Competition between native bees and honey bees on mānuka flowers in New Zealand

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Abstract

Humans have introduced the European subspecies of the Western honey bee (*Apis mellifera*) to every other continent except Antarctica, resulting in the presence of this generalist forager many ecosystems that honey bees are not native to. The impacts of introduced honey bees on these ecosystems are still not well understood. Honey bees were introduced to New Zealand in 1839, and are common visitors to native flowers throughout the country. As honey bees are generalist flower visitors and can present at high abundances, they could potentially be competing with and displacing native flower visitors. The aim of this study was to investigate interactions and possible competition between European-derived honey bees (*A. mellifera* sspp.) and native bee species (*Leioproctus* spp) for mānuka (*Leptospermum scoparium*) floral resources in New Zealand. I assessed a) temporal overlap in activity, b) abundances across time of day, and c) foraging behaviours of honey bees and *Leioproctus* bees. In a combination of field observations and behaviour experiments I found that a) temporal niche partitioning occurs daily and seasonally and b) both *Leioproctus* sp and honey bees display behavioural changes in the presence of the other. My observations suggest that competition does occur between honey bees and *Leioproctus* sp and that both alter their foraging behaviour and activity to reduce this competition. However, more research is required to assess this interspecific competition is great enough to adversely affect either species. Evidence-based understanding of the impacts of honey bees in native ecosystems is critical to our ability to improve honey bee management strategies and/or mitigate adverse effects of honey bee competition to endemic species where honey bees have been introduced.

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Table of Contents

List of Figures

List of Tables

CHAPTER ONE

General Introduction

Organisms require specific resources to survive, reproduce, and pass their genes to the next generation. However, resources are finite, and are unable to sufficiently ensure the survival of all organisms (Darwin, 1859). When organisms with overlapping resource requirements occur within the same ecosystem they must compete for those limited resources to survive and reproduce (Darwin, 1859). There are two categories of ‘real’ competition, interference and exploitation (Holomuzki et al., 2010). An additional, third competition type, ‘apparent competition’, has been described but is not classified as ‘real’ competition (Holomuzki et al., 2010).

Interference competition occurs when an individual/species *directly* impacts the resource-obtaining ability of other individual/species by reducing the ability of the competitor to make use of the shared resource (Holomuzki et al., 2010). This interference involves some form of behavioural or chemical interaction prior to actual use of the resource (Holomuzki et al., 2010), such as aggressive behaviour of lions, *Panthera leo,* facilitating the kleptoparatism of killed prey from spotted hyenas, *Crocuta crocuta*. Prey species represent a shared resource of both lions and hyenas. In this scenario, the aggressive behaviour of the lions directly interferes with the hyenas’ access to the prey, and could impact the fitness of the hyena population if it occurred frequently (Trinkel & Kastberger, 2005).

In contrast, exploitation competition occurs when an individual *indirectly* impacts the resource-obtaining ability of other individuals by reducing the availability of the shared resource (Holomuzki et al., 2010). Revisiting the lion – hyena dynamic: exploitation competition occurs when the prey population is reduced in size as lions hunt and feed. Consequently, this reduces the available prey for hyenas and could therefore lead to a decrease in the spotted hyena population (Hayward & Slotow, 2009).

Apparent competition occurs when individuals do not directly compete for resources, but affect each other indirectly because they are preyed upon by the same predator (Holomuzki et al., 2010). Due to the complexity of multi-species, indirect interactions in changing environmental conditions that often occur at the scale of populations and over long timeframes, apparent competition can be difficult to assess (Frank van Veen et al., 2006). Population dynamics of moose, *Alces americanu*, white-tailed deer, *Odocoileus virginianu,* and gray wolves, *Canis lupus*, illustrate apparent competition (Barber-Meyer & Mech, 2016). Moose and white-tailed deer are both preyed upon by wolves, and their respective population sizes can affect the predation rates of the other, in that if the white-tailed deer population decreases it may lead to increased moose predation by wolves. Conversely, if the white-tailed deer population increases it may lead to reduced moose predation rates. However, over time, a large white-tailed deer population could support an increase in the gray wolf population, thereby increasing moose predation rates to sustain the larger wolf population (Mumma et al., 2018).

Indicators of Competition

Competition comes at a cost to all organisms involved and that cost increases as the specificity of the niche and/or extent of the resources overlap increases (Abrams, 1984; Traveset & Richardson, 2006). Therefore, individuals/species often develop strategies to reduce energetic costs and negative effects of competition, such as temporal niche partitioning, spatial partitioning, and behavioural changes (Grant & Grant, 2006; Hughes & Tanner, 2000). These strategies are often more readily observable than the complex, population-level effects of competition, and can provide valuable insight into the competitive interactions that are likely at play in the environment.

Temporal niche partitioning

Temporal niche partitioning is when individuals/species undergo competing activities at different times to reduce competition (Hu et al., 2016). This may include having differing activity periods over seasons, diurnally/nocturnally, or hourly. Looking again at the lion – hyena dynamic, interference competition is greatly reduced by temporal niche partitioning. Lions are active mainly during the day and hyenas are more active during the night. This avoidance of a temporal overlap reduces the negative effects of interference competition (Hayward & Slotow, 2009; Oriol-Cotterill et al., 2015).

Spatial niche partitioning

Spatial niche partitioning is when individuals/species divide the available space or habitat within a community to reduce competition for resources and increase the potential of coexistence (Schoener, 1974). This can occur across a range of scales and areas within a habitat for example, differing nesting depths in ant communities (Hölldobler & Wilson, 1990), differing foraging heights on trees of warbles foraging for insects of North American warblers (Morse, 1989) or preferential flower species selection of different species of honey bees in India (Young et al., 2021). The avoidance of spatial overlap can reduce the negative effects of both interference and exploitative competition (Nelson et al., 2007; Petroelje et al., 2021; Thorp, 1976).

Behavioural changes

When individuals change their behaviour in direct response to interspecific interactions, this can indicate likely competition occurring between the species. Competition can reduce access to resources and drive species towards temporal/spatial partitioning. This can be exemplified in the mammalian community in a study by Garvey et al. (2015) which shows how stoats harvested less food exhibiting both spatial and temporal avoidance behaviour in the presence of a larger competitor (feral cat). In the pollinator community an study by Balfour et al. (2015) also exemplifies this by showing how the presence of a superior competitor (bumble bee) causes a behavioural response to honey bee foraging behaviours including time spent on patch, flower handling time, interval between probed flowers, proportion of inter-flower flights and flowers rejected. Investigating indicators of competition observationally can be more difficult without the control of the experimental approach, however with rigorous study design and replication one can gain the opportunity to assess the response in a more realistic environment.

Competition between Native and Introduced Species

Competitive interactions can occur when exotic species are introduced and establish in a naïve ecosystem (Richardson et al., 2000). Invasion by exotic species is considered one of the most important threats to conservation and biodiversity globally (Blackburn et al., 2011; Dyer et al., 2017; Early et al., 2016; McGeoch et al., 2010; Pimentel et al., 2000; Schröter et al., 2005; Schweiger et al., 2010; Veldtman et al., 2011; Vilà et al., 2011; Vitousek et al., 1996; Ziska et al., 2011). Invasive species alter the dynamics of native ecosystems via competitive, parasitic, and predatory interactions with native species, habitat alteration, disease vectoring, and/or hybridisation with native species. Ultimately, the impacts of the invasive species threaten the stability of the ecosystem they were introduced into (Pyšek et al., 2012; Traveset & Richardson, 2006; Vilà et al., 2011; Vitousek et al., 1996; Wittenberg & JW Cock, 2001).

The ability of an introduced species to establish in a new ecosystem, and the degree of its impact is a complex interplay of biotic and abiotic influences (Mack & D'Antonio, 1998; Rejmánek & Pitcairn, 2002). Successful invasive species often have an inherent competitive advantage over native species that they are competing with for resources. The introduced species can often secure sufficient resources to successfully establish in the new environment. In the case of the introduction of red-eared sliders, *Trachemys scripta elegans*, into the Spanish terrapin's, *Marelys leprosa*, native range, basking locations were identified as a limiting resource. Red-eared sliders employ their larger size and aggressive behaviour to directly interfere with the Spanish terrapin's access to preferential basking locations (Polo-Cavia et al., 2010). Similarly, the Eastern gray squirrel, *Sciurus carolinensis*, is better able to acclimatise to human development and is able to outcompete native squirrel species for food and territory in Washington, United States (Western gray squirrel, *Sciurus griseus*) and the United Kingdom (Eurasian red squirrel, *Sciurus vulgaris*) (Adams-Wright, 2022; Bryce et al., 2001; Gurnell et al., 2004; Ingles, 1950; Ryan & Carey, 1995; Wauters et al., 2000). In these examples, the natural attributes of the introduced species give the invaders a competitive advantage over the native species which can lead to large scale population declines in native species.

Global Distribution of Honey Bees

Western honey bees, *Apis mellifera*, are native to Europe, Africa, and the Middle East. Several European subspecies of *A mellifera*, notably *A. m. ligustica*, *A. m. mellifera*, and *A. m. carnica*, have been distributed globally by humans and are now established on every continent except Antarctica (Mortensen et al., 2013). Beyond their native ranges there has been substantial genetic admixture of the European subspecies of honey bees, that are more accurately defined as 'European-derived' honey bees, *A. mellifera* sspp. (Sheppard, 1989). For conciseness, European derived honey bees will be referred to simply as 'honey bees' throughout this thesis.

Honey bees do not naturally occur in New Zealand. Honey bees were brought to New Zealand in 1839, and thereafter spread throughout the country as both managed and feral colonies. In 2001, a parasite of honey bees, *Varroa destructor*, was introduced to New Zealand (Beard, 2015; Gillingham, 2012). The accidental introduction of *V. destructor* has reduced the fitness and stability of the feral honey bee population in New Zealand, however, numbers of managed honey bee colonies have continued to grow (from ~380,000 colonies in 2010 to ~900,000 managed colonies in 2020 (MPI, 2012, 2021). This marked increase in colony numbers can be largely attributed to increased demand for the honey made from the nectar of mānuka (*Leptospermum scoparium*) trees (Lloyd et al., 2017).

Environmental Impacts of Introduced Honey Bees

It is somewhat contested as to whether honey bees are considered invasive or naturalised, the latter not having the characteristic negative ecological impacts of invasive species, and the debate is complicated by the clear economic value of honey bees via honey production and pollination of agricultural crops (Cunningham et al., 2022; Moritz et al., 2005; Zhao et al., 2023). Critical to the designation of a species as invasive versus naturalised is an understanding of the nature of the impact(s) that honey bees have on the native environment into which they have been introduced (Huryn, 1997; Paton, 1993; Sugden et al., 1996).

The carrying capacity of the native ecosystems in New Zealand are a point of concern for beekeepers, landowners and ecologists. However, empirical studies of the impacts of introduced honey bees on native ecosystems are limited, with the focus overwhelmingly biased towards the agricultural and economic benefits (Donovan, 1990; Goodwin, 2012; Goodwin et al., 2013; Howpage et al., 2001; Newstrom-Lloyd, 2013; Palmer-Jones & Forster, 1965; Pattemore, 2013).

Native Species of Bees in New Zealand

Honey bees are just one of over 20,000 bee species globally, the majority of which are solitary (>90%) and show a high degree of endemism (Danforth et al., 2006; Delaplane & Mayer, 2000; Michener, 2000). New Zealand hosts 32 species of native bees: 26 endemic (are not found outside of their specific location in New Zealand), one indigenous (can be found naturally occurring elsewhere), and five adventive (population may not be self-sustaining) (Crees & Turvey, 2015; Donovan, 2007; Frank & McCoy, 1995). All of the bee species native to New Zealand have solitary life cycles and fall into three genera – *Leioproctus, Lasioglossum*, and *Hylaeus* (Delaplane & Mayer, 2000; Donovan, 2007). Most of New Zealand's bees are *Leioproctus* species (17 endemic species), and like honey bees, *Leioproctus* spp. obtain critical nutrients from nectar and pollen (Donovan, 2007); Danforth et al., 2006; Delaplane & Mayer, 2000; Donovan, 2007; Grimaldi & Engel, 2005; Michener, 2000) In solitary species, every female is fertile and creates their own nest for their young. As there are no other supporting insects or a worker class, there is no division of labour that occurs, and all tasks required are undertaken by each individual female (Donovan, 1980).

Female solitary bees create a blind tunnel nest in the ground or wood. In these tunnels the female will create cells where she lays individual eggs and provides these cells with the nectar and pollen that the larva requires for development. She then seals the cell and has no further contact with her offspring, and only lives for one season (Donovan, 2007). *Leioproctus* spp. overwinter as a diapausing prepupae in cells within nests. When spring arrives, the prepupa develops into an adult bee, which emerges from the nest between September and December. Adult bees will then begin to forage and mate. While the female begins nesting, males continue with mating attempts. The female individually builds cells and provides each cell with nectar and pollen. It lays a single egg in each cell and seals the entrance. It takes three days for eggs to hatch into small larvae which, over the next 10 days, consume all of the stored food. Within 30 days of oviposition, larvae become prepupae which then diapause until the following spring (Donovan, 1980).

Competition for nesting resources

In contrast to solitary native bees, honey bees are eusocial insects, which is characterised by bees living in a colony, cooperative brood care and a division of labour into reproductive and non-reproductive adults. The colony is made up of a mother (queen) and daughters (workers). The queen is the reproductive adult, while workers carry out the majority of the colony care. While most solitary bees are fossorial, which means they dig nests in the ground, European honey bees are cavity-nesters and construct large hives in natural cavities, particularly in old tree hollows. So, honey bees and solitary bees don't compete for nesting sites, but rather for floral resources. In addition, human beekeeping practices have developed over thousands of years (Gupta et al., 2014) to create artificial hives that simulate natural cavities, but that are transportable, easy to manage, and promote successful inhabitation. This means that honey bees can be readily moved into new areas to exploit floral resources without the need to find a suitable nesting site (Saunders et al., 2021). Native solitary bees are anchored in place due to the location of nesting sites, and they can only forage within flight distance of these sites.

Competition for nutritional resources

Pollinators typically change their foraging behaviour in response to competition, and this behaviour change can be used as an indicator of competition. For example, Balfour et al. (2015) found that excluding superior competitors (bumblebees) saw significant effects on honey bee foraging behaviours, including time spent on a patch, flower handling time, interval between flowers, proportion of inter-flower flights and flowers rejected. Additionally, Balfour et al. (2013) showed that honey bees also showed an avoidance of a preferential foraging source (lavender) in the presence of superior competitors (bumblebees), even when at much higher abundance. Honey bees' natural attributes, such as generalist foraging behaviour and resource hording, often afford a competitive advantage, enabling them to thrive across a range of diverse ecosystems (Goulson, 2003; Gross, 2001; Huryn, 1997; DR Paini, 2004). Therefore, we could expect honey bees to be the dominant or superior competitors when competing with native bees for nutritional resources.

Mānuka

Mānuka (*Leptospermum scoparium*) is one of the most important indigenous shrub species in New Zealand (Stephens et al., 2005). Mānuka has always been of significant value to indigenous Māori, however, since European colonisation the perceived value of mānuka has transitioned from being considered a pasture pest species to having a high economic and ecological value due to the documented medicinal value of the honey that is produced by honey bees from its nectar (Stephens et al., 2005).

Mānuka ranges from a semi-prostrate shrub up to a 12m tall tree and is likely the most widely distributed, abundant and environmentally-tolerant member of the New Zealand indigenous woody flora (Ronghua et al., 1984). It is found throughout the two main islands (North Island and South Island) and its distribution extends from the Three Kings Islands in the north (34˚ 10'S) to Stewart Island in the south (47˚ S) (Allan, 1961). Mānuka occurs from sea level up to altitudes near the regional tree line and is most commonly found as uniformly-aged stands in moist forested regions (Baylis, 1951; Baylis, 1958; Burrows, 1973; Cockayne, 2011; Elder, 1959; Esler & Astridge, 1974; Mark et al., 1964). Mānuka provides two main roles in New Zealand vegetation, as a dominant climax species in extreme environments (such as cliffs or geothermal areas), or as a pioneer species that establishes readily on poor-quality soils such as slip scarps (Burrows, 1973; Wardle, 2001). As a result of the major agricultural land clearance that has occurred in New Zealand, mānuka has been able to greatly expand in extent and dominance (Wardle, 1963, 1991, 2001).

Mānuka has small white flowers classified as open-access with a dish/bowl shape and is visited by a range of insect pollinators (Newstrom & Robertson, 2005). Included in this list of insect pollinators are native bees, flies and moths as well as introduced honey bees (Butz Huryn, 1995; Newstrom & Robertson, 2005). A large proportion of insect-pollinated flora in New Zealand has unostentatious coloured flowers, which has been attributed to the lack of specific insect associations (Godley, 1979; Lloyd, 1985; Wardle, 1991). The mānuka flower blooms annually for approximately 6 weeks and is usually region-specific starting in the north of New Zealand and moving south over the Spring/Summer period (Adcock, 1962; Molan, 2011; Russell et al., 1990).

Mānuka has seen a dramatic change of fortune due to its increased economic and conservational value. The increase in economic value has been driven by the health benefits associated with mānuka honey and other mānuka products (Adams et al., 2009; Lis-Balchin & Hart, 1998; Lis-Balchin et al., 2000; Molan & Rhodes, 2015; Reichling et al., 2005; Weston et al., 1999). The increase in the conservation value can be associated with a recent shift towards restoration of native habitats and mānuka's natural role as a pioneer species which has made the species a prime candidate for early planting efforts. This substantial investment is now driving an increase in demand for research on mānuka and its ecosystems, with stakeholders chasing increased efficacy and return on investment (Hamilton et al., 2013; Marden et al., 2020; McPherson, 2016; Millner et al., 2016; Pizzirani et al., 2019; Timmins et al., 1988). Current popular research areas focus on the medicinal properties of mānuka, mānuka horticulture, and mānuka ecosystems. Our understanding of plant-pollinator relationships of mānuka is comparably still in its infancy, however, the recent increase in demand for mānuka honey has sparked increased interest in the field from both conservation and honey production perspectives.

Value of mānuka honey

Mānuka honey has seen a significant increase in value in recent years. The price of bulk mānuka honey in 2011/2012 season ranged from $8.50 – $45.00 per kilogram, and this price increased, peaking to $12.00 – $148.00 per kilogram in the 2015/2016 season (MPI, 2021). This period spurred on significant investment and expansion in the industry. This financial investment in New Zealand's honey industry has logically driven expansion and a corresponding significant increase in the number of honey bee colonies managed in New Zealand. Between 2012 and 2022 the number of registered honey bee colonies rose from 420,000 to 730,000 (74% increase) which peaked in 2019 at 920,000 colonies (120% increase) (MPI, 2012, 2021). Although the market has cooled more recently, much of the investment remains in infrastructure and more visually, honey bee hives bringing the industry more into the eye of the public.

One concern that has been raised is the potential impacts of increased honey harvesting on New Zealand's native pollinators which typically rely on the pollen and nectar in native ecosystems. Since 2012, we have observed a 47% increase in annual of honey exports with 10,300 ton exported in 2023, with 61% (6300 ton) of exported honey being attributed to mānuka honey (MPI, 2012, 2022). Mānuka stands are monocultural by nature and are normally the main floral resource available during their flowering period (Burrows, 1973). The impact of removing this important resource to native pollinators from their ecosystems is currently not well understood.

