What they do in the shadows: Habitat utilisation and diet of brown kiwi (*Apteryx mantelli*) adults within a high-density island population.

A thesis submitted in partial fulfilment of the requirements for the degree of

Master of Science in Ecology

Massey University, Palmerston North,

New Zealand.

Thomas Dixon

2015

"The natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living."

Sir David Attenborough

Abstract

Exploring the complex interactions between an animal and its spatial environment can reveal much about its biology and behaviour and identify strategies to improve future management. Despite this, surprisingly little research has been undertaken in this field in respect to one of New Zealand's most iconic endangered species, the brown kiwi (*Apteryx mantelli*).

This thesis aims to produce the most comprehensive report to date of brown kiwi spatial behaviour, investigating the habitat utilisation of brown kiwi adults within a high-density population while they are active at night and when roosting during the day. Additionally, the study examines how habitat utilisation varies, and explores the likely drivers of brown kiwi spatial behaviour including food availability, social/reproductive cues, population demographics and environmental variables.

Forty seven radio-tagged brown kiwi adults were tracked across a 1.2km^2 study site on Ponui Island from March 2013 to February 2014. The utilisation of major habitat types (forest, scrub, pasture and swamp) by each bird was measured, plotted upon a generated habitat map, and compared to predicted rates based on habitat availability to assess habitat selection. To assess habitat selection while foraging, brown kiwi were tracked at night using radio telemetry and their positions estimated using a triangulation methodology. Exact bird locations were also recorded during the day to evaluate their roost habitat selection. Roost sites were also classified into four different types of roost (tree burrow, soil burrow, surface, swamp site). Brown kiwi faecal samples were collected over this time and compared with pitfall trap samples to analyse diet and identify spatial patterns in foraging behaviour.

As hypothesised, brown kiwi selected forest habitat most often for both foraging and roosting, also choosing the more structurally stable tree and soil burrow shelter sites. Other habitat types were utilised much less than predicted, though rates varied between seasons, gullies, demographics and behaviours. Pasture was identified as seasonally important for brown kiwi, utilised increasingly by study birds over summer and autumn when foraging. Additionally, a relationship between their spatial behaviour while foraging and while roosting was recognised for the first time, suggesting that these behaviours are not independent. Invertebrate availability was identified as the primary driver of brown kiwi spatial behaviour, with foraging behaviour trends closely matching nocturnal spatial behaviour. Social and breeding behaviours were discussed as other potential drivers, though further research is required to fully understand these relationships. Research findings confirmed that brown kiwi have an opportunistic diet, appearing to select those invertebrate groups that provide the highest protein input more often in their diet. Foraging strategy changed between seasons and locations, likely driven by a combination of changing invertebrate lifecycles, environmental conditions and dietary requirements.

This study has improved our understanding of brown kiwi spatial behaviour, introducing new information and refining previous knowledge. The findings provide valuable information for managers as they work to conserve remaining brown kiwi populations, and will become increasingly relevant in the future as population densities begin to rise.

Acknowledgements

After almost 200 days spent in the field chasing kiwi and what feels like ten times that behind a computer or in the lab, I have finally reached the end of this great adventure! Luckily I have had people to help me every stage of the way. Firstly I need to thank my new family, the Ponui Family:

- To Isabel Castro, the mother of our group. Your supply of enthusiasm and advice is what started us up, kept us going, and helped see us home with a new qualification in tow. Thank you for your support both on and off the island, and for finding the right blend between being our kind mother and (only a little) feared supervisor. A big thank you for introducing me to the world of Kiwi.

- To my Ponui siblings – Alex Brighten, David Izquierdo, Kat Strang and Natasha Bansal, I am lucky to have found a bunch of fellow researchers with whom I get along with so well. Thank you for your companionship in the bush during the unholy hours we frequented, your advice and ideas for the study, and for being a big source of laughter and friendship. Be it poo collecting or finding birds, you all assisted me over my study, for which I am hugely grateful. I am sure we will remain close friends.

- Rounding out the family is the Chamberlin's. I have never met a finer group of people. Thank you all so much for letting us be a part of your island and your life. Dave and Ros, for this analogy to work you will have to be the Ponui Family Grandparents (apologies). Your combined font of knowledge is as unrivalled as it is freely given, and your advice was hugely appreciated throughout the study. Thank you for the time and effort spent transporting me, and ensuring I was never malnourished or lonesome. To the Chamberlin girls (our cousins), thank you for your friendship and advice. That I now consider myself part farm-boy is credit to just how much you and your parents have taught me.

To the other half of my supervisor team - Dianne Brunton, your immense brainpower, help and support during the analysis and write up period helped get me over the line. Thank you for giving up some of your much sought after time to help shape and edit this study.

Thanks also to my unofficial third supervisor – Alex Wilson. The time and energy you spent teaching me how to be an ecologist cannot be understated. Thanks also for your words of encouragement and advice throughout the study.

Thanks to Alisha Thomas, Emily Lindsay, Andrew Babbage, Matt Thomas, Jon Cope, Tracey and Chris Dixon, John and Inge Bolt and Simon and Christine Brotherton for donating some of your time to help in the field. The long days and nights spent in the bush were much brighter when you were around. I am glad you could all share in the Ponui experience. I also want to thank Emily Craig, Anne Kim, Arjane Kerkhoven, Nicki Van Zyl and Rebekah Ingrid for your help in the lab. Thanks also to Beatrix Jones, Daniel Thomas and William Ong for your help with stats, and Alisha Thomas and Aaron Harmer for proof reading drafts!

I had the pleasure of being part of both the Albany and Palmy Ecology groups during my time at Massey. Thank you to the technicians Cleland Wallace, Mark Delaney, Shaun Nielson and Tracy Harris for helping with lab equipment, invert analysis; and Sharon Wright for her tireless work behind the scenes. Huge thanks are required to my fellow postgrad students for forming such a tight knit group. The future of ecology & conservation in NZ looks bright if you lot are anything to go by. Special thanks to Jon, Jacqui, Alaine, Nicki, Lena, Emily, Jess, Luca, Viv and Wesley for your friendship over the study.

Thank you to all my friends who have put up with me constantly being away or else writing. Thanks to my parents and sisters for supporting my decisions and being there through the good and bad in this latest endeavour. I am lucky to have such fantastic family and friends.

Finally, thank you Alisha Thomas. You put up with me being away for weeks on end, every month without complaint, followed by months of write up. The fact you are so happy seeing me achieve my own dreams is just one of the reasons why I love you so much. Without you I would likely have been writing for all of time, so thank you.

This project was funded with the help of the Massey Masterate Scholarship, Lovell and Berys Clark Scholarship and the Ecology Bursary, without which the study would have been impossible. I am extremely grateful for each and every dollar.

Thank you to everyone involved for sharing in my epic adventure.

Table of Contents

List of Tables

List of Figures

List of Plates

List of Appendices

CHAPTER ONE

Introduction

Plate 1.1 - Female brown kiwi Emily has chosen a surface site with very little cover to spend the day in Red Stony gully. Photo by author.

1.1 Spatial Systems

The spatial patterns exhibited by animals within an environment are rarely random (Adams et al., 2013). Instead, they are influenced by an animal's biology, behaviour (Schoener, 1971), and the ecological features of its habitat (Adams et al., 2013). Therefore, an understanding of how an animal interacts with the space around it can reveal much about its ecology. This knowledge can aid conservation initiatives by helping to identify more effective strategies for the management of a species (Holzapfel et al., 2008).

Detailed investigation into an animal's spatial ecology can often prove challenging due to the multitude of factors that can influence spatial behaviour. These include demographic factors such as density (Manly et al., 2002), sex and age ratio (Harris et al., 1990); environmental factors such as habitat structure (MacFaden & Capen, 2002), climate (Stevens, Bayne, & Wellicome, 2011), seasonality (Rice, Ohmart, & Anderson, 1983), resource availability (Rosenzweig, 1991) and levels of competition or predation (Hughes, Ward, & Perrin, 1994), as well as behavioural factors such as territoriality, individuality and reproductive or foraging strategies (Robinson & Holmes, 1982; Bjørneraas et al., 2012; Adams et al., 2013). Often forming complex relationships with each other, these driving factors change over time and between places and can be difficult for researchers to isolate (Rosenzweig, 1991). This difficulty is increased in species which are challenging to monitor. Exploring these driving factors in greater depth will improve our understanding of the spatial ecology of a species.

1.1.1 Habitat Selection

Lack (1933) was among the first to emphasise the occurrence of habitat selection in birds, spawning a new field of study. Since then, the topic has become the focus of numerous studies that span a multitude of species (Reviewed in: Jones, 2001). Habitat selection refers to the behavioural response of an animal to favour certain habitats that aid in fitness or survival (Block & Brennan, 1993). Different habitat types can provide different benefits to avian species, including protection from predation, provision of shelter, nest sites and food, and levels of both inter-specific and intra-specific interaction (Jones, 2001). Habitat utilisation (or use) can help to assess habitat preference by comparing the frequency at which an animal uses a particular habitat with the availability of that habitat. This identifies how often particular habitats are used, suggesting areas that might be important to the animal in its fundamental (realised) niche. Any conclusions made regarding the spatial behaviour of a species are conditional on the spatial scale under investigation (Kristan, 2006). Habitat utilisation can be studied at small (microhabitat) or large (macrohabitat) scales, generating different results (Frye et al., 2013).

Because the drivers behind habitat selection are many, and the relationships between them complex and dynamic (Rosenzweig, 1991), the investigation of habitat utilisation must consider a wide range of ecological factors. While composition of vegetation may play a role in habitat selection, more significance is often attributed to the availability of appropriate resources such as food, cover and shelter sites (Brown, 1988). Interspecific and intraspecific interactions including breeding and social interaction (Harris & Reed, 2002) as well as spatial factors such as density (White & Garrott, 1990) and territoriality (Rosenzweig, 1991) have also been shown to effect utilisation. Additionally, individual animals can show partiality for certain habitats (Bjørneraas et al., 2012), reviewing the costs and benefits of finding and moving to a different habitat as opposed to remaining in one place (Rettie & Messier, 2000). Finally, environmental variables such as climate and weather can affect the rate at which different habitats are used.

1.1.2 Monitoring

Monitoring, by undertaking repeated surveys of a population using standardised methods, is an effective tool for measuring population trends and assessing the impact of management on a population (Gregory, Gibbons, & Donald, 2004). However, when studying avian behaviour a more comprehensive form of monitoring is necessary (McLennan, 1992). Examining spatial behaviour requires a more active approach to monitoring, where individuals can be located on a consistent basis. However many of the techniques which provide this information (stalking, GPS tracking, capture release, dog tracking, remote vocal recognition) are too labour or resource intensive to implement (Gregory, Gibbons, & Donald, 2004), or else change the bird’s behaviour. A turning point in the research of avian spatial systems was the development of lightweight radio transmitters for radio telemetry.

Radio telemetry

Radio telemetry has been widely used to study the spatial systems of many species and is considered an unrivalled technique for determining the activity patterns, movements, home range and habitat use of animals in the wild (Harris et al., 1990; Robertson & Westbrooke, 2005). Remote studies reduce stress and disturbance to avian study subjects, as birds can be monitored from a distance (Lee et al., 1985). This also results in more accurate results, as the behaviour of the bird is no longer impacted by the close proximity of observers. Additionally, there is markedly reduced observer error compared to other techniques. Kufeld, Bowden, and Siperek Jr (1987) found a 95% agreement between observers on classification of signals when listening for the strongest telemetry signal.

The cost of telemetry and limited number of available frequencies (<100) will usually limit the number of study animals involved (Robertson & Westbrooke, 2005; Riber, 2006), a problem often compounded when working with an endangered species. This can make obtaining a sample size which is large enough to take independent data points and avoid pseudo-replication very difficult. In addition, care must be taken to ensure the times between obtaining data points for each sample are far enough apart to ensure that the first measure does not influence the second (White & Garrott, 1990). Further issues can arise ensuring the chosen sample of birds is spatially representative of the entire study site. Telemetry studies also require periodic recapture and bird handling to replace transmitters when the battery runs low or the bird is growing, a process known to elicit a stress response in birds (Straub et al., 2003; Cockrem et al., 2008). Transmitters have been known to get tangled in vegetation (Boyd, 1993), and can only be picked up if the researcher is within a maximum distance, meaning birds which travel far away from the study site may never be picked up again. However, these negatives are generally outweighed by the positives.

Locations of radio-tagged wildlife are generally determined utilising either the ‘homing in’ or triangulation techniques. Homing is where the observer moves in the direction of the strongest signal until the bird is visible. Homing is more accurate than triangulation as specific locations are identified (Keye, 2008). However, this technique is not recommended when tracking nocturnal species that live in closed habitats (Harris et al., 1990), as direct observation is likely to disturb the animal (Chan, 1999). Additionally this technique is more time consuming as only one animal can be followed at any one time, producing fewer samples. Triangulation is an alternative method where an animal’s location is estimated by a process of intersecting multiple bearings taken from known points. This technique allows multiple individuals to be tracked simultaneously with little to no disturbance.

The problem of accuracy

Triangulation studies have inherent inaccuracies. Saltz (1994) identified variance around the bearing, the intersection angle, and distance to the signal source as the most important factors to identify to determine the error of radio telemetry data. A problem with achieving accurate bearings is that radio signals can be blocked or impacted by the topography of an area, resulting in a distorted signal and an unrealistic bearing (Kufeld, Bowden, & Siperek Jr, 1987; Anderson-Sprecher, 1994). These distorted, or ‘bounce’ signals can result in directional accuracy error of many degrees. Bouncing can occur frequently, as often as 37% of the time in a study by Lee et al. (1985), and is particularly common in mountainous terrain. Telemetry instruments also have inherent error, with a standard three element Yagi antenna reported to have a bearing accuracy of about ± 5% (Fuller et al., 2005). Achieving accurate distance estimates can also be problematic. For example, two-stage transmitters often have an effective range of up to 1-2km, which means animals can be monitored without being disturbed. As the bird approaches or gets further away the volume of the transmission will increase or decrease, though this too can also be impacted by topography or land cover (Kufeld, Bowden, & Siperek Jr, 1987; Harris et al., 1990). Finally, when triangulating bearings it is important to consider the intersection angle. Shallower angles between search points provide less accurate locations, while larger angles are considered more accurate (Lee et al., 1985). Angles between 40 and 140 degrees were considered preferable in a previous study (Gibbs, 2000).

These potential errors require some method for outlier rejection to ensure robust estimation. However, when few observations are available for each triangulation, standard techniques for outlier rejection are often impractical (Anderson-Sprecher, 1994). Instead outlier rejection has usually been based on non-statistical considerations, whereby individual bearings are rejected if they are unclear or illogical, if prior knowledge of the terrain suggests a bounced signal or if the animal is at a nonsensical location (Anderson-Sprecher, 1994). While this remains valuable, more statistical methods for reporting error are also desirable. Researchers should attempt to calculate the level of error associated with their specific method and study site (Saltz, 1994).

1.2 Avian Diet

Studies of foraging behaviour and the relationship between birds and their food resources are critical to studies of avian biology and ecology (Sinclair, Fryxell, & Caughley, 2006). Knowledge of a bird's diet can help to explain the spatial behaviours and environmental requirements of a species (Durst et al., 2003; Bjørneraas et al., 2012). This knowledge can lead to direct management implications for the conservation of vulnerable or endangered species (Myles et al., 2009), including helping to develop improved diets for animals in captivity (Potter et al., 2010), and to determine sites appropriate for translocations or habitat management (Morrison et al., 2007; Woolaver et al., 2013). Despite its importance, relatively little is known about the foraging behaviour and diet of many avian species (Rosenberg & Cooper, 1990).

1.2.1 Dietary Factors to Consider

Availability and exploitation

Characterising avian diet requires an understanding of several different factors centred on the availability and exploitation of food resources (Sinclair, Fryxell, & Caughley, 2006).

Food availability is a key determinant of avian habitat use, helping to explain the spatial patterns of foraging behaviour (Razeng & Watson, 2015). Availability of invertebrate food is dependent upon the presence of invertebrates in an area and the ability of a bird to consume them (Wolda, 1990). Constraints imposed by insect biology and vegetation structure help to determine whether or not insects will be present in a habitat (Hutto, 1990). Environmental factors such as rainfall, temperature and soil penetrability may also have significant effects on prey abundance (Sinclair, Fryxell, & Caughley, 2006). Additionally, fluctuations in prey populations due to movements or changes in behaviour of both the predator and its prey can occur within seasons (Sinclair, Fryxell, & Caughley, 2006), years (Szaro, Brawn, & Balda, 1990), and locations (Petit, Petit, & Petit, 1990). Such variation in resource availability suggests that caution be taken when drawing inferences about diet which are based on a few months, or data pooled over several years (Miles, 1990).

The type and rate at which food is exploited results from biological interactions between birds and their prey (Cooper & Whitmore, 1990). Choice of prey depends on foraging behaviours of the species, the methods by which they search for food, and time and place of foraging (Robinson & Holmes, 1982). Birds can practise selective foraging; where food is consumed at rates above their availability, suggesting foraging preference (Stephens, 1990). Exploitation rates can also fluctuate with availability or during times of particular dietary needs such as when breeding (Robel et al., 1995). Competition for resources between species (interspecific) and between individuals of the same species (intraspecific) will limit how much can be exploited by an individual (Szaro, Brawn, & Balda, 1990; Sinclair, Fryxell, & Caughley, 2006). Optimal foraging theory suggests that foraging strategies will be selected to ensure maximum net energy intake whilst minimising other costs, such as thermoregulation or predation risk (Stephens & Krebs, 1986). Therefore, birds are expected to favour certain prey species or habitats when foraging (Stephens, 1990), within the constraints of their realised niche. The complexity of these relationships means that the foraging strategies exhibited by birds are varied, including both generalist and specialist foragers (Catry et al., 2014), and flexible, changing under certain environmental or behavioural circumstances (Durst et al., 2003; Sinclair, Fryxell, & Caughley, 2006).

Nutrient content and digestibility

Foraging behaviour of avian insectivores is often linked to the nutritional content of their prey. However, little information exists on this topic for most avian species (Finke, 2002). Researchers are only now beginning to consider habitat quality in nutritional terms, evaluating if observed patterns of prey selection reflect nutritional value (Razeng & Watson, 2015). This is in turn has helped to inform targeted and effective management actions (Razeng & Watson, 2015), proving particularly important for the conservation of rare species held in captivity (Walker et al., 2013). When studying the energetics of diet, both the nutrient content of available invertebrates and the bird’s ability to digest, and therefore exploit it, must be considered (Bell, 1990).

Invertebrates are an important nutrient source for many animals and their nutrient contents are relatively well known (Finke, 2013). Most invertebrates are protein-rich (Bell, 1990), suggesting protein is an important part of an insectivore’s diet (Minson, 2013). However a substantial amount of that (~33%) is contained in the cuticle (Bell, 1990), of which a significant amount (up to 40%) is stored as chitin (Finke, 2002, 2007), a substance thought to be relatively indigestible in birds (Potter et al., 2006). The percentage of dry weight made up of lipids (fat) varies between different invertebrates (from 5.3%-85.4%; (Finke, 2013)), with some species containing significantly more than others (Barker, Fitzpatrick, & Dierenfeld, 1998). Birds are particularly effective at storing fats as an energy reserve (Blem, 1976). This is important for precocial birds which are born with large lipid reserves (Blem, 1976). The energy content of some taxonomic groups has been reported to differ between locations (Robel et al., 1995), suggesting nutrient content may be partially site-specific. The differences in energy and nutrient content of different categories of invertebrates increases the complexity of the food input variable by several magnitudes (Robel et al., 1995).

A thorough understanding of nutrient assimilation (or digestibility) can give a more accurate notion of the nutrition of an animal (Minson, 2013). Assimilation rate depends upon both the nutrient and animal in question. For example the digestibility of invertebrate protein has been estimated at around 75% to 99% in birds (Bell, 1990).

1.2.2 Sampling Diet

Measuring availability

Ornithological studies use a variety of insect sampling techniques to determine the types, numbers and distribution of invertebrate prey available to birds. Some examples include pitfall traps, light traps, baited traps, leaf litter collection, soil core sampling, sweep netting, transect counts, and quadrat sampling (Cooper & Whitmore, 1990; Prasifka et al., 2007; Schirmel, Buchholz, & Fartmann, 2010). Each technique samples only a portion of the total insect fauna available, so estimates of total abundance using these techniques will be biased accordingly (Prasifka et al., 2007). Most bird species will feed on many types of invertebrates and utilise a variety of different habitats and foraging strategies, presenting a formidable sampling problem (Cooper & Whitmore, 1990). Different types of prey must be sampled in a consistent fashion to allow the researcher to compare the abundance of all types (Standen, 2000). Unfortunately some species are more prone to be captured by a given technique than others, meaning relative abundances in a sample can differ from the actual abundance in the field (Wolda, 1990). As a result it is recommended that more than one method should be used whenever possible, and both the frequency of occurrence and volume should be considered during analysis (Rosenberg & Cooper, 1990; Standen, 2000).

Popular methods for monitoring terrestrial invertebrates such as pitfall trapping or other bulk sampling methods can potentially damage the invertebrate community by harvesting a large number of invertebrates and through by-catch of non-target species (Pearce et al., 2005; Seldon & Beggs, 2010). Consistently killing large numbers of invertebrates at a particular site can take food away from the birds under observation, altering their behaviour. Additionally removing large numbers at a site may bias any subsequent samples (Seldon & Beggs, 2010). Despite these deficiencies, sampling techniques such as pitfall trapping are still considered suitable for monitoring the relative abundance of invertebrates, provided the sample is large enough (Standen, 2000).

Measuring exploitation

Identification of insectivorous bird prey in the field through observation is challenging as they can consume a wide range of taxa, many of which are small and hard to distinguish (Durst et al., 2003). This method is also poor for studying cryptic or nocturnal species (Piggott & Taylor, 2003), or birds with avoidance behaviours, due to the difficulty of observing them for extended periods (Potter, 1989).

Diet sampling in the past necessitated the killing of birds to examine their gut contents (Gurr, 1952), however this is no longer necessary with the advent of stomach flushing or regurgitation. While this is certainly an improvement ethically, the procedure requires animal capture and significant discomfort and can have adverse effects on the sampled birds, limiting its practical use for many studies (Deagle et al., 2007). Samples can also be heavily biased due to the differing digestibility of invertebrates (Hutto, 1990). Results are biased towards invertebrates with sclerotized and chitonous structures (Reid, Ordish, & Harrison, 1982) which persist far longer in the gizzard than softer structures like earthworm chaetae (Watt, 1971). Swanson and Bartonek (1970) found that soft-bodied insects may be absent from gizzards within five minutes of ingestion, whereas hard seeds may persist for several days. Crop contents are thought to be the most unbiased representation of a birds diet (Rosenberg & Cooper, 1990), however not all species possess a well-developed crop.

One of the more demanding techniques, analysis of faecal samples provides an adequate estimation of diet and is used commonly in dietary studies (Dickman & Huang; Rosenberg & Cooper, 1990; MacLeod & Kerly, 1996). Samples can be collected year-round without disturbance to birds (MacLeod & Kerly, 1996), and repeated sampling from known individuals is possible (Rosenberg & Cooper, 1990). Sampling is fast and effortless, with the majority of effort being postponed to the stage of laboratory work (Michalski et al., 2011).

One disadvantage of faecal analysis is the highly digested and fragmented state of the samples. For this reason, biases related to differential digestibility and temporal rates of passage may be more substantial than in stomach or crop samples (Rosenberg & Cooper, 1990). Nevertheless, a close association between faecal and stomach samples has been shown (Rosenberg & Cooper, 1990). Additionally, varying size and consistency of faecal samples could mean that some samples contain more invertebrates than others. Although identification of faecal contents is now possible through genetic analysis (Deagle et al., 2007; Prugh, Arthus, & Ritland, 2008; Boyer et al., 2013), this technique remains costly. Instead, the ability to detect the full range of dietary items present in these samples depends upon learning to identify the specific parts that survive digestion, which are thought to exist for most solid invertebrate foods (Rosenberg & Cooper, 1990; Michalski et al., 2011).

Sampling difficulties

Without knowledge of a bird’s perception, it is hard to know which prey items would be eaten and which ones might be ignored. This makes it difficult to know if you have measured actual food availability or not. Additionally, measures of availability are sampled in a different way and using a different ‘perceptual filter’ than exploitation measures (Hutto, 1990), making comparison between the two problematic. Difficulties in diet studies arise around the need to relate changes in foraging behaviour to changes in food resource (Raphael & Maurer, 1990). While food may be responsible, these changes can also be driven by a myriad of other factors, including spatial behaviours, social behaviours, environmental variables, individuality, density, seasonality and site-specific factors.

1.3 Study Species

This thesis explores how a range of factors contribute to habitat utilisation in the brown kiwi (*Apteryx mantelli*), including an analysis of their diet. Kiwi is a Maori word and as such is the same in singular as it is in plural.

Kiwi are members of the Paleognathae clade, an ancient group of birds separated from 99% of extant avian species due to their unique basal palate structure (Phillips et al., 2010; Mitchell et al., 2014). Comprised of the volant tinamous and flightless ratites, this group has long been viewed as central to understanding the early evolution of birds (Harshman et al., 2008). Kiwi are the smallest member of the ratites, which span many of the southernmost continents, composed largely of giant ground dwelling herbivores such as the ostrich, emu, cassowary, rhea and the now-extinct New Zealand moa and elephant bird of Madagascar (Mitchell et al., 2014). All species of kiwi belong in the genus *Apteryx*, meaning 'without wings', and are endemic to New Zealand.

Due to its unusual features, the kiwi was treated with much scepticism when initial specimens arrived in Europe. However, they are now one of New Zealand's most distinctive animals. The kiwi has become a symbol of New Zealand's unique wildlife and the value of our natural heritage (Holzapfel et al., 2008), and is the country's unofficial national emblem (Herbert & Daugherty, 2002). Despite this, knowledge of kiwi life is still incomplete (Holzapfel et al., 2008), and few New Zealanders have ever seen one in the wild (Peat, 2006).

1.3.1 Classification

There has been debate over the last century concerning the taxonomy of kiwi (Herbert & Daugherty, 2002), however modern genetic analysis has resulted in the current identification of five recognised *Apteryx* species (Burbidge et al., 2003). These are the brown kiwi (*A. mantelli* – previously known as North Island brown kiwi), okarito kiwi (or Rowi; *A. rowi*), southern tokoeka (*A. australis*), great spotted kiwi (*A. haastii*), and little spotted kiwi (*A. owenii*). The brown kiwi is further split into the following races: the Northland, Coromandel, Eastern, and Western populations. Additionally, several races of the southern tokoeka are also recognised: the Haast, Fiordland, and Stewart Island populations. Genetic studies are ongoing and these geographically separated populations may yet be given species or subspecies status.

Research over the past few decades has revealed differences in the mating systems, paternal care and foraging strategies of different species and populations of kiwi (Sales, 2005). As such, care must be taken to distinguish between species and locations when appropriate. This thesis will focus on a population of brown kiwi (*A. mantelli*) on Ponui Island.

1.3.2 Physiology and Behaviour

Brown kiwi possess a raft of characteristics unusual among birds. They are flightless, lacking many common avian structures such as a keel, tail and prominent wings (Van Tuinen, Sibley, & Hedges, 1998). Adults weigh between 1.5kg and 3kg (Sales, 2005) and display reversed sexual size dimorphism, whereby females are up to 25% larger than males (Reid & Williams, 1975), with a disproportionately longer bill (Potter, 1989). Another unusual feature is their low basal metabolic rate, considered one of the lowest among birds (McNab, 1996). Brown kiwi are also long lived, reaching an estimated 18.7 years on average (McLennan et al., 1996), and a maximum of 65 years of age (Robertson, 2004).

Brown kiwi have a large brain compared to their body size, thought to have evolved to accompany the behavioural strategies associated with their niche, that of a flightless nocturnal insectivore (Corfield, 2009). Being mostly active at night, brown kiwi have a poor sense of vision (Martin et al., 2007), instead relying on auditory, tactile and olfactory cues to navigate within their environment (Cunningham, Castro, & Alley, 2007; Martin et al., 2007; Castro et al., 2010; Corfield et al., 2014). Their vocalisations (Corfield, Gillman, & Parsons, 2008) are used for a range of functions, including territory defence, mate attraction, and maintaining contact with conspecifics (Benedict & Krakauer, 2013). Calls are sexually dimorphic, with females producing a low hoarse call, and males a piercing shrill whistle (Digby et al., 2013). Kiwi are the only paleognathous birds to forage by probing, and possess a long slightly curved bill which aids this activity (Cunningham, Castro, & Alley, 2007). Brown kiwi appear to use a combination of tactile and olfactory cues when probing to detect and capture prey both on the surface and in the soil column (Cunningham, Castro, & Potter, 2009). Nares located at the tip of the bill and facial bristles originating at the base aid in locating prey (Cunningham, Alley, & Castro, 2011). The evolution of tactile and olfactory senses over vision in brown kiwi is markedly similar to many nocturnal mammals that exploit a similar niche (Corfield et al., 2014).

Brown kiwi have traditionally been reported as monogamous, establishing long-term pair bonds, although with a high rate of divorce (Potter, 1989; Bassett, McLennan, & Blackwell, 2005; Holzapfel et al., 2008). However, Ziesemann, Brunton, and Castro (2011) found evidence of alternate mating strategies, suggesting their mating system may be more flexible than previously thought. Copulation events begin in the winter (May-June) and eggs can be laid from June-July through to February (Reid & Williams, 1975), with most paired adults attempting one or two clutches per breeding season (Potter, 1989). Females take approximately 20-25 days to form an egg which is allometrically one of the largest of all bird species (400% larger than expected (Calder, 1991)) representing significant investment by the female (Calder, Parr, & Karl, 1978). In a reversal of conventional sex roles (Cockburn, 2006), normally one, but occasionally multiple (Ziesemann, Brunton, & Castro, 2011) males incubate the eggs for 75-84 days (Reid & Williams, 1975), leaving the nest to forage at night for three to six hours (Colbourne, 2002). The incubation time is one of the longest in birds (Calder, Parr, & Karl, 1978), and combined with a nutrient rich egg, allows the chick to develop to an advanced state before it hatches. Chicks are precocial, hatching as developmentally mature, miniature versions of adults (Calder, 1991; Robertson et al., 2003). Chicks will venture out at night independently to explore and forage after approximately five days, and fledge at 24 days on average, no longer returning to the nest (Colbourne, 2002). Brown kiwi grow slowly, slower than many other highly precocial species including the megapodes (Ricklefs, 1979).

