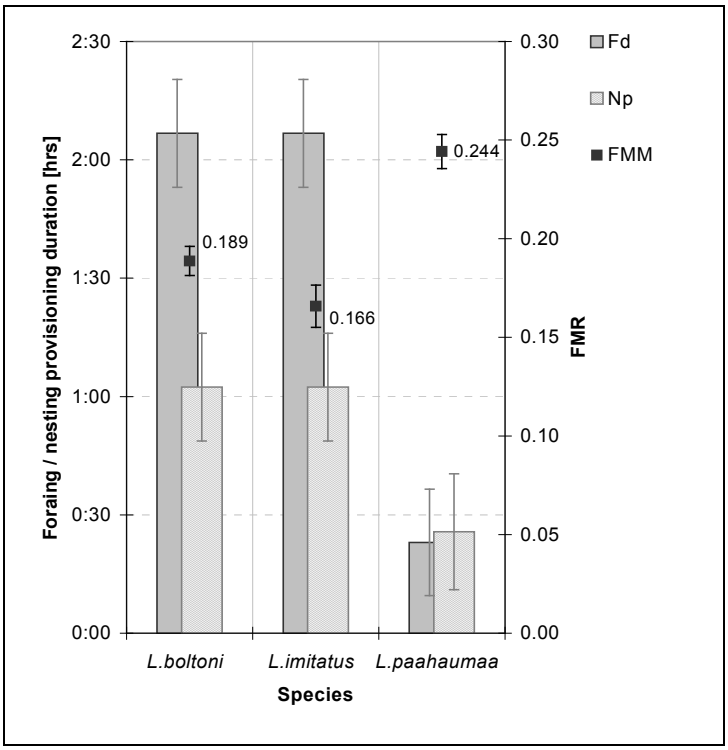

Figure 5.44 Mean foraging (Fd, dark grey) and nest provisioning (Np, light grey) session duration ± SE for three species of New Zealand native bees: *L. boltoni* and *L. imitatus* (foraging duration *n* = 7, nest provisioning sessions *n* = 131); and *L. paahaumaa* (foraging duration *n* = 145, nest provisioning sessions *n* = 300). Compared to mean flight muscle mass (FMM, ■) ± SE for each species, *L. boltoni* (*n* = 16), *L. imitatus* (*n* = 42) and *L. paahaumaa* (*n* = 7)

Figure 5.45 - A below tests the correlation of foraging duration with body length and Figure 5.45 – B tests correlation of foraging duration with flight muscle mass. Results show no correlation of foraging duration with body metrics.

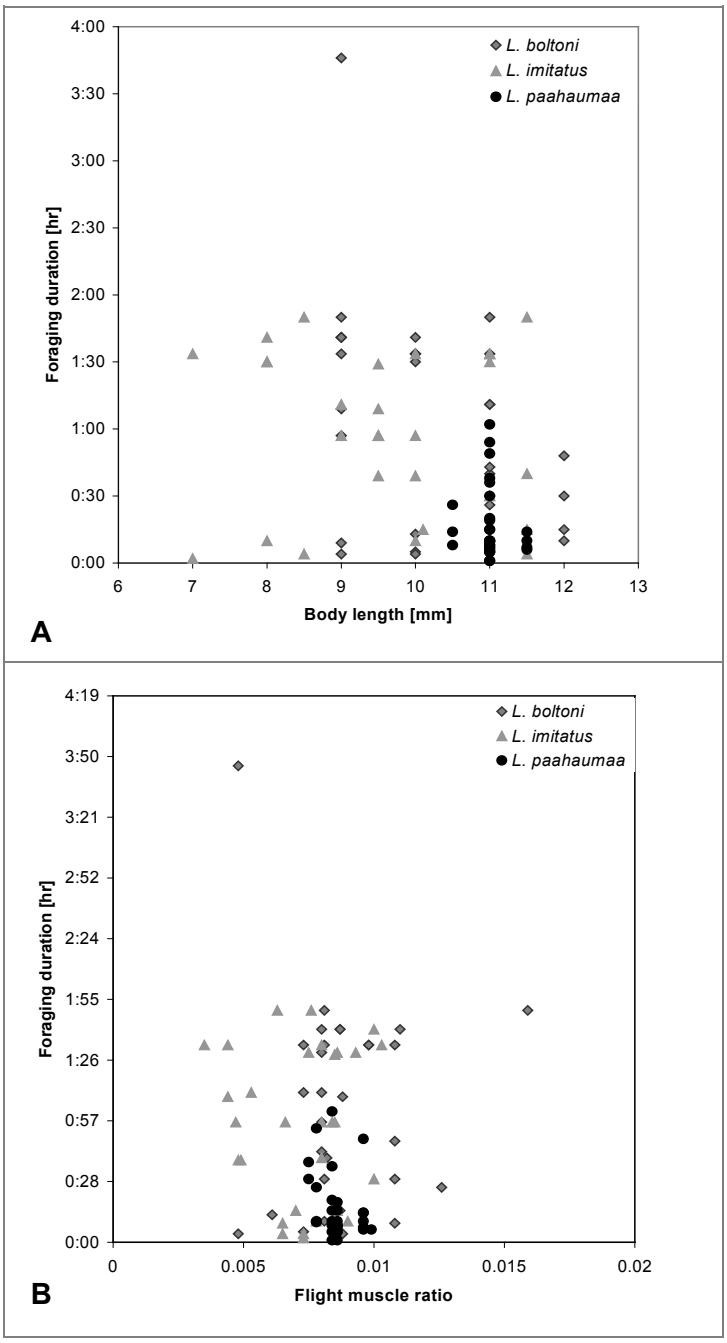

Figure 5.45 Foraging duration (hrs) versus A, body length (mm) and B, Flight muscle mass for three species of New Zealand native bees (n = 30 random samples of body length, flight muscle mass and foraging duration for each species). Foraging duration (hrs) is not highly correlated with body length (mm) or flight muscle mass.

5.5 Discussion

5.5.1 Site description, floral preferences and foraging duration

Pollen analysis of bees collected from nest sites on Mt. Parihaka indicates foraging preferences for some species is highly site dependent. *Leioproctus boltoni* showed a preference for pohutukawa at site 1A and wild carrot at site 1D; *L. imitatus* showed a preference for kanuka and manuka at site 1A and pohutukawa at site 1D. This suggests niche partitioning is influencing native bees foraging behaviours at different locations although further research is necessary to support this hypothesis.

Six species of native bees were found on Mt. Parihaka, five from the genus *Leioproctus* and one species from the genus *Lasioglossum.* A single flowering kanuka at site 1 provided forage for hundreds and thousands of native bees nesting meters from the tree (Figure 4.46 - A). In all three seasons, the tree was enveloped with working bees from most species; in numbers so numerous they created an audible hum. Since the abundance and diversity of native bees is proven to be highly influenced by the abundance and diversity of forage rewards (Potts 2005) this observation raises the question: Could an increase in floral abundance and diversity improve pollinator community structure of New Zealand native bees at certain locations on Mt. Parihaka? Furthermore, foraging duration for *L. boltoni* and *L. imitatus* show some females were foraging for up to 4:28 hrs. This is a comparatively lengthy foraging time. Observations of the behaviour of *L. boltoni* and *L. imitatus* nesting at site 1A indicate many hundreds of bees foraged on the single kanuka tree at the gate entry to Parihaka forest. Although some individuals could have travelled further to forage it was assumed most only travelled 1 – 10 m from their nest site to the single kanuka tree.

The introduced oxeye daisy was found in most areas on Mt. Parihaka. Oxeyes were observed within 2 m of nest aggregations at site 4 (Figure 4.46 - B). Only male *L. paahaumaa* were collected foraging on oxeye daisy at site 4. No female bees from the species were seen on the plant or in flight from their nests to the plant, despite careful repeated attempts to follow the female bees to their forage. Female bees were observed on the wing as they flew east from their sites, over a sheer drop that was covered in gorse, pampas (*Cortaderia spp*.) and cutty grass. It is possible that oxeye daisies were also in this area (underneath gorse, pampas and cutty grass) but confirmation proved too difficult. Foraging duration data for *L. paahaumaa* at site 4 showed that some females forage for up to 1:26 hrs. When compared to the foraging times for *L. boltoni* and *L.*

imitatus, even though *L. paahaumaa* probably travelled further the species had a shorter foraging duration.