Honey bee management practices

Many beekeeping operations prioritise mānuka honey crops over other less valuable honey flows. Consequentially, a period of substantial adaptation in beekeeping management practices has occurred within the industry to maximise return on investment. For example, there have been changes to annual season schedule, increased colony transportation and managing stocking rates. The high value of mānuka honey has also seen increased competition within the industry. Between 2012 and 2022 there was a large increase from 3,800 to 10,000 in the number of beekeeping enterprises. The effect of stocking rates is difficult to investigate due to a combination of the fast-changing industry, honey bees’ wide foraging range, and regulation of stocking rates to areas remaining relatively unrestrictive. Additionally, beekeepers can be reluctant to share information regarding stocking rates in high-density mānuka areas.

Presented with anecdotal evidence of competitive beekeeping practices affecting honey yield, it is hard to ignore what impact these increased stocking rates might be having on native pollinators also foraging in mānuka-dense environments. Some of these adaptations provide reason for potential ecological concern, especially in the native pollinator space. Beekeepers targeting mānuka honey have made a range of adaptations to their historical annual cycle to maximise mānuka honey harvesting potential. Building and timing colony strength to ensure strong healthy colonies are ready to go into the high value mānuka flowering bloom at the cost of chasing lower value honey crops is now commonplace within the industry.

The mānuka flowering bloom is approximately 6 weeks long and starting in the North, moving South, the potential window for mānuka honey harvesters can last from early spring to late summer. Now financially viable, many beekeepers have adapted their practices by transporting honey bee colonies into multiple mānuka-dense ecosystems within a single season. This large-scale focus on mānuka-dense ecosystems has the potential to intensify any ecological impacts, which may have been occurring. Although these changes provide clear economic benefits, the understanding of the ecological impacts remain limited.

Thesis Outline

In this thesis I aim to investigate potential competition between honey bees and native bees in mānuka-dense ecosystems. To do this I used a combination of field observations and an experimental field approach to assess whether temporal niche partitioning and changes in foraging behaviour are occurring. Both of these are potential indicators of competition which could provide valuable information when considering the effects of the introduced honey bee on native ecosystems in New Zealand.

In **Chapter 2**, I used a field study to compare the abundance and behaviour of honey bees and native bees on mānuka crops to determine whether competition could be identified between these species. I was specifically interested in whether there was evidence of temporal niche partitioning and behavioural changes by either bee species in relation to the relative abundance of the other species.

In **Chapter 3**, I used an experimental field approach to assess the effect of native bee presence on the foraging behaviour of honey bees. My previous findings in **Chapter 2** suggested potential avoidance behaviour by honey bees and it was the purpose of this study to investigate the mechanism driving this potential behaviour.

Lastly in **Chapter 4**, I summarise the overall key findings from my thesis, the implications of my results in the context of honey bee management and native bee conservation and discuss possible limitations and future directions.

CHAPTER 2

Abundance and foraging behaviour of *Apis mellifera* and *Leioproctus* spp. on mānuka flowers

Abstract

Honey bees (*Apis mellifera*) effectively exploit new habitats, and, with human assistance, are present on every continent except Antarctica. The impact of introduced honey bees on native flora and fauna is driven by an industry which has experienced a recent period of significant growth. However, their potential impact is also complex when considering the economic benefits of honey bee pollination in productive landscapes and honey production, as well as considering potential negative impacts on native fauna. Interspecific competition for floral resources between introduced honey bees and native fauna is likely to occur with species that have similar resource requirements, traits and behaviours, such as native bee species. This study investigates the interactions between honey bees and native solitary bees (*Leioproctus* spp.*)* foraging on mānuka (*Leptospermum scoparium*) flowers in the Waikato. Honey bee and *Leioproctus* spp. foraging behaviours and potential competitive interactions were observed at the beginning, middle and end of the mānuka flowering season via focal insect observations with behavioural records made including flower visit details and insect interactions. I found that temporal niche partitioning may be occurring both daily and seasonally. Behavioural changes were also identified in response to both changes in honey bee abundance and native bee abundance. These behavioural changes were mainly seen in the native bees, however, honey bees also displayed a behavioural change in response to increase native bee presence. While these results suggest that competition is occurring between honey bees and native bees, much more investigation is required to fully understand the scope of the competition and its potential effects on the bees.

Introduction

Biological invasions involve the introduction of an exotic species, either intentionally or accidentally, and the spread of this species in the new environment to the detriment of native species and ecosystems. Biological invasions can have significant ecological and economic impacts and are one of the most important threats to biodiversity and conservation globally (Dyer et al., 2017; Early et al., 2016; McGeoch et al., 2010; Vilà et al., 2011; Vitousek et al., 1996). The introduction of new species can dramatically impact the native ecosystem, causing a change in the native species' composition or ecosystem functioning (Levine, 2008). These changes can arise through competition, predation, parasitism, disease vectoring, hybridisation, disruptions of mutualistic networks such as pollination and/or habitat alteration by invasive species (Pyšek et al., 2012; Traveset & Richardson, 2006; Vilà et al., 2011; Vitousek et al., 1996; Wittenberg & JW Cock, 2001).

Competition is a common impact of a biological invasions, and occurs most frequently between invasive species and native species that require the same resources (Chesson, 2000). Successful invaders typically have a competitive advantage over a native species that they are competing for resources with (Braks et al., 2004). The two main types of competition are interference competition and exploitation competition. Interference competition occurs when an individual/species directly impacts the resource-obtaining ability of other individuals/species, whereas exploitation competition is when an individual/species indirectly impacts the resource-obtaining ability of other individuals/species (Holomuzki et al., 2010). An example of interference competition is how the invasive red-eared slider turtle (*Trachemys scripta elegans*) directly reduces the resource-obtaining ability of the native endangered Spanish terrapin (*Mauremys leprosa)* through aggression and displacement when competing for basking sites (Polo-Cavia et al., 2010). On the other hand, in urban/suburban habitats throughout the Pacific, the invasive house gecko (*Hemidactylus frentaus*) exhibits superior insect harvesting ability which indirectly impacts the resource-obtaining ability of a native gecko, *Lepidodactylus lugubris,* by reducing the available food source and is an example of exploitation competition (Petren & Case, 1996). Competitive interactions between invasive and native species rarely occur in isolation and often different types of competition across a range of resources are occurring concurrently. Attempting to isolate and investigate an individual competitive interaction can be difficult, often requiring both observational and experimental approaches.

Investigating the presence and impact of invading species in relation to competition can be complex. An initial assessment of indicators or symptoms of competition can help to identify if there is competition occurring. For example, niche partitioning observed between invasive and native species that are potentially competing can indicate behavioural changes by the species to minimise interference competition (Culbertson & Herrmann, 2019; Hairston et al., 1987). Behavioural changes in species can also indicate exploitation competition. For example, female hoverflies, *Episyrphus balteatus*, were found to avoid preferred foraging sources in the presence of competitors (Jeavons et al., 2022). Invasive species often exhibit competitive advantages over native species and these advantages often put native species' populations at risk. It is therefore important to understand the relationships between invasive and any native species which could be at risk.

Western honey bees, *Apis mellifera*, are successful worldwide invaders. Natural attributes such as being generalist foragers, having a eusocial social system, and behavioural plasticity often provide them with competitive advantages over native pollinators and enable them to thrive in a wide range of habitats (Goulson, 2003; Gross, 2001; Huryn, 1997; DR Paini, 2004). Humans have also had a significant influence on the large scale spread of honey bees due to the economic value that honey bees provide via their honey production and pollination services. Today, honey bees inhabit every continent in the world except Antarctica (Mortensen et al., 2013), resulting in widespread impacts on local ecosystems. There is evidence for both negative and positive impacts of honey bees on native ecosystems. For example, honey bees can decrease native pollinator visitation rates to flowers through exploitative or interference competition, which can alter plant genetic structure and potentially negatively affect plant fitness (Celebrezze & Paton, 2004; Dick et al., 2003; Dupont et al., 2004; Gross & Mackay, 1998; Hansen et al., 2002; Huryn, 1997). Alternatively, honey bees can have positive impacts such as becoming a tool for native flora restoration (Hanna et al., 2013). To further exemplify the complexity to understanding the impact of introduced honey bees, there are cases where studies have presented contradictory results. In the review by Russo (2016) it was found that invasive honey bees can positively impact the pollination success of native plants by increasing resilience to human disturbance and climate change, encouraging scientific investigations through lab rearing and supplementing native plant pollination and even rescuing native plant species when their native pollinators are in decline, although their role in the decline of these native pollinators is unclear. The review also found that invasive honey bees can also negatively impact native plants through the alteration of pollination networks, genetic introgression through hybridisation and increasing pollination of exotic weeds leading to decreasing fitness of native species (Russo, 2016).

Honey bees were first documented as being introduced into New Zealand in 1839 and today they are widespread throughout the country (Beard, 2015; Gillingham, 2012). In 2010, New Zealand had 380,000 registered honey bee colonies which greatly increased in number to 900,000 in 2020 (MPI, 2021). This marked increase in colony number can be largely attributed to the significant increase in demand for the honey made from bees foraging on mānuka, *Leptospermum scoparium*, trees (Lloyd et al., 2017). Mānuka honey is prized for its medicinal qualities (Adams et al., 2009; Lis-Balchin & Hart, 1998; Lis-Balchin et al., 2000; Molan & Rhodes, 2015; Reichling et al., 2005; Weston et al., 1999), and its ability to attain premium prices spurring on a period of large investment and expansion in the New Zealand honey industry (Lloyd et al., 2017). The impact of this significant economic up-turn in the industry on New Zealand's native ecosystems are widely discussed anecdotally, however, studies into this impact are limited. Research into the effects of invasive honey bees in New Zealand has focused on impacts such as agricultural economic benefits and conservation benefits (Donovan, 1990; Goodwin, 2012; Goodwin et al., 2013; Howpage et al., 2001; Newstrom-Lloyd, 2013; Palmer-Jones & Forster, 1965; Pattemore, 2013). However, any potentially negative impacts of honey bees due to competition with native species remains mostly unknown.

New Zealand has 32 native bee species belonging to three genera, *Leioproctus, Lasioglossum*, and *Hylaeus*, all of which are solitary (Donovan, 2007). The requirement of New Zealand's native bees for nectar and pollen results in opportunity for competition with introduced honey bees. Indeed, many studies have observed both honey bees and native bees foraging on shared resources (Donovan, 1980; Howlett & Donovan, 2010; Howlett et al., 2015; Malone et al., 2010; Meiners et al., 2019). Competition between introduced honey bees and native bees has been observed in a number of other countries (Cornelissen et al., 2019; Kato et al., 1999; Dean Paini, 2004; Prendergast et al., 2021; Roubik & Wolda, 2001; Russo et al., 2021; Thomson, 2004). Previous research on honey bee/native bee competition has commonly focussed on resource harvesting, visitation rates and floral resource overlap which has been valuable in indicating potential competition (Page & Williams, 2023; DR Paini, 2004).

An early investigation into honey bee/native bee interactions in New Zealand indicated that some native bees had historically successfully competed against the honey bees (Donovan, 1980). Furthermore, the study suggested that due to this historical success, it was likely this success would continue (Donovan, 1980). This was based on honey bee preference for introduced flora and observations of native bees significantly out numbering honey bees during a honey flow (Donovan, 1980). However, at the time, this researcher was unable to predict the growth in the industry and some of their do not take into account contemporary honey bee management practices. For example, many honey bee hives are transported around the country and placed multiple times into the middle of high density mānuka stands to maximise mānuka honey harvesting. In many of these locations there are minimal alternative floral resources in bloom, which would stimulate increased competition. Additionally, anecdotal observations from beekeepers who target mānuka honey report that temporal niche partitioning may be occurring as native bees are observed as the main forager early in the mānuka nectar season, but it appears this switches to a majority of honey bee foragers later in the season. This suggests that competition may be occurring between honey bees and native bees. Although research is limited, some native bee species are now rare and some populations have shown significant declines which may suggest they are being outcompeted in some environments (Beard, 2015; Hart, 2007, 2016).

In this study, I aim to investigate whether competition can be identified between native bees and honey bees on mānuka. Mānuka is widely distributed all throughout New Zealand and grows abundantly across the country (Allan, 1961; Ronghua et al., 1984). As mānuka tends to grow in monoculture stands, it is the main floral resource available to honey bees and native bees during its flowering season (Burrows, 1973). Therefore, we would expect to see both honey bees and native bees foraging on mānuka and possibly competing for the mānuka floral resources. I selected the native bee *Leioproctus* spp. because of their larger size, widespread distribution and abundance, and a natural resource overlap with honey bees. To achieve this, I observed and compared the abundance and behaviour of honey bees and native bees foraging on seasonally flowering mānuka crops to test whether these change with the relative abundance of the competitor species. This study was undertaken on three sites which represent a range of honey bee densities at different stages of the flowering season. If competition is present, I predict temporal niche partitioning to be observed in the abundance surveys and/or behavioural changes by native bees in relation to the relative abundance of native bees and honey bees.

Methods

This study was undertaken over a two-month period, between December 2021 and January 2022. Each site was sampled at three different time periods, to approximately capture the beginning, middle and end of the mānuka flowering season. Each sampling period consisted of two days and each sampling day involved conducting insect abundance surveys, insect behavioural observations, environmental assessments and floral bloom assessments. Each sampling day occurred between 0900 and 1500 to capture the majority of the daily honey bee and native bee foraging activity.

Study sites

Three study sites (Figure 1) were chosen based on a set of criteria. Each site had to be made up of largely mānuka monoculture, located within the Waikato region and had either low, medium or high managed honey bee presence. Feral honey bee colonies are not considered in this study due to presumed current scarcity of feral honey bee colonies in New Zealand following the arrival of the parasitic mite V*arroa destructor*. The low-density honey bee site was located within the Ed Hillary Hope Reserve (Waitetuna, 37°50'02.9"S 175°04'07.3"E) and had no managed honey bee colonies located on the property, although low numbers of bees were foraging in the reserve from other managed colonies nearby. The medium density site was on Stubbs Farm (Waitomo, 38°15'47.3"S 175°01'06.1"E) and had 12 resident managed honey bee colonies. Lastly, the high-density site was located in the Rangitoto Station (Otorohanga, 38°20'26.0"S 175°26'20.2"E) and had no resident managed honey bee colonies, but during the mānuka flowering season, 80 colonies were moved into the site for honey collection. Each site was selected as a mānuka monoculture to limit the subject insects' ability to forage on alternative floral nectar crops. This was important as honey bees have been shown to preferentially forage on introduced flora (Donovan, 1980) and having alternative floral sources available would limit the study's ability to assess their interactions on monoculture ecosystems.

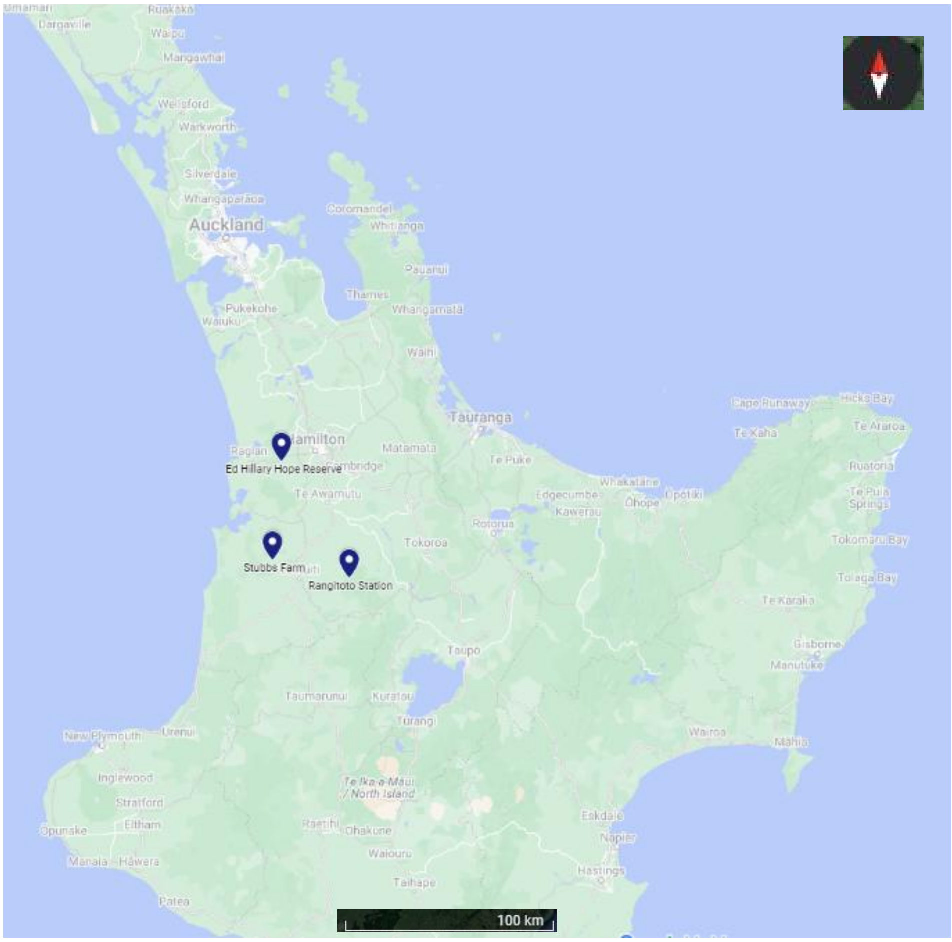


Figure 1: Map showing location of the three study sites in the Waikato region of North Island, New Zealand locations.

Transects

At each site a 20m transect was selected by locating an area with at least seven mānuka trees that lay along the transect. The transect was north facing to ensure that the transect was always sun facing throughout observation period. Flagging tape was used to mark transects to ensure they remained the same for each visit.

Insect abundance surveys

To gain an understanding of what type of foragers, how many foragers and when these foragers are foraging on mānuka flowers during the flowering season, insect abundance surveys were undertaken hourly. This involved identifying and quantifying the species of insect foraging on mānuka flowers in the area. During each survey I walked from the western end to the eastern end of the transect over a 2-minute period. During this walk, I identified and counted all honey bees and *Leioproctus* spp. on mānuka flowers along the transect. I made a concerted effort to avoid counting an individual bee multiple times during a single sampling period.

Individual bee behavioural observations

To assess whether the bees' behaviours changed as relative abundance levels changed, focal observations of honey bees and native bees were undertaken at each transect in-between the hourly abundance surveys. To undertake the behavioural observations, individual native bees and honey bees found foraging on mānuka flowers were randomly selected. For the individual observations I described and recorded the insect's activity using a voice recorder. Each observation started when the subject bee landed on a novel flower. I identified the bee to the species level where possible, with most native bees only identifiable to genus level while in flight, and continued to describe the subject's behaviours until the bee was lost, left the transect or reached the maximum observation length of five minutes. I described each behaviour as it happened, using short code words to create a timestamp for each behaviour. The behaviours recorded were flying, walking, flower visit, nectar foraging, grooming and displacement (intraspecific or interspecific). I made a conscious effort to keep an adequate distance (approximately >0.5 m) from the insects to avoid disturbing their natural behaviours, but remain close enough to accurately observe the behaviours (approximately <3.0 m). I attempted to observe a minimum of two native bees and two honey bees, or eight minutes of recording for each species, between each hourly insect abundance survey. Each individual observation was recorded and saved as an individual file which time-stamped the date and time. Individual insect observations were processed using the software package BORIS version 8.20.3. Information collected on each insect included: flower visit frequency, time spent visiting flower, flying frequency, time spent flying, walking frequency, time spent walking, nectar foraging success frequency, grooming occurrence frequency, interspecific displacement frequency, and intraspecific displacement frequency.

Environmental data

Insect activity can be influenced by environmental factors, therefore directly before each hourly insect abundance survey, potential environmental influences were recorded. Temperature (˚C) and relative humidity (%) were measured with a Kestrel 550 weather meter, light (W/m^2) was measured with a SOLARMETER Model 10.0, and cloud cover percentage (Oktas) was measured using a manual cloud cover assessment (Ahmad et al., 2017).