1.3.3 Conservation

Current status

New Zealand separated from other land masses approximately 80 MYA, a time when birds dominated the world, and few mammals existed. Polynesians arrived in the 13th Century, resulting in major ecological transformations (Gibbs, 2010). It is difficult to understand what the pre-human New Zealand ecosystem was like, as so much has changed since human arrival. The transition of the vertebrate fauna from feathers to fur, with at least 58 bird extinctions and 31 mammal introductions (Tennyson, 2010), and large scale habitat destruction (Stevens et al., 1995) are perhaps the most obvious of a great number of interrelated changes (Sullivan, Kelly, & Ladley, 2010). The native guild of avian ground insectivores present before human arrival has largely disappeared, with nine out of 17 species now extinct (Gibbs, 2010). Predators that may have preyed upon kiwi before are also now extinct or greatly reduced in number, with introduced mammalian predators taking their place. New Zealand’s flightless birds have suffered in particular, with 80% of 30 species now extinct. In the North Island, only two species of flightless birds persist, the brown kiwi and the weka (*Gallirallus australis greyi*) (McLennan et al., 2004). Once abundant throughout New Zealand, all five kiwi taxa now survive only in isolated populations, and are all facing the threat of extinction. The Department of Conservation classes each species as either threatened which includes three levels (nationally critical (rowi), nationally endangered (brown, great spotted), nationally vulnerable (tokoeka)) or recovering (little spotted) (Robertson et al., 2013). The total population of brown kiwi was estimated in 2008 to be around 25,000 (Holzapfel et al., 2008), yet despite conservation efforts numbers continue to decline. This decline highlights the importance of learning more about brown kiwi biology to help manage the remaining wild populations.

Reasons for decline

Brown kiwi evolved in the absence of mammalian predators but today co-exist with several species introduced by humans (Sales, 2005). Unfortunately, their long isolation led to the evolution of a number of behaviours and characteristics which are poorly suited to surviving with these novel predators (McLennan et al., 1996). Young birds are particularly vulnerable, with around 95% failing to reach adulthood largely due to stoat predation rates as high as 60% (McLennan et al., 1996). Stoats and feral cats are considered the main culprits of chick predation and are thought to depredate brown kiwi under 1100g in weight (McLennan et al., 1996). Adults generally have relatively high survival rates, although are still susceptible to predation by dogs (Pierce & Sporle, 1997). Predation of adults in such a long-lived species might prove more important than the frequent predation of young (Robertson et al., 2011).

Humans have modified the habitat of brown kiwi since they arrived in New Zealand via logging, mining, fires, urbanisation and agricultural practices (Stevens et al., 1995). This has led to extensive deforestation, to the point that only about 22% of the original forest cover remains (Mills & Williams, 1979), leaving only fragments of native forest. The majority of land has been converted to grassland, covering almost half (47%) the total area of New Zealand (Blackwell, 2005). This has had a huge impact on the native fauna, most of which were adapted to living in forest ecosystems (Stevens et al., 1995).

Management strategies

The Kiwi Recovery Programme was launched in 1991, kick-starting a coordinated management campaign to save all five taxa from extinction (Robertson et al., 2003; Holzapfel et al., 2008). Since then, translocation of birds to new areas or to areas with low densities has helped to increase the number of populations and the genetic diversity of existing populations. Several ‘kiwi sanctuaries’ have also been established throughout the country to protect populations over their current range, with extensive predator control occurring in parallel with a number of biological studies (Robertson, 2004). These studies have increased our understanding of the impact of pests on native species, aiding in subsequent management of the species (Robertson & Monchy, 2012). Populations of brown kiwi have also been established on a number of offshore islands or fenced ‘mainland island’ sites to ensure their security if management fails on the mainland. The key target in brown kiwi conservation is to achieve many different populations of around 1500 individuals, with 500 effective breeding pairs, ensuring their long term continuity (Peat, 2006).

Operation Nest Egg (ONE), which begun in 1994, seeks to improve the very poor survival rates of brown kiwi chicks. Eggs are removed from the wild to be incubated, hatched and raised in captivity or on pest-free ‘crèche’ islands. Birds are released back into the wild at 1000g, when they are considered large enough to defend themselves against most predators (Colbourne et al., 2005). This technique has been effective in increasing population sizes and building up founder populations for reintroductions or translocations, helping to turn the tide for selected mainland populations of brown kiwi (Colbourne et al., 2005), and is now being expanded to include other kiwi taxa. Despite the success of ONE, it cannot be considered a long term solution as it remains economically unsustainable for large scale management (Colbourne et al., 2005).

An important step in kiwi conservation over the past two decades has been the increased prominence of advocacy and community involvement (James, 2001). Kiwi Recovery Programme initiatives have proven effective at capturing the imagination of the public of New Zealand and educating them about the plight of this treasured species (Colbourne et al., 2005). Today community groups and private organisations actively protect kiwi over a combined area of land almost equal to that managed by the Department of Conservation (Holzapfel et al., 2008).

1.3.4 Monitoring Kiwi

The Kiwi Recovery Plan (Holzapfel et al., 2008) recognises the need to reliably monitor populations of kiwi in order to identify the impacts of management on a population. Unfortunately, the cryptic and nocturnal nature of brown kiwi combined with their avoidance behaviours, large home ranges, and generally low densities limits the number of monitoring methods which can be used effectively (Robertson & Fraser, 2009; Ziesemann, Brunton, & Castro, 2011).

Call count surveying is the most frequently used monitoring method for brown kiwi populations and is considered the simplest way to determine general population trends, highlighting any changes of 25% or more (McLennan, 1992; Pierce & Westbrooke, 2003). Call count surveys involve recording the number of calls heard over a two hour period after dark from several elevated vantage points during five successive nights every five years (McLennan, 1992). The time and direction of calls are then compared between sites to reduce repeated measurements.

To discover more about the behaviour of brown kiwi, a more active approach to monitoring is required. The use of ‘kiwi trained’ dogs enabled researchers to track down brown kiwi to be tagged for capture-recapture studies. However, the real turning point for brown kiwi research was the use of lightweight radio transmitters. Individuals could then be located consistently and with relative ease. This enabled us to learn a great deal more about this cryptic species (Robertson et al., 2011). Increasingly sophisticated and accurate radio telemetry technology which may now include activity timers to document movement and reproductive behaviours (Peat, 2006; Taylor, Nelson, & Ramstad, 2014) and GPS beacons to track movement, means we are better able to investigate how brown kiwi interact with their environment. This has opened up new possibilities for studying brown kiwi spatial systems.

1.3.5 Brown Kiwi Spatial Behaviour

Brown kiwi were initially described as territorial, with pairs defending well defined core areas with minimal home range overlap (McLennan, Rudge, & Potter, 1987). Additionally they have been shown to exhibit high site fidelity, remaining in established territories following logging or drought despite the presence of more suitable areas nearby (Colbourne & Kleinpaste, 1984). Subsequent studies have proven that not all populations follow the same spatial patterns, and that density may play an important role in dictating the spatial systems of brown kiwi (Potter, 1989; Ziesemann, 2011).

Brown kiwi can be considered a generalist species, able to tolerate a wide range of habitat types. Populations have been observed in mature native forest, exotic pine forests, regenerating seral vegetation, tussock grasslands, swamp land, pasture and even sand dunes

(Reid & Williams, 1975; Colbourne & Kleinpaste, 1984; McLennan, Rudge, & Potter, 1987; Potter, 1989, 1990; McLennan, 1992; Miles, 1995; Taborsky & Taborsky, 1995; Chan, 1999; Gibbs, 2000; Forbes, 2009). This suggests considerable flexibility with regard to habitat use. Habitat destruction means brown kiwi are now faced with increasingly fragmented habitats, often a combination of native forest, regenerating scrub and grazed pasture (Potter, 1990). Gibbs (2000) found that chicks that used all three of these habitats had a greater chance of survival when compared to those who used only two. If some habitats are more beneficial for brown kiwi than others, selective habitat use would be expected (Taborsky & Taborsky, 1995).

Little is known about what drives brown kiwi habitat utilisation. It is thought that the direct influence of vegetation may be of minimal importance, with more significance attributed to availability of appropriate food, cover and roost sites (Potter, 1990; Taborsky & Taborsky, 1995). It has been suggested that habitat may also be selected for its social value, such as the availability of breeding partners (Taborsky & Taborsky, 1995) and levels of interaction with conspecifics. Other spatial factors such as density or territoriality also need to be considered (Rosenzweig, 1991). Environmental variables such as climate and weather may also affect the rates at which brown kiwi utilise their habitat. Finally, utilisation rates are expected to vary between seasons and from place to place, depending on multiple factors.

While habitat utilisation can be studied at different scales, previous work on brown kiwi focusing on the microhabitat level (Chan, 1999; Cunningham & Castro, 2011) suggested that utilisation studies at a larger scale could effectively determine habitat use. Measuring habitat availability at finer scale has proved more difficult due to the ever changing nature of microhabitat characteristics such as vegetation and litter composition, litter depth, ground cover, soil penetrability (Chan, 1999).

Nocturnal habitat utilisation

How brown kiwi utilise habitat during their nocturnal activity phase has been studied only four times in the past. These studies each had a narrow focus, investigating habitat utilisation in juveniles (Chan, 1999; Gibbs, 2000), within a low-density population (Taborsky & Taborsky, 1995), and in a fragmented landscape (Potter, 1989). While these studies increased our knowledge of how brown kiwi interact with their spatial environment, they left many questions unanswered.

Table 1.1 - Summary of all previously published studies examining nocturnal habitat utilisation in brown kiwi.

#	Location	Kiwi Density	Years	Lifestage	# Birds	# Fixes	Methodology	Authors
1	Paerata, Northland	0.4 per ha	1985-1988	Adults	24	1447	Homing	Potter, 1989
2	Waitangi, Northland	0.2 per ha	*unknown*	Adults	10	95	Homing	Taborsky & Taborsky, 1995
3	Trounsen, Northland	unknown*	1997-1998	Juveniles	11	236	Homing+Triangulation	Chan, 1999
4	Trounsen, Northland	unknown*	1998-1999	Juveniles	10	254	Triangulation	Gibbs, 2000

All four studies concur that brown kiwi do not use habitat in proportion to its availability. Forest habitat appeared to be preferred by brown kiwi adults (Potter, 1989; Taborsky & Taborsky, 1995). This has reinforced the widely accepted belief that brown kiwi are predominantly forest dwelling. Scrub and bush-edge habitat were also utilised by adults more than expected considering their availability (Potter, 1989; Taborsky & Taborsky, 1995). Cunningham and Castro (2011) found birds had higher foraging success in edge habitats than in forest habitats, suggesting this habitat may be preferred. Pasture habitats were used less than expected by adults in two studies (Potter, 1989; Taborsky & Taborsky, 1995). However, brown kiwi have been shown to disperse over large areas of pasture (Potter, 1990; Forbes, 2009), and have also been observed foraging in pasture (Potter, 1989; Cunningham & Castro, 2011). The latter studies were among the first to document brown kiwi actively exploiting pasture; however their methods did not sample proportionately for pasture so are likely to have underestimated occurrence in this habitat type. Although brown kiwi populations have been found in pine forest plantations (Colbourne & Kleinpaste, 1984), this habitat has generally been avoided by birds, thought to be due to the presence of other more favourable habitats nearby (Taborsky & Taborsky, 1995).

The habitat use of juvenile brown kiwi appears to differ from adults. Immature birds in both Chan (1999) and Gibbs (2000) were found in forest habitat less often than expected, instead favouring scrub and pasture habitat. In total 28.8% of observations found juvenile brown kiwi in pasture, suggesting they were actively utilising this habitat rather than just travelling across it (Gibbs, 2000). The home ranges of chicks and adults were found to overlap significantly in this study despite different use of habitat (Gibbs, 2000), suggesting that birds of different age are selecting habitat types within their home range to meet different requirements. Both researchers suggested that increased shelter from aerial predators, differences in food availability due to differing invertebrate composition and chick's reduced bill length, and the absence of adults in these areas could explain these differences.

The frequency at which each habitat type is used varies seasonally. Although brown kiwi will forage in all habitat types throughout the year (Cunningham & Castro, 2011), pasture use decreases over winter and spring and increases during summer and autumn (Potter, 1989; Gibbs, 2000). Seasonality is also seen in brown kiwi microhabitat utilisation (Cunningham & Castro, 2011). However, none of the four previous studies sampled continuously or consistently over an entire year, thus the true impact of seasonality remains uncertain.

Brown kiwi spend the majority (75%) of their time at night foraging (Cunningham & Castro, 2011), suggesting that food availability may be an important driver of habitat utilisation. Prey capture rates are seen to differ between habitat types and between seasons (Cunningham & Castro, 2011). Male and female brown kiwi appear to feed separately at night (Sales, 2006a). While direct social and courtship interactions are observed only rarely (Taborsky & Taborsky, 1992; Cunningham & Castro, 2011), the impact of social contact may still prove important to spatial behaviour. Research on the great spotted kiwi has found that pairs met regularly at night and spend considerable time foraging with each other (Keye, 2008), though this species also displays cooperative breeding. Both dietary and social factors might prove important drivers to brown kiwi nocturnal habitat utilisation, however this is uncertain due to a lack of information.

These four previous studies (Table 1.1) focused on only a small number of birds (between 10 and 24), with some birds contributing more to the overall analysis than others. While their results were statistically significant, their conclusions should be interpreted with caution. A study of only a few birds may not represent the spatial behaviours of the whole population, and are more likely to be impacted by individual variation (Jones, 2001).

Diurnal habitat utilisation

During the day, brown kiwi take shelter within roost sites of various types, in varying habitat (Jamieson et al., In Prep). Compared to nocturnal utilisation, a substantial amount of prior research has looked at the roosting sites of brown kiwi during the day in adults (McLennan, Rudge, & Potter, 1987; Potter, 1989; Miles, 1995; Taborsky & Taborsky, 1995; Forbes, 2009;

Ziesemann, 2011; Jamieson et al., In Prep) and juveniles (Chan, 1999; Gibbs, 2000; Shapiro, 2005; Forbes, 2009; Wilson, 2014).

Brown kiwi appear to prefer forested habitat for roosting, favouring scrub and native forest over other areas (Jamieson et al., In Prep). This is thought to be due largely to the availability of appropriate roost types. Brown kiwi have been found in a range of roost types including: hollow logs, natural cavities, excavated burrows, swamp or grass plantings, and surface roosts as well as man-made structures (McLennan, Rudge, & Potter, 1987; Potter, 1990; Taborsky & Taborsky, 1995; Forbes, 2009). Potter (1989), Miles (1995) and Forbes (2009) all found that surface vegetation was used markedly more than other roost types, followed by burrows, natural cavities and hollow logs. Roost choice appears highly dependent on macrohabitat type (Miles, Potter, & Fordham, 1997; Forbes, 2009), with surface roosts used more often in grass and scrub habitat than in native forest, where burrows and holes are more commonly used.

When not nesting, brown kiwi will generally roost at a different site each day (Forbes, 2009), although they do occasionally return to previously used sites (McLennan, Rudge, & Potter, 1987; Miles, Potter, & Fordham, 1997). This varies between individuals, with one bird in a study by Potter (1989) using 34 different roosts over a six month period, and another using only five. Some roost sites appear to be favoured and are used by multiple brown kiwi sequentially (Potter, 1989; Ziesemann, 2011).

Brown kiwi spend a large proportion of their time roosting in day-time shelters. Consequently, roosting behaviour may play an important role in their social life (Ziesemann, 2011). Territory neighbours almost never roost together, however breeding pairs often do (Potter, 1989). The type of roost used has been shown to be significantly influenced by the presence or absence of a mate, suggesting roosts may be important for pair bonding (Potter, 1989). Birds which roost together appear to have stable arrangements, persisting over several breeding and non-breeding seasons (Ziesemann, 2011).

Roost site choice has been found to differ significantly between sexes. Forbes (2009) found female brown kiwi in the Coromandel used surface roosts 65% of the time, while males roosted equally often on the surface (46%) as they did in a hole (47%). An earlier study in the Central North Island found the reverse to be true, with males using surface vegetation more often, and females favouring hollow logs and natural cavities (Miles, 1995). This difference may be as a result of varied sex ratios within their sample populations or differences in site characteristics.

Juvenile brown kiwi show different roost choice to adults, with a clear preference for scrub habitat relative to mature forests (Gibbs & Clout, 2003; Shapiro, 2005). Wilson (2014) found juveniles roosted in scrub 56.3% of the time, and in forest 23.4% overall, though even higher rates in scrub (96%) have been documented (Shapiro, Castro, & Colbourne, In Prep). They also tend to roost on the surface in fern fronds and thick scrub rather than in holes (Forbes, 2009). Forbes (2009) found brown kiwi chicks in surface roosts 91% of the time, and sub-adults 79% of the time. Differences in spatial behaviour between age classes could be due to the reduced bill length of juveniles, forcing them to adopt different foraging strategies (Forbes, 2009). It was suggested that the location of the nest site may affect the habitat use of the chick (Taborsky & Taborsky, 1995). However this hypothesis was dismissed because many chicks were found to move large distances from their nest site and were not limited to the habitat found in their natal area (Chan, 1999; Gibbs, 2000).

The type of roost used appears also to vary seasonally (Potter, 1989), with surface roosts used more in the summer, holes or burrows used more during winter and spring, and hollow logs used more in autumn (Potter, 1989; Miles, Potter, & Fordham, 1997; Forbes, 2009).

The selection of a particular roosting habitat and types over others could be due to a number of drivers. The availability of good roosting habitat can influence the likelihood of an animal settling and surviving in an area (Souter, Bull, & Hutchinson, 2004), and can serve to reduce potential predation danger (Tiddeman & Flavel, 1987) and aid in thermoregulation (Walsberg, 1986). Additionally, when birds roost together there can be added social benefits assisting in mate acquisition, breeding, and information transfer between individuals (Marzluff, Heinrich, & Marzluff, 1996; Blanco & Tella, 1999).

Roost choice in brown kiwi might therefore depend on specific feeding or shelter requirements, social influences such as pair bond maintenance, or simply the availability of appropriate roost sites (Taborsky & Taborsky, 1995; Gibbs & Clout, 2003; Forbes, 2009). Characteristics of the site itself may also influence selection, like cover from predation and disturbance or roost microclimate (Potter, 1989; Taborsky & Taborsky, 1995). Density has been shown to have an impact on spatial use patterns (Whyte, Ross, & Buckley, 2014), with social roosting behaviour changing as density increases (Ziesemann, 2011). Environmental factors such as temperature have been shown to effect brown kiwi dispersal behaviour (Wilson, 2014), and thus may have an impact on roosting behaviours. Utilising different habitats for roosting may ultimately increase survival as each can play a different role in protection from weather and provision of warmth and food (Gibbs, 2000). While more is currently known about habitat utilisation of brown kiwi during the day, it remains unclear what factors are driving these patterns.

1.3.6 Brown Kiwi Diet

Diet basics

Nutrition is a critical component of ecology which has received little attention in ratite species (Sales, 2006a). While the nocturnal behaviour of brown kiwi negates direct observation (Reid, Ordish, & Harrison, 1982), only a handful of studies have used other methods to investigate this topic (Table 1.2). This section compiles all prior research to describe what is currently known about brown kiwi diet. Early studies depended largely on the examination of gizzard contents from accidentally killed birds, with faecal analysis being used more recently. Sample sizes have generally been too small and sampling between months too irregular to draw definitive conclusions, particularly concerning seasonal changes in the diet, and none has spanned an entire year continuously. Additionally, only two studies (Kleinpaste & Colbourne, 1983; Shapiro, 2005) assessed both invertebrate availability and exploitation. Despite the limitations of previous studies much has still been discovered about the diet of brown kiwi.

Brown kiwi are insectivores, feeding almost exclusively on invertebrates (between 85% and 95% of the diet) (Sales, 2005), and unlike many birds do not have a crop (Sales, 2006a). They appear to be selectively opportunistic, tending to prey on a given species in proportion to its availability, while selectively foraging for a few important soil dwelling species (Colbourne & Kleinpaste, 1984; Miles, 1995; Shapiro, 2005). Seasonal variations appear to dictate major components of the diet (Kleinpaste & Colbourne, 1983; Miles, Potter, & Fordham, 1997; Shapiro, 2005). Additionally, principal food items and foraging strategies seem to differ between locations (Watt, 1971; Reid, Ordish, & Harrison, 1982). These variations in the diverse feeding habits of brown kiwi indicated to early researchers that a ‘typical’ diet probably does not exist (Reid, Ordish, & Harrison, 1982).

Table 1.2 - Summary of all previously published studies examining the diet of Kiwi.

#	Location	Kiwi Species	Year	Months	Seasons	Method	n	Authors
1	Central North Island	Brown	1882	1	1	Gizzard	2	Gurr, 1952
2	Central North Island	Brown	1956	1	1	Gizzard	1	Bull, 1959
3	Kaitaia, Northland	Brown	1970	2*	2	Gizzard	2	Watt, 1971
4	Northland + Taranaki	Brown	1981	12*	4	Gizzard	50	Reid et al., 1982
5	Waitangi, Northland	Brown	1981-1982	5	2	Faeces+Gizzards	334+3	Kleinpaste & Colbourne, 1982
6	Stewart Island	Southern Tokoeka	1982-1984	11*	4	Faeces	146	Colbourne & Powlesland, 1988
7	Kapiti Island	Little Spotted Kiwi	1984-1985	4*	4	Faeces	61	Colbourne et al., 1990
8	Trounsen, Northland	Brown	1992-1994	14*	4	Faeces	40	Miles, 1995
9	Ponui Island, Hauraki Gulf	Brown (juveniles)	2004-2005	4	2	Faeces	143	Shapiro, 2005
10	Ponui Island, Hauraki Gulf	Brown	2010-2012	**	**	Faeces	30	Strang, 2013

*Sampling between months was not continuous, instead occuring irregularly often over multiple years

**Samples were collected some time over this period, though majority of samples from April 2011

Soil dwelling invertebrates

Invertebrates sourced within the soil column are thought to make up the majority of brown kiwi diet at all life stages (Kleinpaste & Colbourne, 1983; Shapiro, 2005). These invertebrates are most readily available in native forest habitats (Taborsky & Taborsky, 1995), suggesting these areas are important to brown kiwi diet. Due to the clumped distribution of many soil dwelling invertebrates, their availability may often be underestimated using standard sampling methods such as soil core sampling (Shapiro, 2005). As such it is likely that these types of prey are available at higher proportions than documented in most studies and may not be favoured quite as strongly as often suspected.

Long considered the main component of kiwi diet (Sales, 2005), earthworms appear to make up a large part of the diet of brown kiwi (Bull, 1959; Reid, Ordish, & Harrison, 1982; Kleinpaste & Colbourne, 1983; Shapiro, 2005). Earthworm chaetae (hair like sensory structures) have been recorded to occur at rates as high as 94% in gizzard samples (Reid, Ordish, & Harrison, 1982). Chaetae are present within samples in significant numbers throughout the year, even when earthworm availability decreases, suggesting that brown kiwi actively select them. Notably however, the presence of earthworm chaetae in a sample is considered unreliable for determining the number of earthworms eaten, as numbers of chaetae per earthworm differ between species and individuals (Wroot, 1985). Additionally, most chaetae don’t survive digestion, meaning earthworms are probably underestimated in faecal samples. To survive purely on an annelid diet however, brown kiwi would need to locate and extract one per minute during the entire darkness period to gain adequate nutrition (Reid, Ordish, & Harrison, 1982). Therefore a more varied diet is hypothesized.

Other soil dwelling invertebrates such as scarab beetle larvae (Coleoptera) and cicada nymphs (Hemiptera) often contribute a significant amount to brown kiwi diet both numerically and in dry weight (Bull, 1959; Reid, Ordish, & Harrison, 1982; Kleinpaste & Colbourne, 1983; Kleinpaste, 1990; Miles, 1995; Shapiro, 2005). These invertebrates appear to be favoured, consumed in greater numbers than their availability would suggest (Miles, Potter, & Fordham, 1997). They also contribute a large amount of the total dry matter of the diet (Reid, Ordish, & Harrison, 1982), suggesting they are important components of brown kiwi nutrition (Kleinpaste & Colbourne, 1983). Other soil dwelling larvae such as those of crane fly (Tipulid), click beetle (Elateridae) and ground beetle (Carabidae) have also been documented in significant numbers in brown kiwi faecal samples (Shapiro, 2005).

Soil dwelling invertebrates are eaten less frequently by brown kiwi during certain seasons, with numbers exploited peaking in November and then declining over summer and autumn, probably related to their availability and accessibility (Reid, Ordish, & Harrison, 1982; Kleinpaste, 1990; Shapiro, 2005). To counter this, brown kiwi appear to switch foraging strategies over this time to hunt in different habitats (Kleinpaste, 1990), and include more surface-dwelling invertebrates in their diet (Wilson, 2014). A reduction in soil water content combined with high temperatures over summer result in reduced soil penetrability (Cunningham, 2006; Wilson, 2014), impacting the probing behaviour of brown kiwi (Cunningham, Castro, & Alley, 2007). The lifecycles of many soil invertebrates are also expected to play a role in the their availability throughout the year (Colbourne & Powlesland, 1988).

Surface dwelling invertebrates

Coleoptera, Orthoptera, Diptera, Arachnida, and Hemiptera are all orders of surface dwelling invertebrates frequently documented in the diet of brown kiwi (Reid, et al., 1982; Kleinpaste & Colbourne, 1983). Of these, adult ground and scarab beetles (Coleoptera) are consumed in moderate numbers and on the basis of percent occurrence have been documented as the second most eaten invertebrate group (Reid, Ordish, & Harrison, 1982). These beetles are found on the surface, though also shelter in crevices and leaf litter, habitats accessible to a probing species (Colbourne & Powlesland, 1988). Spiders (Arachnida) have been found in faecal samples in large numbers (Miles, 1995), and ground weta (Orthoptera) and centipedes (Chilopoda) are also eaten throughout the year in low numbers (Shapiro, 2005). Black field crickets (Orthoptera) appear to be a major part of brown kiwi diet when available (Kleinpaste & Colbourne, 1983). Interestingly some groups contribute little to the diet despite being available in large numbers. Amphipods are seldom eaten by brown kiwi, probably due to their quick and erratic movements making them difficult prey to capture (Colbourne & Powlesland, 1988).

Surface invertebrates are exploited throughout the year, although rates have been documented to increase over summer and autumn. This could be due to a higher availability of surface invertebrates over this time, largely due to an increase in the number of black field crickets prevalent in pasture habitat (Gibbs, 2000). Numbers of weta and spiders also increase over these months (Colbourne, Baird, & Jolly, 1990; Shapiro, 2005) possibly due to their lifecycles and increased levels of activity at warmer temperatures. In addition, a reduction of available soil dwelling invertebrates may contribute to the larger numbers of surface invertebrates eaten over these months.

Other food items

The importance of plant matter in brown kiwi diet is debated. The presence of vegetation in gut content samples suggests that it is incidentally ingested (Reid, Ordish, & Harrison, 1982), although the physiology of the brown kiwi gastrointestinal tract shows they are adapted to consume some proportion of plant foods (Potter et al., 2006). Seeds have been reported in numerous brown kiwi gizzard (Reid, Ordish, & Harrison, 1982) and faecal samples (Miles, 1995), suggesting fruit may be a diet selection. Buller (1888) proposed that fruit stones may be important for grinding food in the gizzard. However it is known that seeds can persist in the gizzard for weeks (Swanson & Bartonek, 1970), so their importance may have been overstated.

Brown kiwi have been observed capturing and eating frogs, small fish and small eels in captivity, and freshwater crayfish remains have been found in the gizzards of wild birds (Reid, Ordish, & Harrison, 1982). These items are not considered to be an important part of the diet and most likely represent an opportunistic capture. Brown kiwi are able to take aquatic prey due to their ‘mucosal diving nostrils’, a type of nostril that is able to seal underwater, a characteristic otherwise only seen in diving seabirds (Fuller, 1990). This may increase the ease at which they are able to feed in waterlogged swamps, soils and streams.

Competition in diet

Several authors have revealed substantial dietary overlap between brown kiwi and a number of introduced mammalian insectivores including hedgehogs (Berry, 1999), weasels (Strang, 2013) and rats (Shapiro, 2005; Latham, 2006). These competitor species feed on similar surface invertebrates, however are unable to reach most soil dwelling taxa. Thus competition is expected to be particularly detrimental over summer when brown kiwi diet comprises of mostly surface dwelling invertebrates. Brown kiwi evolved with a suite of up to eight other nocturnal insectivorous bird species and a number of ground-active lizard fauna which foraged for invertebrates on the forest floor (Atkinson & Millener, 1991; Gibbs, 2010). It is possible that they evolved with levels of competition similar to the current state, so the effect of inter-specific competition on foraging strategies and diet is likely to be minimal. In higher density populations however intra-specific competition could have a larger impact.