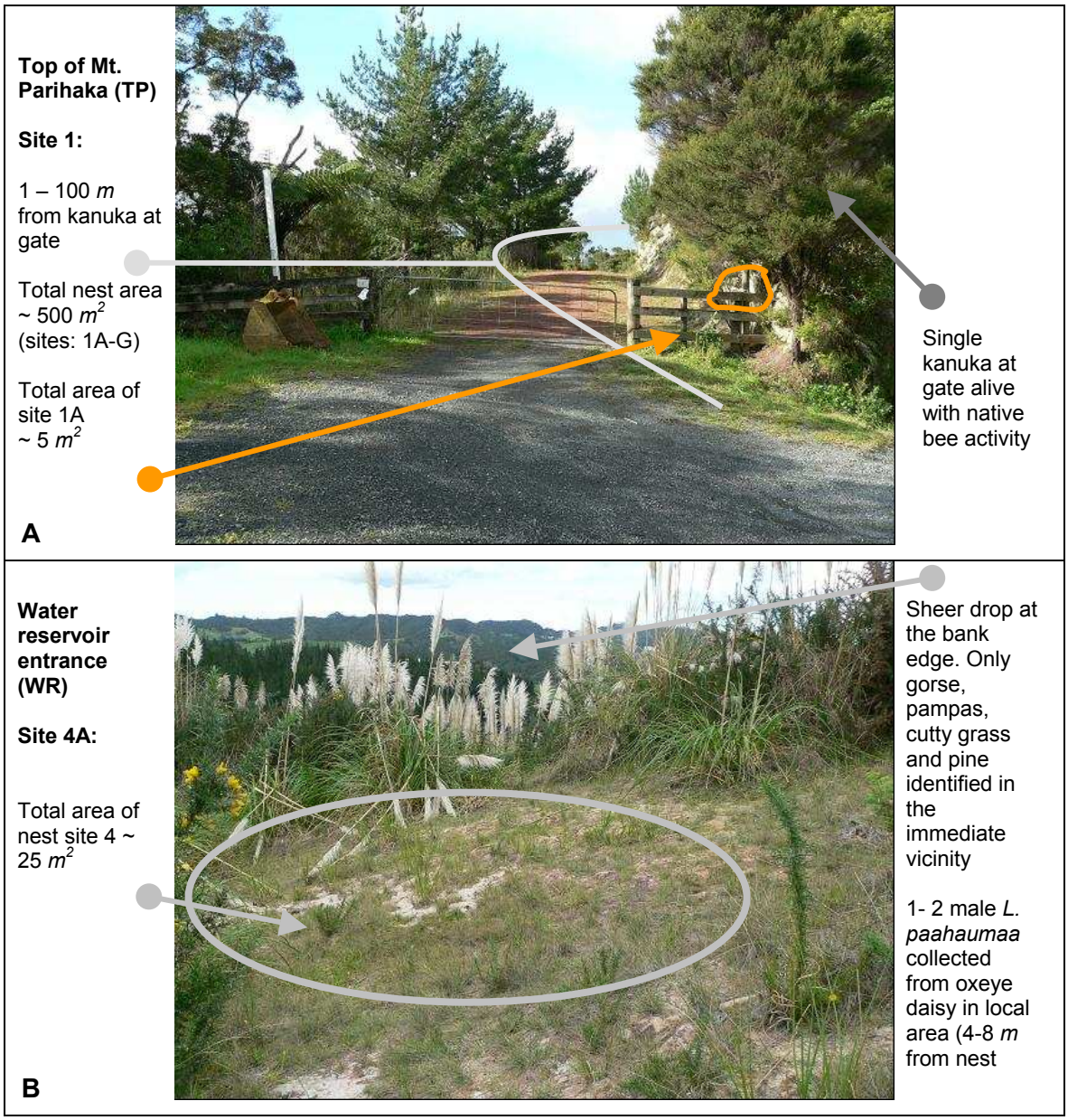

Figure 5.46 Two locations (TP, WR) showing sites of nest aggregations; A, Site 1 at the top of Mt. Parihaka where a large communities of New Zealand native bees were observed (nest sites 1A – G, site 2A, site 3A) and; B, Site 4 at the water reservoir entrance on Mt. Parihaka where two smaller aggregations (nest sites 4A / 4B) were observed.

5.5.2 Foraging duration, foraging range and body metrics

It is difficult to draw robust conclusions about the relationship between foraging duration and the distance New Zealand native bees fly to access floral resources. The terrain on Mt. Parihaka prevented the use of transects to describe the exact distance from nest sites to floral resources. This method is commonly used to asses community floral structure (Paini 2004a). Records of observations of food sources at two locations on Mt. Parihaka TP and WR indicate some resources were available 1 – 10 m from nest sites at both locations. However, foraging duration data was significantly different between the locations. The results demonstrate that even though *L. imita*tus and *L. boltoni* foraged for up to 2 hrs the species probably only travelling 1 – 10 m to access food. In contrast, female *L. paahaumaa* foraged for approximately 0:30 hrs but must have travelled greater than 10 m to access food because no observations were made of female bees foraging within 10 m of nest sites. These results indicate that foraging duration is not necessarily related to foraging range.

Based on the results of this study foraging duration cannot indicate the home range of native bees. This contradicts previous studies (Gathmann & Tscharntke 2002). Gathmann & Tscharntke (2002) also found body length to be the best predictor of the foraging range of solitary bees. This study showed no correlation between the body metrics and foraging duration. Correlation was also tested against flight muscle mass (Figure 4.45 - B) for the three species and no correlation was evident (summarised in Table 5.25 below).

Table 5.25 Correlation coefficient for three species of New Zealand native bees (*n* = 30 for each species). Foraging duration (hr) is not correlated with body length or with flight muscle mass.

Species	Correlation coefficient (r) of foraging duration (hr) versus:	
	Body length [mm]	Flight muscle mass
L. boltoni	- 0.38	- 0.03
L. imitatus	- 0.12	0.00
L. paahaumaa	- 0.12	- 0.27

5.6 Conclusions

It is also concluded that although forage rewards generally determine pollinator community structure nest-sites and nesting resources clearly play an equally important role for native bees on Mt. Parihaka. Aggregations of native bees appeared to be limited by suitable nesting substrate and nest site aspect rather than by local floral community structure. Floral preferences for species varied according to nest site location, further lending support to this theory.

For three species of native bees, pollen composition and plant-associated collections indicated floral preferences vary depending on nest site locations and locally available resources. Records of host plant families for *L. boltoni* show the species has broad foraging tendencies and will forage on introduced and native plants (Donovan 2007). This study confirms existing records (Donovan 2007). *Leioproctus imitatus* displayed specialist foraging tendencies with a distinct preference for plants in the Myrtaceae family. Pollen composition analysis confirms the species prefers native plants in the Myrtaceae family, supporting existing records (Donovan 2007). *Leioproctus (N.) paahaumaa* were collected from only two plant species (oxeye daisy and wild carrot) in two families, Apiaceae and Asteraceae demonstrating specialist foraging tendencies and confirmed a preference for introduced plant species (Donovan 2007).

Foraging duration times have been used to predict the distance travelled by bees to their forage (Gathmann & Tscharntke 2002). Results from this study show foraging duration is not necessarily related to the distance travelled to food resources. Observations of food sources at two locations on Mt. Parihaka (TP, WR) indicate that resources were available 1 – 100 m from nest sites at both locations, but foraging duration data was significantly different between locations. Results demonstrate that even though *L. imita*tus and *L. boltoni* forage for up to 2 hrs the species is probably only travelling 1 – 10 m to access food. In contrast, female *L. paahaumaa* foraged for approximately 0:30 hrs but must have travelled greater than 10 m to access food since no observations were made of female bees foraging within 10 m of nest sites. In addition to foraging duration, body length has also been used to predict the foraging range of solitary bees (Gathmann & Tscharntke 2002). The results of this study do not support that hypothesis; no correlation between foraging duration and body length was found.

Recommendations for the Conservation of Native Bees in Whangarei

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Summary

From December 2004 to January 2007 a study of the biology and behaviour of New Zealand native bees was conducted in Whangarei [1]. Large communities of native bees on Mt. Parihaka were the focus for extensive observations. The results of this study indicate that native bees are contributing to the regeneration of native forests, perhaps in a greater capacity than is realised. This report summarises some of the pivotal findings of the study firstly, to encourage increased awareness of native bees; secondly, to ensure existing communities of native bees on Mt. Parihaka are preserved and protected and; thirdly, to encourage the implementation of conservation management strategies of native bees and their habitats. A complete summary of recommendations is listed below and for more information on New Zealand native bees and topics outlined in this study refer to MSc thesis by Ngaire Hart [2], " New Zealand Native Bees: A Case Study in Whangarei."

RECOMENDATIONS

- Raise awareness of New Zealand native bees and their habitats
- Recognise native bees contribution to New Zealand's natural, agricultural and horticultural pollination systems
- Protect and preserve locations where native bees have established inter generational nest sites.
- Protect and preserve native flora particularly manuka, kanuka, and pohutukawa around established nest sites.
- Continue to build baseline data on the role of New Zealand's native bees in the environment.
- Develop survey strategies and implement long term monitoring programs of native bee diversity and abundance levels locally with a view to nation-wide monitoring.
- Give consideration to native bees habitats in all roadside maintenance plans undertaken by the Whangarei District Council
- Weed spraying undertaken by the Whangarei District Council to be conducted outside native bees active season (November – February)
- With regards to Hydroseeding roadside slips, Hydroseed those slips that require hydro seeding for erosion control only. Allow native bees to develop nest sites where erosion and bank integrity is not a significant issue.

Contents

Introduction

Bees pollinate both natural and cultivated plants and their importance in this role has been recognised worldwide [3, 4]. Regarded as keystone species, bees are vital to the ecosystems in which they live because they help to pollinate plants, which in turn support otherwise separate food webs [5-7]. Conservation of natural habitats depends on the preservation of bee populations, without which the reproduction of native plants would be adversely affected [8]. The common honeybee, which is native to Europe and Africa (and east as far as Western Iran) is the most widely recognised bee and has been exported around the world. It produces honey, pollinates crops, is highly social and has its own means of communication [9]. But although the honeybee is the most studied insect [8], there is growing worldwide interest in native bees, the majority of which are not social and do not produce honey.