Floral bloom assessments

Flowering seasons are variable and influenced by a range of factors, which makes studying ecological behaviours based on this period difficult. Therefore, floral bloom assessments are vital for calibrating how far through the flowering season the mānuka trees are. Floral bloom assessments were undertaken once at 12:30 pm each sample day along the corresponding transect. A minimum of five randomly selected mānuka trees along the transect were photographed for assessment through a 1x1m square frame. Each tree was marked with flagging tape, and each floral bloom assessment was undertaken using the same trees at each of the three sampling periods. Visual estimates were made as to the percentage bloom of each tree with 0% being no flowering and 100% reflecting that all flowers were in bloom and an average taken across the photographed trees to provide a floral bloom percentage for the transect at the date assessed.

Statistical analysis

All statistical analysis were conducted using R statistical software (v4.3.1, R Core Team 2021).

To assess the abundance data, a generalised additive model (GAM) (Hastie, 2023) was used and a pairwise comparison was performed to assess the overall difference between honey bee and native bee abundance for the foraging period. Additionally, an abundance GAM was created for each site and time of season, and used to provide predicted abundance values for both honey bees and *Leioproctus* spp. corresponding to the date and time of each foraging behaviour. Four abundance metrics were chosen to assess the effects of abundance on honey bee and *Leioproctus* spp. foraging behaviours. These were *Leioproctus* spp. abundance, honey bee abundance, total abundance and, the log ratio of *Leioproctus* spp. to honey bees. Correlations between foraging behaviour data and abundance metrics were assessed using Pearson’s product-moment correlations.

Results

Abundance

I observed a total of 2,371 insects over 19 days during 176 abundance surveys across the three sites. Bees accounted for 90.2%, flies 9.3%, and wasps 0.5% of the total insects observed. *Leioproctus* spp. were most abundant at 70.1%, while honey bees made up 18.9% and bumblebees 1.2% of all the insects present. Overall, *Leioproctus* spp. were significantly more abundant than honey bees (Figure 2, Table 1). This trend was observed across most sites and stages of the season except for early and mid-season at Stubbs farm and late season at Rangitoto Station (Figure 3), where the abundances were not significantly different.

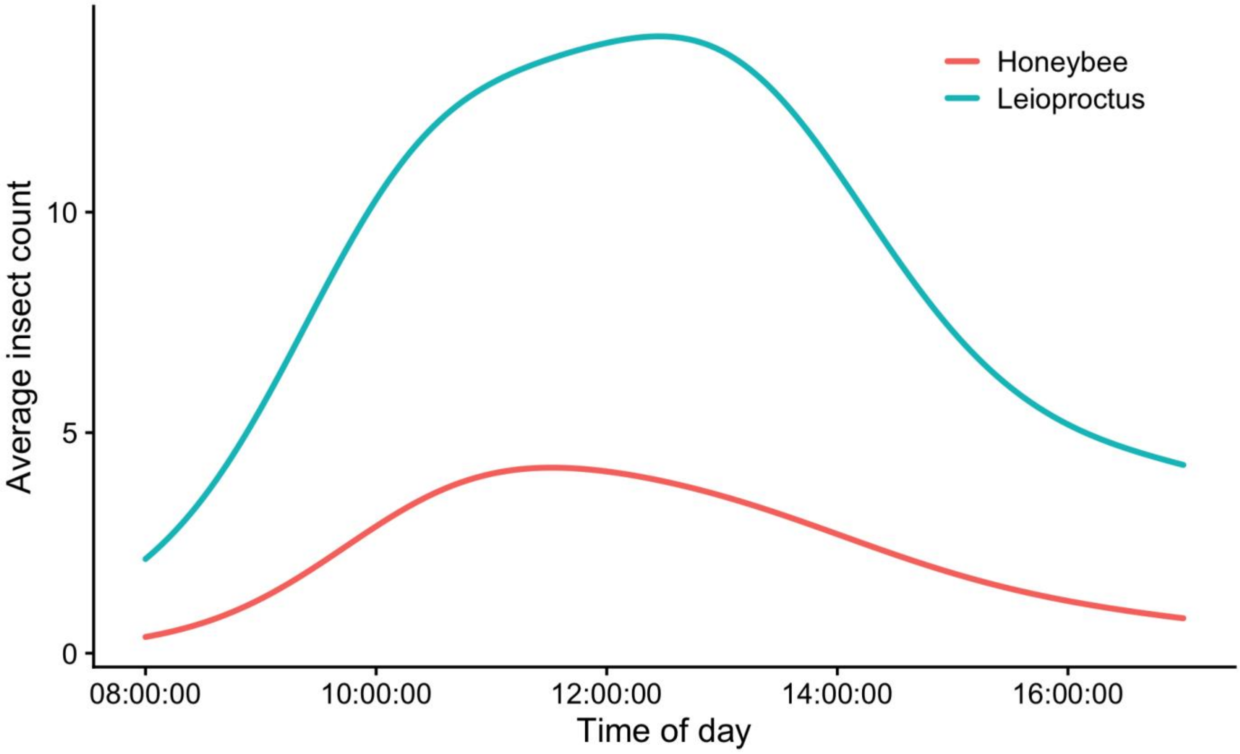


Figure 2: Average Leioproctus spp. and honey bee abundances over the time of day for all sites and stages of season.

Table 1: *Comparison of overall honey bee abundances and overall Leioproctus spp. abundances over the 9hr sampling periods.*

Contrast	ratio	SE	df	t-ratio	p-value
Honey bee / *Leioproctus*	0.294	0.026	341.137	-13.832	<0.001

Overall, *Leioproctus* spp. appeared to have a later daily peak abundance (~13:00 pm) than honey bees (~11:00 am) (Figure 2). When assessing *Leioproctus* spp. and honey bee peak abundances across site and season, there appeared to be differences in the time of day that they occurred, however there are no clear trends in this variation (Figure 3; Table 2; Table 3)

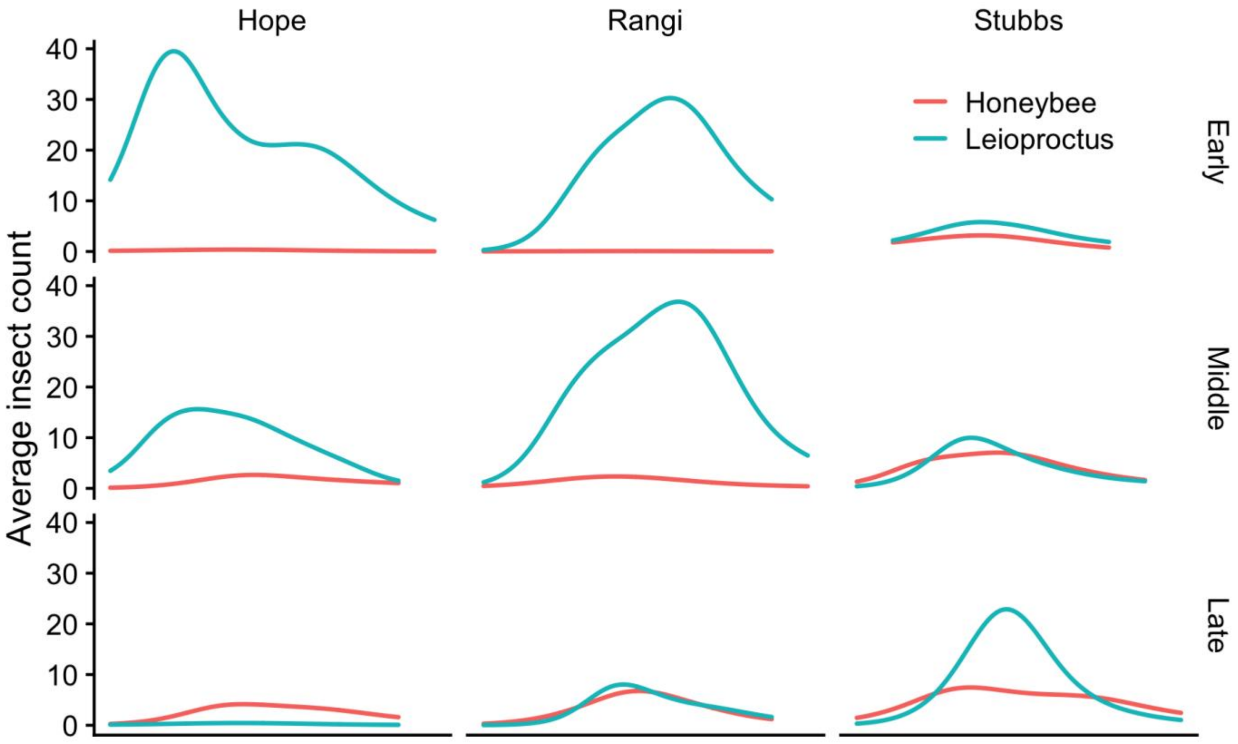


Figure 3: Average Leioproctus spp. and honey bee abundances over the time of day by site (Hope, Rangi, Stubbs) and stage of season (Early, Middle, Late). Hope was the low-density honey bee site, Rangi was the high-density site, and Stubbs was the medium-density site.

***Table 2**: Pairwise comparisons of the difference in abundance between honey bee and Leioproctus spp. at each site across the three sampling seasons. Lines in bold indicate significant differences (P<0.05).*

Season	Site	ratio	df	t-ratio	p-value
Early	**Hope**	**0.017**	**27.680**	**-6.565**	**<0.001**
	Rangi	**0.003**	**28.538**	**-5.050**	**<0.001**
	Stubbs	0.547	22.008	-1.958	0.063
Middle	**Hope**	**0.197**	**27.326**	**-5.143**	**<0.001**
	Rangi	**0.060**	**29.166**	**-9.268**	**<0.001**
	Stubbs	0.886	54.134	-0.617	0.540
Late	**Hope**	**9.386**	**21.461**	**3.509**	**<0.001**
	Rangi	0.828	39.869	-0.839	0.407
	Stubbs	**0.292**	**28.872**	**-5.875**	**<0.001**

Table 3: *Estimated time of daily peak abundance for Leioproctus spp. and honey bees by site and stage of season.*

Season	**Insect**	**Site**		
		Hope	**Rangi**	**Stubbs**
Early	*Leioproctus* spp.	9:30	13:30	11:30
	Honey bee	11:30	n/a	11:30
Middle	*Leioproctus* spp.	10:00	13:45	11:15
	Honey bee	11:45	11:45	11:45
Late	*Leioproctus* spp.	11:30	11:45	12:30
	Honey bee	11:30	12:30	11:00

Behaviour

I conducted a total of 590 insect behavioural observations, summing to 21.9 hours of observations. The average observation duration was 2 minutes and 13 seconds per insect. 63.2% of these observations were *Leioproctus* spp., with a total time of 11.6 hours at an average duration of 1 min and 52 seconds, while I observed honey bees for a total time of 10.3 hours at an average duration of 2 minutes and 50 seconds per individual.

Proportion of time travelling

The proportion of time spent travelling by *Leioproctus* spp. was significantly positively related to honey bee abundance, but was not significantly related to *Leioproctus* spp. abundance, total abundance of bees (combined) or the ratio of *Leioproctus* spp. to honey bees (Figure 4, Table 4). However, honey bee proportion of travelling time was not significantly affected by *Leioproctus* spp. abundance, honey bee abundance, total bee abundance or the ratio of *Leioproctus* spp. to honey bees (Figure 4, Table 4).

Table 4: *Effect of Leioproctus spp. abundance, honey bee abundance, total abundance and the ratio of Leioproctus spp. to honey bee on the proportion of time spent travelling of Leioproctus spp. and honey bees. Lines in bold indicate significant results (P<0.05).*

Predictor	Insect	Cor	t	df	p-value
Abundance: *Leioproctus*	*Leioproctus*	-0.071	-1.339	355	0.181
Abundance: Honey bee	***Leioproctus***	**0.271**	**5.305**	**355**	**<0.001**
Abundance: Total	*Leioproctus*	-0.002	-0.041	355	0.968
Ratio: *Leioproctus*: Honey bee	*Leioproctus*	0.024	0.460	355	0.646
Abundance: *Leioproctus*	Honey bee	0.019	0.275	211	0.783
Abundance: Honey bee	Honey bee	-0.110	-1.614	211	0.108
Abundance: Total	Honey bee	-0.014	-0.201	211	0.841
Ratio: *Leioproctus*: Honey bee	Honey bee	0.080	1.167	211	0.245

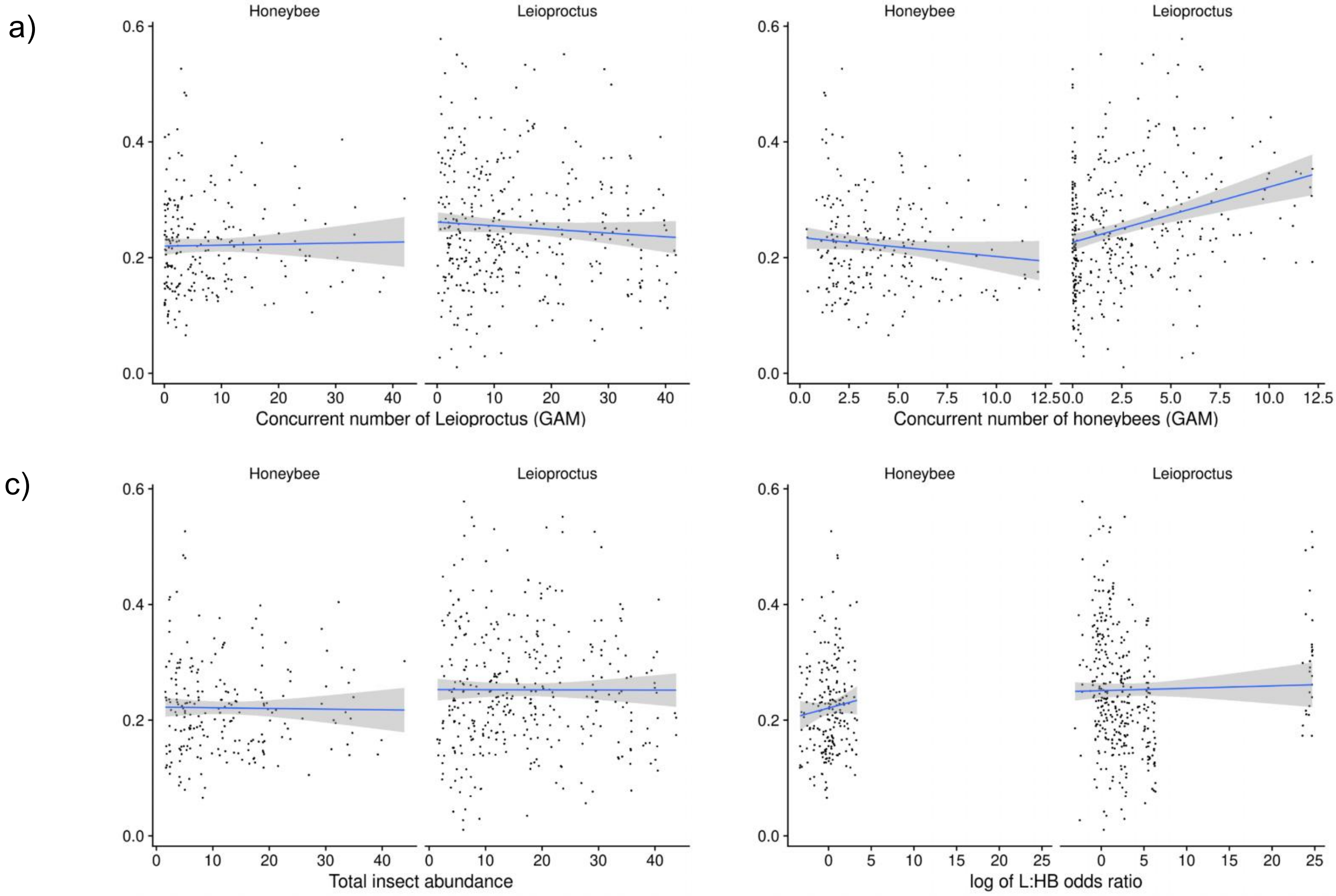


Figure 4: The effect of a) Leioproctus spp. abundance, b) Honey bee abundance, c) total abundance and d) the log ratio of Leioproctus spp. abundance to Honey bee abundance on the proportion of time spent travelling for both Leioproctus spp. and honey bees.

Proportion of time flying

The proportion of time spent flying by *Leioproctus* spp. was not significantly related to *Leioproctus* spp. abundance, total abundance or the ratio of *Leioproctus* spp. to honey bees but was significantly positively correlated with honey bee abundance (Figure 5, Table 5). Honey bee proportion of time flying was not significantly correlated with *Leioproctus* spp. abundance, honey bee abundance, total abundance or the ratio of *Leioproctus* spp. to honey bees (Figure 5, Table 5).