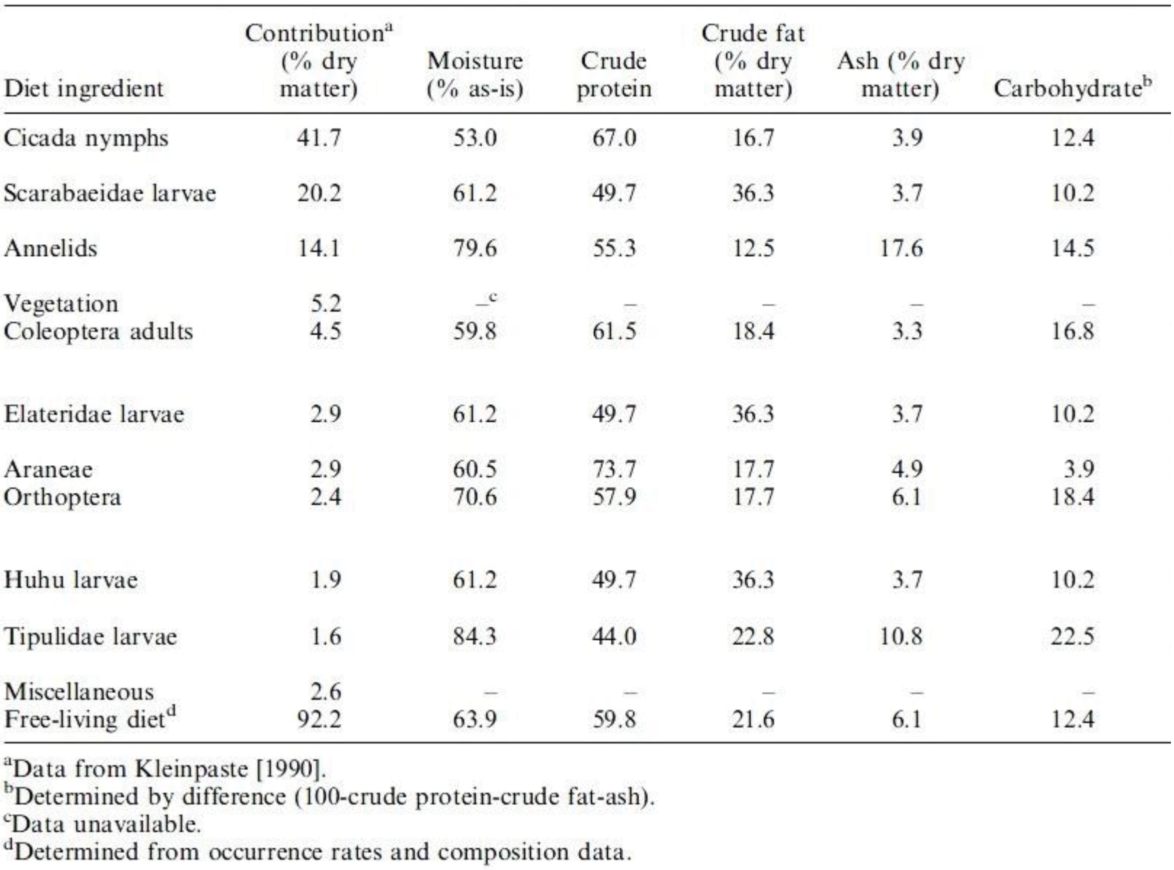
Nutrition

To determine the nutritional benefit of ingested food, both the nutrient content of ingested invertebrates and the bird’s ability to digest those nutrients must be considered (Bell, 1990). Both of these topics have been considered very rarely in kiwi generally and only in relation to captive and not wild diets (Sales, 2006b).

Potter et al. (2010) produced the most complete description of the nutrient content of a range of invertebrates found in wild brown kiwi diet by compiling work from a number of authors (see Table 1.3). This table illustrates that the three soil dwelling invertebrates which appear to contribute the most to the brown kiwi diet (Annelids, Cidada nymphs and Scarabaeidae larvae) all have higher protein measures compared to most other food items. This could explain why these invertebrates were actively selected. The surface invertebrates exploited most frequently (Coleoptera adults, Arachnida, Orthoptera) are also high in protein, suggesting that when foraging changes from targeting mainly soil dwelling to mainly surface dwelling invertebrates brown kiwi may still favour protein-rich invertebrates.

The high intake of protein suggests that brown kiwi either digest protein poorly (especially chitin) so must consume it in large amounts to obtain sufficient quantities, and/or that it is a major source of energy. The apparent high digestibility of protein by brown kiwi (91%) reported by Minson (2013) suggests the latter. However, whether or not they can digest chitin remains unknown. More research into the nutrition of brown kiwi diet is required to ascertain how much this may affect foraging strategies and prey selection.

Table 1.3 – Gross nutrient composition of dietary ingredients regularly consumed by wild brown kiwi. Sourced directly from (Potter et al., 2010, p. 542)



Diet ingredient	Contribution[a] (% dry matter)	Moisture (% as-is)	Crude protein	Crude fat (% dry matter)	Ash (% dry matter)	Carbohydrate[b]
Cicada nymphs	41.7	53.0	67.0	16.7	3.9	12.4
Scarabaeidae larvae	20.2	61.2	49.7	36.3	3.7	10.2
Annelids	14.1	79.6	55.3	12.5	17.6	14.5
Vegetation	5.2	–[c]	–	–	–	–
Coleoptera adults	4.5	59.8	61.5	18.4	3.3	16.8
Elateridae larvae	2.9	61.2	49.7	36.3	3.7	10.2
Araneae	2.9	60.5	73.7	17.7	4.9	3.9
Orthoptera	2.4	70.6	57.9	17.7	6.1	18.4
Huhu larvae	1.9	61.2	49.7	36.3	3.7	10.2
Tipulidae larvae	1.6	84.3	44.0	22.8	10.8	22.5
Miscellaneous	2.6	–	–	–	–	–
Free-living diet[d]	92.2	63.9	59.8	21.6	6.1	12.4

[a] Data from Kleinpaste [1990].
[b] Determined by difference (100-crude protein-crude fat-ash).
[c] Data unavailable.
[d] Determined from occurrence rates and composition data.

1.4 Study Site

1.4.1 Ponui Island

Ponui is a 1770 hectare island located in the Hauraki Gulf, 30 kilometres east of Auckland, New Zealand (Fig. 1.1). Originally inhabited by indigenous Maori people (Ngai Tai), the island has been owned by the pioneering Chamberlin family since 1853 (Brown, 1979). The island is currently split into three separate properties; John Spencer owns the northern part, Richard

Chamberlin own the central area, and Peter and David Chamberlin own the southern section (Miles & Castro, 2000). Farming has occurred on the island since the 1850's (Bellingham, 1979), and approximately two thirds of the land is still grazed by sheep and cattle.

Brown kiwi were translocated to Ponui in 1964 at the request of Peter Chamberlin (Miles & Castro, 2000). Six birds came from Little Barrier Island and another eight from Waipoua, Northland in the same year (Miles & Castro, 2000). These 14 birds had mixed genetic makeup, consisting of birds with Northland and western population heritage (Miles & Castro, 2000). Despite the small founder population and presence of high densities of rats and also feral cats, the population has experienced rapid growth since its introduction.

Exact numbers of brown kiwi currently on Ponui are unknown, although densities were estimated by Miles and Castro (2000) to be around 10 birds per km^2 using call count data. This estimate was considered conservative, especially as the call rates recorded (30.7 calls per hour) greatly exceed rates found in the most prolific Northland populations (19.8 calls per hour) which have up to 100 birds per km^2 (one bird per hectare) (Miles & Castro, 2000). Additionally, densities on other island populations appear to be very high (McLennan, 1992). Castro and Cunningham estimated the density of brown kiwi on Ponui to be at least one bird per hectare (100 per km^2) (Cunningham, Castro, & Alley, 2007). This is similar to proposed pre-human colonisation levels (Reid & Williams, 1975; McLennan et al., 1996), and much higher than the majority of mainland sites (excluding a few in Northland) where density is seldom thought to exceed four adults per km^2 (McLennan, 1992). The recent density estimate would dictate that the Ponui population is around 1,500 birds, or roughly 6% of the entire estimated brown kiwi population (Holzapfel et al., 2008).

The forest fragments of Ponui have a low diversity of birds, dominated by introduced species and small arboreal passerines (Bellingham, 1979). In addition to farmed sheep and cattle and free-ranging donkeys, the only resident mammals on the island are working farm dogs, rats and feral cats. Stoats have been reported on the island in the past, however have never established. It is suspected that cats may manage the stoat numbers via competition, or alternatively stoats may be immigrating to Ponui in such small numbers that by chance a pregnant female has never reached the island to establish a breeding population (Miles & Castro, 2000). Potential predators of brown kiwi on Ponui include feral cats, Morepork and harrier hawks, all which could prey upon chicks. The farm dogs could kill adult brown kiwi, however this rarely happens as the dogs are contained at night.

Figure 1.1 – Aerial photographs of: 1) New Zealand with Auckland highlighted, 2) Auckland with Ponui Island highlighted, 3) Ponui Island with the study site highlighted. Photographs from Google Earth, 2015.

1.4.2 Study Site and Habitat

Most of the northern half of the island is covered by pasture and viniculture orchards. In comparison, the southern half of the island contains a large remnant tract of broadleaf Kauri forest covering approximately 250 hectares, mixed with regenerating scrub and grazed pasture, interspersed with wetlands (Miles & Castro, 2000). This study focuses on a network of three gullies (Kauri, Red Stony and Pipe) and associated ridges, spanning a 1.2km^2 area within the southern third of Ponui Island (Fig. 1.2). The three gullies share similar topography and habitat, including swamp bordering farmland, broadleaf forest in the gullies, regenerating scrub on the slopes and tops of the surrounding ridges and a small stream running along the base of each gully (Shapiro, 2005). These gullies were chosen due to their fragmented nature, containing multiple habitat types, an environment typical of much of the remaining North Island habitat (Potter, 1990).

Four broad macrohabitat types of forest, scrub, swamp and pasture were considered during my study. Pasture and swamp habitats had clear boundaries and thus were easily defined by the predominant vegetation type, while forest and scrub were differentiated on the basis of vegetation type and height using average height measures from Shapiro (2005). Forest primarily consists of a mixture of broadleaf forest and regenerating kauri forest (*Agathis australis*), scrub primarily kanuka (*Kunzea ericoides*), lancewood (*Pseudopanax crassifolius*) and several coprosma species, while swamp vegetation is dominated by raupo (*Typha orientalis*) (Shapiro, 2005). A more detailed description of the vegetation found in each habitat is given in Latham (2006, p. 105).

Ponui is an example of an area of flora that has been altered due to logging and ongoing farming. The forest was logged for Kauri in the early 1900's although small stands remain. Many of the ridges were also burnt off to graze cattle and now consist of mostly regenerating bush (Miles & Castro, 2000). The forested areas of the study site remain unfenced from the adjacent farmland, resulting in a relatively open and sparse understory within the gullies caused by browsing and trampling of livestock (Shapiro, 2005). Studies in other areas of New Zealand have shown that pugging and other damage to soil caused by cattle may alter the soil qualities of gully areas, including water content and soil penetrability (Singleton, Boyes, & Addison, 2000). Recent research also shows that forest fragments accessible to livestock have 10 to 100-fold lower densities of leaf litter invertebrate species compared to areas where livestock are excluded (Didham et al., 2009). Brown kiwi may be further impacted where herbivores remove the dense vegetation that can serve as roost sites for them (Potter, 1989). The combined effects of logging and cattle invasion have meant the flora diversity and potentially abundance of certain invertebrate taxa in the forested areas of Ponui Island are probably limited (Shapiro, 2005).

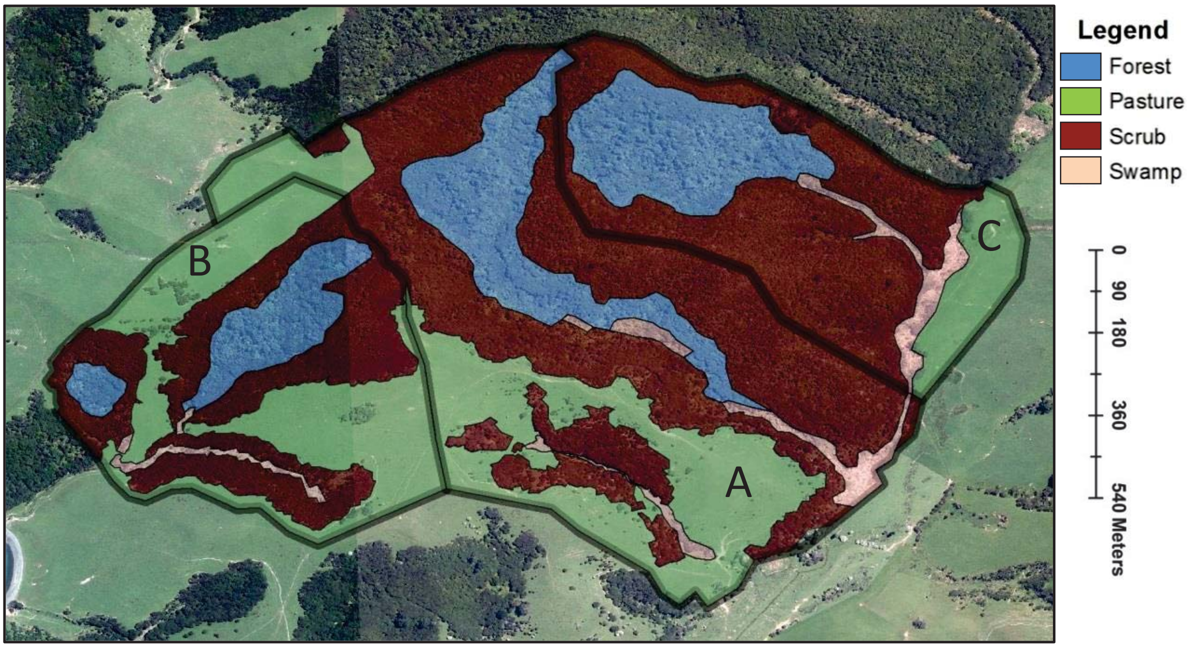


Figure 1.2 – Aerial Photograph of the study site, with gully boundaries and habitat types marked. (A=Red Stony, B=Kauri, C=Pipe).Photograph from LINZ.

1.4.3 Importance

Ponui Island contains one of the highest known densities of brown kiwi in the wild, making it the ideal place to study their behaviour and ecology. Population density is expected to strongly influence a population, potentially altering social, reproductive and spatial behaviours (Rosenzweig, 1991). Adding to our understanding of how brown kiwi behave at high densities will prove important as population densities continue to increase country-wide due to ongoing conservation effort aiming to raise their numbers. Habitat on the island is altered and fragmented, similar to many other sites throughout the country in which brown kiwi are managed now or could be in the future, allowing for comparison.

Due to the mixed origin of brown kiwi on Ponui Island, the population is considered of low conservation concern by the Department of Conservation (DOC), with no plans to use these birds to enhance breeding populations elsewhere. This presents a unique opportunity to study this endangered bird which might not be possible in intensively managed or conservation sensitive populations.

Since 2004 and the creation of the Massey University Kiwi Research Group led by Isabel Castro, brown kiwi within the study site have been intensively monitored. Birds were initially located using specialist dogs or by visual inspection of burrows, physical measurements and DNA samples were then taken, and a radio transmitter placed on their tibiotarsus following the methods laid out by Robertson et al. (2003). Every year all study birds are recaptured, measured and their transmitters are replaced. Birds lost or removed from the study are replaced with other birds found within the study area. The study population over the course of my research consisted of 49 birds (26 male, 23 female). The long term presence of this research group is another point of difference which stands Ponui Island apart from other sites. All birds in the study population have a known history in terms of many aspects of behaviour such as foraging, movements, and breeding, with records often dating back 10 years. Following a long tradition of naming individual kiwi in New Zealand, birds in this thesis will be referred to by name, the only identifier to have remained constant over the course of research on Ponui.

1.5 Research Goals

The central aim of this thesis is to investigate the habitat utilisation and diet of brown kiwi adults in a high-density population within a fragmented landscape. A study of this scale, in a high-density population and comparing a multitude of habitat types has not previously been conducted. This core objective can be broken down into the following four goals:

1) Firstly, this study aims to produce a detailed analysis of the diet of brown kiwi.

This will be the first study to examine diet consecutively over 12 months, including availability and exploitation, serving to increase our understanding of brown kiwi foraging behaviour and how this changes throughout the year. The varied and fragmented habitat of Ponui Island, typical of much of the modern New Zealand, will allow us to generate results applicable to brown kiwi populations across large areas of the North Island. A better understanding of the diet of brown kiwi will aid in the management of wild and captive populations, helping to identify appropriate sites for translocation and management and formulating more suitable diets for birds in captivity.

2) This study aims to produce the first comprehensive report of nocturnal habitat use by brown kiwi throughout the year in a high-density population.

Habitat utilisation studies of brown kiwi are limited, particularly during their nocturnal activity phase. The few studies which have explored this topic in brown kiwi were often restricted by small sample sizes, limited time frame and scope, or methods with large errors in accuracy. These studies did not sample all habitats consistently, often neglecting pasture. In addition difference in methodology, brown kiwi density and a whole host of site specific attributes prevents comparison between each study. As such, it remains unclear what drives habitat utilisation in brown kiwi, leaving this topic ripe for further investigation. This knowledge will allow us to form a more complete picture of how brown kiwi interact with the habitat available to them while active at night.

3) This study aims to produce a more complete picture of brown kiwi roosting behaviour within a high-density population, including habitat and shelter selection.

While a number of studies have investigated the diurnal roosting behaviour of brown kiwi, very few have examined a high-density population, and none have explored the relationship between nocturnal and diurnal habitat utilisation. This study will help to build upon previous findings by identifying which habitats brown kiwi are utilising for roosting throughout the year in a high-density population. It will also compare patterns in nocturnal and diurnal habitat utilisation to identify relationships between brown kiwi foraging and roosting behaviours. This knowledge can be used to enhance the habitat value of managed sites, help select new areas best suited to manage brown kiwi, and to determine which management strategies are likely to prove the most effective.

4) Finally, this study aims to investigate what might be driving the spatial behaviour of brown kiwi within a high-density population.

An important issue that is seldom considered in avian habitat utilisation studies is the lack of certainty around what is driving the behaviours recorded. This is an element of brown kiwi spatial behaviour that remains unclear. This study aims to determine how much effect food availability, social/reproductive cues, population demographics and environmental variables have on nocturnal and diurnal habitat utilisation, while establishing which combination of these factors can best explain the nocturnal spatial patterns of brown kiwi.

By exploring the interactions which occur in a high-density population, we will be more able to manage other brown kiwi populations as they increase in size and thus density in the future, due to concentrated conservation initiatives. Finally, by increasing our understanding of this unusual bird, we may gain some insight into the evolution of its many unique characteristics.

1.5.1 Thesis Structure

The next three Chapters explore the core aims of the project, with the final chapter presenting a summary and brief discussion of what these findings mean and how they relate to each other, as well as limiting factors and implications of the study's results to future brown kiwi conservation. Each core chapter is designed to answer a single part of the project and are written as semi-independent research for ease of publication. Thus slight repetition in text can be expected between chapters, particularly in the introduction and methods sections.

This project was conducted under DoC permits AK-28039-FAU and AK-38796-FAU; and Animal Ethics 11/03 and 14/38. Permission to work on South Ponui Farm was granted by the owners David and Ros Chamberlin and Peter and Pat Chamberlin. Permission to work with a Taonga species was granted verbally by David Beamish of Ngai Tai.

Chapter 2: The Diet of brown kiwi.

- *Document invertebrate availability on Ponui Island.*
- *Assess the diversity of invertebrate food exploited by brown kiwi on Ponui Island.*
- *Compare the availability and exploitation of invertebrate food to assess brown kiwi prey selection and foraging strategies.*

Chapter 3: Nocturnal Habitat Utilisation by brown kiwi

- *Document habitat availability within my study site on Ponui Island.*
- *Assess habitat utilisation rates of brown kiwi at night, including how this may vary with a range of spatial, temporal, demographic and behavioural factors.*
- *Explore potential driving factors and identify those which best explain the observed patterns of brown kiwi habitat utilisation at night.*

Chapter 4: Diurnal Utilisation of Shelters by brown kiwi

- *Document habitat availability within my study site on Ponui Island.*
- *Assess habitat utilisation rates of brown kiwi while roosting, including how this may vary with a range of spatial, temporal, demographic and behavioural factors.*
- *Assess shelter selection of brown kiwi while roosting, including how this may vary with a range of spatial, temporal, demographic and behavioural factors.*
- *Explore the relationship between diurnal roost choice and nocturnal habitat utilisation of brown kiwi on Ponui Island.*

Chapter 5: Patterns in brown kiwi Spatial Behaviour – Conclusions

- *Discuss the relationship between diet, nocturnal and diurnal spatial behaviour in brown kiwi within a high-density population and the implications of this to brown kiwi conservation, while taking into account limitations of the study. Suggest future directions for the study of brown kiwi spatial behaviour.*

CHAPTER TWO

The Diet of Brown Kiwi

Plate 2.1 - Tree weta (*Hemideina thoracica*) up close on Ponui Island. Photo by author.

2.1 Introduction

The interaction between animals and their food has long been of interest to ecologists, as shown by the large amount of published literature exploring this relationship over the last century (Hutto, 1990). A detailed understanding of diet is considered essential to the study of animals, providing insight into many aspects of a species' biology and behaviour (Durst et al., 2003; Sinclair, Fryxell, & Caughley, 2006). Knowledge of diet composition can have direct implications on conservation and management of vulnerable or endangered species (Myles et al., 2009). This can lead to the development of improved diets for animals in captivity (Potter et al., 2010), and help determine the most appropriate areas for translocations or habitat management (Morrison et al., 2007; Woolaver et al., 2013). Although crucial in understanding the habitat requirements of any species, relatively little is known about the foraging behaviour and diet of many avian species (Rosenberg & Cooper, 1990).

Characterising avian diet requires an understanding of several different factors centred on the availability and exploitation of food resources (Sinclair, Fryxell, & Caughley, 2006). However, food resources and foraging behaviours can vary over space and time as well as between individuals, often as a result of environmental changes or shifting dietary requirements (Durst et al., 2003). This makes the study of avian diet particularly complex.

Food availability is a key determinant of avian habitat use, helping to explain the spatial patterns of foraging behaviour (Razeng & Watson, 2015). Availability is dependent upon the presence of food in an area and the bird's ability to consume it, often varying between seasons (Sinclair, Fryxell, & Caughley, 2006), years (Szaro, Brawn, & Balda, 1990), and locations (Petit, Petit, & Petit, 1990). In comparison, the type and rate at which food is exploited is a result of biological interactions between birds and their prey (Cooper & Whitmore, 1990), impacted by foraging preference (Stephens, 1990), inter and intra-specific competition (Sinclair, Fryxell, & Caughley, 2006), or specific dietary needs (Robel et al., 1995). The complexity of these relationships means that the foraging strategies exhibited by birds are varied, including generalist and specialist foragers (Catry et al., 2014), and flexible, changing under certain environmental or behavioural circumstances (Szaro, Brawn, & Balda, 1990). Optimal foraging theory suggests that foraging strategies will be selected to ensure maximum net energy intake whilst minimising other costs, such as thermoregulation and predation risk (Stephens & Krebs, 1986). Therefore, birds are expected to favour certain prey species or habitats when foraging (Stephens, 1990), within the constraints of their realised niche.

Prey selection and foraging strategy are often linked to the nutritional content of prey, including both the nutrients available, and the bird’s ability to digest, and therefore exploit them (Bell, 1990). However, little information exists on this topic for most avian species (Finke, 2002). Researchers are beginning to consider habitat quality in nutritional terms, evaluating whether observed patterns of prey selection reflect nutritional value (Razeng & Watson, 2015). This is in turn has helped to inform targeted and effective management actions (Razeng & Watson, 2015), proving particularly important for the conservation of rare species held in captivity (Walker et al., 2013).

Measuring availability and exploitation can prove challenging, with varying levels of bias present in all sampling methods (Cooper & Whitmore, 1990; Standen, 2000; Ward, New, & Yen, 2001; Pearce et al., 2005; Prasifka et al., 2007). Comparison between food availability and exploitation is also difficult as they are generally sampled through different ‘perceptual filters’ (Hutto, 1990), so often seem more distinct from one another than in actuality.

Though population decline in insectivorous birds is well-documented globally, insectivores have still received less attention than other avian groups in terms of their foraging behaviour and nutrition (Razeng & Watson, 2015). Knowledge of diet might prove particularly important for one insectivorous bird, the kiwi (*Apteryx* spp). Despite its status as New Zealand’s national icon and arguably most cherished species (Herbert & Daugherty, 2002), much still remains unknown about the ecology of this unusual nocturnal, flightless bird. Despite intensive management, populations of all five species continue to decline, highlighting the importance of learning more about their diet in order to improve our management of the remaining captive and wild populations.

Surprisingly little research has focused on the diet of the brown kiwi (Sales, 2006a). The handful of published studies to have investigated diet in this species (see Chapter 1, Table 1.2) have confirmed that brown kiwi feed almost exclusively on invertebrates and identified a number of soil and ground dwelling taxa considered particularly important to their diet (Reid, Ordish, & Harrison, 1982; Kleinpaste & Colbourne, 1983; Miles, 1995; Shapiro, 2005). These studies concur that brown kiwi are selectively opportunistic, preying upon most invertebrates in proportion to their availability, while selectively foraging for a few important soil-dwelling species (Colbourne & Kleinpaste, 1984; Miles, Potter, & Fordham, 1997; Shapiro, 2005). However, variation in invertebrate exploitation between locations (Reid, Ordish, & Harrison, 1982; Miles, 1995), seasons (Kleinpaste & Colbourne, 1983; Miles, Potter, & Fordham, 1997; Shapiro, 2005) and habitat types (Watt, 1971; Kleinpaste & Colbourne, 1983) has led to the suggestion that a 'typical' diet probably does not exist for brown kiwi.

Unfortunately most previous dietary studies of brown kiwi have suffered from small sample sizes, limited time frames, or irregular sampling between months. In addition, none have considered the wider combination of factors which can contribute to diet and foraging behaviour. As a result, a complete and accurate description of the natural diet of brown kiwi and how it varies both spatially and temporally has yet to be given.

In this chapter I will provide a comprehensive analysis of brown kiwi diet, serving to fill some of the gaps remaining in our current understanding of their prey selection and foraging behaviour. The study takes into account both invertebrate availability and exploitation, and is the first to examine brown kiwi diet over a consecutive period of twelve months. In addition, the study will clarify the effects of season, location and habitat related factors to brown kiwi diet, as well as consider how faecal sample quality may affect the accuracy of the exploitation results. The impact of nutrition on brown kiwi foraging behaviour is discussed in relation to availability and exploitation for the first time. This information might prove critical to the species' future survival, helping to identify more effective management for both captive and wild populations. The objectives for this chapter are outlined below, and hypotheses suggested based upon the knowledge gathered in previous studies.

Objective 1: Document Invertebrate availability on Ponui Island.

- *Hypothesis 1.1) The range and abundance of invertebrates present on Ponui Island is comparable to other brown kiwi locations.*
- *Hypothesis 1.2) Invertebrate availability on Ponui Island varies between seasons, habitat types and gullies due to invertebrate lifecycle and environmental changes.*
- *Hypothesis 1.3) Some invertebrate groups have a greater affect upon availability data than others.*

Objective 2: Assess the diversity of invertebrates exploited by brown kiwi on Ponui Island.

- *Hypothesis 2.1) Invertebrate groups are exploited by brown kiwi on Ponui Island at varying abundance and frequency.*
- *Hypothesis 2.2) Invertebrate groups are exploited by brown kiwi on Ponui Island at different rates between seasons and habitat types due to changes in their availability.*
- *Hypothesis 2.3) Variation in faecal sample quality affects the exploitation results, with lower quality faecal samples containing less identifiable invertebrate content.*
- *Hypothesis 2.4) Some invertebrate groups have greater influence on patterns found in exploitation data than others.*

Objective 3: Compare the availability and exploitation of invertebrate food on Ponui Island to assess brown kiwi prey selection and foraging strategies.

- *Hypothesis 3.1) Brown kiwi on Ponui Island are selectively opportunistic foragers, eating some invertebrate groups in line with their availability while favouring others.*
- *Hypothesis 3.2) Brown kiwi on Ponui Island vary their foraging behaviour with seasons and habitats.*
- *Hypothesis 3.3) Nutrition plays an important role in the diet of Ponui Island brown kiwi.*

2.2 Methods

General information regarding the study site and species is given in Chapter 1. Data concerning the diet of brown kiwi were gathered over a twelve month period on Ponui Island from March 2013 to February 2014. Sampling periods were split into four seasons by the traditional seasonal range in New Zealand: summer (December - February), autumn (March - May), winter (June - August) and spring (September - November). Both the availability of invertebrate food resources and the invertebrates exploited by brown kiwi were measured.

2.2.1 Measuring Invertebrate Availability

Invertebrates were sampled each month using a total of 140 pitfall traps installed in 28 randomly determined sites throughout the study area (Fig. 2.1). Pitfall traps are used commonly by researchers because they enable rapid and efficient collection of a large amount of data (Standen, 2000; Seldon & Beggs, 2010; Corti, Larned, & Datry, 2013). Sixteen sites were installed by Lee Shapiro in 2004 and the remaining 12 were set up for this study in February of 2013 using identical methodology (Shapiro, 2005). Sites were spread across four different habitat types: forest, scrub, pasture and swamp-edge. The number of pitfall sites per habitat type mirrored the availability of each habitat within the three gullies. Each gully had at least two pitfall sites for each habitat, while both the larger gullies (Pipe and Red Stony) had three in scrub and in forest due to the larger proportions of those habitat types. The smaller Pohutukawa gully was combined with Kauri gully for this chapter due to similarities in habitat, location, and to increase the area of Kauri gully to a size more comparable with the other two gullies. Previous pitfall studies on the island (Shapiro, 2005; Wilson, 2014) avoided sampling the deep swamp habitat due to flooding and difficulty of installation; however for this study pitfall sites were installed around the edge of swamps to allow comparison with other chapters of the thesis. Hereafter swamp-edge habitat will be referred to as swamp. Site locations were determined by the random selection of points on a grid map of the study site.