Non-*Apis*, native bees play an especially important role in many natural ecosystems because they are among the most critical and effective pollinators of native plants [3, 4, 10, 11]. Many commercial crops: fruits, flowers, vegetables, flaxes, and alfalfa and clover are also bee-pollinated; one out of every four mouthfuls of world food resources depends on insect pollination (estimated at 20-40 billion US dollars per year) [8, 12]. In some instances, native bee efficacy as pollinators of agricultural crops surpasses honeybees [13-15]. Moreover, the invasive varroa mite (*Varroa destructor*) and the acarine mite (*Acarapis woodi*) continue to damage honeybee colonies around the world further adding to the importance of non-*Apis* bees, which are not affect by the mites.

Female native bee on pohutukawa in the Whangarei Town Basin

Bees of the World and New Zealand native bees

Of the 17,000 different species of bees that have been described in the world most are solitary [8]. Unlike highly social bees, such as honeybees which have a caste of cooperating workers directed by a single female, each female solitary bee constructs and provisions her own nest without the help of others [16]. Solitary bees can be classified into two groups; those that construct nests using secretions from their glands (ground burrowing or mining bees) and those that construct nests using resources they have collected from outside of the nest [16].

In New Zealand there are 41 different species of bees and grouped according to their origin, there are 28 native (27 endemic and 1 indigenous) and 12 introduced species (see Appendix A for a complete list of New Zealand taxa). Of the 27 species of bees that are found only in New Zealand (endemic) most are from the primitive Colletidae family, 18 belonging to the genus *Leioproctus* and 6 from the genus *Hylaeus.* The remaining three from the genus *Lasioglossum,* belong to the Halictidae family.

Most species of New Zealand native bees are solitary mining bees (e.g. plasterer and masked bees, which are discussed in the following section). There are around three species that are not solitary, for example, the female *Lasioglossum sordidum*, exhibits some level of social organisation because several females work from the same nest. *Lasioglossum sordidum* are therefore considered partly social [17]. There are at least three rare native species according to Donovan [18] including: *Leioproctus (Leioproctus) otautahi, Leioproctus* (*Nesocolletes*) *nunui* and *Hylaeus* (*Prosopisteron*) *murihiku*.

Female native bee on daisy at Maungatapere farm: Sweat bee (*Lasioglossum spp.*)

Plasterer, masked and sweat bees

Collectively known as plasterer bees, Colletidae is regarded as one of the most primitive families of bees [8]; all members of this family are solitary mining bees. This family can be further divided into two subfamilies, 'hairy colletids' (Subfamily Colletinae, e.g. species *Leioproctus*) and masked bees (Subfamily Hylaeinae – e.g. species *Hylaeus*). Hairy colletids are typically robust, black bees and as the name suggests they are hairy; they range in length from around 5 –13.4 mm. Masked bees on the other hand, have distinctive yellow or white markings on their face (although magnification is needed to see the markings); most species are slender. They are mainly black bees with very few hairs and so are easily mistaken for small flies or wasps.

Halictidae is a large family found in all parts of the world but New Zealand has only four native species; members of this family are considered partly social. They are often called sweat bees because they are attracted to human perspiration. Sweat bees are moderately to sparsely hairy, black or greenish and range in length from 4-8 mm and are also easily mistaken for flies or small wasps.

Tiny female native bee on dandelion at Maungatapere farm: Sweat bee (*Lasioglossum spp.*)

Reproduction and seasonal rhythms

Most solitary bees live for around one year. Plasterer bees (Family Colletidae) hibernate as grubs over the winter in nest cells and in spring the grubs (prepupae) develop into adults and start to emerge (September – December) [17] (See Figure 1). Females are thought to mate once, storing sperm to release as required. They have the capacity to lay up to approximately 30 eggs (and construct up to 30 cells [16, 17]) but when poor weather prevents foraging and nest construction, females have the ability to reabsorb mature eggs as standby food [16]. When a cell is provisioned with a pollen nectar ball, the female lays one egg on the ball and then closes the cell. After around three days the egg hatches into a larval and within a few weeks it has consumed all the food becoming a prepupal which diapauses until the following spring [17]. Although emergence timing is not fully understood, it is proposed that solitary bees can predict cues such as increases in soil temperature/ moisture to time their emergence to coincide with the flowering of their preferred plants [16, 19].

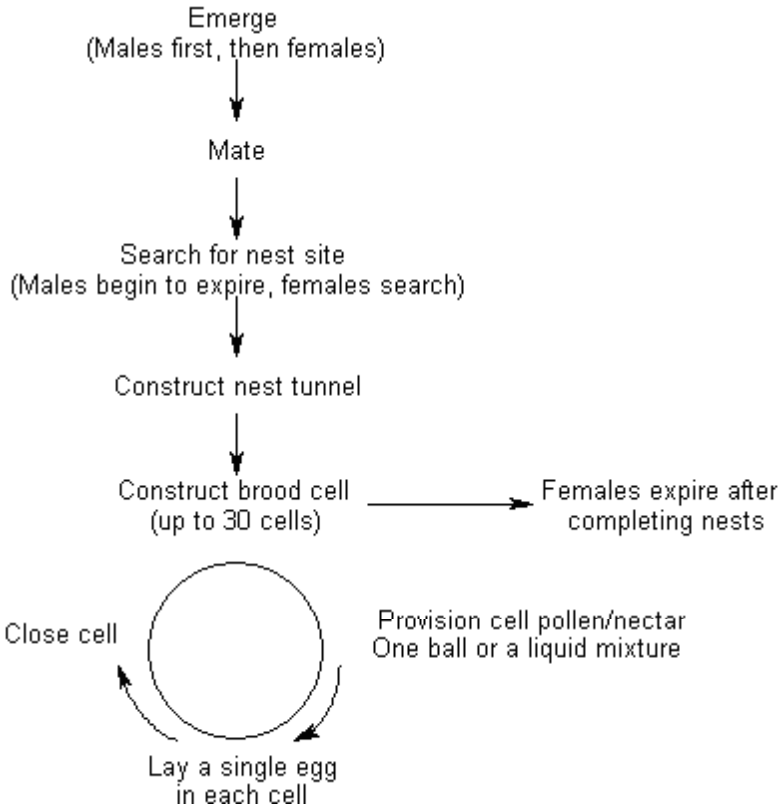


Figure 1 The life cycle common to all solitary bees.

Bee Villages

Many species of solitary mining bees show a strong preference to form large nesting communities, known as aggregations [16], where many species co-exist. For example, an estimated 840,000 bee nests along a 7.5 km road in the McKenzie Basin (Canterbury) was recorded by Quinn [20]. Most mining bees have a strong preference for the type of substrate they nest in [21] and this is one reason native bees form large aggregations.

Flower relationships

Most native bees can be grouped according to their foraging habits and are either generalists, gathering food from a wide range of flowers, or specialists relying on a single plant species (or a closely related group of plants) for food [19]. Myrtaceae is thought to be the primary flowering host family for Colletinae; females forage primarily on native Myrtaceae, Fabaceae or Asteraceae [17]. Some species of hairy colletids (Colletinae) are restricted to a few plants within these families (e.g. *Leioproctus imitatus* visits manuka (*Leptospermum scoparium*), kanuka (*Kunzea ericoides*) and pohutukawa (*Metrosideros excelsa*) and so some of these species would be considered specialists [17]. Other species of Plasterer such as *Leioproctus huakiwi*, have adapted to forage on introduced plants such as kiwifruit (Actinidiaceae *Actinidia*) and onions (Liliaceae *Allium*). Masked bees (Hylaeinae) like hairy colletids (Colletinae), forage on both native and introduced flowers (e.g. manuka and kiwifruit) and some species specialise on plants within a single host plant family. In contrast to Colletidae, most Halictinae are generalist foragers, visiting a wide range of introduced and native plants [17].

Female native bee on pohutukawa at Tahere Farm, Pataua South

A study in Whangarei: Mt. Parihaka nesting communities.

In Whangarei (New Zealand) native bees are located in a variety of ecosystems from regenerative forests such as Mt. Parihaka, to existing native bush such as Raumanga Valley Reserve. Large nest aggregations on roadside banks are commonly seen particularly in rural areas (e.g. Mt. Tiger and Maungatapere). Smaller communities can be found on closer observation, for example, native bees were found nesting in forest undergrowth (Raumanga Valley Reserve) and underneath grass, in moving sands (Ocean Beach), and shelly beaches (Taupiri Bay). Many road side banks have at least small colonies. Native bees were collected from a variety of plants both introduced and native, in rural, agricultural and urban environments.

The large nest areas and variety of species found on Mt. Parihaka were ideal for a medium term case study especially in terms of easy access to the site and limited public disturbance. A plan in 2005 to restore the pine plantation on Mt. Parihaka to natural forest was not anticipated at the start of this study but these developments created a unique opportunity to understand native bee pollinators in the ecosystem in terms of conservation restoration of a native forest.

Eight species of native bees were found in the local Whangarei region; six species were found on Mt. Parihaka, five from the genus *Leioproctus* and one species from the genus *Lasioglossum* (full species list is outlined in Appendix A). Since eight species overall were found in Whangarei, Mt. Parihaka has proved to be representative of Whangarei native bees.