Table 5: *Effect of Leioproctus spp. abundance, honey bee abundance, total abundance and the ratio of Leioproctus spp. to honey bee on the proportion of time spent flying of Leioproctus spp. and honey bees. Lines in bold indicate significant results (P<0.05).*

Predictor	**Insect**	**Cor**	**t**	**df**	**p-value**
Abundance: *Leioproctus*	*Leioproctus*	-0.065	-1.233	355	0.218
Abundance: Honey bee	***Leioproctus***	**0.293**	**5.784**	**355**	**<0.001**
Abundance: Total	*Leioproctus*	0.010	0.185	355	0.853
Ratio: *Leioproctus*: Honey bee	*Leioproctus*	0.019	0.363	355	0.717
Abundance: *Leioproctus*	Honey bee	-0.025	-0.358	211	0.720
Abundance: Honey bee	Honey bee	-0.087	-1.272	211	0.205
Abundance: Total	Honey bee	-0.048	-0.705	211	0.482
Ratio: *Leioproctus*: Honey bee	Honey bee	0.019	0.283	211	0.778

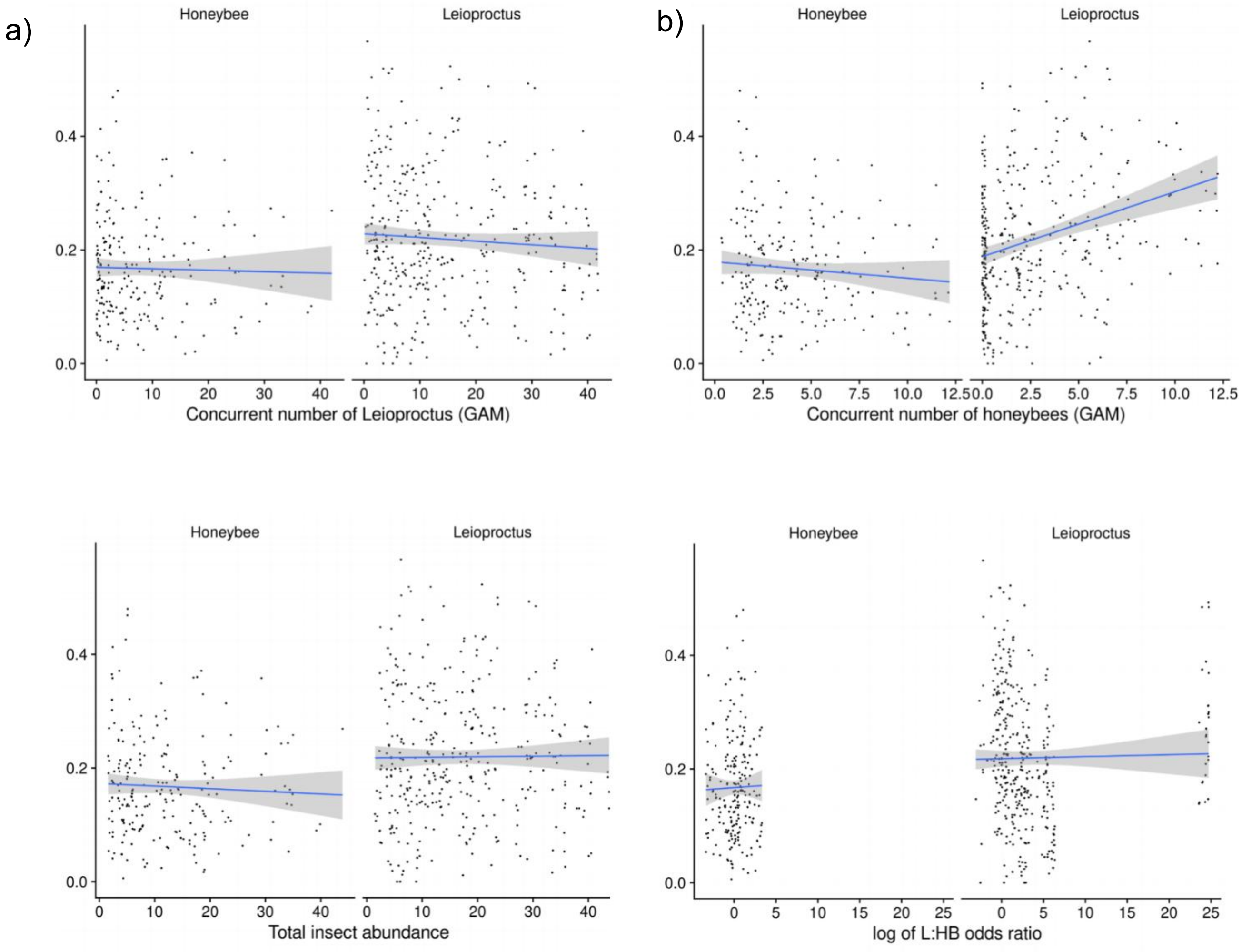


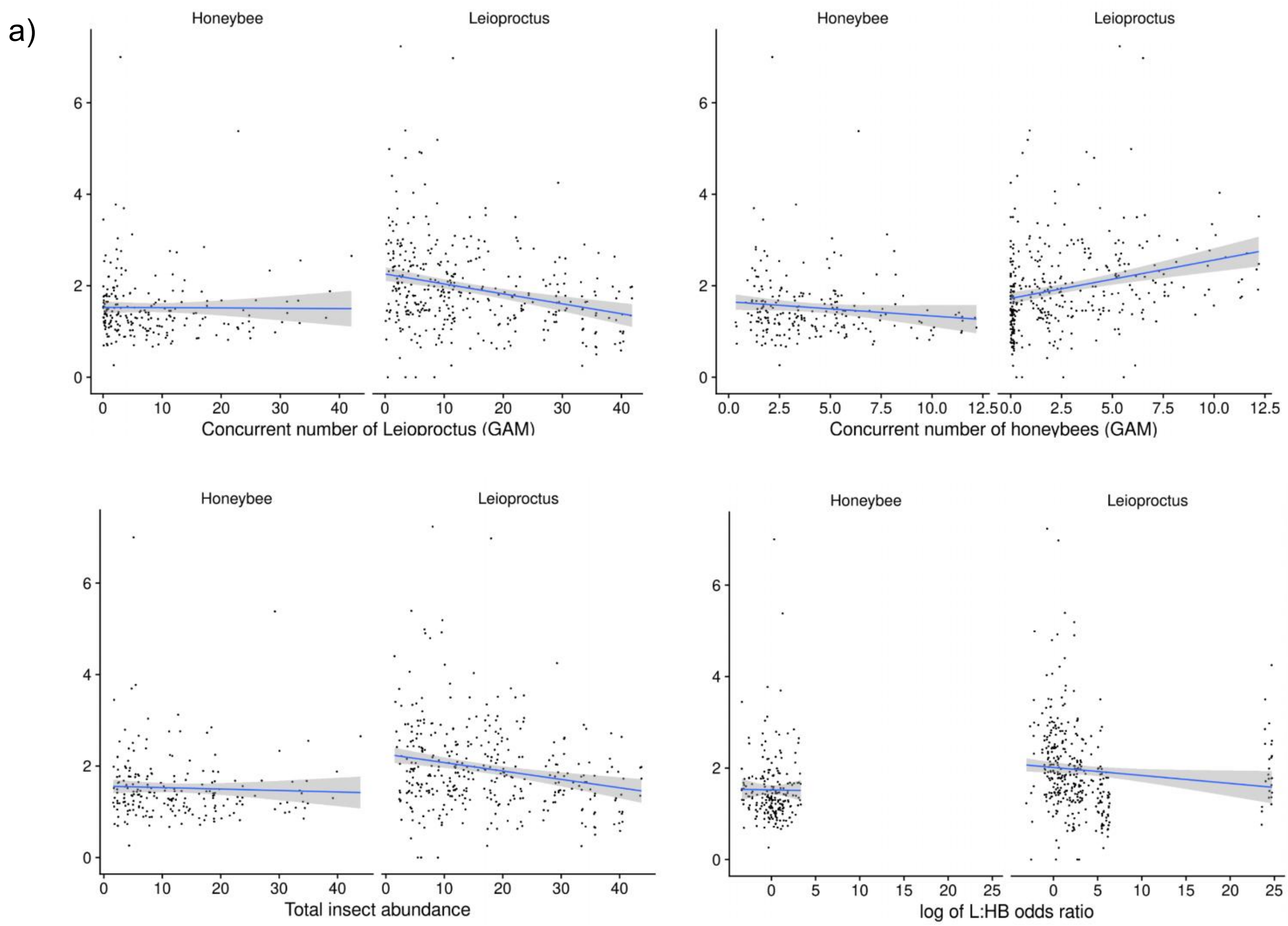
Figure 5: The effect of a) Leioproctus spp. abundance, b) Honey bee abundance, c) total abundance and d) the log ratio of Leioproctus spp. abundance to Honey bee abundance on the proportion of time spent flying for both Leioproctus spp. and honey bees.

Mean flying duration

Leioproctus spp. mean flying duration was significantly negatively correlated with *Leioproctus* spp. abundance, total abundance and the ratio of *Leioproctus* spp. to honey bees, but significantly positively affected by honey bee abundance (Figure 6, Table 6). Honey bee mean flying time duration was not significantly correlated with any of the variables measured (Figure 6, Table 6).

***Table* 6*:** Effect of Leioproctus spp. abundance, honey bee abundance, total abundance and the ratio of Leioproctus spp. to honey bee on the mean flying duration of Leioproctus spp. and honey bees. Lines in bold indicate significant results (P<0.05).*

Predictor	Insect	Cor	t	df	*p*-value
Abundance: *Leioproctus*	***Leioproctus***	**-0.264**	**-5.156**	**355**	**<0.001**
Abundance: Honey bee	***Leioproctus***	**0.259**	**5.052**	**355**	**<0.001**
Abundance: Total	***Leioproctus***	**-0.210**	**-4.051**	**355**	**<0.001**
Ratio: *Leioproctus*: Honey bee	***Leioproctus***	**-0.113**	**-2.150**	**355**	**0.032**
Abundance: *Leioproctus*	Honey bee	-0.008	0.122	211	0.903
Abundance: Honey bee	Honey bee	-0.115	1.688	211	0.093
Abundance: Total	Honey bee	0.041	0.590	211	0.550
Ratio: *Leioproctus*: Honey bee	Honey bee	-0.008	0.114	211	0.909



abundance and d) the log ratio of Leioproctus spp. abundance to Honey bee abundance on the mean duration of flight for both Leioproctus spp. and honey bees.

Proportion of time walking

The proportion of time spent walking by *Leioproctus* spp. was significantly negatively correlated with honey bee abundance but was not significantly related to any of the other variables measured (Figure 7, Table 7). Honey bee proportion of time walking was significantly positively related to the ratio of *Leioproctus* spp. to honey bees but was not significantly correlated with any of the other variables (Figure 7, Table 7).

Table 7: *Effect of Leioproctus spp. abundance, honey bee abundance, total abundance and the ratio of Leioproctus spp. to honey bee on the proportion of time spent walking of Leioproctus spp. and honey bees. Lines in bold indicate significant results (P<0.05).*

Predictor	Insect	Cor	t	df	p-value
Abundance: *Leioproctus*	*Leioproctus*	0.005	0.101	355	0.919
Abundance: Honey bee	***Leioproctus***	**-0.225**	**-4.349**	**355**	**<0.001**
Abundance: Total	*Leioproctus*	-0.055	-1.037	355	0.301
Ratio: *Leioproctus*: Honey bee	*Leioproctus*	0.014	0.258	355	0.797
Abundance: *Leioproctus*	Honey bee	0.116	1.693	211	0.092
Abundance: Honey bee	Honey bee	-0.034	-0.493	211	0.623
Abundance: Total	Honey bee	0.100	1.459	211	0.146
Ratio: *Leioproctus*: Honey bee	**Honey bee**	**0.146**	**2.142**	**211**	**0.033**

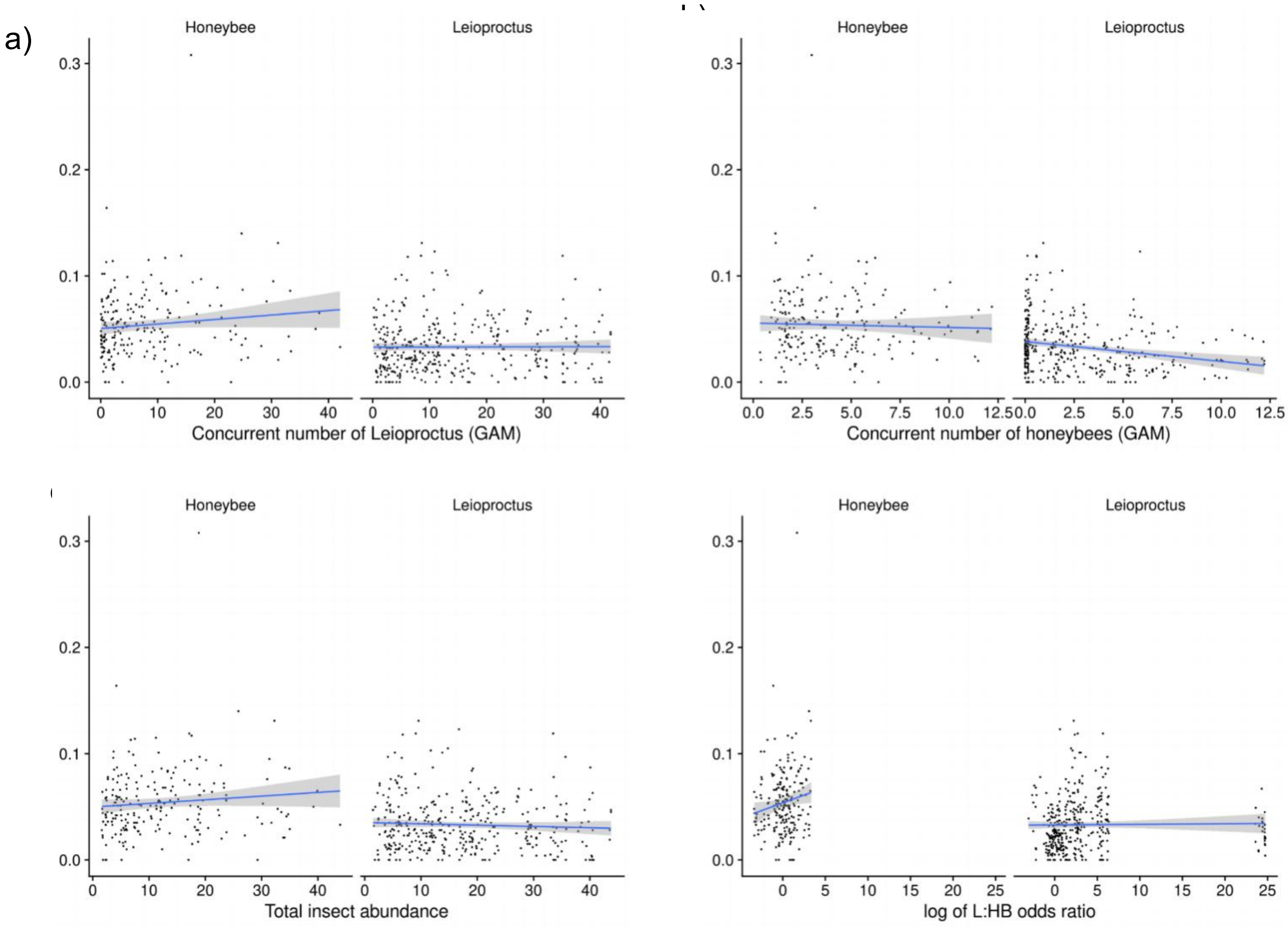


Figure 7: The effect of a) Leioproctus spp. abundance, b) Honey bee abundance, c) total abundance and d) the log ratio of Leioproctus spp. abundance to Honey bee abundance on the proportion of time spent walking for both Leioproctus spp. and honey bees.

Mean walk duration

Leioproctus spp. mean walking duration was significantly negatively affected by honey bee abundance and significantly positively affected by the ratio of *Leioproctus* spp. to honey bees but was not significantly affected by *Leioproctus* spp. abundance or total abundance (Figure 8, Table 8). Honey bee mean walking duration was significantly positively affected by *Leioproctus* spp. abundance but was not significantly affected by honey bee abundance, total abundance or the ratio of *Leioproctus* spp. to honey bees (Figure 8, Table 8).

Table 8: *Effect of Leioproctus spp. abundance, honey bee abundance, total abundance and the ratio of Leioproctus spp. to honey bee on the mean walking duration of Leioproctus spp. and honey bees. Lines in bold indicate significant results (P<0.05).*

Predictor	Insect	Cor	t	df	*p*-value
Abundance: *Leioproctus*	*Leioproctus*	-0.001	-0.018	355	0.986
Abundance: Honey bee	***Leioproctus***	**-0.146**	**-2.778**	**355**	**0.006**
Abundance: Total	*Leioproctus*	-0.040	-0.760	355	0.447
Ratio: *Leioproctus*: Honey bee	***Leioproctus***	**0.125**	**2.377**	**355**	**0.018**
Abundance: *Leioproctus*	**Honey bee**	**0.137**	**2.012**	**211**	**0.046**
Abundance: Honey bee	Honey bee	-0.062	-0.898	211	0.370
Abundance: Total	Honey bee	0.112	1.641	211	0.102
Ratio: *Leioproctus*: Honey bee	Honey bee	0.121	1.773	211	0.078

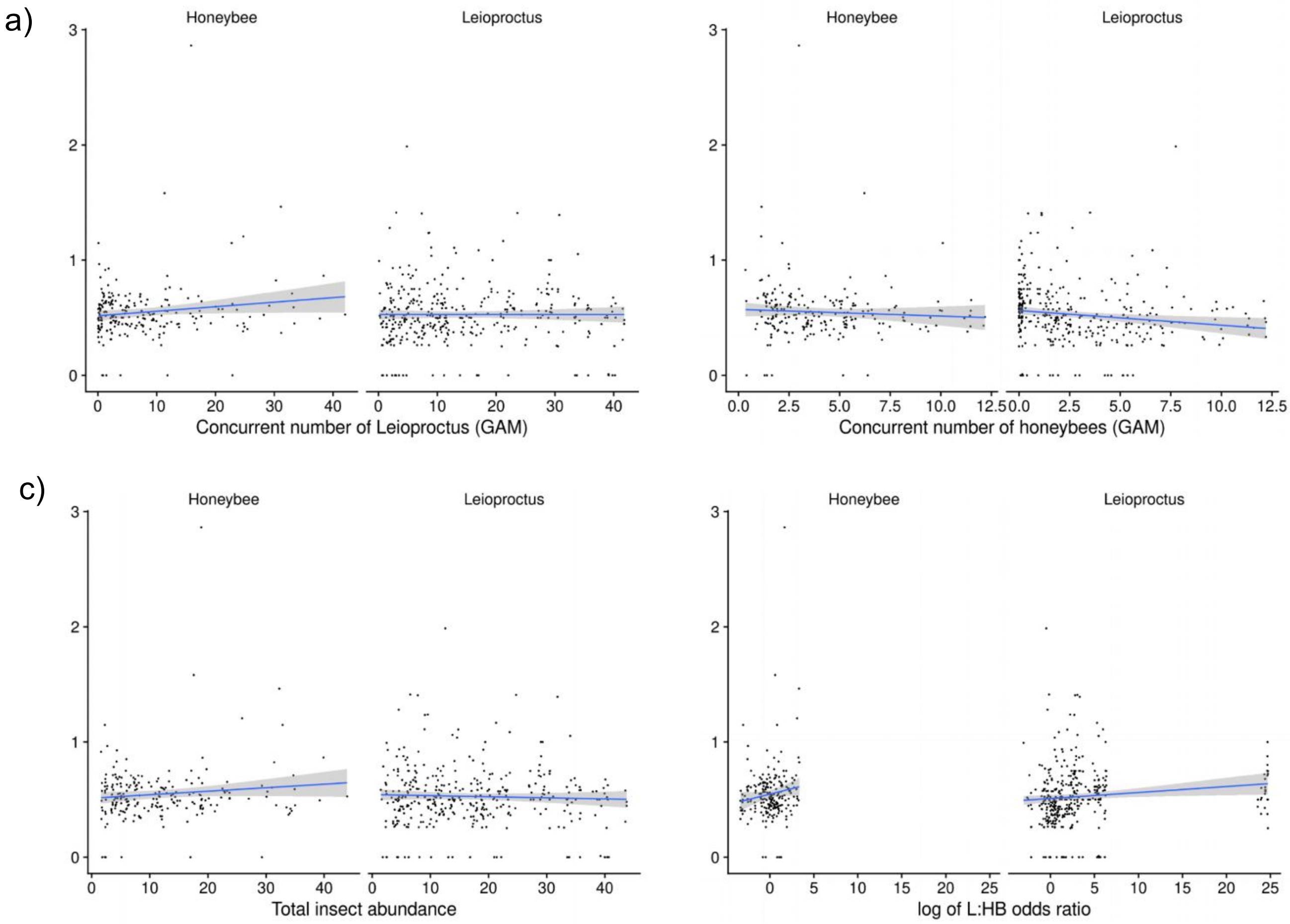


Figure 8: The effect of a) Leioproctus spp. abundance, b) Honey bee abundance, c) total abundance and d) the log ratio of Leioproctus spp. abundance to Honey bee abundance on the mean duration of walking for both Leioproctus spp. and honey bees.

Proportion of time visiting flowers

The proportion of time *Leioproctus* spp. spent visiting flowers was not positively correlated within any of the variables measure, and was only significantly negatively correlated with honey bee abundance (Figure 9, Table 9). There was no relationship between the proportion of time honey bees spent visiting flowers and any of the variables measured (Figure 9, Table 9).