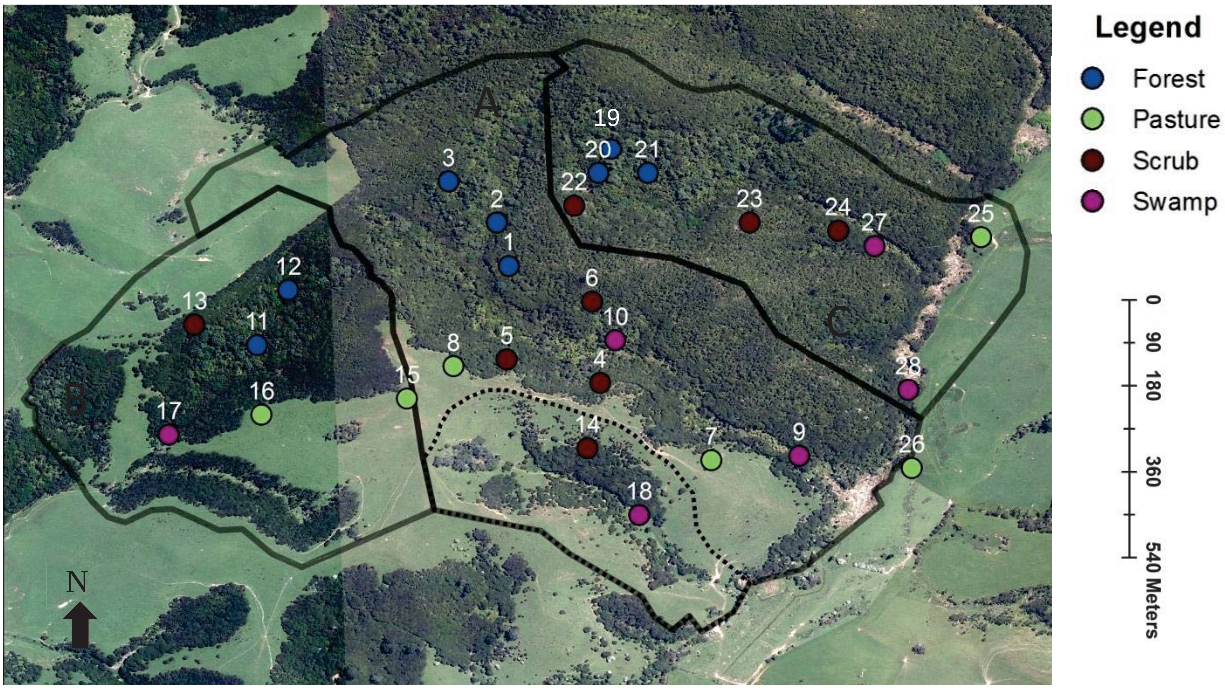


Figure 2.1 – Map of the Study area and gully boundaries with pitfall sites marked and labelled. (A=Red Stony, B=Kauri, C=Pipe). Dotted outline represents Pohutukawa Gully. Photograph from LINZ.

At each site five pitfall kill-traps were placed in a square pattern encompassing $15m^2$ with one trap at each corner and one in the centre of the square. Pitfall traps consisted of a 20cm deep circular hole, approximately 8cm in diameter. Each hole contained a 20cm-long pipe set flush with the ground surface. A 200ml plastic cup containing 20ml of antifreeze (ethyl glycol) was placed inside each pipe, ensuring the top of the cup was flush to the top of the pipe with no gap between them that insects could fall through. Traps were covered with a 30cm x 30cm metal lid placed 2-3cm above the ground, to limit the amount of plant material and rainwater entering the cup.

Each trap was cleared and reset every 26-31 days, and the contents sieved and stored in a 70% ethanol solution for later identification. Identification took place at a high taxonomic level, with invertebrates identified either to class, order, or family depending on their perceived importance using an identification guide (Naumann et al., 1991). Based on prior knowledge of the size of invertebrate prey in both the brown kiwi (Reid, Ordish, & Harrison, 1982) and little spotted kiwi diet (Colbourne, Baird, & Jolly, 1990), only invertebrates 8mm or larger were considered available to kiwi and thus recorded in this study. All invertebrates were identified and the total number of individual invertebrates of each invertebrate group was recorded for each pitfall site before the entire sample was dried and weighed (Sunbeam Food Dehydrator DT5600). Samples were weighed at two hour intervals throughout dehydration until a constant mass was reached, and the final dry biomass weight was recorded for each pitfall site. In some months, individual pitfall traps were flooded or disturbed by livestock and as a result contained no invertebrate content so could not be used. To account for this the average dry weight per pitfall trap (n=5) for each site was used for analysis each month, rather than the total dry weight of biomass. Weight of invertebrates is thought to present the most relevant depiction of availability, as it accounts for the size of invertebrates and thus the overall nutritional potential to brown kiwi. However, to increase understanding of the results, both weight and proportion of invertebrates were used during analysis.

Arthropod sampling is complicated due to irregular distributions that can vary substantially in time and space (Cooper & Whitmore, 1990; Smith & Rotenbetty, 1990), as well as variation in their behaviour and ecology. It is therefore recommended that several sampling techniques are used to assess food availability (Cooper & Whitmore, 1990; Standen, 2000). The collection and analysis of leaf litter, a stratum brown kiwi are known to use for foraging (Cunningham, 2006), was considered. However, Shapiro (2005) found that litter dwelling invertebrates were easily disturbed and moved away prior to collection, concluding that pitfall traps present a more accurate representation of surface and litter dwelling invertebrate availability. Likewise, soil core sampling for the collection of soil dwelling invertebrates would have limited accuracy if used in the large study site, due to the ‘random clumped distribution’ of many soil dwelling taxa on Ponui Island (Shapiro, 2005). To increase precision, the required number and frequency of soil core samples would raise dramatically, something the land owner and I agreed would result in excessive damage to the site. As such, pitfall trap sampling was used singularly to measure invertebrate availability.

2.2.2 Measuring Invertebrate Exploitation

Kiwi faecal samples were collected opportunistically over the course of the study to determine what invertebrates were exploited by brown kiwi on Ponui Island. Unlike other methods such as gut content analysis or direct observation, this method does not result in death or disturbance to the animal (Rosenberg & Cooper, 1990; MacLeod & Kerly, 1996), samples are easily collected (Deagle et al., 2007), and yield reliable estimates of the diet of insectivorous animals (Dickman & Huang, 1988). Faecal analysis is the most practical method of studying the diet of secretive or endangered species where direct observations or culling are not possible (MacLeod & Kerly, 1996)

Samples were collected throughout the wider study site to avoid site specific bias and to increase the potential sample size. The habitat type in which each sample was collected was recorded as scrub, pasture or forest. Faecal samples were not collected from swamp habitat as intact samples could not be found consistently throughout the year due to flooding. The size and consistency of each faecal sample were recorded to estimate the age of the sample and indicate the potential impact quality of faeces could have on invertebrate content. Samples were classed into small, normal or large size categories, and liquid, normal or dry consistency categories at the researcher’s discretion. It was ensured that at least 10 faecal samples were collected from each of the three habitat types every month to allow comparison. This would result a significantly larger sample size than previous studies. Samples were frozen for up to six months until they could be analysed in the lab.

In the lab, samples were defrosted and washed through a gradation of different sized sieves (4000µm, 500µm, 250µm & 125µm) enabling the collection of varying sized fragments of digested material. The largest sieve separated any vegetation which may have been picked up with the sample, while the smallest sieve contained particles too small to analyse in a timely manner. The remaining material was transferred to a Petri dish and examined under an Olympus sz40 dissection microscope at 8x magnification. Insect and plant material was removed by hand and any fragments not similar to those already encountered were photographed at 6x magnification. The ability to identify the full range of dietary items rests on learning the specific parts which will survive digestion, for which clues exist for most soil foods a bird will eat (Rosenberg & Cooper, 1990; Michalski et al., 2011). Fragments were identified to order, or for Coleoptera to family level, using an identification guide (Naumann et al., 1991) and a Ponui Island invertebrate reference collection created by Denny (2009). A distinction was made between adult and larvae of particular taxa where appropriate. The number of each type of fragment within a sample was recorded before all material was stored in a 70% Ethanol solution and labelled.

Invertebrates were counted in a conservative manner using the most conspicuous remains (i.e., the foretibias of cicada nymphs, heads and mandibles of beetles and chelicerae of spiders). For each appendage or structure found in a sample, the frequency of that structure was divided by the number expected on a single individual. All fractions were rounded up to the closest whole number. If there were multiple different parts of the same order or family within one sample (e.g. heads, legs and mandibles) then the largest whole number of those parts was used to represent the number of individuals for that sample. Whole invertebrates which appeared completely undigested were excluded from the analysis as they are likely to have been unintentionally collected with the faecal sample.

The number of individuals per sample and frequency of occurrence were both used for analysis of exploitation data to increase validity of the results as suggested by previous research (Dickman & Huang, 1988; Rosenberg & Cooper, 1990). Only the presence or absence of Annelid chaetae were used for analysis, as Wroot (1985) found that these structures are not a reliable indicator of Annelid numbers.

2.2.3 Statistical Analyses

Multivariate statistical analyses were performed using Primer v6.1.13 and Permanova v1.0.3. Microsoft Excel 2010 and Graph Pad Prism 6 were used to generate graphs and tables. A probability of ≤ 0.05 was deemed statistically significant.

Abundance data from pitfall and faecal sampling were analysed separately. Both datasets were transformed using an overall square root transformation, serving to reduce the importance of the most abundant taxa (Clarke & Gorley, 2006). Only the average weight per pitfall data, included with abundance of available invertebrates, was left untransformed. Resemblance matrices were created using the Bray-Curtis measure of similarity. Multidimensional scale plots (nMDS) were then produced by plotting samples into a 2d space based on their resemblance. This illustrated any differences between factors, serving as a visual aid to interpret the data. Each nMDS plot includes a measure of stress; this represents the accuracy of the plot. Final stress values should ideally be smaller than 10% and definitely not in excess of 30% to represent species abundance data accurately (Clarke & Gorley, 2006). If the stress value for a 2D MDS solution was relatively high (>0.20) then the 3D MDS solution would be checked to confirm accuracy by ensuring trends were similar with a lower recorded stress value.

One-way ANOSIM routines were run on both availability and exploitation data for each factor (season, habitat type, gully, faecal size and consistency) to analyse for similarity, testing the null hypothesis of no difference between groups (R=0). The ANOSIM test gives a ‘Global R’ value, a comparative measure of the degree of separation of groups within a factor. R values close to zero represent very little separation between groups, while values close to one represent perfect separation (Clark & Gorley, 2001). If the observed R value was found to exceed 95% of the simulated R values, then the null hypothesis was rejected at the 5% confidence level. Differences were plotted on bar graphs for visualisation. In addition, Two-way ANOSIM routines were performed combining multiple factors to assess whether this increased the R values or significance levels for each factor.

ANOSIM is sensitive to differences in multivariate dispersion among groups (Anderson, Gorley, & Clarke, 2008), and runs best when within-group dispersion is homogeneous between groups. Therefore PERMDISP routines were also run on each factor to compare the distances for each group of observations to their group centroid. This allows for the assessment of both within and between-group variation for each factor, where within-group variance represents the variation we would expect simply by chance and between-group variance represents variation attributable to the factor. Increased within-group dispersion from sampling error will affect the results of between-group variation.

BEST routines using Spearman rank correlation were run for each dataset to find which invertebrate groups acted as the best explanatory variables in the resemblance matrices of invertebrate availability and utilisation data. The procedure aims to find the best match between the multivariate among-sample patterns and environmental variables associated with those samples, identifying those invertebrate groups which had the greatest effect.

To compare availability and exploitation both sets of data were plotted using their proportion of abundance. This was generated by dividing the number of individuals of each group with the total number of invertebrates for that month, converted to a percentage. Only invertebrate groups present in both datasets were included for this analysis. A combined dataset of both availability and exploitation was put through the same ANOSIM and PERMDISP tests mentioned above. Additionally, a PERMANOVA test was run to compare brown kiwi diet availability and exploitation and produce a final measure of variance, describing the difference between Invertebrate availability and exploitation.

2.3 Results

2.3.1 Invertebrate Availability

A total of 28,546 individual invertebrates were caught and identified in 1,595 pitfall traps, at an average of 85 individuals per pitfall site sampled (±6.4 SE). These invertebrates represented a combined dry weight per pitfall of 151.09g (Appendix B). Eighty five pitfall traps were considered non-viable due to damage or flooding. Sixteen different invertebrate groups were represented within pitfall trap samples (Fig. 2.2) (see Appendix A for common names). Of these, Isopoda were by far the most frequently identified taxa (accounting for almost 50% of all invertebrates), with Orthoptera, Arachnida, Amphipoda and Coleoptera also caught in substantial numbers (Appendix C). Together these five groups made up over 85% of all the invertebrates caught. Hymenoptera, Gastropoda, Blattodea and Diptera were present in small numbers, while all other groups of invertebrates including Oligochaeta and Hemiptera were present in much lower proportions.

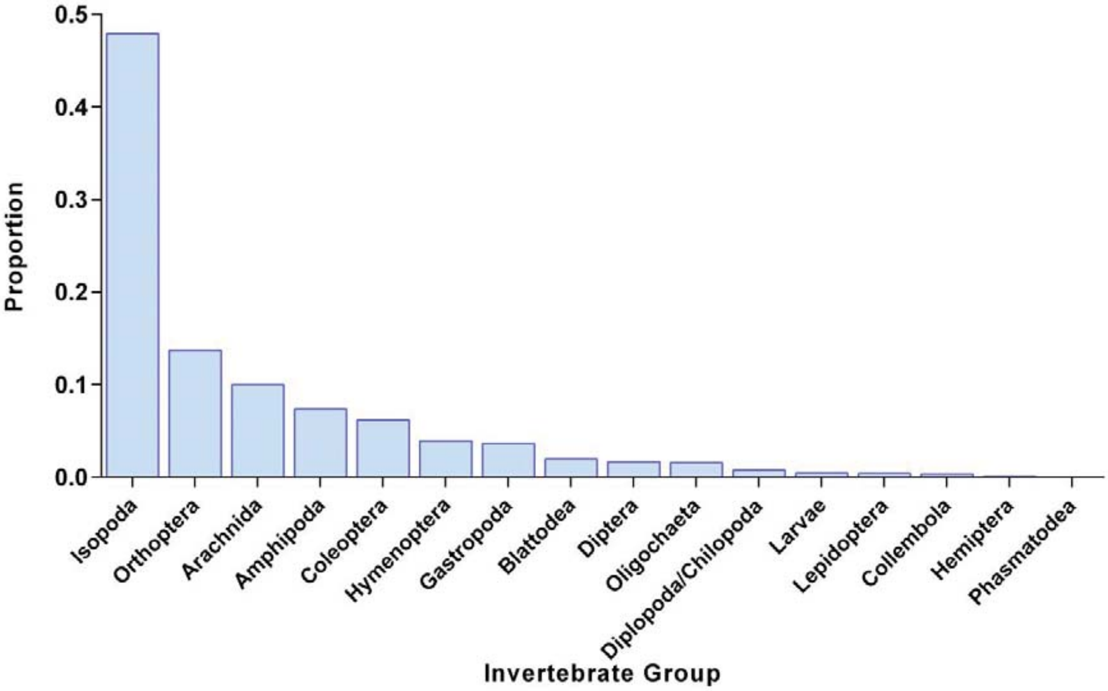


Figure 2.2 - Proportion of all invertebrates made up by each invertebrate group identified in pitfall traps on Ponui Island, in order of most abundant.

Seasonal variation

Invertebrate availability (weight + number) differed significantly between seasons (one-way ANOSIM; Global R=0.137; P<0.001) (Appendix D). However, a low R value indicated that this difference was small. This is reflected in the considerable overlap of samples when plotted as points in a multidimensional space (Fig. 2.7A). Monthly invertebrate dry weight per pitfall started at a moderate level in March, declined steadily until midwinter in July before increasing again, peaking dramatically over summer in January and February 2014 (Fig. 2.3).

Seasonal fluctuations were evident in the proportion of available invertebrates (Fig. 2.4). Isopoda were caught throughout the year, though they represented a higher proportion of individuals caught in winter. Orthoptera also had a pronounced seasonal trend, peaking in proportion over summer and autumn. Arachnida, Amphipoda and Coleoptera were present in a moderate proportion of samples throughout the year. Hymenoptera, Blattodea and Diptera were caught at higher rates during summer and autumn, while Gastropoda showed the opposite trend, increasing in proportion in winter and spring. Oligochaeta were caught relatively infrequently, but appeared to increase in proportion over winter and spring. Other invertebrate groups present at low densities showed no apparent seasonal trends.

Pairwise comparisons (Appendix D) show that winter and summer were least similar in terms of invertebrate availability (one-way ANOSIM: Global R=0.302, P=0.001). In comparison, availability remained very similar between autumn and summer (one-way ANOSIM: Global R=0.052, P=0.001), autumn and spring (one-way ANOSIM: Global R=0.075, P=0.001), and spring and summer (one-way ANOSIM: Global R=0.083, P=0.001). When season was considered in a two-way test with habitat type the difference between seasons was more evident (two-way ANOSIM: Global R=0.246, P=0.001) (Appendix D).

Results of the PERMDISP test suggest that there is a difference in within-group variance between seasons (F=3.968, P=0.016) (Appendix E). This can be seen visually in the multidimensional plot (Fig. 2.7A), where samples from spring are clustered together in the middle of the plot while those from winter have a wider spread. Z scores generated during the test conformed to this trend, with spring having the lowest score (Appendix E). The other three seasons showed much greater variance in dispersion, with winter the most scattered and with the highest Z score, followed closely by autumn and summer.

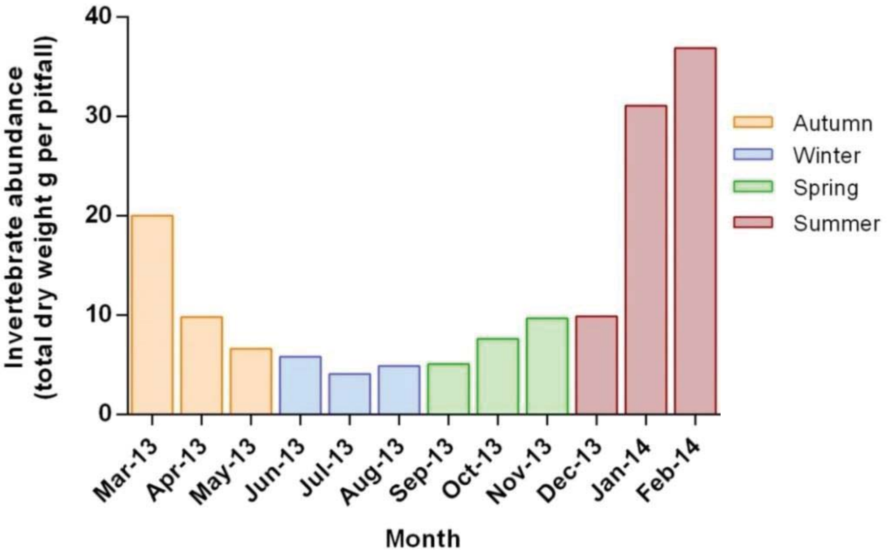


Figure 2.3 - Combined monthly invertebrate abundance (measured in combined average weight (g) per pitfall) caught over 12 months in pitfall traps on Ponui Island, coloured for season.

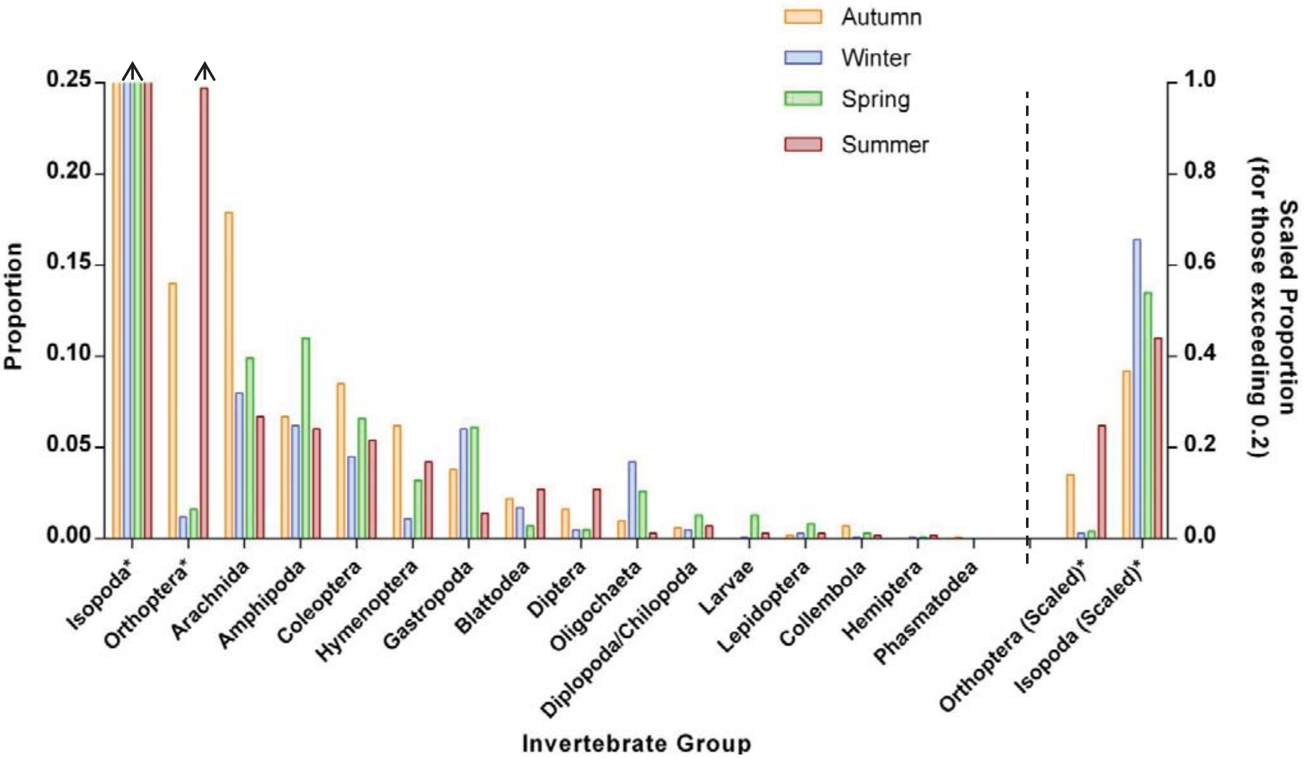


Figure 2.4 – Proportion of individuals of each group identified in pitfall traps on Ponui Island over the course of four seasons, in order of most abundant. * and ^ represent taxa which exceed the left y axis, and thus are plotted at a different scale on the right y axis.

Habitat variation

There was a significant difference in invertebrate availability between habitat types on Ponui Island (one-way ANOSIM; Global R=0.362; P<0.001) (Appendix D). Habitat showed well defined separation between groups when plotted as points in a multidimensional space (Fig. 2.7B), reflected in a moderate R score. Variation between habitat types can be seen in both invertebrate quantity (total weight per pitfall) (Fig. 2.5) and composition (proportion of invertebrates) (Fig. 2.6). Pasture consistently had the highest invertebrate weight throughout the year, while also showing the most variation seasonally. Composition of invertebrates also varied between habitat types. Isopoda and Orthoptera were both present at higher proportions within pasture habitat. Coleoptera were found more frequently in forest and swamp habitat, while Blattodea were most common in scrub. Arachnida made up a large proportion (over 20%) of all invertebrates caught in forest and scrub. Numbers of all other orders remained relatively consistent between each of the four habitat types.

Pairwise comparisons (Appendix D) highlight the differences between forest and pasture (one-way ANOSIM: Global R=0.712, P=0.001), and scrub and pasture (one-way ANOSIM: Global R=0.571, P=0.001). Forest and scrub on the other hand had similar invertebrate availability (one-way ANOSIM: Global R=0.208, P=0.001). Swamp habitat was similar to all other habitat types. When habitat was considered in a two-way test with season the difference between habitat types was more pronounced, with an increased R score (two-way ANOSIM: Global R=0.455, P=0.001).

The PERMDISP test suggested that there was a difference in within-group dispersion between habitat types (PERMDISP: F=7.781, P=0.001) (Appendix E), reflected in the increased scatter between groups in the multidimensional space (Fig. 2.7B). However, the Z scores produced for each habitat type were very similar, which may prove important for the results of the ANOSIM, which assumes homogenous dispersion.

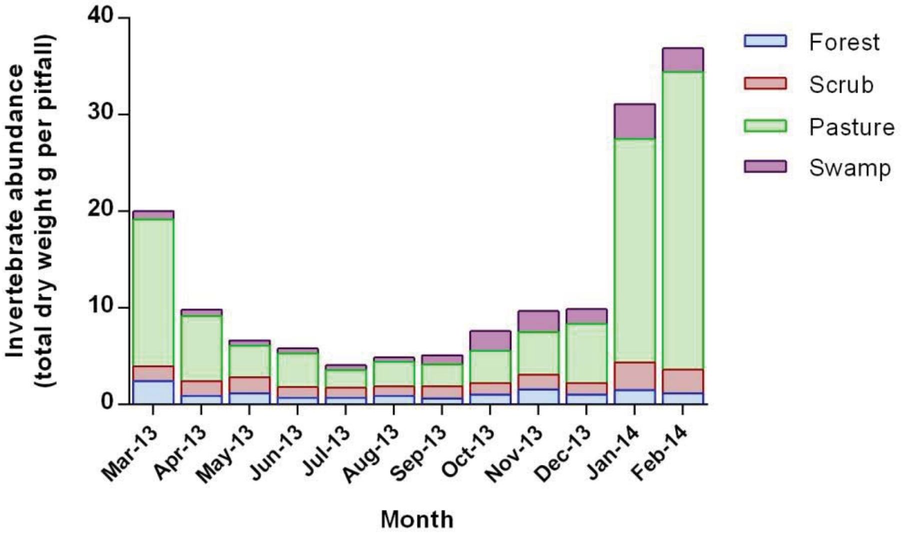


Figure 2.5 – Combined monthly invertebrate abundance (measured in combined average weight (g) per pitfall) caught over 12 months in pitfall traps on Ponui Island, coloured for habitat type.

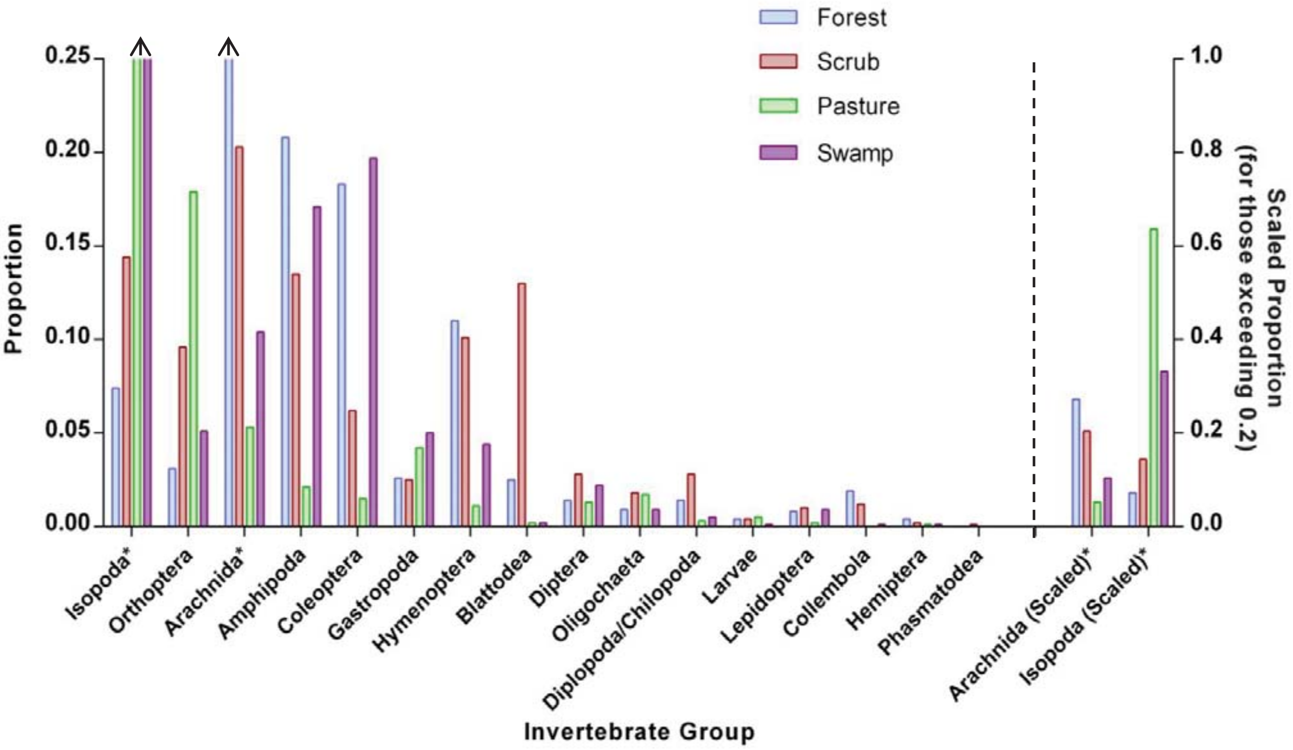


Figure 2.6 - Proportion of all individuals of each group caught in pitfall traps on Ponui Island in different habitat types, in order of most abundant.* and ^ represent taxa that exceed the left y axis, and thus are plotted at a different scale on the right y axis.