Female native bee on parsley at Tahere Farm, Pataua South

Understanding the native bee community organization on Mt. Parihaka is the first step towards the management of pollinator biodiversity and conservation in a rejuvenating native ecosystem. The following sections outline the important findings of the community study on Mt. Parihaka in relation to existing literature on the conservation of native bees including:

- **Habitat requirements**
  - Location and description of nest sites
  - Floral resources

- **Conservation considerations**
  - Contribution to pollinating systems in a rejuvenating forest
  - Recommendations for conservation management

Female native bee on pohutukawa in the Whangarei Town Basin

Female native bee on parsley at Tahere Farm, Pataua South

Habitat requirements

Most species handled in this study were seasonally abundant and in their peak flight season (November – January) observations of native bees on Mt. Parihaka by far out numbered those of honeybees (*Apis mellifera*) and bumblebees (*Bombus spp*). Although suitable forage [21, 22] is a significant factor determining the success of native bees, nest site suitability is more than likely equally important [16, 21, 23-26] and trends on Mt. Parihaka support this notion. Observations of floral community structure on Mt. Parihaka indicate that forage rewards were no greater at large nest aggregations (i.e. site 1, Figure 2 and Table 1) when compared to smaller aggregations (i.e. site 3). Both sites 1 and 3 had similar floral diversity and abundance but a greater area of substrate and an ideal north-facing bank provided more nesting areas at site 1 compared to the small south east facing bank at site 3.

Figure 2 Gated entry to forestry area on Mt. Parihaka on the left and Memorial Drive on the right. In the centre a single kanuka tree that was a popular source of food for many native bees nesting on both sides of the bank.

Location and description of nest sites

Table 1 below lists several main nest aggregations found on Mt. Parihaka. The general ecology of the area of each location is described.

The density of nesting bees varied between sites from 14 - 22 nests per m^2. At premium sites especially, the density of nests appeared evenly distributed. From observation, sites 1A – D and 2A in particular have supported many generations of native bees and continue to be a popular spot for current generations (Figure 3 - A).

Table 1 Locations on Mt. Parihaka where New Zealand native bees have been observed.

Location	Nest site & code	Location	General Ecology
Top of Mt. Parihaka (TP) Mt. Parihaka, Riverside. Whangarei. Main entrance at the very end of memorial drive. Car park leading to walking access war memorial on the right hand side and gated forestry area (restricted access) on the left hand side.	**Site 1A**: By gate, at the entry to forestry area. First bank on right-hand side.	**S** 35^{O} 42' 43.04 " **E** 174^{O} 20' 18.62" **HAE** 261 m	Pine forest plantation. First generation regenerative forest. Some gorse, pampas (*Cortaderia spp*.) and cutty grass.
	Site 1D: Second bank under transmission tower.	**S** 35^{O} 42' 42.97" **E** 174^{O} 20' 20.18" **HAE** 260 m	
	Site 2A: Down from gate entry. Third major bank in forestry area, on the right hand side.	**S** 32^{O} 46' 43.03" **E** 174^{O} 20' 22.01" **HAE** 258 m	
	Site 3A: Down from gate. Small bank on left hand side in the forestry area	**S** 32^{O} 46' 43.03" **E** 180^{O} 20' 21.01" **HAE** 242 m	
Water reservoir (WR) Mt. Parihaka, Riverside. Whangarei. Before memorial car park, half way up memorial drive. On the right hand side gated entrance into water tower reservoir area	**Site 4A**: Water tower entrance, over mound on the left hand side	**S** 35^{O} 43' 01.96" **E** 174^{O} 20' 37.34" **HAE** 192 m	Pine forest plantation. First generation regenerative forest. But mainly gorse, pampas and cutty grass in the immediate vicinity of nest site. Some cleared areas.
	Site 4B: Five m down from mound, on steep bank.	**S** 35^{O} 43' 01.34" **E** 174^{O} 20' 37.35" **HAE** 192 m	

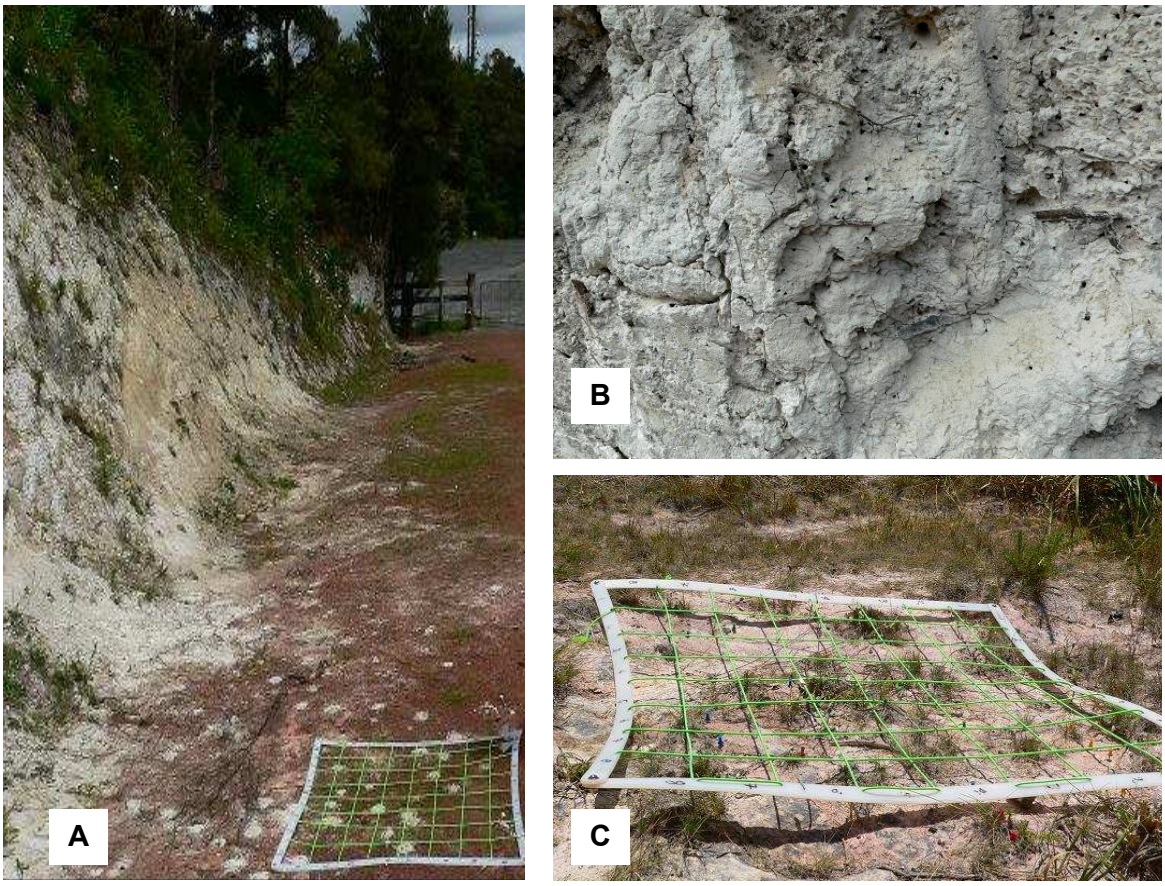
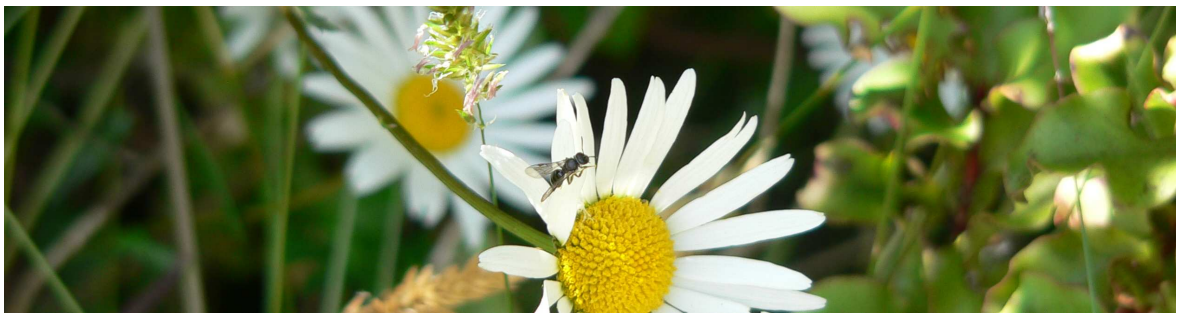


Figure 3 Nest sites; A, Ground nests (site 1D) beside bank at site 1 with approximately 35 visually active nests per m^2 and; B, Dense aggregations on North East facing cliff face at site 2A with approximately 1700 nest entrances per m^2 and; C, Ground nests of small localised community of *L. paahaumaa* with approximately 20 active nests per m^2 (with around 500 active nests over the entire 25 m^2 area).

Floral resources

For some species of native bees on Mt. Parihaka, floral preferences vary depending on nest site locations and locally available resources [1]. One such species is *Leioproctus boltoni,* which is known to have broad foraging tendencies and will forage on introduced and native plants [18]. Depending on the exact nest site location on Mt. Parihaka the species was shown to forage on pohutukawa (Myrtaceae) at site 1A or wild carrot (Asteraceae) at site 1D. Another species, *L. imitatus,* was shown to have specialist foraging tendencies with a distinct preference for native plants in the Myrtaceae family. *Leioproctus imitatus* carried mainly kanuka and manuka at site 1A and pohutukawa at site 1D. Finally, *Leioproctus (N.) paahaumaa* (which also displayed specialist foraging tendencies), were collected from only two plant species (oxeye daisy and wild carrot at site 4) in two families, Apiaceae and Asteraceae.