Table 9: *Effect of Leioproctus spp. abundance, honey bee abundance, total abundance and the ratio of Leioproctus spp. to honey bee on the proportion of time spent visiting flowers of Leioproctus spp. and honey bees.*

Predictor	**Insect**	**Cor**	**t**	**df**	***p*-value**
Abundance: *Leioproctus*	*Leioproctus*	0.057	1.083	355	0.280
Abundance: Honey bee	***Leioproctus***	**-0.259**	**-5.050**	**355**	**<0.001**
Abundance: Total	*Leioproctus*	-0.009	-0.168	355	0.866
Ratio: *Leioproctus*: Honey bee	*Leioproctus*	-0.026	-0.496	355	0.620
Abundance: *Leioproctus*	Honey bee	-0.021	-0.311	211	0.756
Abundance: Honey bee	Honey bee	0.108	1.584	211	0.115
Abundance: Total	Honey bee	0.011	0.159	211	0.874
Ratio: *Leioproctus*: Honey bee	Honey bee	-0.076	-1.110	211	0.268

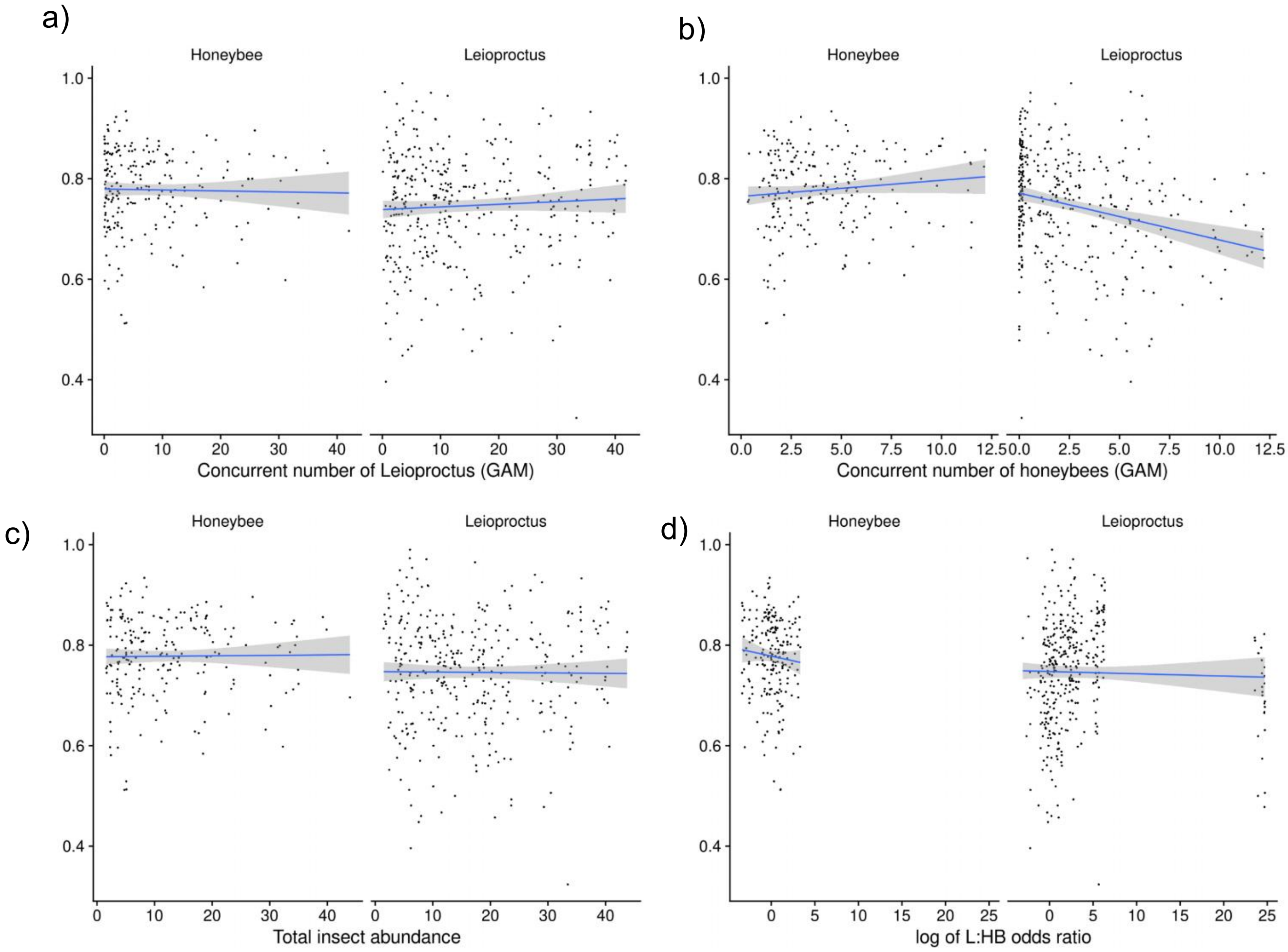


Figure 9: The effect of a) Leioproctus spp. abundance, b) Honey bee abundance, c) total abundance and d) the log ratio of Leioproctus spp. abundance to Honey bee abundance on the proportion of time spent visiting flowers for both Leioproctus spp. and honey bees.

Mean flower visit duration

Leioproctus spp. mean flower visit duration to a flower was significantly negatively correlated with *Leioproctus* spp. abundance and total bee abundance but was not significantly correlated with honey bee abundance or the ratio of *Leioproctus* spp. to honey bees (Figure 10, Table 10). Honey bee mean flower visit duration was not significantly correlated with any of the variables measured (Figure 10, Table 10).

Table* 10*: Effect of Leioproctus spp. abundance, honey bee abundance, total abundance and the ratio of Leioproctus spp. to honey bee on mean flower visit duration of Leioproctus spp. and honey bees. Lines in bold indicate significant results (P<0.05).

Predictor	Insect	Cor	t	df	p-value
Abundance: *Leioproctus*	***Leioproctus***	**-0.139**	**-2.647**	**355**	**0.008**
Abundance: Honey bee	*Leioproctus*	-0.065	-1.226	355	0.221
Abundance: Total	***Leioproctus***	**-0.165**	**-3.154**	**355**	**0.002**
Ratio: *Leioproctus*: Honey bee	*Leioproctus*	-0.097	-1.829	355	0.068
Abundance: *Leioproctus*	Honey bee	-0.005	-0.074	211	0.941
Abundance: Honey bee	Honey bee	-0.035	-0.513	211	0.609
Abundance: Total	Honey bee	-0.015	-0.217	211	0.828
Ratio: *Leioproctus*: Honey bee	Honey bee	-0.082	-1.200	211	0.232

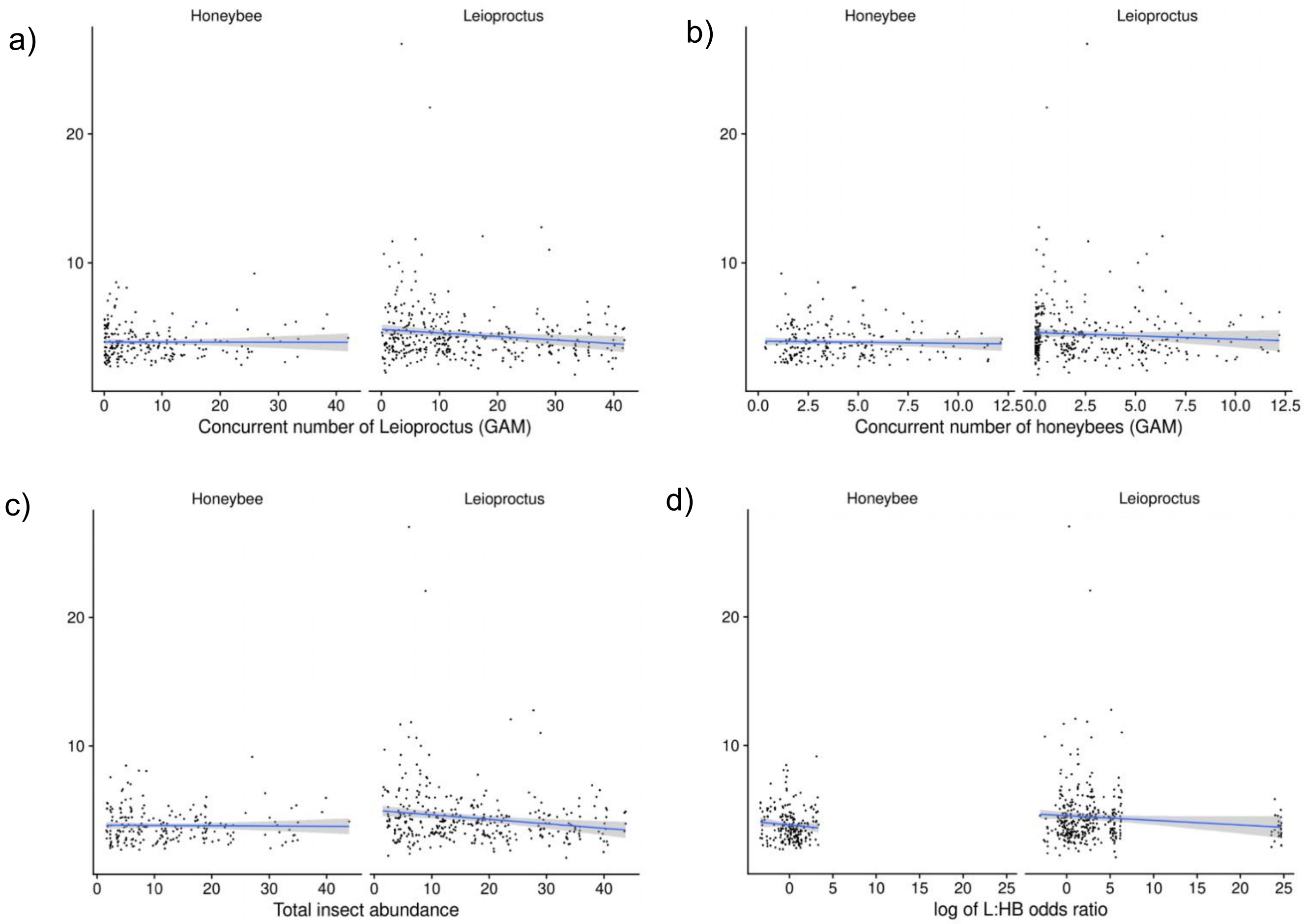


Figure 10: The effect of a) Leioproctus spp. abundance, b) Honey bee abundance, c) total abundance and d) the log ratio of Leioproctus spp. abundance to Honey bee abundance on the mean duration of flower visits for both Leioproctus spp. and honey bees.

Flower visitation rate

Leioproctus spp. flower visitation rate was significantly negatively correlated with *Leioproctus* spp. abundance, total abundance and the ratio of *Leioproctus* spp. to honey bees but was not significantly affected by honey bee abundance (Figure 11, Table 11). Honey bee flower visitation rate was not significantly correlated with any of the variables measured (Figure 11, Table 11)

Table* 11*: Effect of Leioproctus spp. abundance, honey bee abundance, total abundance and the ratio of Leioproctus spp. to honey bee on flower visitation rate of Leioproctus spp. and honey bees. Lines in bold indicate significant results (P<0.05).

Predictor	Insect	Cor	t	df	*p*-value
Abundance: *Leioproctus*	***Leioproctus***	**-0.184**	**-3.526**	**355**	**<0.001**
Abundance: Honey bee	*Leioproctus*	0.011	0.213	355	0.831
Abundance: Total	***Leioproctus***	**-0.192**	**-3.688**	**355**	**<0.001**
Ratio: *Leioproctus*: Honey bee	***Leioproctus***	**-0.109**	**-2.061**	**355**	**0.040**
Abundance: *Leioproctus*	Honey bee	0.018	0.259	211	0.796
Abundance: Honey bee	Honey bee	-0.072	-1.053	211	0.294
Abundance: Total	Honey bee	-0.004	-0.057	211	0.955
Ratio: *Leioproctus*: Honey bee	Honey bee	-0.060	-0.873	211	0.383

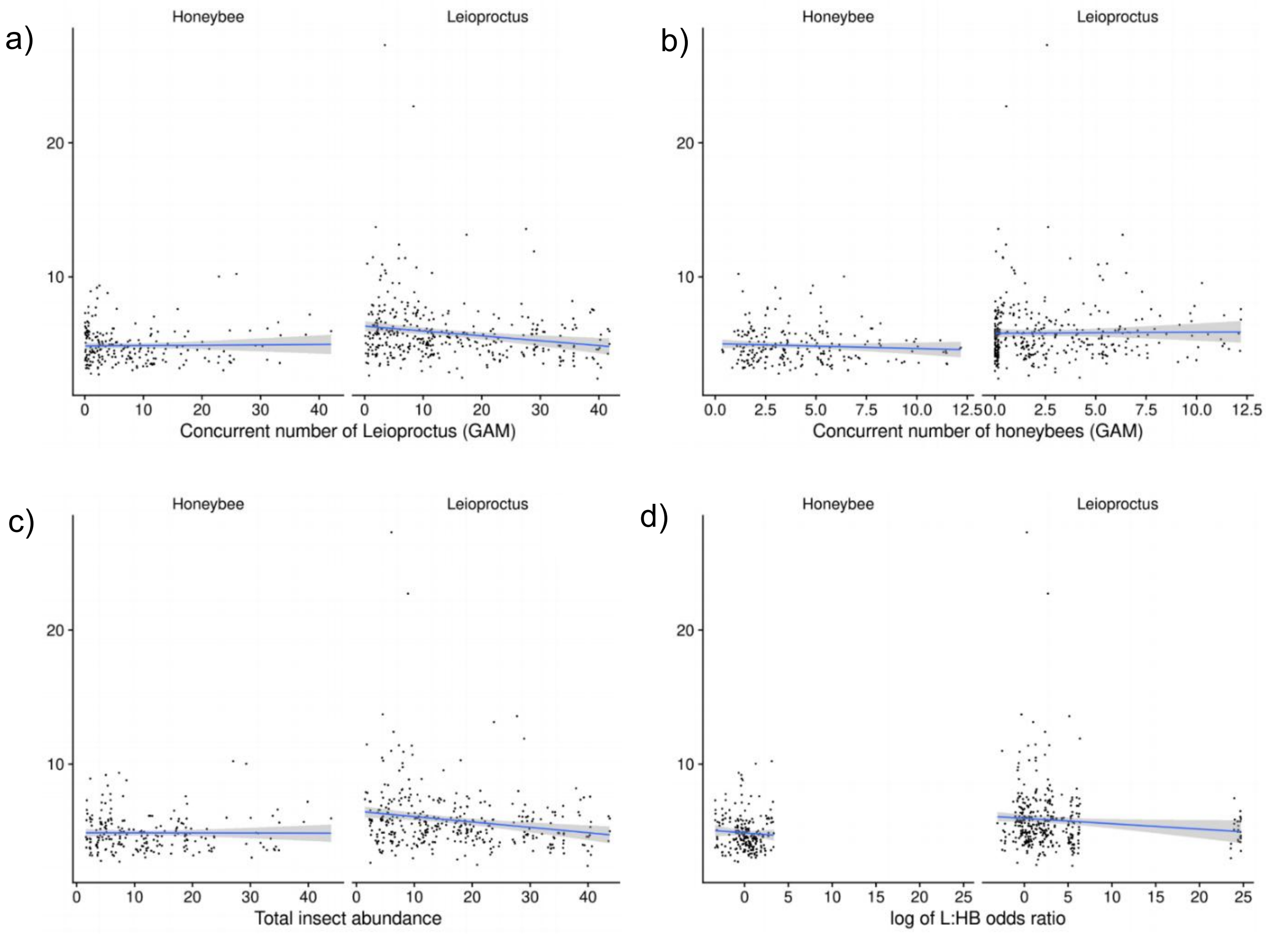


Figure 11: The effect of a) Leioproctus spp. abundance, b) Honey bee abundance, c) total abundance and d) the log ratio of Leioproctus spp. abundance to Honey bee abundance on the flower visitation rate for both Leioproctus spp. and honey bees.

Flower visit success

Leioproctus spp. flower visit success was significantly negatively affected by *Leioproctus* spp. abundance and total abundance; however, *Leioproctus* spp. flower visit success was significantly positively affected by honey bee abundance (Figure 12, Table 12). Honey bee flower visit success was significantly negatively affected by the ratio of

Leioproctus spp. to honey bees however honey bee flower visit success was significantly positively affected by honey bee abundance (Figure 12, Table 12).

Table 12: *Effect of Leioproctus spp. abundance, honey bee abundance, total abundance and the ratio of Leioproctus spp. to honey bee on percentage of flower visit success of Leioproctus spp. and honey bees. Lines in bold indicate significant results (P<0.05).*

Predictor	Insect	Cor	t	df	p-value
Abundance: *Leioproctus*	***Leioproctus***	**-0.217**	**-4.191**	**355**	**<0.001**
Abundance: Honey bee	***Leioproctus***	**0.202**	**3.893**	**355**	**<0.001**
Abundance: Total	***Leioproctus***	**-0.176**	**-3.364**	**355**	**<0.001**
Ratio: *Leioproctus*: Honey bee	*Leioproctus*	-0.020	-0.374	355	0.709
Abundance: *Leioproctus*	Honey bee	-0.131	-1.926	211	0.055
Abundance: Honey bee	**Honey bee**	**0.155**	**2.277**	**211**	**0.024**
Abundance: Total	Honey bee	-0.080	-1.166	211	0.245
Ratio: *Leioproctus*: Honey bee	**Honey bee**	**-0.174**	**-2.570**	**211**	**0.011**

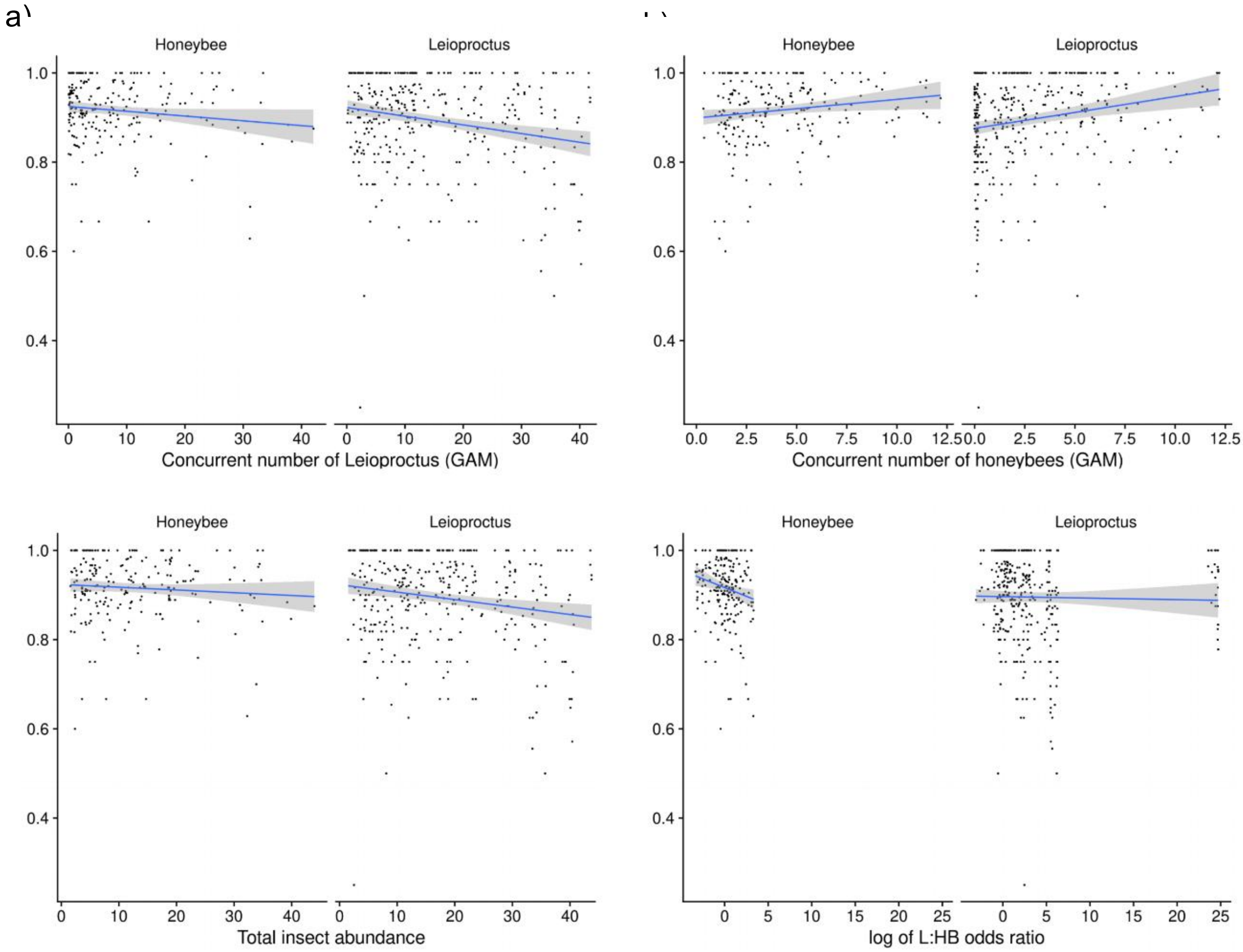


Figure 12: The effect of a) Leioproctus spp. abundance, b) Honey bee abundance, c) total abundance and d) the log ratio of Leioproctus spp. abundance to Honey bee abundance on the percentage of flower visit success for both Leioproctus spp. and honey bees.