Gully variation

There was a significant difference in invertebrate availability between gullies on Ponui Island (one-way ANOSIM; Global R=0.044; P<0.001) (Appendix D). However, a low R value indicates that differences between gullies were very small. This close similarity remains true for all pairwise comparisons, with R scores for all comparisons falling below 0.010. These patterns are apparent when samples are plotted as points in a multidimensional space (Fig. 2.7C), with little separation to distinguish between groups.

There is no evidence to suggest a difference in within-group dispersion between gullies on Ponui Island (PERMDISP: F=1.368, P=0.344) (Appendix E). It is therefore assumed that samples from the three gullies are evenly dispersed. This is reflected in the very similar Z scores calculated for each gully. This is important for the results of the ANOSIM, which assumes homogenous dispersion.

BEST analysis

The BEST analysis identified the five invertebrate taxa considered to have the greatest effect upon differences seen within the invertebrate availability data. These taxa were Amphipoda, Arachnida, Coleoptera, Isopoda and Orthoptera. These five invertebrate groups were considered by the analysis to be driving the assemblage structure of the generated resemblance matrix. These were also the groups caught at the highest abundances, together making up over 85% of all the invertebrates caught.

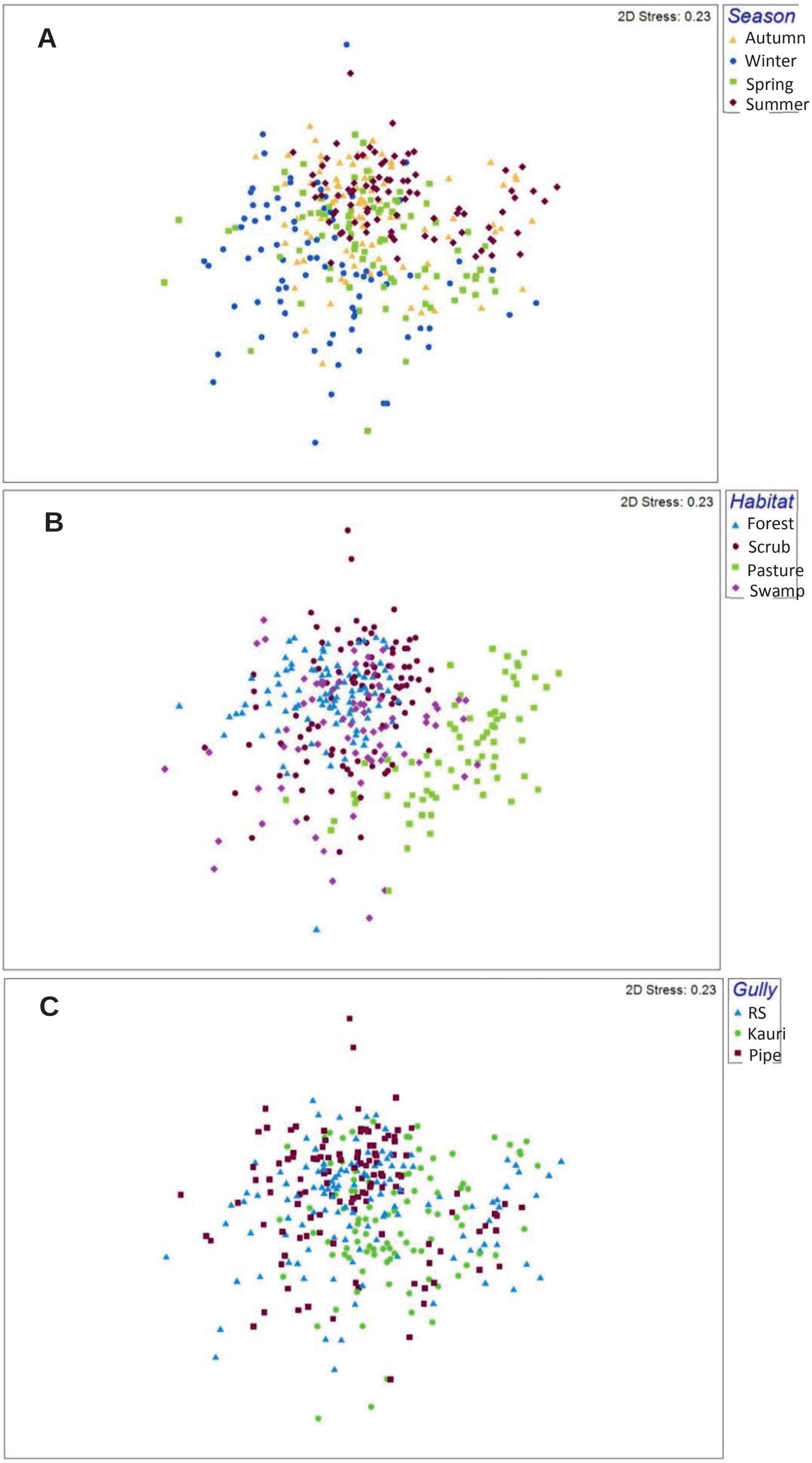


Figure 2.7 – Non-metric MDS ordination; Comparison of invertebrate availability on Ponui Island between: A = seasons, B = Habitat types and C = Gullies. Created using the total abundance of 16 different invertebrate groups and average weight per pitfall data collected from 336 pitfall samples. Data were pre-treated using a Square Root transformation, and Bray Curtis similarity matrix created. Axes lack labels as an MDS only shows information on the relative similarities between points, hence the scale is arbitrary.

2.3.2 Brown Kiwi Diet: Invertebrate Exploitation

A total of 442 brown kiwi faecal samples were collected and analysed for invertebrate content during the study. Out of a total of 9696 invertebrate fragments separated from samples, 9382 were identified to order or family level, accounting for a total of 4279 estimated individuals (Appendix F + Appendix G). In total, sixteen different groups of invertebrates were identified in the faecal samples to order or family (Fig. 2.8A+B) (see Appendix A for common names). Coleoptera occurred the most frequently, present in 89.3% of the samples. They were also the most dominant taxa numerically, accounting for 65.2% of all the invertebrates identified. Hemiptera and Diptera occurred in around half of the samples and accounted for almost 20% of all invertebrates identified. Orthoptera and Arachnida were present in around a quarter of all samples and made up a proportion of roughly 10%. There was evidence of Oligochaeta in 13% of all samples. Excluding Oligochaeta, which could not be accurately counted; these five groups accounted for almost 88% of all invertebrates identified within the faecal samples.

Most other invertebrate groups were identified relatively infrequently within faecal samples. Two of the most highly available taxa (See Fig. 2.2) Isopoda and Amphipoda, occurred infrequently and at low proportions in the faecal samples. Acari, Blattodea, Hymenoptera, Chilopoda and Diplopoda were all present in less than 20% of samples and at low to moderate proportions, while all other groups of invertebrates were present at much lower frequencies and densities.

Due to their apparent importance to brown kiwi diet, Coleoptera were analysed further to family level. A total of eight different coleopteran families were identified within the faecal samples (Fig. 2.8C+D). Scarabaeidae, Carabidae and Elateridae families occurred most frequently within samples, including both adults and larval forms, and made up the greatest proportion of all Coleoptera identified in the samples.

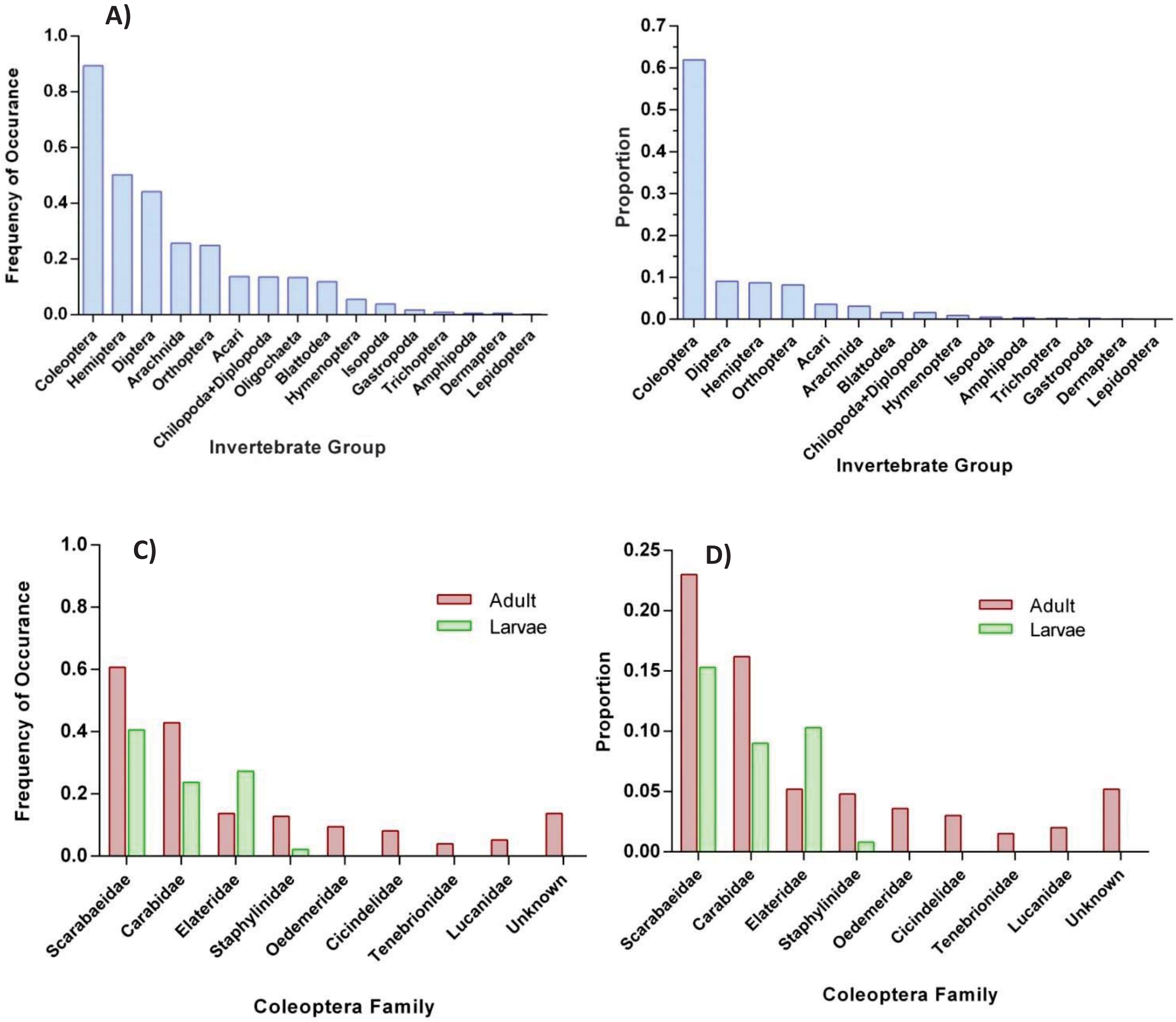


Figure 2.8 – Frequency of occurrence and proportions for each of the 16 invertebrate groups and Coleoptera families identified over 12 months within 442 brown kiwi faecal samples on Ponui Island. A) Frequency of occurrence of all 16 invertebrate groups, in order of most abundant. B) Proportion of all individuals made up by 15 counted invertebrate groups, in order of most abundant. C) Frequency of occurrence of all Coleoptera, including both adult and larval stages. D) Proportion of all Coleoptera made up by each Coleoptera family, including both adult and larval stages.

Seasonal variation

Rates of invertebrate exploitation in brown kiwi differed between seasons (one-way ANOSIM; Global R=0.076; P<0.001) (Appendix H). However, the low R value indicates that any difference was small. This is reflected in the considerable overlap of samples when plotted as points in a multidimensional space (Fig. 2.12A).

While utilisation rates of most invertebrate taxa did not differ substantially, there was evidence of seasonality in the abundance of certain exploited invertebrate foods (Fig. 2.9). Orthoptera, Arachnida and Blattodea all occurred significantly more frequently in summer and autumn, while Acari and Chilopoda / Diplopoda were present in faeces more often over winter and spring. Coleoptera, the most commonly exploited taxa found in the faecal samples year round, showed seasonal trends when explored to a family level (Fig. 2.10). The proportion of Scarabaeidae consumed by brown kiwi peaked over spring and summer, while Carabidae increased in autumn and Elateridae during summer. Coleoptera adults were exploited more frequently during summer and autumn and less frequently over winter and spring (Fig. 2.11). Conversely, Coleoptera larvae were evident in faecal samples in greater proportions over winter and spring, and less so during summer and autumn.

Pairwise comparisons (Appendix H) showed that autumn and spring were the most different to each other when considering invertebrate exploitation (one-way ANOSIM; Global R=0.141; P<0.001). However, even these two seasons show considerable overlap when plotted as points in a multidimensional space (Fig. 2.12A). Invertebrate exploitation rates were very similar between winter and spring (one-way ANOSIM; Global R=0.011; P<0.062), and autumn and summer (one-way ANOSIM; Global R=0.045; P<0.001). When season was considered in a two-way test with habitat type the difference between seasons was slightly more evident (two-way ANOSIM: Global R=0.094, P=0.001), though still minor (Appendix H).

The PERMDISP test suggests that there is very little difference in within-group dispersion between seasons (PERMDISP: F=0.718, P=0.616) (Appendix E; Fig. 2.12A), where samples from all four seasons appear evenly scattered. Z scores from each season are all very similar, demonstrating homogenous within-group dispersion.

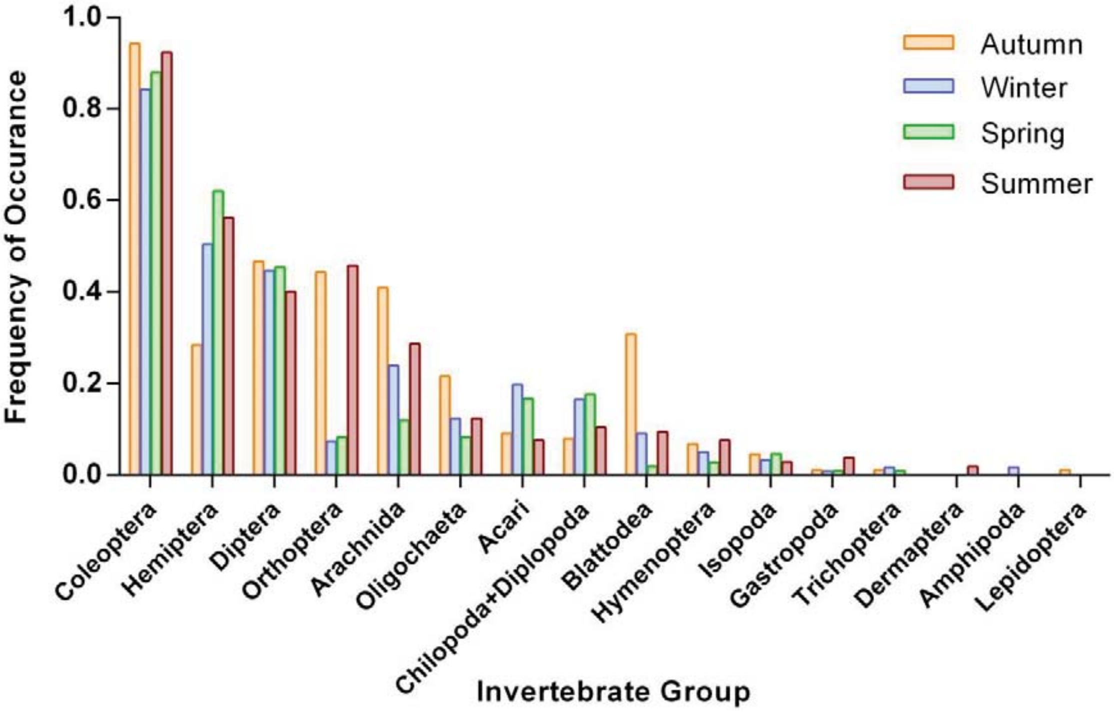


Figure 2.9 – Frequency of occurrence rates for each group identified in brown kiwi faecal samples collected on Ponui Island over the course of four seasons, in order of most abundant.

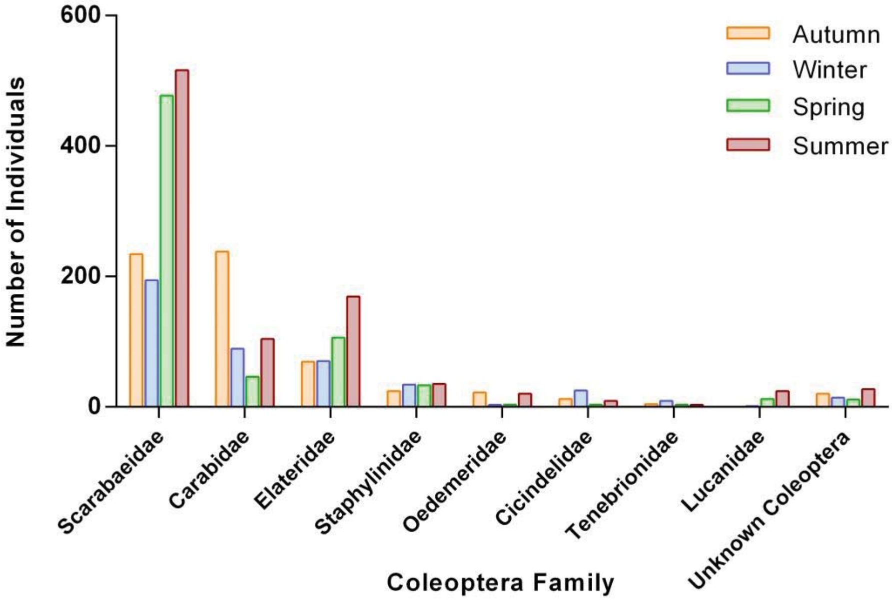


Figure 2.10 – Total number of individuals of each Coleoptera family identified in brown kiwi faecal samples collected on Ponui Island over the course of four seasons.

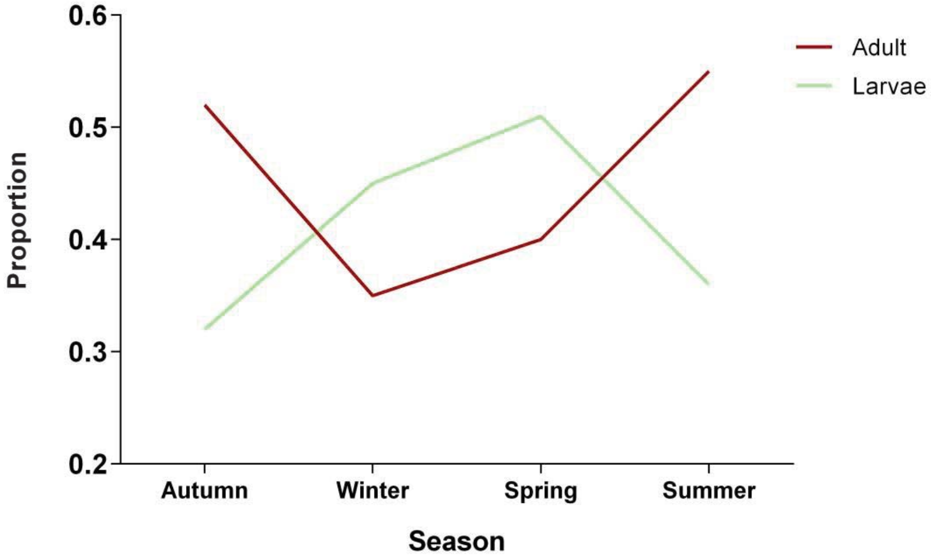


Figure 2.11 – Proportion of all Coleoptera at adult and larvae stages identified in brown kiwi faecal samples collected on Ponui Island over the course of four seasons.

Habitat variation

No significant differences in invertebrate exploitation were found between habitat types on Ponui Island (one-way ANOSIM; Global R=0.009; P<0.028) (Appendix H). While the global R value does not indicate perfect similarity, the observed R value was not higher than 95% of the simulated R values, and thus no difference was seen to occur.

The similarity in invertebrate exploitation rates between habitat types remained true for all pairwise comparisons (Appendix H), with R scores for all comparisons falling below 0.016. This can be seen when samples are plotted as points in a multidimensional space (Fig. 2.12B). When considered in a two-way test with season the difference between habitats was further reduced (two-way ANOSIM: Global R=0.003, P=0.003), with habitats showing near perfect similarity (Appendix H).

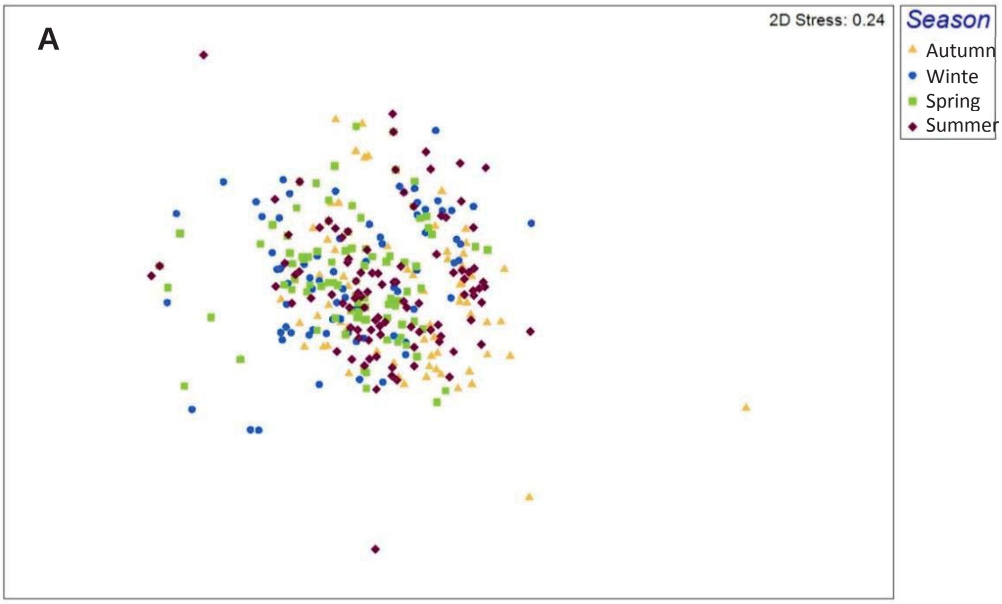
Results from the PERMDISP test suggests there is no difference in within-group dispersion between habitat types on Ponui Island (PERMDISP: F=1.525, P=0.225) (Appendix E; Fig. 2.12B). Although the Z score for scrub is lower than other habitat types, suggesting a larger dispersion, it can still be assumed that samples from each habitat show homogenous dispersion due to the non-significance of the PERMDISP test.

Faecal sample differences

No significant difference was found in invertebrate exploitation on Ponui Island between groupings in both faecal size (one-way ANOSIM; Global R=0.015; P<0.172) and consistency (one-way ANOSIM; Global R=-0.004; P<0.551) (Appendix H). This similarity remains true for most pairwise comparisons, with R scores for all but one comparison falling below 0.036. Invertebrate exploitation rates differ most between faecal samples of small and large sizes (one-way ANOSIM; Global R=0.092; P<0.005), however these still remain very similar.

BEST analysis

The BEST analysis determined the five invertebrate taxa considered to have the greatest effect upon differences seen within the invertebrate exploitation data. These taxa were Oligochaeta, Coleoptera, Diptera, Hemiptera and Orthoptera. These five invertebrate groups were considered by the analysis to be driving the assemblage structure of the generated resemblance matrix. Excluding Oligochaeta, which could not be accurately counted; the remaining four groups were those which were identified at the highest abundances in the faecal samples, accounting for almost 88% of all invertebrates identified.



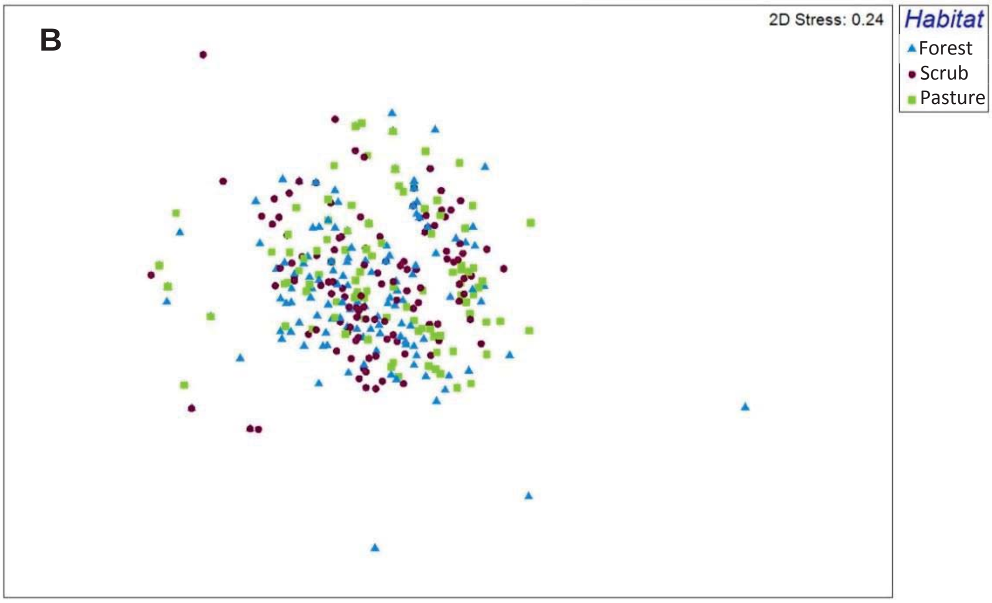


Figure 2.12 - Non-metric MDS ordination; Comparison of invertebrate exploitation by brown kiwi on Ponui Island between: A = Seasons and B = Habitat types. Created using abundance data from 442 faecal samples. Data were pre-treated using a Square Root transformation, and Bray Curtis similarity matrix created. The axes lack labels as an MDS only shows information on the relative similarities between points, hence scale is arbitrary.

2.3.3 Exploitation vs Availability

A significant difference was found between the composition of invertebrates available in the study site and the composition of invertebrates exploited (one-way ANOSIM; Global R=0.792; P<0.001). A high F value generated in a PERMANOVA test serves to confirm this result (PERMANOVA; F=348.24, P=0.001). The difference between invertebrate availability and exploitation rates are comprehensive, represented by a large global R value and clearly defined groupings when samples are plotted in a multidimensional space (Fig. 2.13).

Of the twelve invertebrate groups common to both sampling techniques, only three appeared to have similar rates of availability and utilisation. These were Blattodea, Chilopoda/Diplopoda and Lepidoptera. All other groups were either available in higher proportions to rates of exploitation, or were exploited at proportions much higher than their availability (Fig. 2.14).

There is evidence to suggest a difference in within-group dispersion between samples of invertebrate availability and exploitation (PERMDISP: F=3.283, P=0.086). This suggests that the level of within-group dispersion between factors is not homogenous, an assumption which should be met for both ANOSIM and PERMANOVA routines.

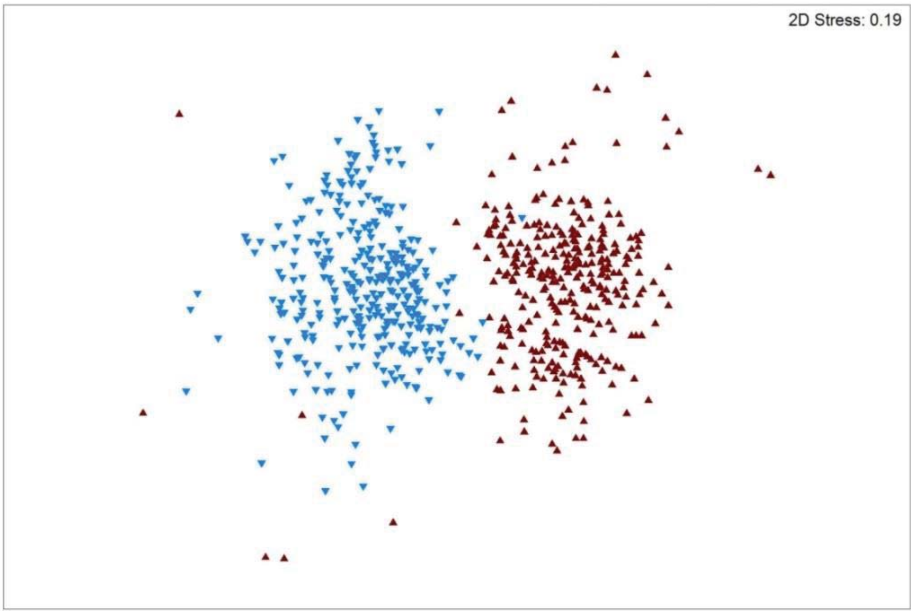


Figure 2.13 - Non-metric MDS ordination; Comparison of invertebrate availability (▼) and invertebrate exploitation by brown kiwi (▲) over a 12 month period on Ponui Island. Only invertebrate groups common to both were included. Data was pre-treated using a Square Root transformation, and Bray Curtis similarity matrix created. Axes lack labels as an MDS only shows information on the relative similarities between points, hence scale is arbitrary.