In addition to floral preferences, foraging duration data on these species demonstrates that even though *L. imita*tus and *L. boltoni* forage for up to 2 hrs the species is probably only travelling 1 – 10 m to access food; for example, the kanuka positioned at the gate entrance to Mt. Parihaka forest is only meters from nest sites (refer to Figure 2). In contrast, female *L. paahaumaa* foraged for approximately 0:30 hrs but must have travelled greater than 10 m to access food since no observations were made of female bees foraging within 10 m of nest sites. It is therefore likely that many species of native bees on Mt. Parihaka rely on forage local rewards, requiring food resources within 100 m of nest sites.

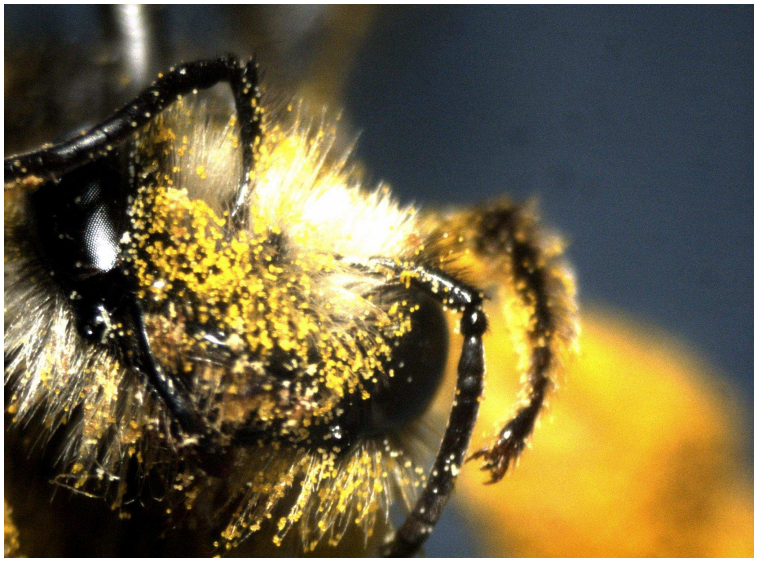


Native bee on oxeye daisy at Mt. Parihaka: Sweat Bee (*Lasioglossum spp.*)

Conservation considerations

The contributions of native bees to the pollination systems on Mt. Parihaka have not been fully quantified. However, the abundance of native species is an indicator that they are a valuable resource particularly in a regenerating forest. Observations of native bees throughout the study showed they far out numbered bumblebees and honeybees (the later of which have been adversely effected by the varroa mite). At least two species of native bees on Mt. Parihaka (*L. imitatus* and *L. boltoni*) forage on native plants species such as kanuka, manuka and pohutukawa. In studies elsewhere, native bees have been shown to be extremely effective, important pollinators of native plants in particular [27, 28].

Conservation of native bees relies on an increased awareness of their biology and the role they play in the environment. During the course of this study several accounts of homeowners spraying entire banks with fly spray to “kill little black wasps” were relayed. Members of the public regularly stopped to show interest in the study on Mt. Parihaka and were often intrigued and delighted to discover the “flies” on the bank were New Zealand native bees. In two seasons (2006 and 2007) Department of Conservation field workers carried out weed spraying on banks where native bees are nesting, unaware of the existence of the pollinators. In other areas around Whangarei, the practice of hydro-seeding slips (Whangarei District Council, Roading Division) prevents native bees from nesting in otherwise ideal semi natural sites. Since, for the most part, hydroseeding is used for cosmetic purposes only it should be possible to leave at least some areas free for native bees to develop nest aggregations.



Close up photo of a New Zealand native bee with pollen on her facial hair: Hairy colletid (*Leioproctus spp.*)

It therefore seems important to raise awareness of the biology of native bees and especially to disseminate such facts as:

- They very rarely sting
- If they do sting it is comparable to a mosquito bite
- They are not aggressive and do not swarm aggressively
- They are fully active for only a few months of the year
- Most species only produce one generation per year
- They are important pollinators of native plants

Fact sheets for general distribution are currently being compiled by Hart [29] and for more information refer to " Apoidea, Fauna of New Zealand" by Donovan [18] or visit the website "Community Pollination Project " by Landcare Research [30].

Supporting native bee populations on Mt. Parihaka

Native bees are thriving in many areas on Mt. Parihaka. It is anticipated their success will continue and also the benefits of the essential pollination services they provide in the regenerating forest. Native bee populations can be supported by the following actions.

- Increasing available foraging habitats to include a range of plants.
- Protecting existing forage near nest sites.
- Creating and preserving existing nest sites.
- Reducing their exposure to pesticides and herbicides during their active season (Late October through to Late March).

Close up photo of a New Zealand native bee: Hairy colletid (*Leioproctus spp*.)

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Appendix A

Table 2 New Zealand Native Bee Taxa (Donovan 2007)

Superfamily **APOIDEA**
Family **Colletidae**
Subfamily **Colletinae**
Genus ***Leioproctus*** Smith, 1853
Subgenus *Leioproctus* Smith, 1853
boltoni Cockerell, 1904
huakiwi (Donovan 2007)
imitatus Smith, 1853
maorium Cockerell, 1913
viridibasis Cockerell, 1936
kanapuu (Donovan 2007)
keehua (Donovan 2007)
metallicus (Smith, 1853)
Andrena trichopus "White", Butler, 1874
otautahi (Donovan 2007)
pango (Donovan 2007)
purpureus (Smith, 1853)
vestitus (Smith 1876)
waipounamu (Donovan 2007)
Subgenus *Nesocolletes* Michener, 1965
fulvescens (Smith 1876)
hirtipes (Smith 1878)
opacior (Cockerell, 1936)
hudsoni (Cockerell 1925)
maritimus (Cockerell, 1936)
monticola (Cockerell 1925)
nunui (Donovan 2007)
paahaumaa (Donovan 2007)
pekanui (Donovan 2007)

Subfamily **Hylaeinae**
Genus ***Hylaeus***
Subgenus *Prosopisteron* Cockerell, 1906
agilis (Smith 1876)
laevigata (Smith, 1854)
laevigatulus Michener, 1965
laevigatus (Hutton, 1904)
maoriana (Cockerell, 1909)
maorica (Kirkaldy, 1909)
ssp. *laevigata* (Cockerell, 1916)

Continued -
Subfamily **Hylaeinae**
Genus ***Hylaeus***
Subgenus *Prosopisteron* Cockerell, 1906
capitosus (Smith 1876)
capitorus (Kirby, 1884)
capitosa (Dalla Torre, 1896)
innocens (Cameron 1898)
kermadecensis (Donovan 2007)
matamoko (Donovan 2007)
murihiku (Donovan 2007)
relegatus (Smith 1876)
cameroni (Cockerell 1905)
hudsoni Cockerell, 1925
maoriana (Cockerell, 1909)
maorianus (Meade-Waldo 1923)
relegata (Dalla Torre, 1896)
sulcifrons (Cameron 1898)

Family **Halictidae**
Subfamily **Halictinae**
Tribe Halictini
Genus ***Lasioglossum*** Curtis, 1833
Subgenus *Chilalictus* Michener, 1965
cognatum (Smith, 1853)
haematostoma (Cockerell, 1914)
inclinans (Smith, 1879)
subinclinans (Cockerell, 1915)
Subgenus *Austrevylaeus* Michener, 1965
mataroa (Donovan 2007)
maunga (Donovan 2007)
sordidum Smith, 1853)
familiaris (Smith 1876)
huttoni (Cameron, 1900)
smithii (Dalla Torre, 1896)
smithii var. *a* (Cockerell, 1916)

Table 3 New Zealand Native Bee Species Collected from areas around Whangarei

Collected from Mt. Parihaka
1. *Leioproctus (Leioproctus) boltoni* (Cockerell)
2. *L. (L.) huakiwi* (Donovan)
3. *L. (L.) imitatus* (Smith)
4. *L. (N.) paahaumaa* (Donovan)
5. *L. (L.) pango* (Donovan) (Hymenoptera: Colletidae)
6. *Lasioglossum (Austrevylaeus) sordidum* (Smith) (Hymenoptera: Halictidae)
Other areas around Whangarei
7. From the Morningside subdivision, another species from the genus *Lasioglossum, Lasioglossum (Chilalictus) cognatum* (Smith) was collected.
8. Finally, one species from the genus *Hylaeus, Hylaeus* (*Prosopisteron*) *relegates* (Smith) (Hymenoptera: Colletidae), was collected from Raumanga Valley.
• Note: *Leioproctus boltoni* was also collected from Ngaiotonga Valley and *L. imitatus* was collected from Mair Park.

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Appendix A2

Collection Records

Table A2.26 Insect collections in season one (2004 - 2005).