Discussion

This chapter investigated whether competition could be identified between *Leioproctus* spp. and introduced honey bees foraging on mānuka flowers at three locations. To identify potential competition, I first confirmed that the subject groups have a niche overlap. Both *Leioproctus* spp. and honey bees were observed at all three sites foraging on mānuka flowers during the season. This supports my hypothesis that these groups have a niche overlap. Next, I analysed abundance data taken throughout the season to identify whether temporal niche partitioning was occurring during the day and over the season. I found that temporal niche partitioning may be occurring during the day, with *Leioproctus* spp. overall having a later peak abundance than honey bees. Additionally, temporal partitioning may also be occurring seasonally, with *Leioproctus* spp. having greater abundances earlier in the season and honey bee abundances increasing later in the season. Lastly, I investigated the effect of *Leioproctus* spp. and honey bee abundances on a range of behaviours to provide evidence for/against exploitative and interference competition between *Leioproctus* spp. and honey bees. The results from the behavioural observations indicate that exploitative and interference competition may be occurring as some *Leioproctus* spp. and honey bee behaviours were correlated with variation in intra- and interspecific abundance.

Abundance

The results from my abundance observations indicate that competition is likely present, as evidenced by the overlap in abundance between *Leioproctus* and honey bees during mānuka flowering. Additionally, I found support for temporal niche partitioning which implies that some of this competition is being avoided. Evidence for temporal niche partitioning was observed both seasonally and in daily foraging activity. At all three sites there are stages of the season where honey bees and *Leioproctus* spp. have differing peak abundance times. Additionally, at all three sites, native bee abundances were higher in early and mid-season but decreased by late season, whereas the honey bee abundance increased in the late season. There is evidence that at the Hope and Rangi sites, there is a decrease in *Leioproctus* spp. abundance late in the season, suggesting that seasonal temporal partitioning may be occurring. There was also evidence for temporal niche partitioning in daily activity patterns with *Leioproctus* spp. overall showing a later peak in activity however this pattern was reversed at some sites and stages of the flowering season.

These results are similar to studies done abroad by Young et al. (2021) and Smith et al. (2017). Both studies found evidence for temporal niche partitioning with co-occurring bee species. Young et al. (2021) found that in Bangalore, India, *Apis cerena* forages earlier in the morning while, *Apis florea*, forages later in the day on the similar nectar crops. Smith et al. (2017) similarly found that night flying sweat-bees *Megalopta genalis*, forage into the evening in the presence of diurnal bee species, such as honey bee and stingless bees. Additionally, like my results, a study by Ginsberg (1983) showed how honey bees and native bees *(Halictus ligatus)* partitioned goldenrod nectar where native bees were found more abundant foraging on early spring blooming goldenrod species and honey bees were more abundant foraging on late summer blooming goldenrod species.

Foraging behaviour of Leioproctus spp.

When assessing the foraging behaviours of *Leioproctus* spp. and honey bees, I broke this down into two main categories: travelling between flower behaviours and flower visiting behaviours. Subject insects were foraging insects and were always classified as undertaking a behaviour falling into one or both categories. Travelling behaviours were then further broken down into two categories, flying and walking. As abundances of both interspecific and intraspecific competitors changed, I expected to see changes in the moving and flower visiting behaviours as insects adjusted to changes in competition. Studies on honey bees and bumble bees show that they are sensitive to changes in floral rewards and that the abundance of these species on flowers was directly related to available nectar resources (Free, 1968; Heinrich, 1976; Seeley, 2009) Accordingly, I expected that when there were higher amounts of nectar available there would be higher abundances of both species, and therefore greater potential for competition.

Proportion of time travelling

I predicted that as competitor species abundance increased, species exhibiting avoidance behaviour would forage on less desirable patches of flowers and would therefore have an increased proportion of time travelling between flowers. I found that the proportion of time that *Leioproctus* spp. spent travelling increased with the abundance of honey bees. This behaviour was not affected by the three other abundance metrics, which indicates that the effect is interspecific competition. These results align with my prediction and are similar to a study by Balfour et al. (2015) where the honey bee proportion of inter-flower flights was greater when the superior competitor (bumblebees) were present. Similarly, I hypothesise that as honey bee abundance increases, *Leioproctus* spp. are exhibiting avoidance behaviour to preferential patches of flowers and travelling further to patches where honey bees are less present.

Flying behaviour

I assessed two flying behavioural metrics to see if they were affected by the four abundance metrics. The first was proportion of time flying which includes the variables of flying occurrences and flying duration. The second was the mean flying duration, which describes the average flight time for the insects. Following on from the expectation that travel time would increase as competitor abundances increase, I expected to see the proportion of time spent flying and mean flying duration to increase as competitor abundances increase. Similar to the proportion of time spent travelling, the proportion of time that *Leioproctus* spp. spent flying increased as honey bee abundance increased. This is correlated with the changes in the proportion of time spent travelling, as almost 60% of the 15,000 travelling behaviours assessed were flying behaviours. However, I found that *Leioproctus* spp. mean flying duration was variably affected by the four abundance metrics. Honey bee abundance had the predicted positive effect on *Leioproctus* spp. mean flying duration, increasing as honey bee abundance increased and indicating a change of behaviour as a result of potential exploitative or interference interspecific competition. Interestingly, *Leioproctus* spp. mean flying duration was negatively affected by *Leioproctus* spp. abundance, total abundance and ratio of *Leioproctus* spp. to honey bees which contrasts expectation. I expected intraspecific abundance to also positively affect flight duration, however this could be potentially explained by scramble competition. Scramble competition is an evolutionarily stable strategy which involves individuals increasing their foraging speed as competitor density increases (Beauchamp, 2012; David et al., 2014). Therefore, this suggests that intraspecific competition would decrease mean flight duration in *Leioproctus* spp. whereas interspecific competition increases mean flight duration.

Walking behaviour

Forty percent of travelling behaviours were categorised as walking. Again, I split walking behaviour into the proportion of time spent walking and the mean walk duration. Walking is the slower of the two travelling behaviours and therefore takes the insect longer to reach its next flower, however it is less metabolically expensive mode of travel, especially when travelling between two close flowers (Harrison & Fewell, 2002; Kammer & Heinrich, 1978; Wolf et al., 1989). Walking is categorised as a travelling behaviour and would be expected to increase as competitor abundance increases, however I predicted that the proportion of time spent walking would decrease as abundances increase. This is because the metabolic cost of flying would be outweighed by the reward of getting to more flowers quicker. I found *Leioproctus* spp. proportion of time walking to be negatively affected by honey bee abundance and not affected by the other abundance metrics (*Leioproctus* spp. abundance, total abundance and ratio of *Leioproctus* spp. to honey bees). This indicates that *Leioproctus* spp. are not being affected by the abundance of their conspecifics, but are affected by honey bee abundance. This could potentially be evidence for exploitative and/or interference competition. When competitor abundance is high, this is likely corresponding to a high availability of nectar (Free, 1968; Heinrich, 1976; Seeley, 2009). Mānuka flowers bloom in bunches and both *Leioproctus* spp. and honey bees can often walk between flowers. Therefore, when abundance is high, I expected the mean walk duration to decrease due to the closeness of suitable flowers once the bee has arrived at a suitable patch. In this study I found that *Leioproctus* spp. mean walking duration was negatively affected by honey bee abundance and positively affected by the ratio of *Leioproctus* spp. to honey bee abundance, but was not affected by *Leioproctus* spp. abundance or total abundance. The significant negative relationship between *Leioproctus* spp. mean walk duration and honey bee abundance could suggest that interspecific interference competition may be occurring rather than exploitative competition. If exploitative competition was the main driver, I would have expected to also see a significant effect of increasing numbers of conspecific competitors (total abundance and *Leioproctus* spp. abundance). The significant positive relationship between *Leioproctus* spp. mean walk duration and the ratio of *Leioproctus* spp. to honey bees further reinforces this implication that as the ratio decreases (more honey bees per *Leioproctus),* *Leioproctus* spp. mean walk duration decreases. Again, this finding suggests that interference competition is likely a factor driving the variation in walking behaviours.

Flower visiting and foraging behaviours

In addition to travelling behaviours, I assessed the effect of competitor abundance on *Leioproctus* spp. foraging behaviours on mānuka flowers, which included the proportion of time spent visiting flowers, mean time visiting a flower, flower visitation rate and the proportion of flower visits that were successful. Competitor abundance is likely positively related to flower nectar production (Free, 1968; Heinrich, 1976; Seeley, 2009), which for mānuka starts earlier in the day, rises to a peak in the middle period of the day, and falls towards the end of the day, often reflecting the temporal patterns of the pollinators (Pacini & Nepi, 2007; Sheridan, 2019). I predicted that as competitor abundance increases, the proportion of time insects spend visiting flowers would decreases as insects increase their travelling time. I also predicted that as competitor abundance increased, insect mean flower visit duration would decrease. This is due to the assumption that when abundance is high, nectar availability is also high, therefore spending less time on each flower and maximising the number of flowers visited and potential nectar uptake, in a shorter amount of time, is more beneficial as competitor abundances increase. Lastly, I predicted that as competitor abundance increases, the proportion of successful flower visits would decrease due to the increased flower visitation rates of competitors expected.

My study found the proportion of time *Leioproctus* spp. spent visiting flowers was negatively affected by honey bee abundance but was not affected by the other assessed metric abundances. This is line with my prediction that as honey bee abundances increased, *Leioproctus* spp. spends less time visiting flowers and more time travelling to suitable flowers. This implies that both scramble competition and interference competition may be occurring, as *Leioproctus* spp. may be increasing their foraging speed to maximise nectar uptake and/or may be spending more time travelling between flowers in order to avoid honey bees already on flowers.

Similarly *Leioproctus* spp. mean flower visit duration was negatively affected by *Leioproctus* spp. abundance and total abundance but not by the other two assessed abundance metrics (honey bee abundance and the ratio of *Leioproctus* spp. to honey bees). The effect of total abundance may be due to the large numbers of *Leioproctus* spp. recorded and not the honey bees as mean flower visit duration was not affected by honey bee abundance. This suggests that it is likely intraspecific competition (i.e., scramble competition) rather than interspecific competition effecting the mean duration of flower visits for *Leioproctus* spp.

The results show that *Leioproctus* spp. flower visitation rate was negatively affected by conspecific abundance, total abundance and the ratio of *Leioproctus* spp. to honey bees. This again suggests that *Leioproctus* spp. are experiencing intraspecific competition, which could be exploitative and/or interference. I would not suggest that the effect observed by total abundance and the ratio of *Leioproctus* spp. to honey bees indicates potential interspecific competition for two reasons. Firstly, there was no effect of honey bee abundance and secondly the relatively large numbers of *Leioproctus* spp. recorded in abundance surveys may be driving the effects observed in the total abundance and the ratio of *Leioproctus* spp. to honey bees.

This study found that the *Leioproctus* spp. percentage of successful flower visits was negatively affected by *Leioproctus* spp. abundance, which suggests that there could be intraspecific exploitative competition occurring. Although total abundance also is negatively affecting *Leioproctus* spp. flower visit success, a combination of relatively high *Leioproctus* spp. numbers recorded in abundance surveys and no effect observed of the ratio of *Leioproctus* spp. to honey bees, suggests that it is the intraspecific competition causing this effect rather than the interspecific competition. Interestingly, however, *Leioproctus* spp. flower visit success is positively affected by honey bee abundance, contradictory to my prediction. This effect could potentially be explained by the interspecific competition being interference competition rather than exploitative competition and therefore, nectar availability is still high despite increased honey bee abundance, whereas high abundances of *Leioproctus* spp. decreases successful flower visits as nectar availability will begin to decrease due to exploitative competition.

Foraging behaviour of Honey bees

Honey bee foraging behaviour was not significantly affected by any of the four abundance metrics, except for walking behaviour and percentage of successful flower visits. This is similar the study of Balfour et al. (2015) that found that the superior or dominant species was not affected by the competitor, however in this study I did find that some behaviours were affected.

Honey bee proportion of walking time was positively affected by the ratio of *Leioproctus* spp. to honey bees. Similar to the proportion of time spent walking, the mean walk duration of honey bees was positively affected by *Leioproctus* spp. abundance but not significantly affected by the other three abundance metrics assessed. Interestingly, the proportion of time spent walking is affected by just the ratio of *Leioproctus* spp. to honey bees, while mean walk duration is affected by just *Leioproctus* spp. abundance, but neither are affected by the total abundance.

A change of behaviour driven by the relative abundance of these potentially competing species is a strong indicator that competition is occurring, and in this case it is honey bees that are altering their behaviour. It is important to note that some of these significant effects could be the result of some sites having very low honey bee numbers relative to *Leioproctus* spp. early in the season, and further investigation would be required to identify factors causing this result.

Honey bee flower success was positively affected by honey bee abundance but negatively affected by the ratio of *Leioproctus* spp. to honey bees. There was not a statistically detectable effect of *Leioproctus* spp. abundance or total abundance on honey bee flower visit success. This suggests that honey bees’ interference competition with *Leioproctus* spp. may be benefiting honey bees as successful flower visits increase as honey bee density increases, and *Leioproctus* spp. honey bee avoidance behaviour increases.

Summary of behavioural changes

The significant changes in foraging behaviour and the type of competition suggested by these changes are summarised below (Table 13). *Leioproctus* spp. foraging behaviour was affected by honey bee abundance for every behaviour assessed except for the mean duration of a flower visit and flower visitation rate. These results indicate that interspecific competition is occurring between *Leioproctus* spp. and honey bees on mānuka flowers. Additionally, some of the *Leioproctus* spp. foraging behaviours (Table 13) were also affected by *Leioproctus* spp. abundance and total abundance, indicating that intraspecific competition is also occurring, particularly scramble competition. Interestingly, some honey bee foraging behaviours (Table 13), were affected by *Leioproctus* spp. abundance or the ratio of *Leioproctus* spp. to honey bees, suggesting that the interspecific competition between honey bees and *Leioproctus* spp. affects both bee types.

Table 13: Summary table of the significant effects of Leioproctus spp. abundance, honey bee abundance, total abundance and the ratio of Leioproctus spp. to honey bees on the foraging behaviours of both Leioproctus spp. and honey bees, and suggested attribution to the type of competition that may be occurring.

Behaviour	Bee	*Leioproctus* abundance	Honey bee abundance	Total abundance	*Leioproctus* to honey bee ratio	Interspecific competition	Intraspecific competition
Prop. time travelling	*Leioproctus*		+			exploitative and/or interference	
	Honey bee						
Prop. time flying	*Leioproctus*		+			exploitative and/or interference	
	Honey bee						
Mean flight time	*Leioproctus*	-	+	-	-	exploitative and/or interference	scramble
	Honey bee						
Prop. time walking	*Leioproctus*		-			exploitative and/or interference	
	Honey bee				+	exploitative and/or interference	
Mean walking time	*Leioproctus*		-		+	interference	
	Honey bee	+				exploitative and/or interference	

Table 13 cont.: Summary table of the significant effects of Leioproctus spp. abundance, honey bee abundance, total abundance and the ratio of Leioproctus spp. to honey bees on the foraging behaviours of both Leioproctus spp. and honey bees.

Behaviour	Bee	*Leioproctus* abundance	Honey bee abundance	Total abundance	*Leioproctus* to honey bee ratio	Interspecific competition	Intraspecific competition
Prop. time visiting flowers	*Leioproctus*		-			interference	scramble
	Honey bee						
Mean flower visit time	*Leioproctus*	-		-			scramble
	Honey bee						
Flower visitation rate	*Leioproctus*	-		-	-		exploitative and/or interference
	Honey bee						
Flower visitation success %	*Leioproctus*	-	+	-			exploitative and/or interference
	Honey bee		+		-	interference	

CHAPTER 3

The effect of the presence of *Leioproctus* spp. models on *Apis mellifera* foraging behaviour

Abstract

Competition is a common consequence of the introduction of a new species, and successful invasive or introduced species usually have a competitive advantage over native species. Honey bees were introduced to New Zealand in 1836 and are generally considered dominant over native pollinator species. However, little research has experimentally assessed competition between honey bees and native pollinators in New Zealand. Recent research has suggested that, despite being considered the dominant species, honey bees may display avoidance behaviour in the presence of native competitors. To assess the avoidance behaviour of honey bees further, I investigated the floral resource selection of honey bees when potential native bee competitors are present. To do this I presented honey bees with a choice of two floral resources, one with no competitors and the other with varying densities of decoy native bees present. I found that honey bees tended to choose the floral resource without any native bee decoys present, however, the density of the native bee decoys had no effect on honey bee floral resource choice. These results suggest that honey bees display avoidance behaviour to reduce competition with native bees, however, further research into the foraging behaviour of honey bees in the presence of competitors would be beneficial. These results can help inform the management of honey bees hives for mānuka honey operations.

Introduction

Biological invasions are the introduction and spread of exotic species to an ecosystem (Richardson et al., 2000). These can occur naturally, accidentally, or intentionally and can have significant ecological and/or economic impact. Biological invasions are considered one of the most important threats to conservation and biodiversity globally (Dyer et al., 2017; Early et al., 2016; McGeoch et al., 2010; Vilà et al., 2011; Vitousek et al., 1996). Invasive species can change the dynamics of an ecosystem causing an unbalancing of a native ecosystem (Schröter et al., 2005; Vitousek et al., 1996). This change is a result of the variety of interactions that invasive species can have on native species including competition, disease vectoring, habitat alteration, hybridisation, parasitism, and predation (Pyšek et al., 2012; Traveset & Richardson, 2006; Vilà et al., 2011; Vitousek et al., 1996; Wittenberg & JW Cock, 2001).

Competition is a common consequence of biological invasions and the greater the niche overlap of the invader and native species, the greater the competition will be (Chesson, 2000). Therefore, successful invasive species can often attribute their success to having a competitive advantage over native species (Braks et al., 2004). Competitive advantages can arise when an invader's natural attributes allow them to acquire resources or reproduce more efficiently than native species. These attributes may include faster reproduction, faster growth and maturation, broad dietary requirements, a lack of natural predators or disease, tolerance to environmental conditions and/or more efficient resource use (Alonso & Castro-Díez, 2012; David et al., 2017; Hellmann et al., 2008; Niu et al., 2013; Scheba et al., 2017; Vargas Salinas, 2006).