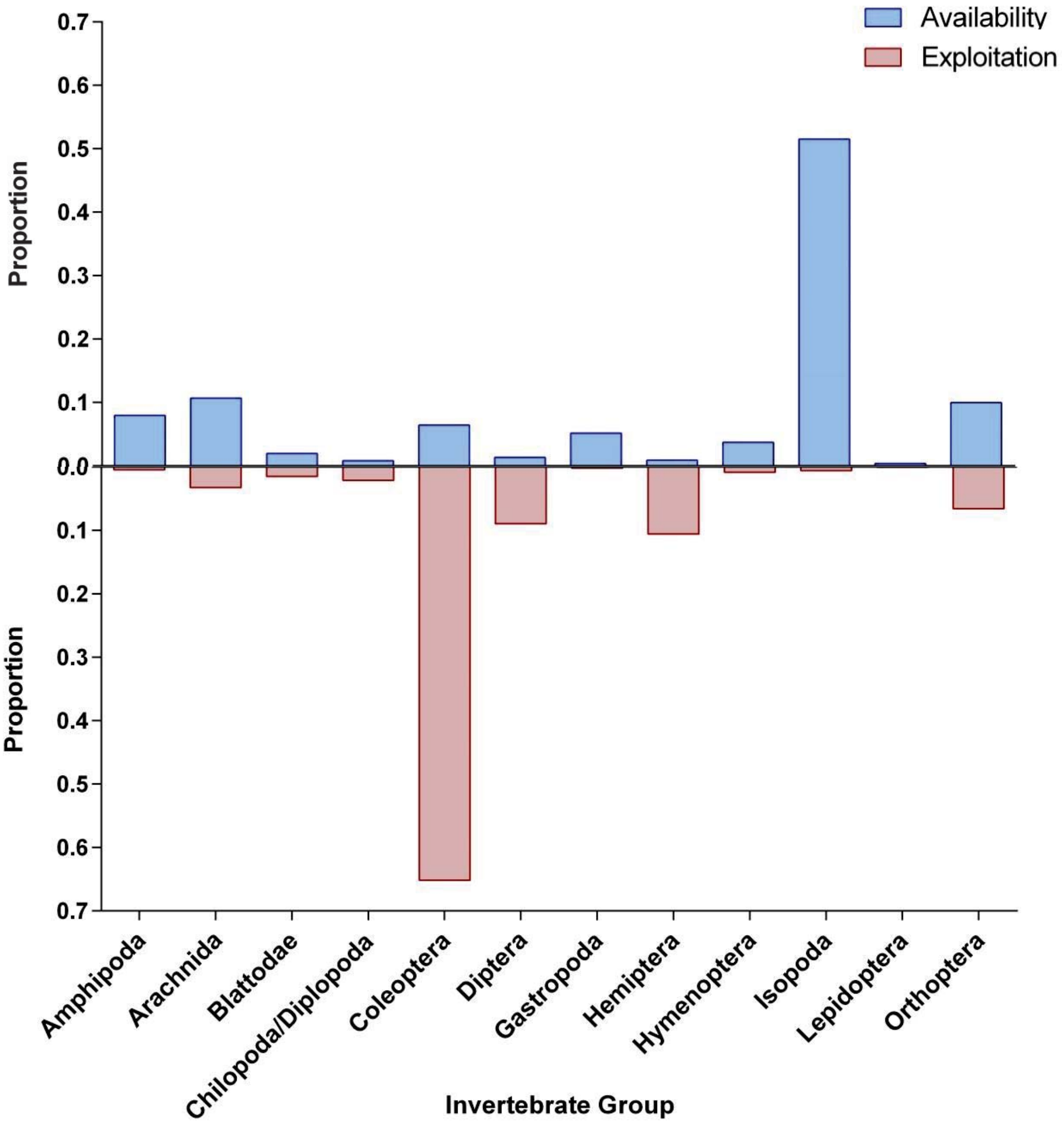


Figure 2.14 – Proportion of all invertebrates common to both availability and exploitation datasets identified in Pitfall traps and brown kiwi faecal samples on Ponui Island over the course of four seasons, ordered alphabetically.

2.4 Discussion

2.4.1 Invertebrate Availability

Out of the 16 invertebrate groups identified on Ponui Island, Isopoda, Orthoptera, Arachnida, Amphipoda and Coleoptera were found to have the greatest effect on spatial and temporal differences in invertebrate availability. Other invertebrate groups traditionally thought to be important to the diet of brown kiwi were rarely detected in pitfall traps within the study site, including Hemiptera and Oligochaeta.

Four of the five most prominent invertebrate groups in this study were also dominant in previous studies of invertebrate availability on Ponui Island utilising comparable methodology (Shapiro, 2005; Morgan & Castro, 2014; Wilson, 2014). In fact, the makeup of the 11 most prominent invertebrate groups in my research were also the most common in Wilson (2014), and in much the same order of abundance. Coleoptera were the only group to show significantly increased availability compared with previous studies on Ponui Island. Pitfall trap studies elsewhere in New Zealand have also found an almost identical composition of invertebrate groups (Reid, Ordish, & Harrison, 1982; Miles, 1995). Therefore, any conclusions made on invertebrate availability and how this may impact brown kiwi foraging behaviour are likely to be applicable to other areas of New Zealand, and other populations of brown kiwi.

Seasonal variation

The number and dry weight of invertebrates caught in pitfall traps on Ponui Island differed significantly between seasons. Invertebrate availability was at its peak in summer and lowest in winter, while seasons occurring in succession were more similar to one another. This is unsurprising, as changes in environmental conditions on Ponui Island such as rainfall, temperature and soil penetrability are most evident in winter and summer (Wilson, 2014). The composition of available invertebrates also varied between seasons, with different groups peaking in availability in different seasons. Seasonal variation in resource abundance is a feature recorded in many other avian studies and presents a problem for a multitude of avian species to overcome (Moeed & Meads, 1985; Poulin, Lefebvre, & McNeil, 1992; Atkinson & Merton, 2006; Romanowski & Mihorski, 2008; Castillo-Guerrero et al., 2009; Mulwa et al., 2014; Lindsay, Allen, & Major, 2015). However, Mulwa et al. (2014) suggests that insectivorous birds appear to be the most susceptible to seasonal fluctuations in food availability.

Invertebrate lifecycles play a large role in the temporal availability of certain invertebrates (Colbourne & Powlesland, 1988). Many of the trapped Coleopteran and Dipteran species spend winter and spring as larvae in the soil column before moving closer to the surface and emerging in early summer as adults '*en masse'* (Moeed & Meads, 1985; Walker, 2000). This corresponds to a peak in occurrence in pitfall traps for many important invertebrate groups over summer and autumn. This time also coincides with the breeding season of most Coleopteran and Orthopteran species, which prefer to reproduce during warmer months (Moeed & Meads, 1985). In this way, important invertebrates may swing into or out of reach of availability over the course of a year (Wolda, 1990). The large proportion of Orthoptera caught in warmer seasons is largely due to the explosion of black field crickets (*Formicidae*) in pasture habitat over this time, signifying their potential importance to brown kiwi diet. The peak in Arachnids over autumn may also be explained by their lifecycle and behaviour, whereby activity increases over warmer months (Crowe, 2007), increasing the likelihood of them encountering a pitfall trap. Additionally, warmer temperatures over these seasons can also lead to the development of cracks and crevices in the hard soil, particularly within pasture, providing extra habitat for a range of surface dwelling invertebrates (Colbourne, Baird, & Jolly, 1990).

Other groups peaked in availability during the spring and/or winter. Increased rainfall during winter and spring may have forced Oligochaeta species to the soil surface, raising the likelihood of being caught in pitfall traps. The reduced proportion of many soil dwelling species in pitfalls over summer and autumn is probably due to a decrease in soil moisture close to the surface, forcing them to retreat to lower, moister levels (Kleinpaste & Colbourne, 1983). While pitfall traps are unable to accurately measure soil-dwelling invertebrates (Prasifka et al., 2007), previous studies taking soil core samples have suggested that this group are available in large numbers within the upper soil column during the winter and spring (Kleinpaste & Colbourne, 1983; Shapiro, 2005). Amphipods prefer damper conditions under forest hummus and leaf litter (McColl, 1981), and thus may have increased in availability during spring due to increased rainfall.

Habitat variation

Invertebrate availability on Ponui Island varied spatially, with both the number and dry weight of invertebrates caught in pitfall traps varying strongly between four different habitats, reflected in a relatively high global R score. Pasture consistently contained the highest invertebrate content, displaying different invertebrate availability to forest and scrub. Forest and scrub were shown to have similar invertebrate availability, a result shared by Shapiro (2005), while swamp was considered similar to all other habitat types.

Differences in invertebrate availability between habitat types are best explained by biology of the prey. The eruption of cricket (*Formicidae*) numbers in pasture over the summer is the most obvious driver of this dramatic increase in dry weight content. However, pasture provides ideal habitat for invertebrates such as Isopoda and Orthoptera year round, particularly in crevices or the walls of sheer banks (Miles, Potter, & Fordham, 1997). This is reflected in the presence of these invertebrate groups in pasture throughout the year. Likewise pasture provides habitat for a range of exotic Oligochaeta species that feed on grass debris, which although underestimated in the pitfall traps are likely to be available in high numbers within the soil column in pasture habitat (Shapiro, 2005). Forest habitat on the other hand contained the highest numbers of Coleoptera and Arachnida, possibly due to the presence of more preferable sheltered habitat or else a higher availability of prey species (Spence & Niemela, 1994). Amphipods were also most prevalent in forest and swamp habitats, where moisture content is highest.

Invertebrates in pasture and swamp habitats may have been underrepresented. Fewer pitfall sites were installed within these habitats compared to forest and scrub. As a result several important invertebrate taxa may have been underestimated due to their clumped distribution. Additionally, pasture and swamp habitats were more likely to be flooded and washed out each month. For these reasons, weight per pitfall is perhaps the more accurate indicator of habitat importance when comparing invertebrate availability between habitats in this study.

Gully variation

Despite their close proximity and similar topography, invertebrate availability differed between the three gullies of my study site. Availability was lowest in Pipe and highest in Red

Stony, while rates remained very similar between Kauri and Red Stony. This difference is probably a reflection of the location of each gully, with Red Stony and Kauri receiving more sunlight hours each day compared to Pipe due to their north facing aspect. Increased sunlight will result in higher average temperatures, a quality which has been linked with increased invertebrate availability in the past (Wilson, 2014). This also impacts soil quality, increasing the soil moisture content of Pipe gully. Research has suggested that higher soil moisture levels will reduce the overall invertebrate diversity and biomass of an area (Richardson et al., 2010). Variation between locations suggests that when managing brown kiwi in large areas, a variety of gullies facing different aspects with different composition of habitat might prove beneficial.

Sampling Bias

Despite being one of the most commonly used methods to survey invertebrate populations, pitfall trap sampling has many biases that impact the sampling of invertebrates (Spence & Niemela, 1994). The most obvious of these is that some invertebrate groups are more likely to be caught than others (Cooper & Whitmore, 1990). Most ground dwelling invertebrates can be adequately sampled using this methodology (Prasifka et al., 2007), however soil dwelling invertebrates such as Oligochaeta or Coleoptera larvae (Schirmel, Buchholz, & Fartmann, 2010) and flying invertebrates such as Diptera and Hemiptera (Standen, 2000) will often be underestimated. This makes it difficult to know if actual food availability has been measured (Hutto, 1990). Shapiro (2005) found that Oligochaeta species and soil dwelling larvae were available in higher numbers than my study suggested, in part because he used both pitfall and soil core sampling methods. As a result of this, the availability of soil dwelling invertebrates such as Oligochaeta and Hemipteran or Coleopteran larvae was most likely underestimated in my study. We must therefore assume that soil dwelling invertebrates are likely to be available at higher numbers than indicated by the results, particularly during the wetter winter and spring months. This would lead to a reduction in the overall variation in availability between seasons but further emphasis on differences in composition. It is worth noting that variation in availability could also be partially attributed to the random selection of pitfall sites throughout the study site.

2.4.2 Invertebrate Exploitation

Of the sixteen different invertebrate groups identified within brown kiwi faecal samples on Ponui Island, five were shown to have the largest effect on spatial and temporal differences in invertebrate exploitation. These groups were Oligochaeta, Coleoptera, Diptera, Hemiptera and Orthoptera. Most other invertebrate groups were identified very infrequently within faecal samples.

The invertebrates exploited by brown kiwi in this study are similar to those recorded in previous studies. Coleoptera and Hemiptera have previously been shown to be an important part of brown kiwi diet, contributing a large amount both numerically and in terms of dry weight (Bull, 1959; Reid, Ordish, & Harrison, 1982; Kleinpaste & Colbourne, 1983; Colbourne & Kleinpaste, 1990; Miles, 1995; Shapiro, 2005). Orthoptera, Diptera and Arachnida have also been frequently documented within faecal samples of brown kiwi in the past (Kleinpaste & Colbourne, 1983; Miles, 1995; Shapiro, 2005). Similarities between the invertebrates exploited in my study and previous studies suggests that brown kiwi select for certain invertebrates, including them in their diet at similar rates despite varying levels of invertebrate availability. This in turn suggests that despite the early conclusions of Reid, Ordish, and Harrison (1982), a ‘typical’ diet for brown kiwi may exist. Insectivorous birds around the world exploit many different types of invertebrates, though several other studies have recorded a preference for larger prey items including Hemiptera, Coleoptera and Arachnida (Durst et al., 2003; Lindsay, Allen, & Major, 2015).

Interestingly Oligochaeta, long considered the staple food of kiwi (Sales, 2005), were present in only 13% of all samples in my study. This represents an exploitation rate much lower than previous studies which recorded rates as high as 94% in brown kiwi gizzards (Reid, Ordish, & Harrison, 1982). It is likely that invertebrate groups like Oligochaeta were underrepresented due to bias in the chosen sampling method. Biases relating to differential digestibility of invertebrates are more substantial in faecal samples than in stomach or crop samples (Rosenberg & Cooper, 1990). As a result, invertebrates with hard bodied chitinous remains such as Coleoptera or Orthoptera are more likely to persist through digestion to be present in faecal samples than their soft bodied counterparts. Additionally, the presence of earthworm chaetae in a sample is considered an unreliable means for determining the number of earthworms eaten (Wroot, 1985). Despite this, Oligochaeta occurred commonly in faecal samples in Kleinpaste & Colbourne (1982), suggesting either brown kiwi on Ponui

Island consume fewer earthworms, or that some of the microscopic chaetae may have been overlooked when analysing the faecal samples. It is possible that soft bodied invertebrates such as Oligochaeta are exploited more than was suggested.

Acari (specifically ticks) were recorded in brown kiwi faecal samples at moderate numbers. These were identified as kiwi ticks (*Ixodes anatis*), a parasite specific to their host for which there is a paucity of information regarding their biology (Swift, Heath, & Jamieson, 2015). This is the first time they have been documented in brown kiwi diet and suggests that birds may be consuming them as they preen themselves or their conspecifics. This behaviour might be isolated to Ponui Island and requires further investigation to determine if these nutrient rich, blood filled invertebrates are important to brown kiwi nutrition or are instead consumed inadvertently.

Seasonal variation

Brown kiwi on Ponui Island exhibited variation between seasons in the type and rate at which they exploited invertebrates. Exploitation was most similar between winter and spring versus summer and autumn, while the largest differences were seen between winter vs summer, and spring vs autumn. However, any difference between seasons overall was considered small. Therefore, it can be assumed brown kiwi on Ponui Island exploit invertebrates in a similar way over the year, with only a few key exceptions.

Seasonal variation may be related to changing environmental conditions impacting what food can be exploited by brown kiwi. In a recent study on Ponui Island, increases or decreases in average temperature and rainfall were linked to changes in soil penetrability (Wilson, 2014). When rainfall increases over winter and spring, the soil becomes easier for the birds to penetrate, while during the drier seasons of summer and autumn penetrability can reduce to the extent that birds will not even attempt to probe (Cunningham, 2006). Research on sandpipers (*Calidris spp.*) has revealed a similar pattern whereby birds will switch from hunting by probing to hunting by sight for prey on the surface when the substrate becomes more difficult to probe (Gerritson & Vanheezik, 1985).

Birds will respond to seasonal fluctuations in the availability of food resources, impacting strongly the type of prey and rate at which it is consumed (Mulwa et al., 2014). Both Orthoptera and Arachnida were most abundant in the faecal samples during summer and autumn, which are also the seasons in which they peaked in availability within the study site. Hemiptera larvae were commonly exploited over winter, spring and summer, with numbers found within faecal samples peaking in spring. This could be related to both increased soil penetrability and their lifecycle; in which nymphs will move closer to the surface in spring before emerging as adults (Colbourne & Kleinpaste, 1990). Coleoptera were exploited consistently over the year, though show stronger seasonal trends when explored to a family level. The numbers of Scarabaeidae consumed by brown kiwi peaked over spring and summer while Carabidae numbers increase in autumn and Elateridae during summer. Seasonal trends were also apparent between Coleoptera adults and larvae, with soil dwelling larvae consumed more frequently during the wetter months and surface dwelling adults over the summer. These patterns reflect the different lifecycles of each taxa, resulting in increased availability at certain times of the year (Colbourne & Powlesland, 1988). The distribution of peaks in exploitation for Coleopteran families over the year helps to explain why Coleoptera were exploited so frequently throughout the study.

Habitat variation

Habitat was not found to have an impact upon invertebrate exploitation rates of brown kiwi on Ponui Island, despite significant differences in invertebrate availability recorded between habitat types in my study site. The exploitation of different food resources across different habitats has been documented in many New Zealand endemic birds, including the kakapo (Atkinson & Merton, 2006), takahe (Baber & Craig, 2003) and brown kiwi (Kleinpaste & Colbourne, 1983). This result is almost certainly a reflection of bias in the sampling method rather than actual exploitation patterns. Faecal samples were collected in each habitat to avoid biasing collection, and were never expected to represent actual exploitation in each habitat. Although the habitat in which each faecal sample was collected was recorded, without direct observation up until the moment of excretion it is impossible to know where invertebrates were actually consumed. Brown kiwi in my study travelled large distances and were often found in multiple habitat types each night (See Chapter 3). Therefore faecal samples will almost certainly contain invertebrates from multiple habitat types. Even if an individual was known to be present in one habitat for an extended period of time before excreting, it remains unknown how long each invertebrate will persist in the digestive tract (Hutto, 1990). Soft-bodied invertebrates that were eaten in one habitat type may be rapidly digested, whereas harder bodied invertebrates which were eaten elsewhere hours earlier may persist. In high intake the interval between ingestion and defecation was found to be 70-85 minutes (Reid, Ordish, & Harrison, 1982), suggesting that faecal samples may in fact only represent prey taken in the period immediately prior to excretion.

Further exploration of variation between habitats in a more controlled environment may yield significantly different results. To reduce sampling bias future studies could make use of captive birds, or examine a population located only within a contiguous piece of native forest. Despite the results of my study, it should be assumed that habitat may indeed have a role to play in brown kiwi diet.

Faecal sample variation

Variation in both the size and consistency of faecal samples on Ponui Island were shown to have no effect on the invertebrates found within. This was consistent across all pairwise comparisons. This result is interesting, as it suggests that no matter the size, state or age of a faecal sample, it will yield similar results. This contradicts my initial hypothesis (2.3) that poor quality faecal samples will result in less detailed information. It is interesting that a larger sample appears to yield the same results as a smaller one. This result could aid future brown kiwi dietary studies that use faecal samples, as researchers could feasibly collect more samples without worrying about their condition. The low variation between faecal samples of different qualities may be better explained by bias present in the identification methodology, including differential digestibility and observer error.

Sampling Bias

It is recommended that caution is taken during analysis of faecal samples to ensure the many potential sources of bias are considered (Dickman & Huang, 1988). Samples may be biased due to the differing digestibility of invertebrates (Hutto, 1990), whereby hard bodied invertebrates are likely to persist for longer in the digestive tract than their soft bodied counterparts (Reid, Ordish, & Harrison, 1982). The highly digested and fragmented state of faecal samples means that biases related to differential digestibility and temporal rates of passage may be more substantial than in stomach or crop samples (Rosenberg & Cooper, 1990). Therefore, it is likely that while some of the more chitonous invertebrates such as Coleoptera, Orthoptera and Hemiptera were accurately sampled; other soft bodied invertebrates might have been underrepresented within the samples. Smaller, less recognisable, or more digested invertebrate body parts present in the samples may have also been missed by the researcher or left unidentified, increasing bias toward certain invertebrates. Despite the potential for significant bias in faecal sampling, this remains the best method to examine the diet of brown kiwi. Samples can be easily collected year-round without the need to observe or disturb the bird (Rosenberg & Cooper, 1990; MacLeod & Kerly, 1996), making this method the most feasible option when working with the cryptic and endangered brown kiwi, where direct observations or and stomach samples are not possible (MacLeod & Kerly, 1996).

The foraging behaviour of each individual bird can impact the foods it chooses to exploit (Woo et al., 2008). For example both generalist and specialist individuals were found in a recent study of Black-Tailed Godwits (Catry et al., 2014). As samples were collected opportunistically, we are unable to measure this potential effect. However, due to the large number of samples it is likely that any individual bias was reduced.

2.4.3 Foraging Patterns: Exploitation vs Availability

There was low similarity between the proportions of different invertebrate groups detected in pitfall traps and those identified in brown kiwi faecal samples (Fig. 2.14). It is worth noting that the documented non-homogenous within-group dispersion will have reduced the accuracy of these statistics. This result suggests that either brown kiwi on Ponui Island do not exploit invertebrate resources based on their availability, or else sampling biases inherent to both data collection methods have caused an artificial separation between exploitation and availability. It is likely that a combination of both of these factors has influenced the diet and foraging behaviour of brown kiwi in this study. Therefore, a comparison of trends to assess patterns in foraging might prove more valuable than comparing datasets directly.

Prey selection

Similar to the conclusions of several previous dietary studies (Colbourne & Kleinpaste, 1984; Miles, 1995; Shapiro, 2005), brown kiwi on Ponui Island appeared to be selectively opportunistic in their utilisation of invertebrate prey. This type of prey selection is common among insectivorous birds in order to meet dietary requirements (Razeng & Watson, 2015).

Many invertebrate groups occurred in the diet of brown kiwi at a similar proportion to their availability throughout the year. This included Orthoptera, Blattodea and also Arachnida and Diptera when biases in sampling methods are considered. Some invertebrate groups including Isopoda, Amphipoda and Hymenoptera were consumed by brown kiwi less than their availability would suggest. This is likely a reflection of their quick, erratic movements and small size, making them difficult to locate and capture (Colbourne & Powlesland, 1988). Others, such as Coleoptera and Hemiptera larvae were exploited in numbers far exceeding their availability, suggesting they may be actively sought out by brown kiwi. Both of these groups still appear to be favoured even when soil dwelling invertebrates are artificially increased in availability to account for pitfall trap sampling biases. Lindsay, Allen, and Major (2015) found a similar preference for large adult and larval invertebrates in diet of the white-fronted chat, while other studies have also observed the presence of preferred prey items in avian subjects (e.g. O’Donnell & Dilks, 1994). These findings indicate that overall food abundance is unlikely to be the main determinant of foraging site selection, with more importance placed on access to favoured invertebrate prey.

While my study was unable to accurately sample the availability or exploitation rate of Oligochaeta due to biases in the methodology, it is likely that this group is also particularly important to the diet of brown kiwi. Previous authors have documented much higher rates of exploitation for this group, even when availability is reduced over the warmer seasons (Reid, Ordish, & Harrison, 1982; Kleinpaste & Colbourne, 1983; Shapiro, 2005). This suggests that Oligochaeta may be another group which is actively sought out by brown kiwi.

Seasonal prey switch

Brown kiwi on Ponui Island exploited different resources throughout the year, confirming the thoughts of many authors (Kleinpaste & Colbourne, 1983; Miles, Potter, & Fordham, 1997; Shapiro, 2005) that seasonal variations dictate major components of brown kiwi diet. Seasonal changes in diet have been recently reported in a number of different avian species, including the takahe (Baber & Craig, 2003), kakapo (Atkinson & Merton, 2006), long-eared owl (Romanowski & Mihorski, 2008), marbled godwit (Castillo-Guerrero et al., 2009), white-fronted chat (Lindsay, Allen, & Major, 2015) and a number of omnivorous New Zealand birds (O'Donnell & Dilks, 1994).

The foraging strategies of brown kiwi on Ponui Island differed between seasons based on the food resources which were most readily available. During the wetter winter and spring months invertebrates which were available in the soil column were exploited more frequently. Coleopteran and Hemipteran larvae in particular as well as Oligochaeta made up a large portion of the diet during this time. Forest and swamp habitats provided more of these particular invertebrate groups and are particularly important over these seasons. However, in drier summer and autumn months brown kiwi switched their foraging strategy, placing a heavier reliance on surface invertebrates which were more readily available and accessible at that time, including Coleoptera adults, Arachnids and Orthopterans. Over these seasons pasture habitat was the most important for brown kiwi diet. These findings are similar to Lindsay, Allen, and Major (2015) in suggesting that both the abundance of preferred food, as well as varied foraging habitats are important to avian diet.

This pattern may reflect a seasonal change in the priorities of brown kiwi, with summer and autumn important for building up weight and condition for breeding. Seasonal change in foraging strategy is common among other avian species, with diet often switching as priorities change from survival to breeding or migration (Poulin, Lefebvre, & McNeil, 1992; Castillo-Guerrero et al., 2009; Michalski et al., 2011). For example, takahe family groups will use seasonally available seed heads with the specific aim of supporting growth in their young (Baber & Craig, 2003). These changes are often accompanied by a switch in foraging strategy. Many seabirds will switch either their foraging habitat or method of foraging as environmental or substrate conditions change (Gerritson & Vanheezik, 1985; Castillo-Guerrero et al., 2009). It is likely that brown kiwi are maximising their net energy intake similarly by adapting their foraging strategies to current substrate conditions (Cunningham, 2006), in addition to responding to changing invertebrate availability.

The increased exploitation of surface invertebrates in pasture during warmer seasons, including Scarabaeidae (grass grub) adults and field crickets, suggests that pasture may be of particular importance to the diet of brown kiwi over this time. Many introduced or exotic invertebrates appear to prefer this habitat, whereas shady forest habitats are colonised by these species to a much smaller degree (Brockerhoff et al., 2010). This supports the findings of Watt (1971) that brown kiwi are successfully adapting to the novel environments and species introduced by humans. This recognises the fact that both the invertebrate fauna and the suite of insectivorous animals have changed dramatically since human colonisation, likely impacting the relative food availability for brown kiwi in various habitats (Gibbs, 2010).

Foraging strategy

Brown kiwi on Ponui Island were generalist foragers, exploiting different types of invertebrates from a range of different habitat types. This trait is one which they share with a number of extant New Zealand birds (O'Donnell & Dilks, 1994). Brown kiwi exhibited considerable flexibility in their choice of prey, switching foraging strategies to target specific invertebrates when they became available at different times of the year. A generalist or flexible feeding ecology is thought to be best suited where multiple habitats containing appropriate food sources are available to a species (Sinclair, Fryxell, & Caughley, 2006). Optimal foraging theory proposes that an animal will select the foraging strategy that maximizes its net intake of energy per whilst minimizing other costs like thermoregulation or predation risk (Stephens & Krebs, 1986). The flexible and broad diet documented in my study may reflect the need for brown kiwi to maximise energy intake in a changing landscape. These specific foraging strategies have perhaps developed over the brown kiwis' long evolution specifically to cope with the changing availability of resources during periods of natural climate and habitat change. Alternatively, such flexible foraging behaviour may be a reflection of the highly competitive niche they evolved in, which historically contained a large suite of other nocturnal insectivorous bird species and lizard fauna foraging on the forest floor (Atkinson & Millener, 1991; Gibbs, 2010). The foraging behaviours documented in this thesis will continue to prove beneficial to the survival of brown kiwi in New Zealand, whose diet now overlaps considerably with introduced mammals such as the Hedgehog (*Erinaceus europaeus*) (Colbourne & Kleinpaste, 1990), Weasel (*Mustela nivalis vulgaris*) (Strang, 2013) and Ship Rat (*Rattus rattus*) (Shapiro, 2005).

Nutrition

The importance of nutrition to the diet and foraging behaviour of birds has gained a groundswell of interest in recent years and is now seen as vital to the long term sustainability of avian populations (Razeng & Watson, 2015). Nutrient composition of food sources is vitally important for the health and welfare of the animal, including the concentration of important minerals (Fidgett & Gardner, 2014). Recent research has shown that insectivores in Southern Australia favour invertebrate groups in their diet which contain higher fractions of crude protein and total fat content, as well as those with greater concentrations of seven different micronutrients (Razeng & Watson, 2015). These results indicate that the nutritional quality plays an important role in prey selection in insectivores (Razeng & Watson, 2015).

Historically nutritional information of the domestic fowl was extrapolated and applied to ratites (Sales, 2006a). However, most subsequent work has focused on the ostrich, largely because this species has commercial value and is commonly farmed (Labaque et al., 2013). Only in recent years have authors such as Potter et al. (2010) and Minson (2013) explored the importance of nutrition to brown kiwi diet, improving our knowledge in this area. Potter et al. (2010) have provided a complete description of the nutritional content of those invertebrates considered most important to the diet of brown kiwi (see Chapter 1, Table 1.3)

By comparing my results with this research, it is clear that those invertebrates selected for by brown kiwi in my study (Coleoptera, Hemiptera, Oligochaeta) contained the highest levels of protein and fat. A similar trend was seen for those surface invertebrates which were favoured over summer and autumn (Orthoptera, Coleopteran adults). Therefore patterns in both prey selection and foraging strategies might be explained by the nutrient content of their prey. This adds weight to the suggestions of Minson (2013) that brown kiwi utilise protein as their major source of energy and those of Potter et al. (2010) that brown kiwi appear to favour high protein invertebrates, confirming my hypothesis (3.3) that nutrition plays an important role in the diet of Ponui Island brown kiwi. The importance of protein and fat in the diet of brown kiwi might be related to the energetic needs required to produce a rich egg and highly precocial young of this species.

Further research is required to understand more about the link between energy, nutrition and diet in brown kiwi. A good starting point may be to determine just how effectively this species can utilise chitin (Minson, 2013), a significant component of protein (Finke, 2007).

2.5 Summary

Objective 1: Document invertebrate availability on Ponui Island.

Invertebrate availability on Ponui Island was similar to previous studies of brown kiwi in this and in other locations, suggesting validity and applicability to the North Island as a whole. Availability changed significantly throughout the year, varying between habitat types and gully locations. Differences were greatest between winter and summer, with summer sharing similar trends to autumn and winter to spring. Changes appeared to be driven by a combination of invertebrate lifecycle and environmental conditions. Bias inherent in the methodology meant several important invertebrate taxa may have been underestimated.