Date Collected	Site Code	Reason Collected	Collection Method	Species	No.	M	F	ID'd By	Date ID'd
20/12/04	1D	LL & FMM	BV exiting nest	*Leioproctus huakiwi*	**5**	♂♂		NH	03/04/06
20/12/04	1D	LL & FMM	BV exiting nest	*Leioproctus huakiwi*	**1**		♀	NH	03/04/06
20/12/04	1D	LL & FMM	BV exiting nest	*Leioproctus huakiwi*	**5**	♂♂		NH	03/04/06
20/12/04	1D	LL & FMM	BV exiting nest	*Leioproctus huakiwi*	**1**		♀	NH	03/04/06
24/12/04	6	ID & Ref.	BV grapefruit	*Lasioglossum sordidum*	**1**		♀	BD	11/11/05
24/12/04	6	ID & Ref.	BV grapefruit	*Lasioglossum sordidum*	**1**		♀	BD	11/11/05
26/12/04	8	ID & Ref.	BV nest area	*Lasioglossum cognatum*	**1**		♀	BD	11/11/05
26/12/04	8	ID & Ref.	BV nest area	*Lasioglossum cognatum*	**1**		♀	BD	11/11/05
27/12/04	6	ID & Ref.	BV nest area	*Leioproctus imitatus*	**1**		♀	BD	11/11/05
27/12/04	6	ID & Ref.	BV nest area	*Leioproctus imitatus*	**1**		♀	BD	11/11/05
28/12/04	3	ID & Ref.	BV nest area	*Leioproctus boltoni*	**1**		♀	NH	30/03/06
28/12/04	3	ID & Ref.	BV nest area	*Leioproctus boltoni*	**1**		♀	NH	30/03/06
04/01/05	7	ID & Ref.	BV nest	*Leioproctus imitatus*	**1**		♀	NH	30/03/06
04/01/05	7	ID & Ref.	BV nest	*Leioproctus imitatus*	**1**		♀	NH	30/03/06
16/01/05	5	ID & Ref.	BV exiting nest	*Leioproctus boltoni*	**3**		♀♀	NH	03/04/06
16/01/05	5	ID & Ref.	BV exiting nest	*Leioproctus boltoni*	**3**		♀♀	NH	03/04/06
17/01/05	2	LL & FMM	BV exiting nest	*Leioproctus boltoni*	**8**		♀♀	NH	03/04/06
17/01/05	4A	ID & Ref.	BV exiting nest	*Leioproctus boltoni*	**1**		♀	NH	03/04/06
17/01/05	4A	ID & Ref.	BV exiting nest	*Leioproctus paahaumaa*	**2**		♀♀	NH	03/04/06
17/01/05	2	LL & FMM	BV exiting nest	*Leioproctus boltoni*	**8**		♀♀	NH	03/04/06
17/01/05	4A	ID & Ref.	BV exiting nest	*Leioproctus boltoni*	**1**		♀	NH	03/04/06
17/01/05	4A	ID & Ref.	BV exiting nest	*Leioproctus paahaumaa*	**2**		♀♀	NH	03/04/06

Table A2.27 Key to Abbreviations.

Area Code		**Reason Collected**		**Collection Method**	
1, 2, 3 & 4	Mt. Parihaka	ID & Ref.	For reference collection	SW	Sweep net
5	Ngaiotonga Valley	LL	For load-lifting experiments	BV	Bug vacuum
6	Raumanga Valley	FMM	Muscle mass measurements	**Identified by (ID'd by)**	
7	Mair Park	PM	Pollen mass measurements	NH	N. Haigh
8	Morningside subdivision	DNA	For DNA analysis	BD	B. Donovan
9	Opposite Warehouse				
10	Whangarei marina				
11	Mount Tiger				

Table A2.28 Scientific and common names of plant species associated with native bee collection.

Scientific name	**Common name**
Apiaceae *Daucus carota*	Wild carrot
Asteraceae *Leucanthemum vulgare*	Oxeye daisy
Asteraceae *Taraxacum sp.*	Dandelion
Cunoniaceae *Weinmannia racemosa*	Kamahi
Myrtaceae *Kunzea ericoides*	Kanuka
Myrtaceae *Leptospermum scoparium*	Manuka
Myrtaceae *Metrosideros excelsa*	Pohutukawa
Pinaceae *Pinus radiata*	Pine
Rutaceae *Citrus grandis* × *reticulata*	Grapefruit
Rutaceae *Citrus reticulata*	Mandarin
Fabaceae *Ulex europaeus*	Gorse
Rosaceae *sp.*	Rose

Table A2.29 Insect collections (season two 2005 – 2006).

Date Collected	Site Code	Reason Collected	Collection Method	Species	No.	M	F	ID'd By	Date ID'd
17/10/05	1D	ID & Ref.	BV nest	*Leioproctus boltoni*	3	♂♂		BD	11/11/05
26/10/05	6	ID & Ref.	BV nest	*Lasioglossum sordidum*	**1**		♀	BD	11/11/05
27/10/05	1A	ID & Ref.	BV nest	*Leioproctus imitatus*	**1**	♂		BD	11/11/05
27/10/05	1A	ID & Ref.	BV nest	*Leioproctus imitatus*	**3**	♂♂		BD	11/11/05
27/10/05	1A	ID & Ref.	BV nest	*Leioproctus pango*	**1**	♂		BD	11/11/05
14/11/05	1A	PM & FMM	SN over kanuka	*Leioproctus boltoni*	**1**		♀	NH	09/12/05
14/11/05	1D	ID & Ref.	SN over pine	*Leioproctus boltoni*	**1**		♀	NH	09/12/05
14/11/05	1A	PM & FMM	SN over kanuka	*Leioproctus imitatus*	**9**		♀♀	NH	09/12/05
16/11/05	1A	ID & Ref.	BV nest area	*Leioproctus pango*	**2**		♀♀	NH	09/12/05
20/11/05	6	ID & Ref.	SN over rose	*Hylaeus relegatus*	**1**		♀	BD	09/12/05
20/11/05	2	ID & Ref.	SN over shrubs	*Leioproctus boltoni*	**4**	♂♂		BD	09/12/05
20/11/05	1A	DNA	SN over kanuka	*Leioproctus boltoni*	**12**	♂♂		BD	13/12/05
20/11/05	3	ID & Ref.	SN over shrubs	*Leioproctus boltoni*	**39**	♂♂		BD	09/12/05
20/11/05	6	ID & Ref.	SN wild carrot	*Leioproctus boltoni*	**1**		♀	BD	09/12/05
20/11/05	1A	DNA	SN over kanuka	*Leioproctus boltoni*	**1**		♀	BD	13/12/05
20/11/05	2	ID & Ref.	On ground, unwell?	*Leioproctus boltoni*	**1**		♀	BD	09/12/05
20/11/05	2	ID & Ref.	SN over shrubs	*Leioproctus imitatus*	**18**	♂♂		BD	09/12/05
20/11/05	1A	DNA	SN over kanuka	*Leioproctus imitatus*	**3**	♂♂		BD	13/12/05
20/11/05	3	ID & Ref.	SN over shrubs	*Leioproctus imitatus*	**4**	♂♂		BD	09/12/05
20/11/05	2	ID & Ref.	SN over shrubs	*Leioproctus imitatus*	**16**		♀♀	BD	09/12/05
20/11/05	1A	DNA	SN over kanuka	*Leioproctus imitatus*	**17**		♀♀	BD	13/12/05
20/11/05	1A	DNA	SN over kanuka	*Leioproctus imitatus*	**1**	♂		BD	13/12/05
20/11/05	2	ID & Ref.	SN oxeye daisy	*Leioproctus imitatus*	**1**		♀	BD	09/12/05
20/11/05	2	ID & Ref.	SN oxeye daisy	*Leioproctus paahaumaa*	**2**	♂♂		BD	09/12/05
20/11/05	2	ID & Ref.	SN oxeye daisy	*Lasioglossum sordidum*	**2**		♀♀	BD	09/12/05
21/11/05	2	ID & Ref.	SN oxeye daisy	*Leioproctus boltoni*	**1**	♂		BD	09/12/05
21/11/05	2	ID & Ref.	SN over shrubs	*Leioproctus boltoni*	**20**	♂♂		BD	09/12/05
21/11/05	1C	DNA	SN over manuka	*Leioproctus boltoni*	**21**	♂♂		BD	13/12/05

Table A2.29 Insect collections continued (season two 2005 - 2006).

Date Collected	Site Code	Reason Collected	Collection Method	Species	No.	M	F	ID'd By	Date ID'd
21/11/05	1C	DNA	SN over manuka	*Leioproctus boltoni*	**21**	♂♂		BD	13/12/05
21/11/05	1E	ID & Ref.	SN over shrubs	*Leioproctus boltoni*	**2**	♂♂		BD	09/12/05
21/11/05	2	ID & Ref.	SN over shrubs	*Leioproctus boltoni*	**1**		♀	BD	09/12/05
21/11/05	1C	DNA	SN over manuka	*Leioproctus boltoni*	**1**		♀	BD	13/12/05
21/11/05	1C	DNA	SN over manuka	*Leioproctus huakiwi*	**1**	♂		BD	13/12/05
21/11/05	1C	DNA	SN over manuka	*Leioproctus huakiwi*	**2**	♂♂		BD	13/12/05
21/11/05	2	ID & Ref.	SN over shrubs	*Leioproctus imitatus*	**21**	♂♂		BD	09/12/05
21/11/05	1C	DNA	SN over manuka	*Leioproctus imitatus*	**24**	♂♂		BD	13/12/05
21/11/05	2	ID & Ref.	SN over shrubs	*Leioproctus imitatus*	**2**		♀♀	BD	09/12/05
21/11/05	2	ID & Ref.	SN small daisy	*Leioproctus imitatus*	**1**		♀	BD	09/12/05
21/11/05	1C	DNA	SN over manuka	*Leioproctus imitatus*	**4**		♀	BD	13/12/05
21/11/05	1C	DNA	SN over manuka	*Leioproctus imitatus*	**1**	♂		BD	13/12/05
21/11/05	2	ID & Ref.	SN oxeye daisy	*Leioproctus paahaumaa*	**2**		♀♀	BD	09/12/05
21/11/05	1E	ID & Ref.	SN over shrubs	*Leioproctus pango*	**4**	♂♂		BD	09/12/05
21/11/05	1E	ID & Ref.	SN over shrubs	*Leioproctus pango*	**4**		♀♀	BD	09/12/05
26/11/05	6	ID & Ref.	BV grapefruit	*Lasioglossum sordidum*	**2**		♀♀	BD	11/11/05
27/11/05	1D	PM & FMM	BV entering nest	*Leioproctus boltoni*	**1**		♀♀	NH	09/12/05
27/11/05	1D	PM & FMM	BV entering nest	*Leioproctus imitatus*	**7**		♀♀	NH	09/12/05
28/11/05	6	ID & Ref.	BV mandarin	*Leioproctus boltoni*	**1**		♀	BD	11/11/05
28/11/05	6	ID & Ref.	BV mandarin	*Leioproctus pango*	**1**		♀	BD	11/11/05
06/12/05	1D	Sex ID	5 X SN nest	Mixed	**75**	30	45	NH	06/12/05
06/12/05	1D	Sex ID	5 X SN nest	Mixed	**92**	40	52	NH	06/12/05
06/12/05	1A	Sex ID	5 X SN nest	Mixed	**76**	34	42	NH	06/12/05
06/12/05	1A	PM & FMM	BV entering nest	*Leioproctus boltoni*	**5**		♀♀	NH	12/12/05
06/12/05	1A	PM & FMM	SN over kanuka	*Leioproctus huakiwi*	**1**	♂		NH	09/12/05
06/12/05	1A	PM & FMM	SN over kanuka	*Leioproctus imitatus*	**6**	♂♂		NH	09/12/05
06/12/05	1A	PM & FMM	BV entering nest	*Leioproctus imitatus*	**20**		♀♀	NH	12/12/05
06/12/05	1A	PM & FMM	SN over kanuka	*Leioproctus imitatus*	**1**	♂		NH	09/12/05