Competition is energetically expensive so populations will often exhibit behavioural changes to reduce competition, such as niche partitioning (Grant & Grant, 2006; Hughes & Tanner, 2000). Niche partitioning can occur through spatial or temporal changes in behaviour that promote the avoidance of the competitor and reduce the overlap in their niches. Spatial niche partitioning is when competitors forage in, or inhabit, different areas and thus minimise contact with the other species, whereas temporal niche partitioning involves the competing species having peak activity at different times. This could be over a 24hr period or seasonally. Alternatively, one or more species may change their foraging behaviour to include foraging on different food sources or prey species to reduce competition. For example, Sumatran tigers, *Panthera tigris sumatrae*, Sunda clouded leopards, *Neofelis diardi*, Asiatic golden cats, *Catopuma temminckii*, marbled cats, *Pardofelis marmorata*, and leopard cats, *Panthera pardus*, are able to co-exist through niche partitioning. Each cat uses a different elevation, increasing spatial separation, and they also have differences in choice of prey size. However, as prey size similarities increase between cat species, temporal avoidance also increases (Sunarto et al., 2015). These behavioural changes can occur in either or both/all species that are competing over a shared resource. Accordingly, we can use these behavioural changes to identify if competition is occurring in an ecosystem.

Honey bees, *Apis mellifera*, are a classic example of a successful invader species, which, largely through human intervention, are now found on every continent across the globe, except Antarctica (Mortensen et al., 2013). What makes honey bees such a successful invasive species, and gives them a competitive advantage over native species, is a combination of their generalist foraging behaviour, eusocial structure, and human-management practices (Goulson, 2003; Kremen et al., 2002; Steffan-Dewenter & Tscharntke, 2000). Initially valued for their wax and honey, their introductions to novel territories continued and are now also economically valued for their pollination (Kuropatnicki et al., 2018; Roffet-Salque et al., 2015; Southwick & Southwick Jr, 1992). Globally, honey bees are the most economically important pollinators of crop (McGregor, 1976; Southwick & Southwick Jr, 1992; Watanabe, 1994). Although honey bees do visit the target crops, they have also been documented as having a foraging range of up to 285 square kilometres (Beekman & Ratnieks, 2000). This implies that they are highly likely to spill-over into floral territories relied upon by other nectivorous species, including native pollinators. Competition is therefore highly likely to occur between honey bees and native bee species as their foraging ranges would greatly overlap.

In New Zealand, manuka, *Leptospermum scoparium*, honey has recently become an important economic crop which is prized by beekeepers due to high international demand and prices. Each year, large numbers of honey bee colonies are transported around the country into high density mānuka ecosystems by beekeepers chasing the mānuka nectar flow. However, the nectar and pollen from mānuka, a native shrub, is relied upon by a variety of native pollinators, including native bees (Bennik, 2009; Butz Huryn, 1995; Iwasaki, 2017; Murphy, 1996). Competition between invasive honey bees and native bees has been studied internationally with a focus on floral resource overlap, visitation rates and resource harvesting. However, there is limited investigation into the mechanisms driving these behavioural responses (Cornelissen et al., 2019; Kato et al., 1999; DR Paini, 2004; Prendergast et al., 2021; Roubik & Wolda, 2001; Russo et al., 2021; Thomson, 2004). Furthermore, studies into honey bee/native bee competition in New Zealand are limited and very little is known about the impacts of honey bees on native bee foraging behaviour (Bennik, 2009; Butz Huryn, 1995; Iwasaki, 2017; Murphy, 1996). In Chapter Two of this thesis, I presented evidence supporting competition through temporal partitioning and behavioural changes of both honey bees and native bees, suggesting that both display changes in their foraging behaviour when competitor abundances increase. This study aims to investigate further into the mechanisms behind these behavioural changes by observing honey bee floral resource selection in the face of native bee presence. Research on how honey bees select resources has often focussed on the olfactory, electromagnetic and visual cues from the floral resource itself (Dötterl et al., 2014; Greggers et al., 2013; Iwasaki, 2017; Murphy, 1996; DR Paini, 2004; Wright &

Schiestl, 2009). Although honey bees are considered dominant pollinators in many ecosystems (Brittain et al., 2013; Danforth, 2007; Weekers et al., 2022), there are examples of honey bees exhibiting avoidance of competitors, which is symptomatic of competition reducing behaviours (Sidhu & Wilson Rankin, 2016; Wright & Schiestl, 2009). Here, I focus on honey bee floral resource selection when competitors are present. I offer foraging honey bees a selection between two identical floral resources, only differing by the presence of native bee decoys across a range of densities. I predict that honey bees will preferentially select the foraging source that has no native bee decoys present to reduce interspecific competition. Additionally, I predict that this preference will become more apparent with increasing density of native bee decoys.

Methods

Study site

This study was undertaken at the Plant and Food Research NZ Ltd (PFR) facility in Ruakura, New Zealand. The experiments were undertaken on three separate days over a two-week period in February 2022. To assess whether foraging honey bees preferentially select foraging sources where native bees are absent, two identical forage sources (flower boards) were provided to honey bees foraging in a pasture area, differing only by presence of native bee decoys. This design required foraging honey bees to select one of the flower boards over the other as its initial foraging choice.

Study species: Honey bees

The honey bees observed in this study were most likely from colonies managed by PFR. There were 48 honey bee colonies of varying size, strength, and structure within a 50 m radius of any sampling location within the pasture area. However, honey bees were not restricted from moving in and out of the sampling area and have been reported as having a 280 km^2 foraging range (Beekman & Ratnieks, 2000), so while it is likely that most honey bees arriving at my experiments were from local colonies, I cannot rule out that honey bees were not visiting from further afield.

Native bee decoys

Native bees from the genus *Leioproctus* spp. were the only native bees observed foraging concurrently with honey bees on mānuka flowers in the Waikato (**Chapter 2**). Therefore, I chose to model the native bee decoys based on the attributes of this genus. The native bee decoys were designed by James Pinfold (Research Technologist, PFR) approximately to the scale of commonly observed *Leioproctus* spp. species in New Zealand (height: 5 mm; length 12 mm). The decoys were designed to be made up of two parts, body (including head, thorax, abdomen, legs and antenna) and wings. The body was coloured in black to reflect the majority of *Leioproctus* spp. found in New Zealand and the wings transparent and laid down flat on the posterior side of the body. This design was then sent to Zelta3D, a 3D printing manufacturer, who printed 20 native-bee decoys. The bodies were printed in nylon on a Hewlett Packard Multi Jet Fusion printer, and the wings were printed on a smaller stereolithography (SLA) printer in clear resin (Figure 13).

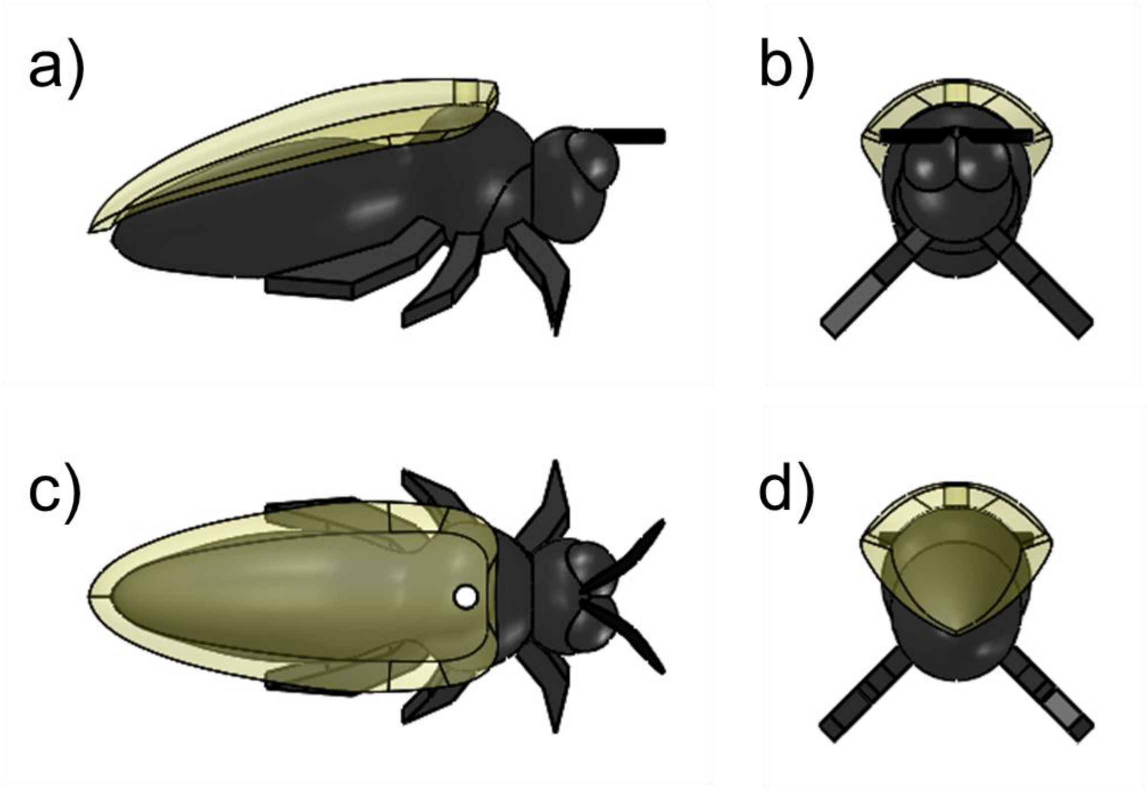


Figure 13: Design of the decoy Leioproctus spp. bees made into 3D models. a) lateral view, b) anterior view, c) dorsal view, d) posterior view.

Flower boards

Two identical flower-boards were designed to simulate a generic foraging source (*i.e.,* a tree or bush; Figure 14). During trials, flower boards were placed 200 mm apart on the ground, perpendicular to the managed honey bee colonies in the immediate area. Flower boards were made from green painted plywood for the board face and timber for the legs. The face was 500 mm x 500 mm, and the feet raised it 100 mm off the ground. The flowers were yellow, made of thin cardboard and glued to the board face arranged in a 4 x 4 square (Figure 15). At the centre of each flower a 9.9 mm hole was drilled, and a 1.5 ml centrifuge tube pushed through for the nectar source. The nectar tubes were filled with 67 Brix white sugar (sucrose) syrup.

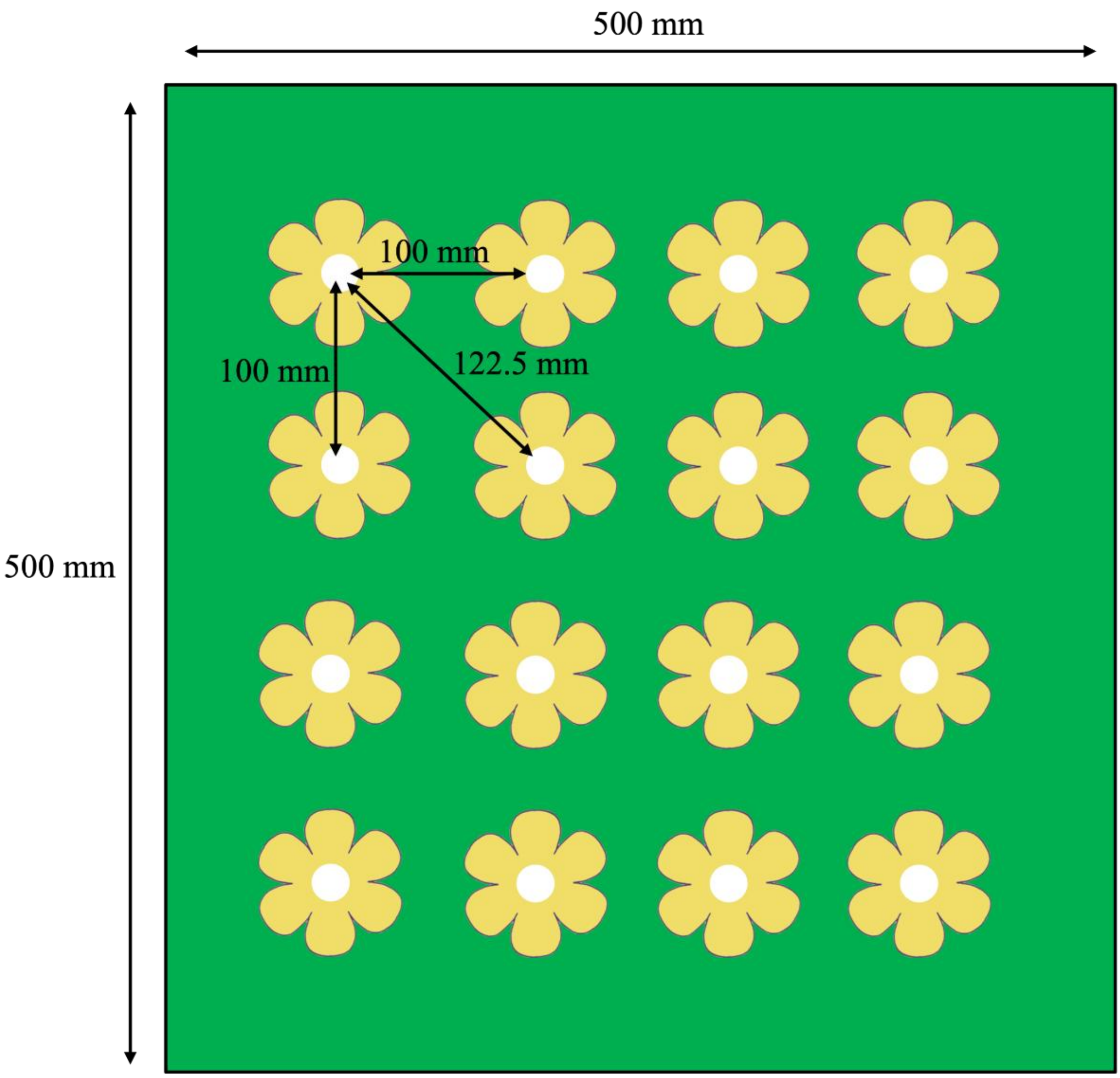


Figure 14: Diagram of flower board with measurements.

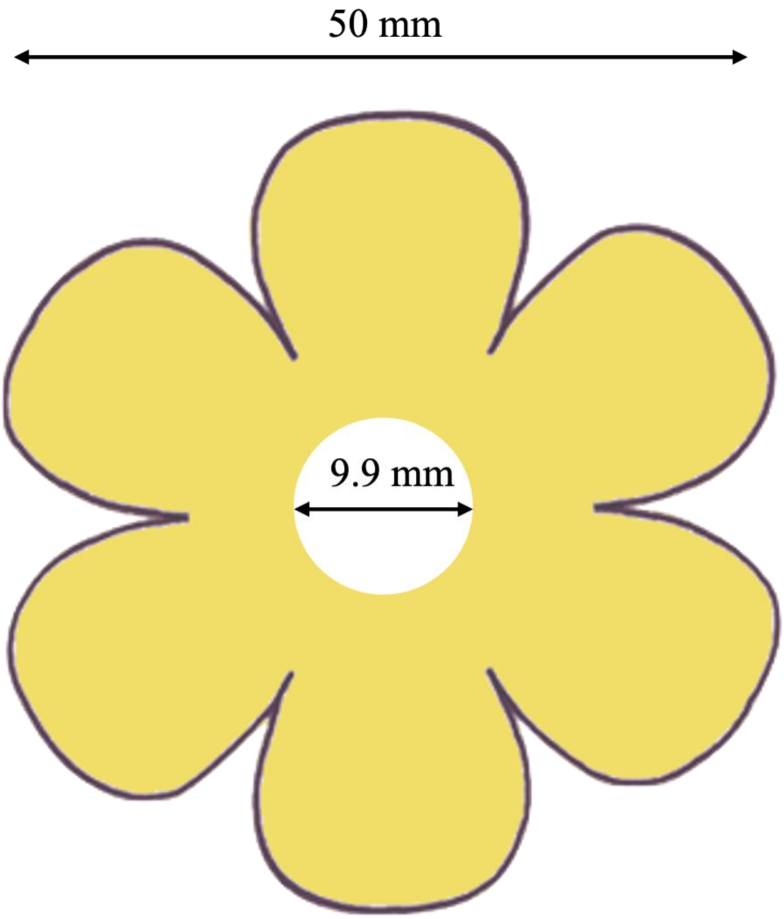


Figure 15: Diagram of flowers from flower board with measurements.

Experimental design

Five different densities of native bee decoy presence were tested; 0, 4, 8, 12, and 16, arranged randomly on the flower board flowers (maximum of one native bee decoy per flower). The treatment flower board (with native bee decoys) and control board (without decoys) were switched after each round. The native bee decoy densities were randomly selected for each round of observations. Each replicate was undertaken at a new location, and each location was randomly selected from an area within 100m of the resident managed honey bee colonies.

Behavioural observations

Each trial consisted of five rounds using one each of the five different densities of native bee decoys for a total of nine replicates. For each round of observational periods I recorded the first flower visit by a honey bee, the flower board visited and the total number of flower visits by honey bees. A first visit was classified as a honey bee that is identified as visiting a flower for the first time in that current round. The total number of visits was total number of successful flower visits (i.e. it could include multiple visits by the same bee moving from flower to flower, either on the same board or adjacent board). A successful flower visit was only recorded if the honey bee was observed dipping its tongue into the tube with the sugar syrup. Each replicate started with a two-minute acclimatisation period where the simulation flowers were filled with sugar syrup and flower boards were placed on the ground. After the acclimatisation period, the flower boards were removed, simulation flowers refilled with sugar syrup, native bee decoys positioned, and re-placed on the ground to their original positions. The observational period for each round started once the flower boards were placed on the ground and ended once the 20th first-visit of a honey bee had been observed. The minimum duration of an observational period was 2 minutes, and the maximum duration was 17 minutes, with a mean duration of 5 minutes. Once the round was complete, the flower boards were removed, simulation flowers refilled, the next corresponding native bee decoys deployed, and then replaced on the ground to their original positions. After five rounds were completed the flower boards were moved to the new location to begin the next replicate. For each round of observations, the time of day, cloud coverage and temperature were also recorded.

Statistical analysis

Linear regression models were used to determine the relationship between first visits or total visits and three environmental variables: time of day, cloud cover percentage, and temperature. Analysis of Variance was used to determine the relationship between the proportion of first visits or total visits to the control board and the native bee decoy treatment (0, 4, 8, 12, 16.). All models were checked and fitted the assumptions of homogeneity of variance.

Results

Environmental effects

Honey bee behavioural responses were not significantly related to time of day or temperature for both the initial bee visit and total bee visits (Table 14). Similarly, initial bee visit was unrelated to cloud cover percentage, however, total bee visits was significantly affected by cloud cover, with total bee visits increasing as cloud cover increased (Table 14).

Table 14: *Effect of environmental factors on honey bee and Leioproctus spp. behavioural responses.* Significant effects are indicated in bold text.

Response	Fixed Effect	Estimate	SE	*p*-value
	Time of day	0.002	0.002	0.465
First Visits	Cloud Cover	0.245	0.159	0.131
	Temperature	-0.123	0.147	0.406
	Time of day	-0.010	0.011	0.337
Total Visits	**Cloud Cover**	**3.734**	**0.566**	**< 0.0001**
	Temperature	1.206	0.704	0.094

Native bee decoy presence

The number of decoy native bees was not correlated with the proportion of honey bees visiting the control vs treatment board for the first time ($F_{4,40} = 1.308$, $p = 0.284$) (Table 15, Figure 16). Similarly, there was no significant relationship between the number of decoy native bees present and the proportion of honey bees visiting the control board when considering the total number of honey bee visits ($F_{4,40} = 1.042$, $p = 0.398$) (Figure 17).