Objective 2: Assess the diversity of invertebrate food exploited by brown kiwi on Ponui Island.

Invertebrates exploited by brown kiwi on Ponui Island were almost identical to those documented in previous studies, with several groups exploited above their availability and others exploited in line with or below levels of availability. The invertebrates exploited varied between seasons in terms of both frequency of occurrence and composition, following similar trends to availability, however remained similar between habitats. Quality of faecal samples had no effect on the results generated. Changes are likely driven by varying invertebrate availability and changes in dietary requirements. Soft-bodied taxa including Oligochaeta (earthworms) were underrepresented due to bias in the methodology.

Objective 3: Compare the availability and exploitation of invertebrate food on Ponui Island to assess brown kiwi prey selection and foraging strategies.

This study supports the hypotheses that brown kiwi are selectively opportunistic in their choice of prey, and that they change their foraging strategies seasonally based on the availability of certain invertebrates. The similarities between these results and previous studies at other locations indicate that a typical diet likely does exist for brown kiwi. Nutrition was identified as a potential driver of invertebrate selection for brown kiwi, and the value of pasture to brown kiwi diet was revealed.

CHAPTER THREE

Nocturnal Habitat Utilisation by Brown Kiwi

Plate 3.1 - An unidentified brown kiwi on Ponui Island foraging at night on the Red Stony track. Photo by Kathryn Strang, Massey University.

3.1 Introduction

Habitat selection refers to the behavioural response of an animal to favour certain habitats that aid in fitness or survival (Block & Brennan, 1993; Dechant et al., 2002). Different habitat types can provide different benefits to avian species, including protection from predation, provision of shelter, nest sites and food, and levels of both inter and intra specific interaction (Jones, 2001). Currie et al. (2005) found that of 51 avian species studied in the Bahamas, almost all occurred across a range of habitats. Habitat utilisation (or use) is often used to assess habitat preference, and compares the frequency at which an animal uses a particular habitat with its availability. This identifies areas that might be important to the animal in its fundamental (realised) niche. This knowledge can aid wildlife conservation by identifying more effective strategies for future management of the species (White & Garrott, 1990; Holzapfel et al., 2008). For example, understanding habitat selection can aid in identifying favourable sites for translocation or management based on the composition of available habitat (Morrison et al., 2007).

Detailed investigation into habitat selection can often prove challenging (MacFaden & Capen, 2002). This is because the spatial patterns of animals within an environment are influenced by a multitude of driving factors, encompassing aspects of biology and behaviour (Schoener, 1971), as well as the characteristics of its habitat (Adams et al., 2013). Habitat selection also varies between various ecological guilds, with each interacting with their environment differently (Rice, Ohmart, & Anderson, 1983). Often forming complex relationships, these driving factors change over time and space and can be difficult for researchers to unravel (Rosenzweig, 1991). This is particularly so in species where monitoring is difficult. Any investigations into habitat utilisation must therefore consider a wide range of ecological factors, including demographic factors such as density (Manly et al., 2002), sex and age ratio (Harris et al., 1990); environmental factors such as habitat structure (MacFaden & Capen, 2002), climate (Stevens, Bayne, & Wellicome, 2011), seasonality (Rice, Ohmart, & Anderson, 1983), resource availability (Rosenzweig, 1991) and levels of competition or predation (Hughes, Ward, & Perrin, 1994); as well as behavioural factors such as territoriality, individuality and reproductive or foraging strategies (Robinson & Holmes, 1982; Bjørneraas et al., 2012; Adams et al., 2013).

A further challenge faced by researchers is the question of scale. Any inferences about the factors that influence ecological process are conditional on the spatial scale under investigation (Kristan, 2006), with responses varying between microhabitat and macrohabitat utilisation (Frye et al., 2013). Avian models in particular often emphasize the importance of vegetation structure and composition as variables for habitat selection, overlooking factors impacting on a larger scale, such as climate and land cover (Stevens, Bayne, & Wellicome, 2011).

Despite the many benefits of spatial studies and vast number of studies looking at avian habitat selection, surprisingly little research has been undertaken in this field looking at New Zealand’s most iconic species, the kiwi (*Apteryx* spp.). Indeed, much remains unknown about the unusual behaviour and ecology of this nocturnal, flightless bird. With numbers of the most commonly occurring species, the brown kiwi (*Apteryx mantelli*), continuing to decline, the importance of learning more about their spatial systems to improve our management has been highlighted.

Habitat utilisation of brown kiwi during their nocturnal activity phase has been explored specifically only four times in the past (see chapter 1, table 1.1). These studies each had a narrow focus, investigating habitat utilisation in juveniles (Chan, 1999; Gibbs, 2000), within a low-density population (Taborsky & Taborsky, 1995), and in a particularly fragmented landscape (Potter, 1989). Differences in tracking methodologies, location, population density, time of year, length of study and a host of other site specific attributes between these previous studies makes comparison difficult. Despite these limitations, these studies have increased our understanding of how brown kiwi interact with their spatial environment.

All four studies concur that brown kiwi do not utilise habitat in proportion to its availability. Adults use forest and scrub habitat more than expected, while pasture is used only sparingly compared to its availability (Potter, 1989; Taborsky & Taborsky, 1995). Forest and scrub edge habitats are considered particularly important, perhaps due to a greater availability of food resources (Ismail, 1993; Cunningham & Castro, 2011). Introduced pine forest habitat is avoided when other more suitable habitat is available (Taborsky & Taborsky, 1995). Habitat utilisation of juveniles appears to differ from adults despite considerable home range overlap, with scrub and pasture habitat utilised more often (Chan, 1999; Gibbs, 2000).

Utilisation is also thought to vary between seasons, (Potter, 1989; Gibbs, 2000; Cunningham & Castro, 2011) and locations (Potter, 1989; Ziesemann, 2011).

Little is known concerning what is driving the habitat utilisation patterns seen in brown kiwi. As they spend the majority (75%) of their time foraging when active at night (Cunningham & Castro, 2011), food is expected to be a major driver. Sociality may also play some role in habitat use, although direct social interactions while active at night have been observed only rarely (Taborsky & Taborsky, 1992; Cunningham & Castro, 2011). The availability of breeding partners and level of interaction with conspecifics have both been suggested as potential social drivers of habitat selection (Taborsky & Taborsky, 1995). The individual nature of each bird, which often differ in temperament and behaviour (Potter, 1989; Chan, 1999; Gibbs, 2000), is another aspect to consider. Other factors including seasonality, density, age, and sex ratio of the population, as well as climate and weather might also affect spatial behaviour.

This chapter will comprehensively explore the habitat utilisation of brown kiwi while they are active at night, improving upon previous observations which were limited in scale and focus. How this behaviour varies both spatially and temporally will be explicitly explored for the first time, as well as differences between birds in different demographic or behavioural groups. With a larger sample size, time scale and a more holistic approach than attempted before, this study will build a clearer picture of the nocturnal spatial behaviours of brown kiwi. Additionally, this study aims to establish the impact of food availability, social/reproductive cues, population demographics, environmental variables and individuality on nocturnal habitat utilisation, while establishing which combination of these driving factors can best explain the spatial patterns seen in brown kiwi. This will fill a large hole in our understanding of brown kiwi ecology, and may prove vital to the future survival of the species, leading to an improved ability to manage populations in the wild. The objectives for this chapter are outlined below, and hypotheses suggested based upon the knowledge gathered in previous studies.

Objective 1: Document habitat availability within my study site on Ponui Island.

- *Hypothesis 1.1) Forest, scrub, pasture and swamp habitat cover varying proportions of the study site.*
- *Hypothesis 1.2) Each of the three gullies within the study site possess different proportions of these four habitat types.*

Objective 2: Assess habitat utilisation rates of brown kiwi on Ponui Island at night, including how this may vary with a range of spatial, temporal, demographic and behavioural factors.

- *Hypothesis 2.1) Brown kiwi do not utilise the habitats available to them at rates predicted by availability, instead utilising forest more than other habitats.*
- *Hypothesis 2.2) Habitat utilisation of brown kiwi varies between seasons, time of night, and gullies.*
- *Hypothesis 2.3) Habitat utilisation of brown kiwi varies between birds of different sex, age, social grouping and breeding status.*

Objective 3: Explore potential driving factors and identify those which best explain the observed patterns of brown kiwi habitat utilisation at night.

- *Hypothesis 3.1) Multiple factors contribute to where brown kiwi are found at night with each explaining some of the variation seen within factors.*
- *Hypothesis 3.2) The habitat that brown kiwi are found at night is driven largely by their foraging and breeding behaviours.*

3.2 Methods

General information regarding the study site and species is given in Chapter 1. Locations of brown kiwi during their nocturnal activity phase were observed over a nine month period on Ponui Island from June 2013 to February 2014. Sampling periods were split into three seasons as follows; winter (June - August), spring (September - November) and summer (December - February). A short trial study was run over autumn to test and refine the triangulation methodology. However, these results were excluded from the analyses. Environmental and demographic information related to the study site and population was collected throughout the year. Invertebrate availability data from Chapter 2 were also used to further expand the statistical model developed in this chapter.

3.2.1 Sample Population

In March 2013, as part of the Ponui Kiwi Research Programme, 49 adult brown kiwi were fitted with radio transmitters (WildTech Ltd., Havelock North, NZ) following the protocols described in the Kiwi Best Practise Manual (Robertson et al., 2003). Each radio weighed 21g on average (~1% of average adult body mass), had a range of up to five km, and a battery life of 14 months. Forty six of the birds were already banded from previous years as part of the ongoing research programme. Therefore, most birds have a known history including pairing status, home range and social interactions. Three new birds (Adriana, Vaughan and Leigh) were found within burrows and added to the study population to replace birds which were lost from the study the year before through transmitter failure. Each transmitter had its own radio frequency, ensuring birds could be individually identified. All transmitters included chick timer technology. This technology consists of a data logger that records the daily activity patterns of the bird, using this information to tell the observer (via the receiver) the current reproductive state and daily activity of each bird. Birds were sexed using DNA analysis of feather samples, and classed into three different age groups based on their estimated age (less than five, between five and ten, and more than ten years). Birds known to have been born in the past five years were easily grouped, as were those that were banded when the study began ten years prior. The age of remaining birds was estimated by comparing morphometric measurements for each year the individual occurred in the study with other birds of known ages.

3.2.2 Habitat Analysis

Habitats within the 1.2km^2 study site were classed as one of four broad macrohabitat types consisting of forest, scrub, pasture and swamp, and plotted onto a map using Arc GIS (Fig. 3.1). Pasture and swamp habitats had clear boundaries which were easily defined by their predominant vegetation type as outlined in Chapter 1. The extent of pasture considered available to brown kiwi was extended far enough from each gully to include 95% of all location fixes of birds found in pasture. Recent GPS data marking the boundaries between scrub and forest taken by Sarah Jamieson (unpublished data, 2012) were used with her permission to distinguish the extent of these two remaining habitat types within the study site. Jamieson gathered this GPS data by walking the border between habitats, marking her location at regular intervals. To ensure accuracy a random sample of 50 of these GPS points were selected and ground-truthed by finding their precise location and ensuring the point did indeed lie on the border of these two habitats. The area (in km^2) covered by each habitat type within the study site and within each individual gully was measured using the calculator function in Arc GIS. The relative proportion of each habitat type was then calculated to determine its availability to brown kiwi within the study site.

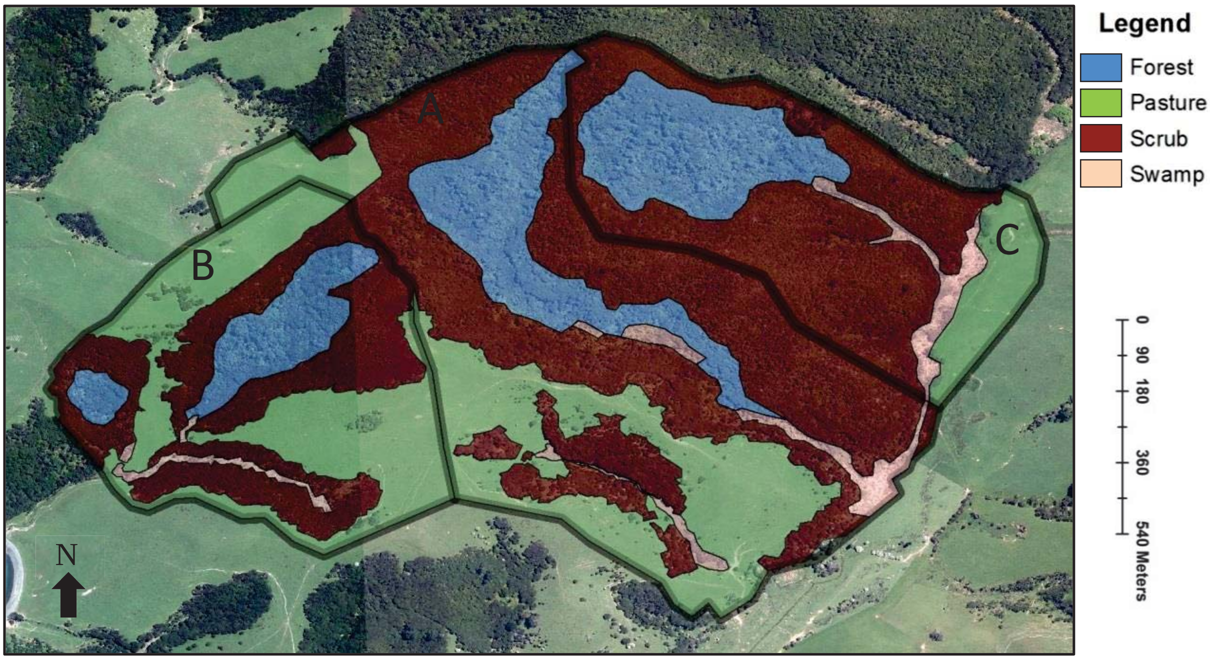


Figure 3.1 – Habitat map of the study site on Ponui Island. Showing the area of Forest, Pasture, Scrub and Swamp habitat within each of the three gullies. (A=Red Stony, B=Kauri, C=Pipe). Photograph from LINZ.

3.2.3 Collecting Brown Kiwi Location Data

Forty seven of the 49 banded brown kiwi adults were tracked using a Telonics TR4 receiver and Yagi three element antenna to detect transmitter signals. These included 26 males and 21 females spread across all three gullies (see Appendix I).

Radio telemetry is considered an unrivalled technique for determining the activity patterns, movements, home range and habitat use of animals in the wild (Harris et al., 1990; Robertson & Westbrooke, 2005) and has been used to study a multitude of different species around the world. Radio telemetry reduces stress and disturbance to avian study subjects, resulting in more accurate data as the behaviour of the bird is not impacted by the close proximity of observers. Additionally, there is markedly reduced observer error compared with other techniques. Kufeld, Bowden, and Siperek Jr (1987) found a 95% agreement between observers on classification of signals when listening to the strongest signal.

Brown kiwi were tracked over nine nights each month by the same observer. Due to the size of the study site a single gully was chosen each night, ensuring that all of the gullies were sampled for three nights each month. Tracking took place over three shifts lasting 3-4 hours each, starting at sunset, midnight, and around 3am, recorded as shifts 1-3. Each night a single shift was randomly chosen for sampling. Starting times changed slightly throughout the year due to daylight saving and as hours of darkness increased and decreased. It was ensured that each gully was sampled during all three shifts every month.

Locations of brown kiwi at night were obtained using the triangulation method. This involved estimating a bird’s location by analysing the intersection of multiple bearings taken from known points. This technique is recommended when tracking nocturnal species that live in closed habitats allowing for a greater number of birds to be tracked at once, from a distance where their behaviour will not be disturbed (Harris et al., 1990).

Tracking followed a pre-set route along a grid of known points marked with GPS coordinates (Figure 3.2). Grid points were located 100m apart in open habitat, and 50m apart in more dense forest habitat. This gave the observer an increased amount of places to stop at within dense habitat to ensure accuracy. Grid routes generally followed higher terrain to reduce the impact of signal bounce. The researcher stopped every 100m along the grid. At each point, the time, direction, signal strength and estimated distance of every bird which could be picked up by the receiver were recorded, before moving on to the next point. Direction of the strongest signal was obtained using a compass, while the distance from the observer to the bird was estimated in the field based on signal strength. Increased time was allocated to searching for the signal of known inhabitants, while birds unlikely to be found in that gully were scanned more quickly. If a banded bird was ever opportunistically encountered and disturbed then no subsequent bearings were taken for that individual in that shift. Additional notes included sightings or calls of known birds, and identification of topographical features potentially impacting the telemetry signal.

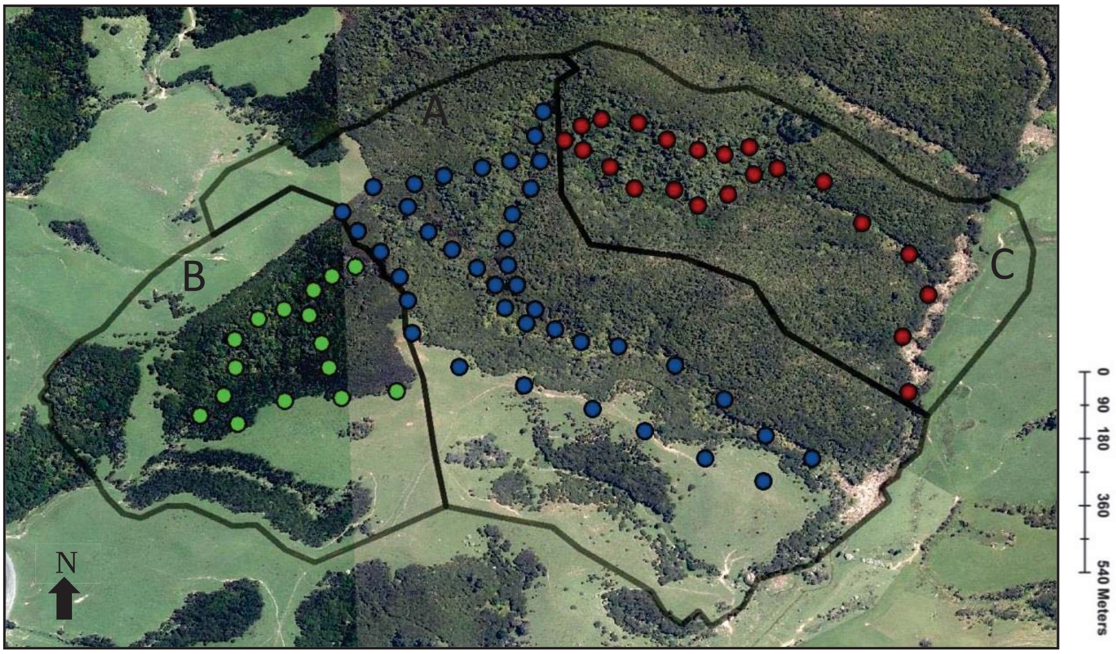


Figure 3.2 – Grid map of the study site on Ponui Island. Showing the locations of every grid station within each of the three gullies. (A=Red Stony, B=Kauri, C=Pipe). Photograph from LINZ.

Bearings and distances collected on a given night were entered into Google Earth for each individual brown kiwi in the form of lines heading away from grid stations (Figure 3.3). Based on the overlap of lines from multiple locations it was possible to ascertain the locations of each bird over that shift to generate GPS point data. A slow and methodical approach was taken, with points which appeared nonsensical based on the topography or a bird's previous location discarded. Only locations confirmed by multiple bearings were included. Estimated distances sometimes had to be slightly extended or reduced, but directions were considered highly accurate. The identification of locations in this manner required an in depth knowledge of the topography of the study site, behaviour of individual birds, and how telemetry signals behave within each gully on Ponui Island.

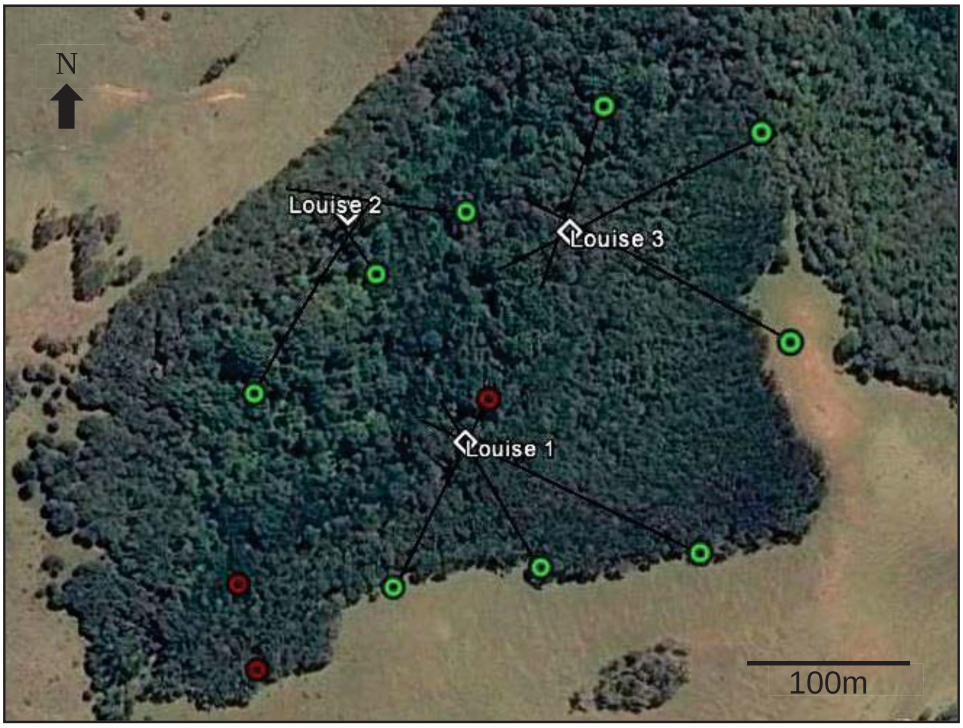


Figure 3.3 – Example of the triangulation methodology in Kauri Gully , with bearings and distances for the brown kiwi Louise on the 28/05/2013 indicated by black lines from each of the grid stations (circles) marked on google maps. Stations where bearings for Louise were removed due to errors on that night are in red. White diamonds indicate the estimated locations for Louise that night. Not all triangulations were as obvious as those shown this example. Photograph from LINZ.

Lastly, GPS coordinates of all brown kiwi locations at night were input into mapping software Arc GIS version 10.2.2, and layered over the top of the previously produced habitat map (Fig. 1.2). Using the Editor Toolbar, locations were then assigned a habitat type based on which habitat polygon each GPS point was contained in.

The month, season (winter, spring or summer), shift (1-3), gully (Red Stony, Kauri, Pipe), sex (male or female), age (1-5, 6-10, <10), social grouping (paired, group, alone), breeding status (currently incubating, not incubating), breeding season (yes or no), average shift temperature (˚C), estimated shift rainfall (light, medium, heavy), average daily rainfall (mm), average min and max temperature (˚C), and food availability (average weight of invertebrates per pitfall) were also recorded with each brown kiwi location.

Other Data Collection

Environmental variables were also measured over the course of the study. Temperature was recorded using six Hobo data loggers placed in randomly selected sites along the base of each gully. These data loggers recorded temperature every half hour for 12 months. This was later used to calculate average temperature for the gully being sampled over the precise sampling hours for that night. This provided accurate measures of microclimate for each gully. Additionally, average temperature, rainfall, humidity and wind data at Waiheke Island (the closest weather station) was downloaded from NIWA. Invertebrate availability was sampled throughout the study following the methodology laid out in Chapter 2.

3.2.4 Radio Telemetry Error

Signal accuracy

When animal locations are estimated based on the angle of signals it is important signals have a high level of accuracy (Kufeld, Bowden, & Siperek Jr, 1987). A problem with achieving accurate bearings is that telemetry signals can be impacted by the topography of an area, resulting in a distorted or ‘bounced’ signal and an incorrect bearing (Kufeld, Bowden, & Siperek Jr, 1987; Anderson-Sprecher, 1994). Bouncing can occur frequently in mountainous terrain (Lee et al., 1985), and was identified as an issue during a triangulation pilot study on Ponui Island in the past (Castro et al., *unpubl. data*). Additional care must be taken to ensure that the topography and/or land cover between the observer and receiver is not affecting the signal volume (Kufeld, Bowden, & Siperek Jr, 1987; Harris et al., 1990), impacting upon the estimation of distance.

To reduce the chance of incorrect readings we used a method of outlier rejection. However with only two or three observations typically available for each triangulation, standard statistical techniques for outlier rejection are often impractical in the wildlife setting (Anderson-Sprecher, 1994). The non-statistical identification and rejection of inaccurate bearings relies upon knowledge of the topography of the study site and significant telemetry experience to recognize how telemetry signals behave within it. Hence, a four month trial period was undertaken in this study before any data collection occurred.

To calibrate readings, a beacon study was undertaken to provide a quantifiable measure of error in the radio-tracking method. People with radio-transmitters attached to their ankle (at a similar height to transmitters attached to brown kiwi legs) were tracked through the study area while recording their own locations every ten minutes using a GPS. This enabled me to simulate the movement of transmitters that occurs at night. Out of a total 18 fixes, the mean linear error was 59m (± 44.9 SD), with 66% of fixes having an error < 50m. This level of error was considered acceptable for studying brown kiwi macrohabitat use in this study, which occurred over a wide area with numerous samples.

Finally, when triangulating bearings it is important to consider the intersection angle. Shallower angles between search points provide less accurate locations, while larger angles are considered more accurate (Lee et al., 1985). As such, during the trial period distances between sampling sites along the grid were increased from 50m to 100m. This resulted in larger angles between bearings, with most sitting between 40 and 140 degrees, the range considered most preferable (Lee et al., 1985).

Pseudo-replication

Pseudo-replication is another common source of error in triangulation studies (Kufeld, Bowden, & Siperek Jr, 1987). Obtaining a large number of spatially representative and temporally independent samples can often prove challenging, particularly when working with an endangered or threatened species like the brown kiwi. This is compounded by the significant cost of telemetry and limited number of frequencies available to researchers (Robertson & Westbrooke, 2005; Riber, 2006).

Measures were taken to ensure samples were as independent as possible. Bearings used to identify a single bird’s position were always obtained within 30 minutes of each other. This was considered enough time for the researcher to travel between sites while minimizing disturbance and also corresponds to the findings of Miles (1995) that brown kiwi will forage in a site for 30 minutes on average before moving on. Additional care was taken to ensure the time between obtaining multiple locations of a single bird in one night was far enough apart so that the first measure had no influence on the second (White & Garrott, 1990). In this case, one hour was considered long enough between locations to negate the chances of pseudo-replication.

Ensuring samples were spatially representative was more difficult as I worked with a sample of preselected monitored birds that shared a particular area. Brown kiwi live within home ranges in our study site, with many marked birds sharing overlapping home ranges. Historically birds were selected in order to study their social interactions and to avoid those birds which favoured the less accessible swamp habitat. A few areas existed in the study site in which there are no home ranges of marked birds, including below about half way down RSHG and Pipe Gully, although many unmarked birds are seen in these areas regularly. The focus of this research was therefore to examine the use of habitat of our marked birds.

3.2.5 Statistical Analyses

Multivariate statistical analyses were performed using SPSS 20 and R version 3.2.1. Microsoft Excel 2010 and Graph Pad Prism 6 were used to generate further graphs and tables. A probability of ≤ 0.05 was deemed statistically significant.

Habitat Utilisation

The frequency of brown kiwi locations within each habitat type over the entire study was compared to predicted habitat use based on the availability of each habitat within the study site. A one-sample chi squared test was used to determine if apparent differences between actual habitat use and the expected habitat use were significant, with the expected values entered into the matrix by hand. Additional Pearson chi squared tests were carried out to assess variation in habitat utilisation rates within each of the different potential drivers, including temporal, spatial, demographic and behavioural factors. Due to the large number of variables tested (7), probability was corrected for using Holm-Bonferroni Sequential Correction (see Holm, 1979). This method presents a less conservative correction than the standard Bonferroni, and is used frequently in Ecological studies (Nakagawa, 2004). Corrected P values are presented in the results.

Drivers of Habitat Utilisation

A Generalised Linear Mixed Model (GLMM) using multinomial logistic regression was run to determine the effects of a range of potential drivers (fixed effects) on the habitat type brown kiwi were located in (target effect). Multinomial logistic regression allows the analysis of factors for which there are more than two possible responses, for example four seasons or three gullies. This type of model is useful in that it allows for the analysis of many different variables, whether they are categorical, nominal or ordinal (Field, 2013).

Multinomial logistic regression requires careful consideration of the sample size to ensure adequate samples for each group within a factor. This was not considered a problem due to the large number of samples collected in this study. The identity of each bird was included as a random effect to account for any individual variation. The model identified which factors were the most important to determine habitat utilisation rates of sample birds in my study.

A wide range of temporal, spatial, demographic, environmental and behavioural factors were collected each night to be input into the model for analysis. This included season, month, shift, gully, sex, age, social grouping, breeding status, breeding season, shift temperature, max daily temperature, min daily temperature, daily rainfall, shift rainfall and food availability. Factors were tested for correlation with one another, with those that showed a strong correlation with another factor removed prior to analysis.

Once the initial model had run, stepwise backwards elimination was used to remove the least significant factor, before re-running the model. This step was replicated until the model no longer increased in accuracy (measured by a reduction in AICC and BIC scores of at least 100) with the removal of a factor. The resulting F-values measure the overall goodness of fit for each factor to the model. A high F value (or equivalently a small p-value) signifies that the overall model fits the data quite well, and that the variation among group means is more than you would expect to see by chance. Two and three way interactions between fixed effects were added to the model one at a time, however none proved significant, nor did they increase model accuracy, so were left out of the analysis and final model.