Table A2.29 Insect collections continued (season two 2005 - 2006).

Date Collected	Site Code	Reason Collected	Collection Method	Species	No.	M	F	ID'd By	Date ID'd
06/12/05	1A	PM & FMM	BV entering nest	*Leioproctus pango*	**1**		♀	NH	12/12/05
06/12/05	1A	PM & FMM	SN over kanuka	*Leioproctus pango*	**2**	♂♂		NH	09/12/05
18/12/05	1D	ID & Ref.	On bank - expired	*Leioproctus imitatus*	**1**		♀	NH	30/03/06
20/12/05	4C	ID & Ref.	SN over pohutukawa	*Leioproctus boltoni*	**11**	♂♂		NH	30/03/06
20/12/05	2	ID & Ref.	BV oxeye daisy	*Leioproctus boltoni*	**1**		♀	NH	30/03/06
20/12/05	1D	ID & Ref.	SN over gorse	*Leioproctus boltoni*	**2**		♀♀	NH	30/03/06
20/12/05	1D	ID & Ref.	SN over gorse	*Leioproctus huakiwi*	**13**	♂♂		NH	30/03/06
20/12/05	4C	ID & Ref.	SN over pohutukawa	*Leioproctus huakiwi*	**2**	♂♂		NH	30/03/06
20/12/05	1D	ID & Ref.	SN over gorse	*Leioproctus imitatus*	**1**	♂		NH	30/03/06
20/12/05	3	ID & Ref.	BV oxeye daisy	*Leioproctus imitatus*	**1**		♀	NH	30/03/06
20/12/05	1A	ID & Ref.	BV oxeye daisy	*Leioproctus paahaumaa*	**2**	♂♂		NH	30/03/06
20/12/06	1D	ID & Ref.	BV oxeye daisy	*Leioproctus paahaumaa*	**1**		♀	NH	30/03/06
20/12/05	1E	ID & Ref.	BV oxeye daisy	*Leioproctus paahaumaa*	**1**		♀	NH	30/03/06
20/12/05	1B	ID & Ref.	BV wild carrot	*Leioproctus paahaumaa*	**3**		♀♀	NH	30/03/06
20/12/05	1D	ID & Ref.	SN over gorse	*Leioproctus pango*	**3**	♂♂		NH	30/03/06
20/12/05	4C	ID & Ref.	SN over pohutukawa	*Leioproctus pango*	**19**	♂♂		NH	30/03/06
20/12/05	1B	ID & Ref.	BV wild carrot	*Lasioglossum sordidum*	**2**		♀♀	NH	30/03/06
13/01/06	4A	ID & Ref.	BV oxeye daisy	*Leioproctus paahaumaa*	**1**	♂		NH	30/03/06
13/01/06	4B	ID & Ref.	BV nest	*Leioproctus paahaumaa*	**1**	♂		NH	30/03/06
17/01/06	4A	ID & Ref.	Expired	*Leioproctus paahaumaa*	**1**		♀	NH	30/03/06
18/01/06	4B	ID & Ref.	On ground nest	*Leioproctus huakiwi*	**1**		♀	NH	30/03/06
18/01/06	4B	ID & Ref.	BV nest	*Leioproctus boltoni*	**1**	♂		NH	30/03/06
18/01/06	4A	ID & Ref.	BV nest - tiger beetle	*Leioproctus boltoni*	**1**		♀	NH	30/03/06
20/01/06	4A	ID & Ref.	BV oxeye daisy	*Leioproctus paahaumaa*	**3**		♀♀	NH	30/03/06
21/01/06	4A	ID & Ref.	BV nest - tiger beetle	*Leioproctus boltoni*	**1**	♂		NH	30/03/06
31/01/06	4A	PM & FMM	BV entering nest	*Leioproctus paahaumaa*	**7**		♀♀	NH	30/03/06

Table A2.29 Insect collections continued (season three December 2006).

Date Collected	Site Code	Reason Collected	Collection Method	Species	No.	M	F	ID'd By	Date ID'd
08/12/06	1A	ID & Ref.	SN over kanuka	*Leioproctus boltoni*	1	♂		NH	14/12/06
08/12/06	1A	ID & Ref.	SN over kanuka	*Leioproctus pango*	8	♂♂		NH	14/12/06
08/12/06	1A	ID & Ref.	SN over kanuka	*Leioproctus pango*	1		♀	NH	14/12/06
08/12/06	1A	ID & Ref.	SN over bank	*Leioproctus imitatus*	11	♂♂		NH	14/12/06
08/12/06	1A	ID & Ref.	SN over bank	*Leioproctus boltoni*	10	♂♂		NH	14/12/06
12/12/06	3A	ID & Ref.	SN over bank	*Leioproctus boltoni*	36	♂♂		NH	14/12/06
12/12/06	3A	ID & Ref.	SN over bank	*Leioproctus imitatus*	20	♂♂		NH	14/12/06
12/12/06	1F	ID & Ref.	SN over bank	*Leioproctus boltoni*	42	♂♂		NH	14/12/06
12/12/06	1F	ID & Ref.	SN over bank	*Leioproctus imitatus*	9	♂♂		NH	14/12/06
12/12/06	1F	ID & Ref.	SN over bank	*Leioproctus huakiwi*	5	♂♂		NH	14/12/06
12/12/06	11	ID & Ref.	SN over bank	*Leioproctus boltoni*	4		♀♀	NH	14/12/06
12/12/06	11	ID & Ref.	SN over bank	*Leioproctus boltoni*	23	♂♂		NH	14/12/06
12/12/06	11	ID & Ref.	SN over bank	*Leioproctus huakiwi*	29	♂♂		NH	14/12/06
12/12/06	2A	ID & Ref.	SN over nest	*Leioproctus boltoni*	3	♂♂		NH	14/12/06
12/12/06	1G	ID & Ref.	SN over nest	*Leioproctus boltoni*	12	♂♂		NH	14/12/06
12/12/06	10	ID & Ref.	BV over pohutukawa	*Leioproctus pango*	1		♀	NH	14/12/06
12/12/06	9	ID & Ref.	SN over pohutukawa	*Leioproctus boltoni*	1	♂		NH	14/12/06
12/12/06	9	ID & Ref.	SN over pohutukawa	*Leioproctus pango*	8	♂♂		NH	14/12/06
12/12/06	9	ID & Ref.	SN over pohutukawa	*Leioproctus pango*	1		♀	NH	14/12/06
12/12/06	1E	ID & Ref.	SN over kamahi	*Leioproctus pango*	3	♂♂		NH	14/12/06
12/12/06	1E	ID & Ref.	SN over kamahi	*Leioproctus boltoni*	1	♂♂		NH	14/12/06
28/12/06	5	ID & Ref.	SN over nest	*Leioproctus huakiwi*	78	♂♂		NH	14/12/06
28/12/06	5	ID & Ref.	SN over nest	*Leioproctus huakiwi*	1		♀	NH	14/12/06
28/12/06	5	ID & Ref.	SN over nest	*Leioproctus boltoni*	31	♂♂		NH	14/12/06
28/12/06	5	ID & Ref.	SN over nest	*Leioproctus imitatus*	4	♂♂		NH	14/12/06
28/12/06	5	ID & Ref.	SN over nest	*Leioproctus imitatus*	3		♀♀	NH	14/12/06
12/12/06	1E	ID & Ref.	SN over kamahi	*Leioproctus boltoni*	1	♂♂		NH	14/12/07

Appendix A3

Harmonic radar studies

Table A3.30 Studies using harmonic radar, target insects and antenna specifications (O'Neal et al. 2004)