Table 15: *Mean and standard deviation of the proportion of first visits to the control boards at five levels of native bee decoy density.*

Number of native bee decoys	Replicates	Mean	Std dev
0	9	0.572	0.100
4	9	0.600	0.079
8	9	0.572	0.112
12	9	0.644	0.081
16	9	0.650	0.117

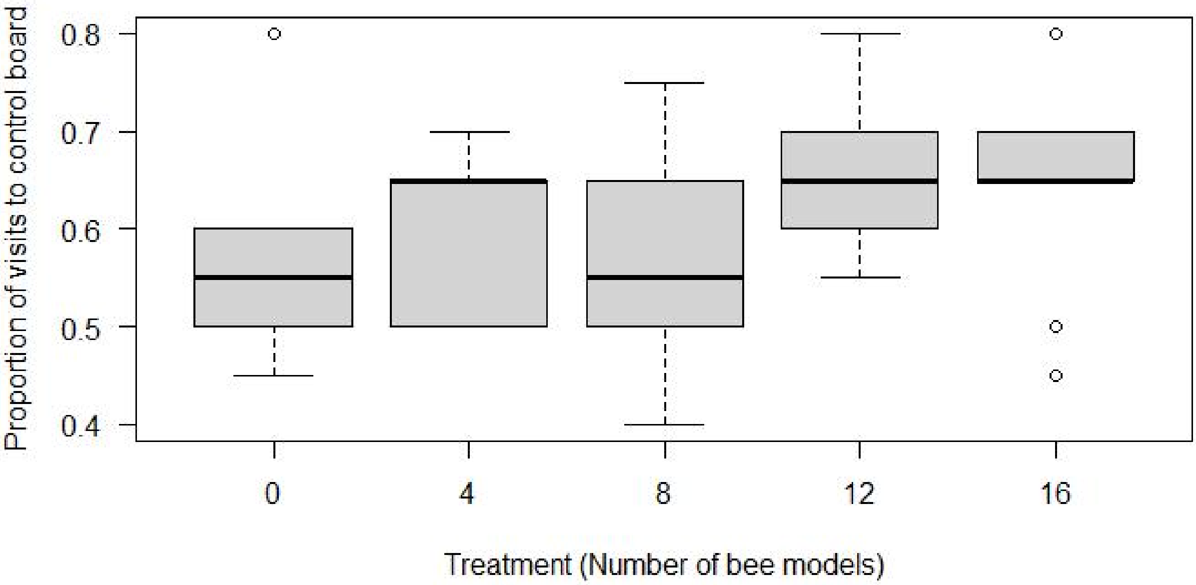


Figure 16: The proportion of first visits to the control board at five different levels of native bee decoy densities. The box represents the upper and lower quartiles, while the dark black line represents the median.

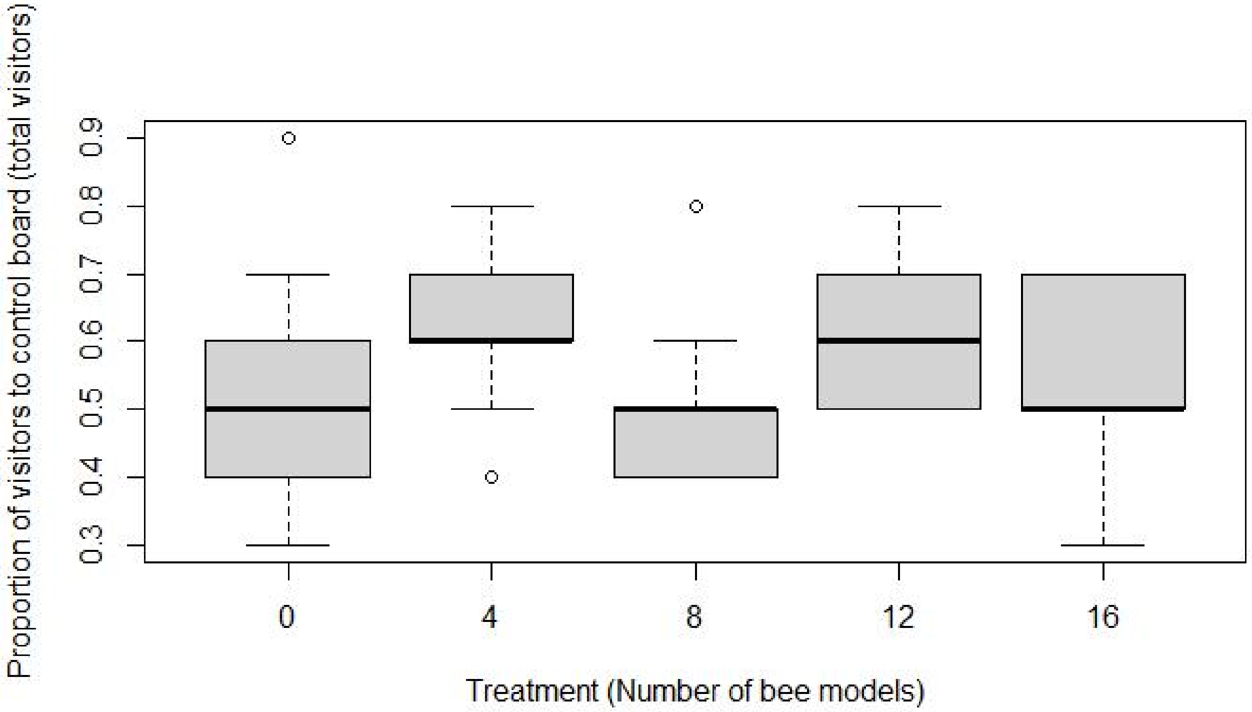


Figure 17: The proportion of total visits to the control board at five different levels of native bee decoy densities. The box represents the upper and lower quartiles, while the dark black line represents the median.

Presence/Absence

Overall, there was a higher number of honey bee visits to the control board where there were no native bee decoys present (mean = 23.7, SD = 8.63), versus visits to the treatment board (mean = 17.8, SD = 6.11) (t = 3.159, df = 35, p = 0.003) (Figure 18). Note that for this analysis the trials where the native bee treatment was 0 were removed to leave 36 trials at 4, 8, 12, or 16 native bee decoys.

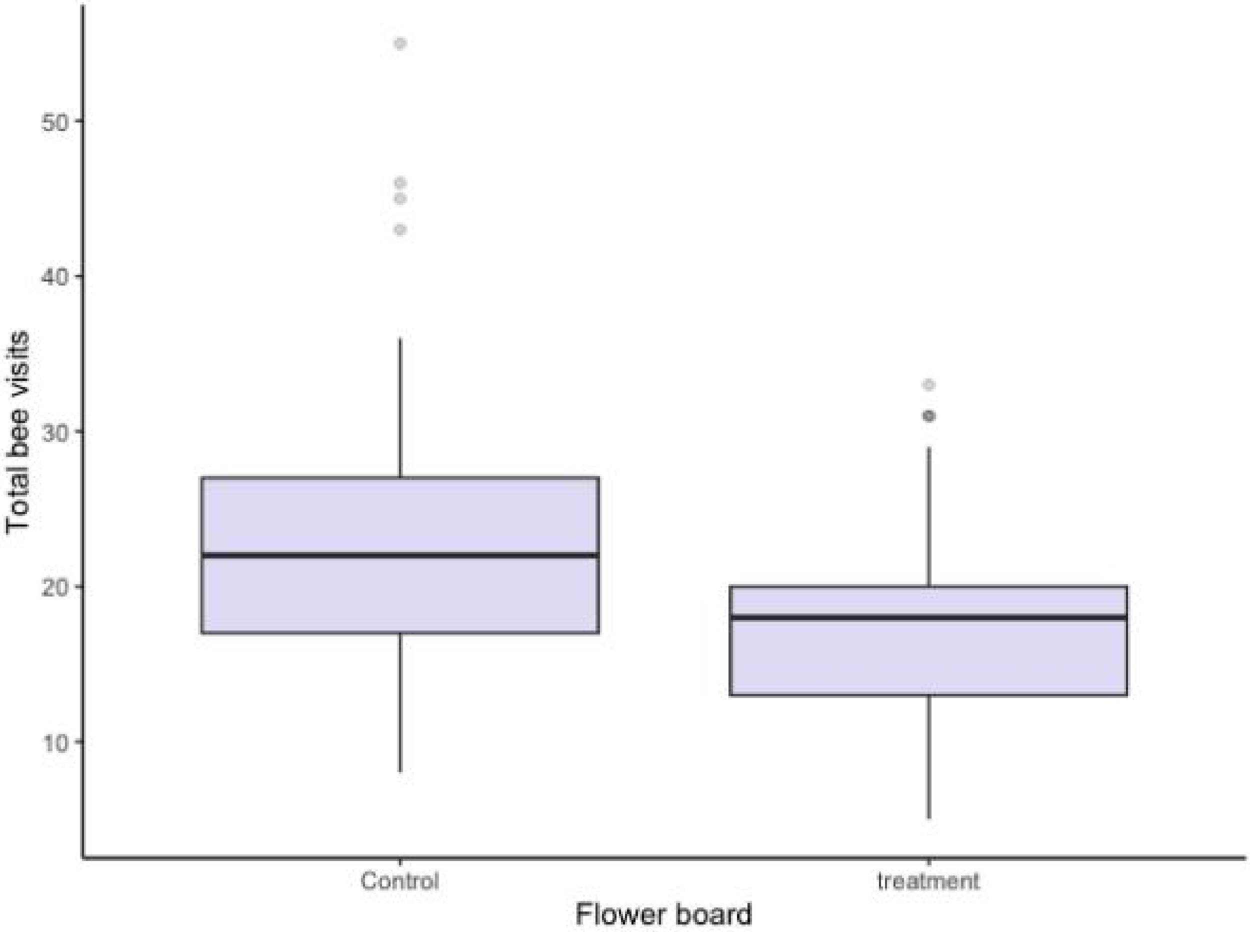


Figure 18: The comparison of total number of visits of honey bees to the control board vs the total number of visits of honey bees to the board with native bee decoys present. The box represents the upper and lower quartiles, while the dark black line represents

Discussion

In this trial of the effect of native bee decoys on honey bee foraging behaviours, I did not find a correlation between the density of native bee decoys and increasing preference of the honey bees for the floral source without decoys. However, overall there were more visits of honey bees to the control boards than to the boards with one or more native bee decoys. In chapter two, I explored the potential that honey bees exhibit avoidance behaviours in the presence of *Leioproctus* spp., especially at high abundances. This study was designed to explore this hypothesis, with the aim to expose the mechanism driving this potential behaviour. If avoidance behaviour was to be identified, I would expect to see a negative relationship between honey bee flower visits and the number of native bee decoys. However, the number of decoy native bees did not have a significant effect on the proportion of honey bees visiting the control board vs treatment board for both initial visits and total number of visits. However, the data for first-visits (Figure 16), show a positive trend that suggests that the limited replication of this study was not sufficient to demonstrate this relationship. The results should not be taken as demonstration of no relationship; further investigation with increased replication and even higher native bee decoy densities would be required to increase confidence in the result.

To assess whether future investigation into this study could benefit from increased replication, I analysed the data through a simplified lens to compare the effect of the presence of native bee decoys versus the absence of native bee decoys on total honey bee visits. The analysis found that there were significantly higher mean visits to control boards where there were not native bee decoys present versus treatment boards with native bee decoys present. Note that for this analysis, trials where the treatment board had no native bee decoys present (i.e. treatment level 0 was removed). This result supports the hypothesis that honey bees exhibit avoidance behaviour in the presence of foraging *Leioproctus* spp. This study provides a foundation for future research to further investigate this hypothesis.

Temperature and time of day did not significantly affect honey bee behavioural responses for both the initial bee visits and total bee visits. Similarly, initial honey bee visits were unaffected by cloud cover, however, total honey bee visits increased with increasing cloud cover. Typically, pollinator and honey bee activity is negatively related to an increase in cloud cover (De Mattos et al., 2018; Sjödin, 2007; Vicens & Bosch, 2000), however when interrogating the data further, my result is probably due to low sample size and cloud cover outliers. For eight of the nine sampling rounds, cloud cover was one okta or lower, and for one round cloud cover ranged from 4 – 7 oktas. Therefore, it is difficult to make any conclusions about the relationship between cloud cover and honey bee activity in this study.

CHAPTER 4

General Discussion

In this thesis I aimed to investigate whether or not competition between honey bees and native bees in mānuka-dense ecosystems could be identified through temporal niche partitioning and changes to foraging behaviours relative to the abundance of interspecific competitors. In Chapter 2, I found evidence for temporal niche partitioning and in Chapter 2 and 3 I provide some evidence for change in foraging behaviour in both *Leioproctus* spp. and honey bees in response to competitor presence. Here I will discuss the overall implications from both chapters.

Honey bee behaviour in the presence of competitors

Despite my assumption that honey bees were the superior forager, in Chapter 2 and Chapter 3 I found evidence supporting a change in foraging behaviour (mean walking time & flower board choice) in response to *Leioproctus* spp. abundance or decoy presence respectively. Additionally, supported by the evidence for temporal niche partitioning in Chapter 2, this thesis has implications for beekeeping management practices. It is in the best interest of mānuka harvesting beekeepers to transport their honey bee colonies into mānuka stands at the right time to maximise honey profits. Since honey bees are exhibiting avoidance behaviour (Chapter 3) when *Leioproctus* spp. foraging abundances are high, honey bees may be flying further away to forage on less preferential nectar crops. Therefore, beekeepers should be transporting their hives in a more targeted approach and delay moving honey bee hives early in the season when native bees like *Leioproctus* spp. are at high abundance. This would be beneficial to the reproductive success of native bee species as well as for the production of honey for beekeepers.

To gain clearer understanding of the potential competition between native bees and honey bees, it is important to investigate the potential concurrent intraspecific competition that may be affecting both groups and in turn, how these interactions describe what is occurring in these environments. In this study I found that honey bee behaviour was only affected by conspecific abundance in one instance, where I found a positive relationship between flower visitation success and honeybee abundance. This would be valuable information and a foundation for methodology for future studies useful to the mānuka honey industry. A key avenue to explore would be to investigate honey bee stocking rates, using flower visitation success rates to identify when stocking rates are too high and flower visitation becomes less efficient.

Native bee behaviour in the presence of competitors

While there is economic benefit for the honey bee industry in understanding these interactions, for *Leioproctus* spp*.,* and by proxy all native bees in New Zealand, the priority is the consideration of how to protect their populations. The majority of the native bee foraging behaviours assessed were significantly affected by honey bee abundance, indicating potential exploitative and/or interference interspecific competition. This indicates that honey bees do have an effect on native bees and native ecosystems. However, to understand the specific effects and impacts, particularly potential adverse effects, further study is required.

The *Leioproctus* spp*.* in this study showed a significantly higher abundance than honey bees overall on mānuka flowers, and therefore higher potential opportunity for intraspecific competition. In Chapter 2 of this thesis, I identify a number of behavioural changes in *Leioproctus* spp. in response to conspecific abundance which I suggest could be a result of both exploitative and interference intraspecific competition, as well as being symptomatic of the scramble effect described by David et al. (2014). Historically speaking, before the introduction of honey bees and without the benefit of historic records, I think it would be safe to assume that there would have been high densities of native bees foraging on mānuka flowers and that adaptations may already have developed to minimise the effects of this intraspecific competition. Donovan et al. (2010) showed how artificially established populations of *Leioproctus huakiwi* were able to expand by 8-25 times over three years, which is evidence that *Leioproctus* spp. have the ability to maintain or grow their populations even in the presence of competition with a supposedly superior competitor (honey bees). The high abundance of native bees early in the flowering season may provide them a competitive advantage over honey bees during this period, which could allow them to at least maintain their population levels. However, long-term population studies would be required to confirm this. It may also mean that the interspecific competition between native bees and honey bees might not be as detrimental to native bees as feared. Lastly, the seasonal temporal niche partitioning evidence from this thesis, in combination with the population expansion ability of *L.huakiwi* demonstrated by Donovan et al. (2010), could provide a potential foundation for the development of conservation practices to reduce the negative impact of honey bee nectar harvesting in mānuka blocks on native bees.

Future Research

Generally, economically driven priorities conflict with conservation driven priorities. Research in this field has the rare potential opportunity to benefit both the economically driven party (beekeepers) and conservationists. For example, research investigating nectar productivity of mānuka throughout the day/season can be used to relate to insect abundance surveys and assess insect foraging trends and standing nectar crop. Understanding mānuka nectar production would be directly beneficial for beekeepers and mānuka honey operations but could have indirect beneficial implications for native bee populations. Mānuka honey is more valuable when it is purer, so beekeepers time their transportation of hives into mānuka crops to avoid dilution of the honey crop. Dilution can occur due to bees foraging on other flowering species which flower leading up to and out of the mānuka flowering season. Additionally, if hives are in mānuka stands when nectar production is lower than the cost of energy required by the colonies, the honey bees will be eating more nectar/honey than they are storing, literally eating away their profits. In order to ensure beekeepers do not miss the optimal timing, or the possibility of losing yield to competitors, beekeepers often take a cautious approach, and put their hives into mānuka stands earlier than the optimal time. Accordingly, if this optimal time was better understood, and it led to beekeepers introducing their hives into mānuka stands later, this would make a substantial amount of nectar available early in the season to native pollinators in a win-win situation for beekeepers and conservationists.

Due to the limited research into the impact of introduced honey bees on native bees, not only in New Zealand but internationally, the research completed in this thesis only begins to scratch the surface of what is required to answer this question. Future studies should build on these findings and methods, and focus on identifying specific competitive interactions between honey bees and native bees. They should also focus on how these interactions influence reproductive success at both the individual insect level and population level of native bees. Refining methodologies to be practical in the current economic climate would encourage industry interest and allow for vital aggregation of currently limited data.

It is important to note that human honey bee management practices create an artificial environment with regards to the honey bee lifecycle. Honey bee population dynamics may not be as relevant, and each season can be treated independently. This is due to there being no seasonal carry-over effects as a result of factors like competition or nectar/pollen availability, whereas these factors would have a much greater seasonal carry-over effect for native bees. For example, the abundance of honey bees present each season is not directly impacted by the reproductive success of the previous season, but native bee abundance will be directly impacted by the reproductive success of previous season(s). For this reason, I recommend that long term studies on native bee populations be prioritised, in order to understand and mitigate the impact of honey bees on native bee populations in mānuka.

Limitations

The experiment conducted in Chapter 3 would have benefited from increased replication. I would hypothesise that the predicted negative linear relationship between increased native bee decoy presence and honey bee avoidance would likely be found with greater replication. Additionally, due to the high abundance of *Leioproctus* witnessed in my study in Chapter 2, a higher density of native-bee decoys could be valuable in attempting to expose the relationship. Currently the maximum number of native-bee decoys was 1 per flower but increasing this to a maximum of 2 per flower may better simulate a native-bee-saturated patch of flowers.

Further analysis and research which elucidates more context to the observed themes would be beneficial. For example, analysis into the effect of site based on the management practises and density of site would have been beneficial to look into. Additionally, further analysis into the occurrence ratio of flying and walking, grooming behaviours and displacement behaviours would help to provide increased context to the discussion of competition. Expanding on these examples, occurrence ratio of flying and walking would provide context around bees' decision to walk or fly at different times of day or abundances. This would provide an opportunity to investigate the decision-making process in the context of metabolic energy expenditure and the cost/benefit of potential rewards and how this might be affected by competition. Assessing how displacement occurrences might respond to increased abundance and how grooming behaviours are affected by competitor abundance, and what these the mean with regard to the pollen availability and its potential implications on the fecundity of these species would also have been helpful to further our understanding.

Concluding remarks

I believe I have taken one of the first steps to identifying competition between honey bees and native bees in New Zealand, however the next step is to investigate whether or not this competition is having a negative effect on the native bee populations. Ideally these questions would be addressed through long-term population studies and/or fecundity studies which are a logical next step for future research to build on the work done in this thesis.

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