Insect Studied			Antenna Tag		
Species	**Body mass (mg)**	**Dispersal Mode**	**Tag mass (mg)**	**Tag length (cm)**	**Reference Study**
Coleoptera					
Pterostichus melanarius	160	Walking	30 – 80	20	(Wallin & Ekbom 1988) (HDF)
Pterostichus cupreus	70	Walking	30 – 80	20	(Mascanzoni & Wallin 1986) (HDF)
Pterostichus niger	220	Walking	30 – 80	20	(Wallin & Ekbom 1994) (HDF)
Scarites quadricepts Harpalus pennsylvanicus	-		21- 26	8-16	(O'Neal et al. 2004) (HDF)
Lepidoptera					
Parnassius sminthius	350	Flying	0.4	8	(Roland et al. 1996) (HDF)
Malacosoma disstria	200	Flying	0.4	8	(Caldwell 1997) (HDF)
Erebia epipsodea	150	Flying	0.4	8	(Caldwell 1997) (HDF)
Diptera					
Arachnidomyia aldrichi	55 - 75	Flying	0.4	8	(Roland et al. 1996) (HDF)
Patelloa pachypyga	45 - 60	Flying	0.4	8	(Roland et al. 1996) (HDF)
Glossina morsitans morsitans	50	Flying	1	-	Riley et al. Unpublished (HSR)

Note: Harmonic direction finder (HDF) and Harmonic scanning radar (HSR) studies

Measurement records for each insect tested

Table A3.31 Measurement records

Collection	Species	Sex		Body length	Mt [g]	Pm [g]	Mb [g]	Mf [g]	Load mass [g]
BV entering nest	*L. boltoni*		♀	8.5	0.031	0.005	0.024	0.005	0.005
SN over kanuka	*L. boltoni*		♀	9	0.053	0.000	0.053	0.009	0.000
BV entering nest	*L. boltoni*		♀	9	0.082	0.005	0.043	0.007	0.005
BV entering nest	*L. boltoni*		♀	9	0.041	0.002	0.034	0.006	0.002
BV entering nest	*L. boltoni*		♀	9	0.039	0.006	0.030	0.005	0.006
BV entering nest	*L. boltoni*		♀	10	0.056	0.008	0.046	0.011	0.008
BV entering nest	*L. boltoni*		♀	10	0.097	0.006	0.057	0.009	0.006
BV exiting nest	*L. boltoni*		♀	10	0.055	0.000	0.042	0.009	0.009
BV exiting nest	*L. boltoni*		♀	10	0.051	0.000	0.039	0.008	0.009
BV entering nest	*L. boltoni*		♀	11	0.057	0.007	0.051	0.011	0.007
BV exiting nest	*L. boltoni*		♀	11	0.096	0.000	0.060	0.013	0.031
BV exiting nest	*L. boltoni*		♀	11	0.056	0.000	0.044	0.008	0.009
BV exiting nest	*L. boltoni*		♀	12	0.080	0.000	0.062	0.010	0.012
BV exiting nest	*L. boltoni*		♀	12	0.081	0.000	0.067	0.016	0.008
BV exiting nest	*L. boltoni*		♀	12	0.063	0.000	0.047	0.008	0.013
BV exiting nest	*L. boltoni*		♀	13	0.078	0.000	0.056	0.008	0.017
BV exiting nest	*L. huakiwi*	♂		7	0.037	0.000	0.010	0.001	0.0026
SN over kanuka	*L. huakiwi*	♂		7.5	0.033	0.000	0.033	0.003	0.0000
BV exiting nest	*L. huakiwi*	♂		8	0.038	0.000	0.026	0.004	0.0105
BV exiting nest	*L. huakiwi*	♂		9	0.012	0.000	0.010	0.003	0.0008
BV exiting nest	*L. huakiwi*	♂		9	0.030	0.000	0.023	0.004	0.0048
BV exiting nest	*L. huakiwi*			9	0.016	0.000	0.015	0.003	0.0010

Table A3.31 Measurement records continued.

Collection	Species	Sex		Body length	Mt [g]	Pm [g]	Mb [g]	Mf [g]	Load mass [g]
SN over kanuka	*L. imitatus*	♂		7	0.036	0.000	0.036	0.005	0.000
SN over kanuka	*L. imitatus*	♂		7.5	0.023	0.000	0.023	0.003	0.000
SN over kanuka	*L. imitatus*		♀	8	0.038	0.000	0.038	0.007	0.000
SN over kanuka	*L. imitatus*	♂		8	0.044	0.000	0.044	0.006	0.000
SN over kanuka	*L. imitatus*	♂		8	0.033	0.000	0.033	0.004	0.000
SN over kanuka	*L. imitatus*	♂		8	0.033	0.000	0.033	0.005	0.000
BV entering nest	*L. imitatus*		♀	8.5	0.042	0.005	0.043	0.007	0.005
SN over kanuka	*L. imitatus*		♀	8.5	0.061	0.003	0.028	0.009	0.003
SN over kanuka	*L. imitatus*		♀	9	0.049	0.000	0.049	0.008	0.000
SN over kanuka	*L. imitatus*	♂		9	0.030	0.000	0.030	0.005	0.000
SN over kanuka	*L. imitatus*		♀	9	0.043	0.001	0.021	0.004	0.001
SN over kanuka	*L. imitatus*		♀	9	0.047	0.003	0.023	0.008	0.003
SN over kanuka	*L. imitatus*		♀	9	0.052	0.002	0.029	0.009	0.002
SN over kanuka	*L. imitatus*		♀	9.5	0.053	0.000	0.053	0.009	0.000
SN over kanuka	*L. imitatus*		♀	9.5	0.030	0.000	0.030	0.005	0.000
SN over kanuka	*L. imitatus*	♂		9.5	0.043	0.000	0.043	0.007	0.000
BV entering nest	*L. imitatus*		♀	9.5	0.069	0.001	0.032	0.009	0.001
BV entering nest	*L. imitatus*		♀	9.5	0.034	0.005	0.027	0.008	0.005
BV entering nest	*L. imitatus*		♀	9.5	0.060	0.006	0.045	0.008	0.006
SN over kanuka	*L. imitatus*		♀	9.5	0.050	0.002	0.026	0.009	0.002
SN over kanuka	*L. imitatus*		♀	9.5	0.047	0.002	0.027	0.008	0.002
SN over kanuka	*L. imitatus*		♀	9.5	0.047	0.001	0.025	0.007	0.001
SN over kanuka	*L. imitatus*		♀	10	0.057	0.000	0.057	0.007	0.000
BV entering nest	*L. imitatus*		♀	10	0.067	0.005	0.043	0.008	0.005
BV entering nest	*L. imitatus*		♀	10	0.097	0.001	0.039	0.008	0.001
SN over kanuka	*L. imitatus*		♀	10	0.064	0.001	0.029	0.009	0.001
SN over kanuka	*L. imitatus*		♀	10	0.051	0.003	0.026	0.008	0.003
SN over kanuka	*L. imitatus*		♀	10	0.061	0.001	0.032	0.009	0.001

Table A4.31 Measurement records continued.

Collection	Species	Sex		Body length	Mt [g]	Pm [g]	Mb [g]	Mf [g]	Load mass [g]
SN over kanuka	*L. imitatus*		♀	10	0.057	0.001	0.030	0.009	0.001
SN over kanuka	*L. imitatus*		♀	10	0.052	0.001	0.027	0.008	0.001
BV entering nest	*L. imitatus*		♀	10.1	0.055	0.001	0.029	0.007	0.001
SN over kanuka	*L. imitatus*		♀	10.5	0.047	0.000	0.047	0.008	0.000
SN over kanuka	*L. imitatus*		♀	10.5	0.047	0.000	0.047	0.008	0.000
SN over kanuka	*L. imitatus*		♀	10.5	0.046	0.000	0.024	0.007	0.000
BV entering nest	*L. imitatus*		♀	11	0.067	0.000	0.067	0.010	0.000
BV entering nest	*L. imitatus*		♀	11	0.071	0.003	0.041	0.007	0.003
BV entering nest	*L. imitatus*		♀	11	0.092	0.003	0.051	0.010	0.003
BV entering nest	*L. imitatus*		♀	11	0.060	0.007	0.057	0.009	0.007
BV entering nest	*L. imitatus*		♀	11	0.070	0.009	0.058	0.008	0.009
BV entering nest	*L. imitatus*		♀	11.5	0.068	0.013	0.056	0.009	0.013
BV entering nest	*L. imitatus*		♀	11.5	0.063	0.006	0.057	0.009	0.006
BV entering nest	*L. imitatus*		♀	11.5	0.050	0.006	0.041	0.007	0.006
BV entering nest	*L. paahaumaa*		♀	10.5	0.048	0.004	0.038	0.010	0.004
BV entering nest	*L. paahaumaa*		♀	11	0.047	0.000	0.047	0.010	0.000
BV entering nest	*L. paahaumaa*		♀	11	0.031	0.000	0.031	0.009	0.000
BV entering nest	*L. paahaumaa*		♀	11	0.043	0.003	0.034	0.009	0.003
BV entering nest	*L. paahaumaa*		♀	11	0.039	0.004	0.031	0.008	0.004
BV entering nest	*L. paahaumaa*		♀	11	0.048	0.005	0.038	0.008	0.005
BV entering nest	*L. paahaumaa*		♀	11.5	0.038	0.005	0.032	0.008	0.005
SN over kanuka	*L. pango*	♂		7	0.015	0.000	0.015	0.002	0.000
BV entering nest	*L. pango*		♀	7	0.024	0.004	0.024	0.004	0.004
SN over kanuka	*L. pango*	♂		7.5	0.017	0.000	0.017	0.004	0.000