Predicted value coefficients for each grouping within the remaining fixed effect factors in the final model were plotted with two times standard error, illustrating how the categories within each factor impacted the likelihood of brown kiwi being found in a certain habitat type in comparison to the reference category of forest, after the effect of the other factors had been taken into account. The smaller the error bar, the more certain we can be of the GLMM estimate for that coefficient.

Individual Variation

A Hausman test was carried out in R to assess how much affect individuality may have had on the spatial patterns of brown kiwi recorded. This test compares a fixed effects model with a random effects model to determine which one provides the best explanation of the data. In this case the random effect was individual bird ID and the fixed effects were all of the considered potential driving factors. The result of this test is a chi square value with an associated p-value. If the p-value is significant then the model with the highest p-value is seen to offer a better explanation of the data (Hausman, 1978). A non-significant p-value means that the models are different, and thus adding the random effect factor has not helped to better explain the data.

3.3 Results

3.3.1 Habitat Availability

The four habitats considered in this study were available in differing proportions within the study site (Table 3.1). Scrub was the most prevalent habitat type, covering almost half of the available area. Pasture and forest habitat covered a large proportion of what remained, with swamp only sparsely available. Each gully had a different overall distribution of habitat types (Fig. 3.4). The difference between gullies was most pronounced between Pipe and the other two gullies, with less forest and more swamp habitat available proportionally.

Some areas of the study site were never used by the sample of brown kiwi tracked on Ponui Island, particularly the large area to the SE of the site (Fig. 3.5). This is likely because they were not part of the bird’s home range. An attempt was made to remove these areas from the availability analysis based on the locations of study birds. However, despite the removal of these areas, the proportion of each habitat within the study site was only changed marginally, by an average of 2% (forest up 2%, scrub down 3%, pasture up 2%, swamp down 1%). As the home range of each the study birds was unknown, and calculating it was outside the scope of this study, removal of habitat was relatively anecdotal, with no quantitative process. Given the small impact this would have had on results, and non-robust approach of removal, we decided to simply include this area in the availability analysis and instead discuss why it may not have been used by sample birds later in the chapter.

Table 3.1 – Total area and proportions of the study site on Ponui Island covered by each of the four main habitat types.

Habitat	Area (Km^2)	Proportion of Study Site
Forest	0.21	19%
Scrub	0.54	48%
Pasture	0.33	29%
Swamp	0.05	4%

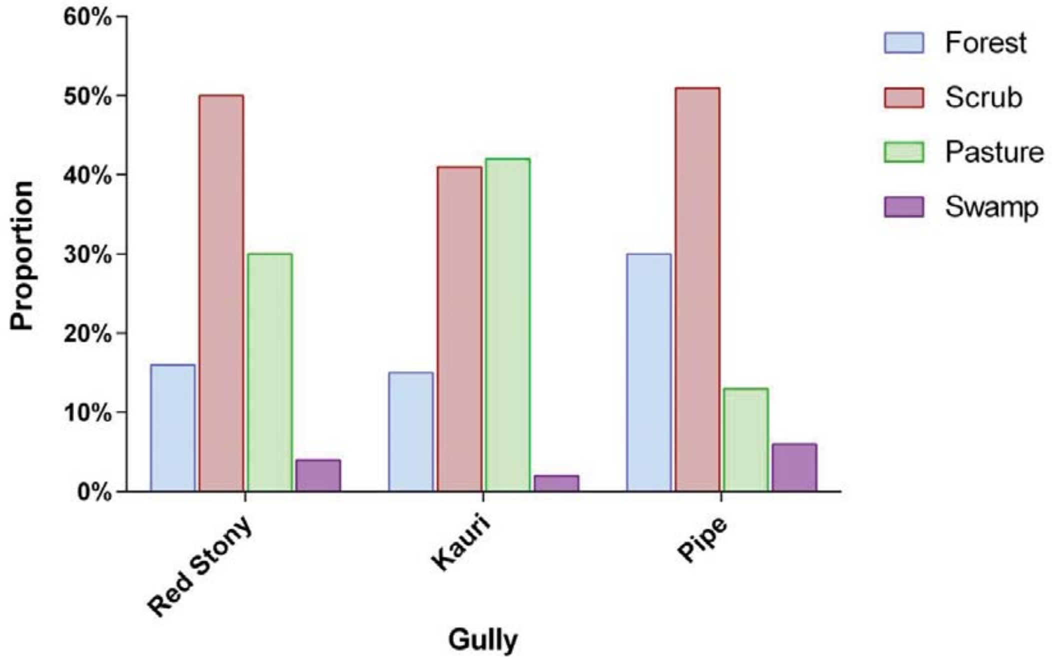


Figure 3.4 – Comparison of the availability of each of the four main habitat types between the three gullies sampled within the study site.

3.3.2 Habitat Utilisation

Forty seven brown kiwi were located a total of 2377 times during their nocturnal activity phase over nine months on Ponui Island. These location fixes were spread throughout the majority of the study site and occurred within all four habitat types (Fig. 3.5). Data collection was evenly spread, with similar numbers of location fixes recorded for each season, gully, shift and sex (Appendix M). Samples were also spread evenly across the 47 tracked birds (Appendix I), with an average of 51 nocturnal location fixes per bird (± 1.98 SE). All 47 birds were located in forest and scrub at least once, while 23 birds occurred in 3 different habitats, and 11 were found in all four over the course of the study (Appendix J).

Brown kiwi were located within each habitat type at differing proportions (Table 3.2). Birds were predominantly found within forest habitat, followed by scrub, and then pasture. Few birds were located within swamp habitat. Habitat utilisation differed significantly from predicted rates based on habitat availability (One sample Chi Squared Test; Chi Square=1570.747, df=3, P<0.001) (Appendix K). Overall, brown kiwi on Ponui Island were located within forest habitat more often and in all other habitats less often than the availability of these habitats would suggest (Fig 3.6).

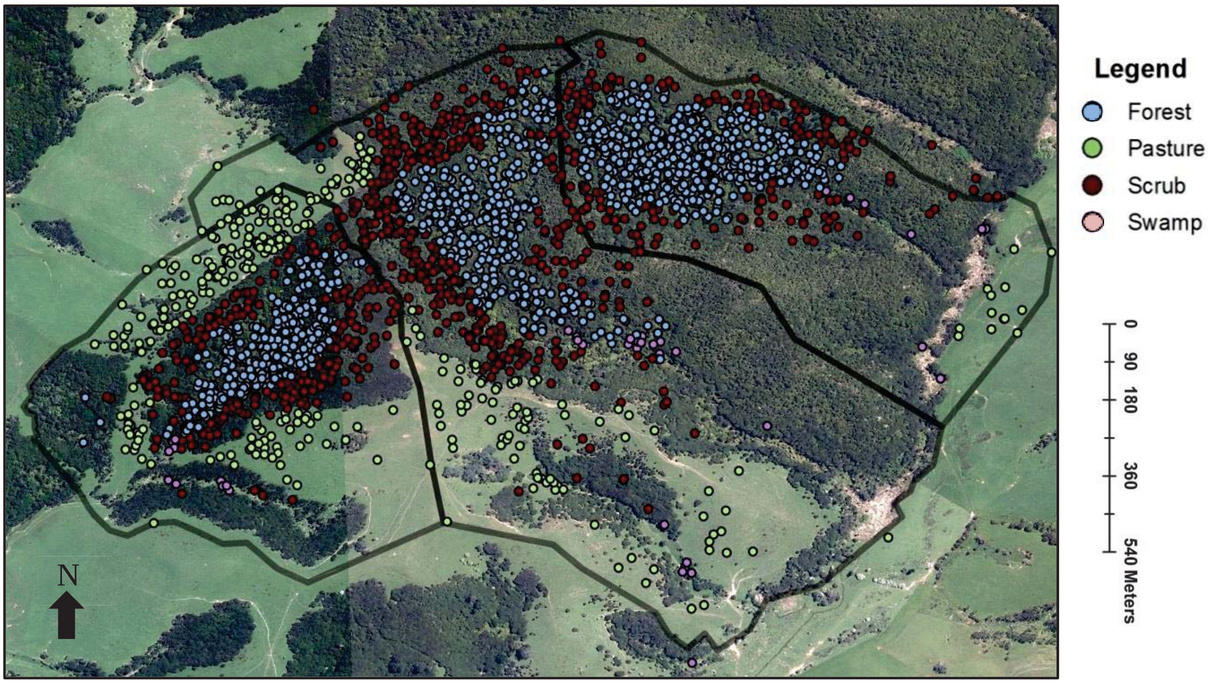


Figure 3.5 – GIS map illustrating all 2377 nocturnal locations of brown kiwi on Ponui Island over the course of the study, with the corresponding habitat type for each point identified by colour. Dark lines represent the boundary of each gully following the contour of the study site. Photograph from LINZ.

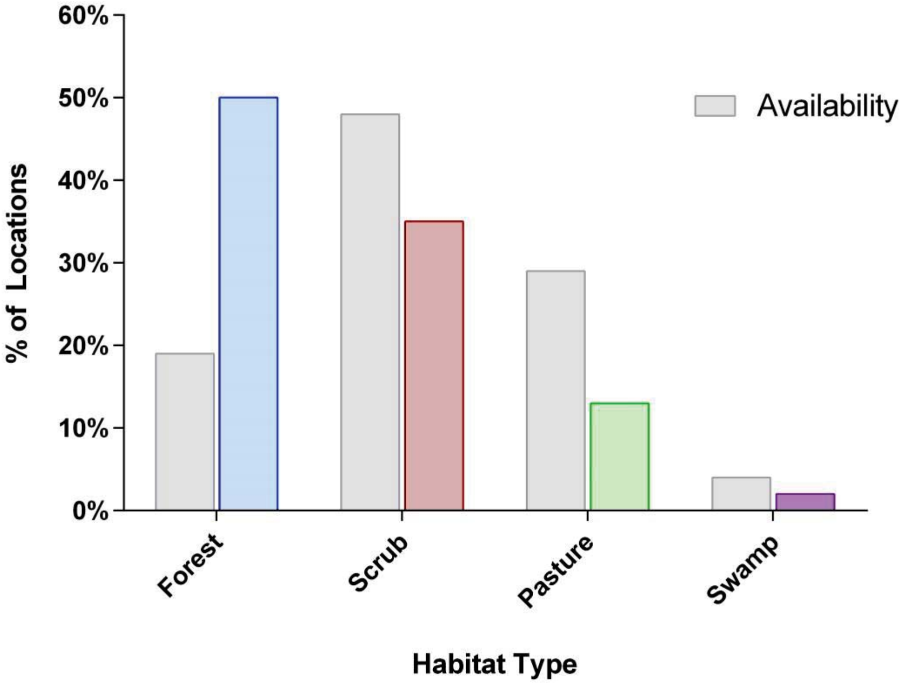


Figure 3.6 – Percentage of nocturnal locations of brown kiwi found within each of the four main habitat types over the course of the study, compared to the expected utilisation rates based on habitat availability.

Table 3.2 – Table showing the total number and proportions of nocturnal locations of brown kiwi on Ponui Island over the course of the study between each of the four main habitat types.

Habitat	# Locations	Proportion of Total Locations
Forest	1195	50%
Scrub	825	35%
Pasture	315	13%
Swamp	42	2%

Telemetry Error

In total, 7571 bearings were recorded over the course of the study. Of these, 613 (8%) were suspected to be erroneous and were not used to aid in the triangulation of brown kiwi locations. Two hundred and sixty of these were discarded as they appeared nonsensical or erroneous based on previous locations and knowledge of the topography of the study site. The remaining 353 were discarded because the bird was estimated to be too far away to ensure accuracy. Removed bearings were spread unevenly across all individual birds, with a mean of 13 errors per bird (± 1.3 SE).

Spatial Variation

Forest habitat was used by brown kiwi more than expected and all other habitat types less than expected in all three gullies. However, the rate at which each habitat was utilised varied between gullies (Pearson Chi Squared Test; Chi Square=249.576, df=6, P=0.007) (Appendix K).

Compared to the availability of habitat, Red Stony and Kauri gullies had very similar utilisation for forest, scrub and swamp, but Kauri birds used pasture less often compared to its availability (Fig. 3.7). Birds from Red Stony were located the most often in scrub habitat, followed closely by forest and finally pasture then swamp (Fig. 3.8A). Kauri birds showed similar use of habitat to Red Stony, though they were found within forest more than scrub and in pasture more often than the other gullies. Pipe gully showed markedly different patterns of habitat utilisation to the other two gullies. Pipe birds were very rarely found within pasture habitat, instead located predominantly in forest (Fig. 3.8A). Pipe birds utilised forest habitat much more than its availability would suggest, while utilising scrub much less than expected (Fig. 3.7). When Pipe gully is excluded from the analysis the difference between habitat utilisation rates and habitat availability is increased in significance (One sample Chi Squared Test; Chi Square=1570.747, df=3, P=0.007) (Appendix K).

Temporal Variation

Though forest habitat was utilised the most year round, the rate at which habitat was utilised by brown kiwi differed between seasons (Pearson Chi Squared Test=35.851, df=6, P=0.007) (Appendix K). Forest and scrub habitats were utilised the most during winter and spring before dropping slightly over summer, where a marked increase in pasture utilisation occurred (Fig. 3.8B). These trends are more pronounced when results from pipe gully are excluded (Fig. 3.8C).

Rates of habitat utilisation in brown kiwi on Ponui Island were similar throughout the night between all three sampling shifts (Chi Square=9.377, df=6, P=0.153) (Fig. 3.8D) (Appendix K).

Demographic Variation

Male and Female brown kiwi in my study site utilised the habitat available to them similarly, with forest utilised the most, followed by scrub, pasture and then swamp. However, variation between sexes was identified in the rate at which each habitat was used (Chi Square=16.237, df=3, P=0.007) (Appendix K). Males were located slightly more frequently within forest, scrub and swamp habitat than females, while females were more likely to be located in pasture (Fig. 3.9A).

Additionally, habitat utilisation rates were observed to differ between birds of different age groups (Chi Square=34.091, df=6, P=0.007) (Appendix K). Birds estimated to be between one and five years old were located less often in pasture and swamp than other age groups and more often in forest and scrub habitats (Fig. 3.9B). Birds estimated to be between the ages of six and ten and those which were over ten had similar rates of utilisation.

Behavioural Variation

Habitat utilisation of brown kiwi on Ponui Island differed depending on a bird’s social grouping (Chi Square=58.862, df=6, P=0.007) (Appendix K). Birds which sheltered alone were located more often in swamp and scrub habitat than others but were less likely to be found in pasture (Fig. 3.9C). Paired birds were found most often within forest habitat, while those which sheltered as part of a group were found more often within scrub and pasture habitats.

Rates of habitat utilisation of brown kiwi on Ponui Island also differed according to the breeding status of birds (Chi Square=19.336, df=3, P=0.007) (Appendix K). Incubating birds (and their suspected partners if known) were found within forest habitat more often and in any other habitat less often than birds which were not incubating (Fig. 3.9D).

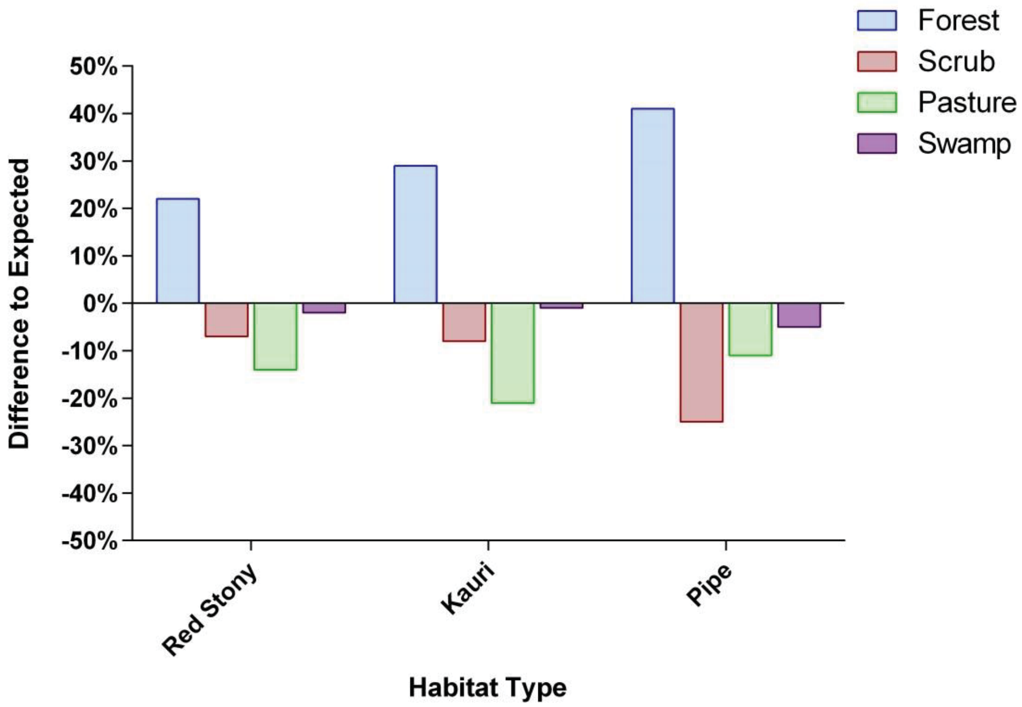


Figure 3.7 - Percentage of nocturnal locations of brown kiwi found within each of the three sampled gullies, compared to the expected utilisation rates based on habitat availability.

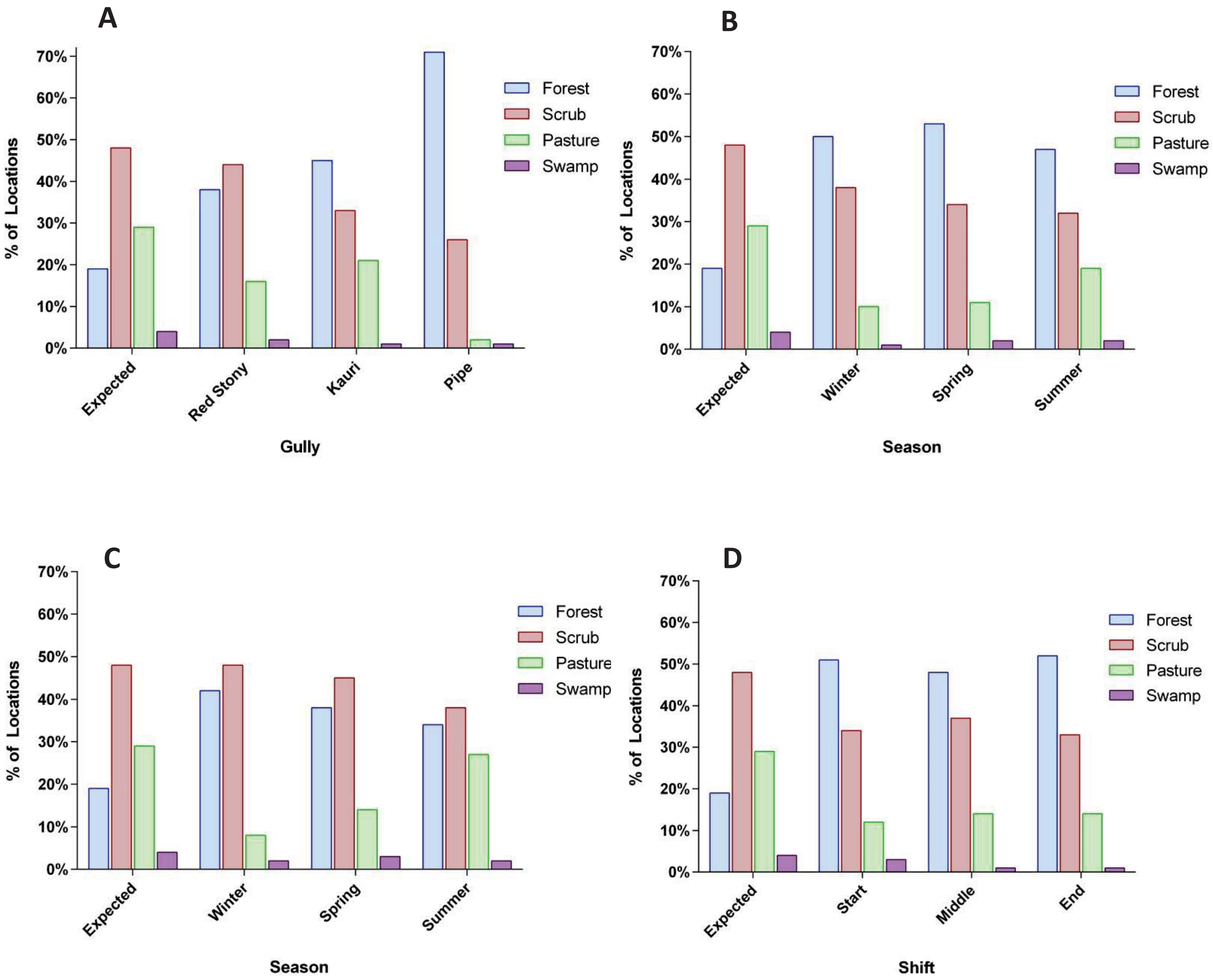


Figure 3.8 – Variation in nocturnal habitat utilisation rates of brown kiwi in four habitat types on Ponui Island compared to expected rates based on habitat availability, across a number of potential driving factors:

A = Percentage of nocturnal locations of brown kiwi found in each habitat type within each of the three gullies.

B = Percentage of nocturnal locations of brown kiwi found in each habitat type during three seasons of sampling.

C = Percentage of nocturnal locations of brown kiwi found in each habitat type during three seasons of sampling over the course of the study EXCLUDING pipe gully,

D = Percentage of nocturnal locations of brown kiwi found in each habitat type during the three sampling shifts.

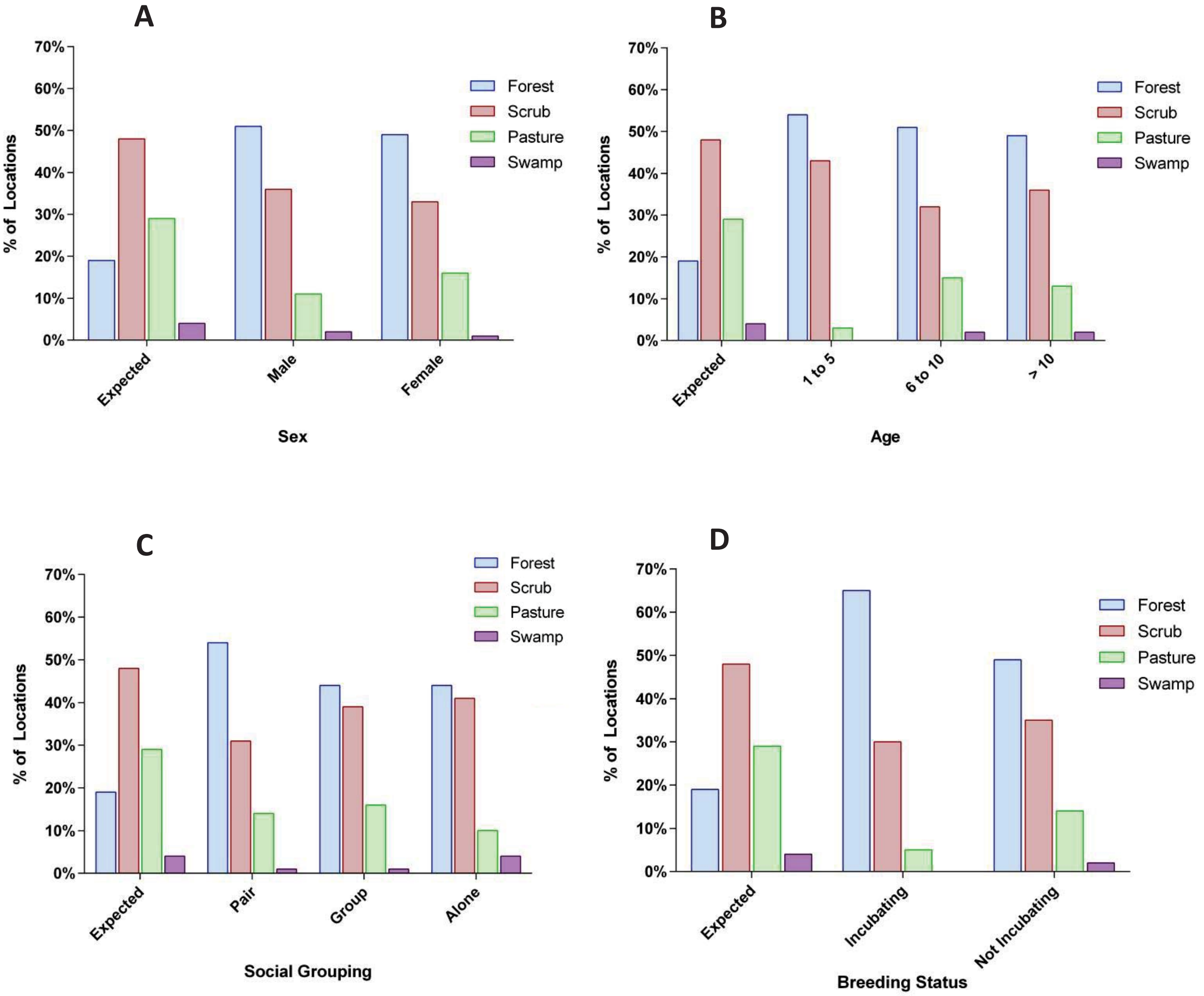


Figure 3.9 - Variation in nocturnal habitat utilisation rates of brown kiwi in four habitat types on Ponui Island compared to expected rates based on habitat availability, across a number of potential driving factors:

A = Percentage of nocturnal locations of male and female brown kiwi found in each habitat type.

B = Percentage of nocturnal locations of brown kiwi in three age groups found in each habitat type.

C = Percentage of nocturnal locations of brown kiwi in three social groupings found in each habitat type.

D = Percentage of nocturnal locations of brown kiwi either currently undertaking incubation or not incubating found in each habitat type.

3.3.3 Habitat Utilisation Drivers

Several factors were found to be correlated with one another and thus were removed before the model was run. This included month and breeding season (correlated with season), max and min temperature (correlated with shift temperature), and shift rainfall (correlated with daily rainfall). Four factors were identified in the final model as the most important drivers of habitat utilisation in this study (Table. 3.3). The model itself was significant, as were the four factors of invertebrate availability, season, gully and social grouping. These four were also the only significant factors in the full model when all 10 fixed effects were considered together prior to reverse elimination (Table 3.4) (Appendix L).

Table 3.3 – Results of the final GLMM, showing results of the overall model, as well as the four most important driving factors of habitat utilisation in brown kiwi on Ponui Island.

Factor	F statistic	df	P
Final Model	21.894	21	<0.001
Invertebrate Availability	128.479	3	<0.001
Season	30.661	6	<0.001
Gully	9.132	6	<0.001
Social Grouping	3.385	6	0.003

Table 3.4 – Results of the first GLMM, showing results of the overall model. Includes the four most important driving factors of brown kiwi habitat utilisation, followed by those factors that were removed during stepwise backwards elimination. Including associated AIC and BICC values for each model upon removal of that factor. Removed factors are listed in order of their removal from first to be removed to last to be removed.

Factor	F statistic	df	P	AICC	BIC
Overall Model	10.45	45	<0.001	46704.7	46722.0
Invertebrate Availability	127.228	3	<0.001	-	-
Season	12.647	6	<0.001	-	-
Gully	7.916	6	<0.001	-	-
Social Grouping	3.718	6	0.001	-	-
Sex	0.323	3	0.808	46204.3	46221.6
Age	0.755	6	0.605	43761.2	43788.5
Breeding Status	0.818	3	0.484	41995.2	42012.5
Daily Rainfall	1.388	3	0.245	41828.1	41845.3
Shift	1.506	6	0.172	41545.3	41562.6
Shift Temp	1.193	3	0.311	41351.6	41368.9

Figure 3.10A shows variation in habitat utilisation explained by the spatial factor of gully. Birds in Red Stony gully were less likely to be found in pasture, scrub and swamp habitats than in forest. Kauri birds were more likely to be found in pasture habitat than forest, and a little less likely to be found within scrub and swamp habitats than in forest. Pipe birds were far less likely to be found in scrub habitat, and slightly less likely to be found within pasture and swamp habitats than in forest.

Figure 3.10B shows variation in habitat utilisation explained by the temporal factor of season. Birds are more likely to be found within forest than other habitat types in every season. In winter, birds are much less likely to be found in pasture and swamp habitat than forest compared to other seasons. In both spring and summer, birds are less likely to be found within all three other habitat types than in forest. This is especially pronounced for the likelihood of being found in pasture during summer.

Figure 3.10C shows variation in habitat utilisation explained by the behavioural factor of social grouping. Paired birds were less likely to be found in other habitats than in forest, especially pasture and swamp. Birds which sheltered in a group were less likely to be found in pasture than forest, and had a similar chance to be found in scrub or swamp than forest. Alternatively, birds which sheltered alone were more likely to be found in scrub, pasture and swamp than forest habitat.

Figure 3.10D shows variation in habitat utilisation explained by the environmental factor of average invertebrate weight per pitfall. As the weight of invertebrate content within a habitat increases, the likelihood of a brown kiwi being found in that habitat type instead of forest also increases. This is true for all three of the compared habitat types. Pasture shows a particularly strong positive correlation between invertebrate availability and the likelihood to be found in that habitat. A high coefficient score was generated for all three habitat types compared to other factors, suggesting that much of the variation is explained by this factor.

The final factor considered in the model was the random effect of Individual ID. The results of the Hausman Test (Hausman Test; Chi Squared=112.11, df=4, P=<0.001) suggest that the fixed effect variables offer a better explanation of the data than the random effect. Although individuality may still have some effect on the results, this has likely been reduced due to the large number of samples recorded for each bird, made possible by using the triangulation methodology in this high-density island population.

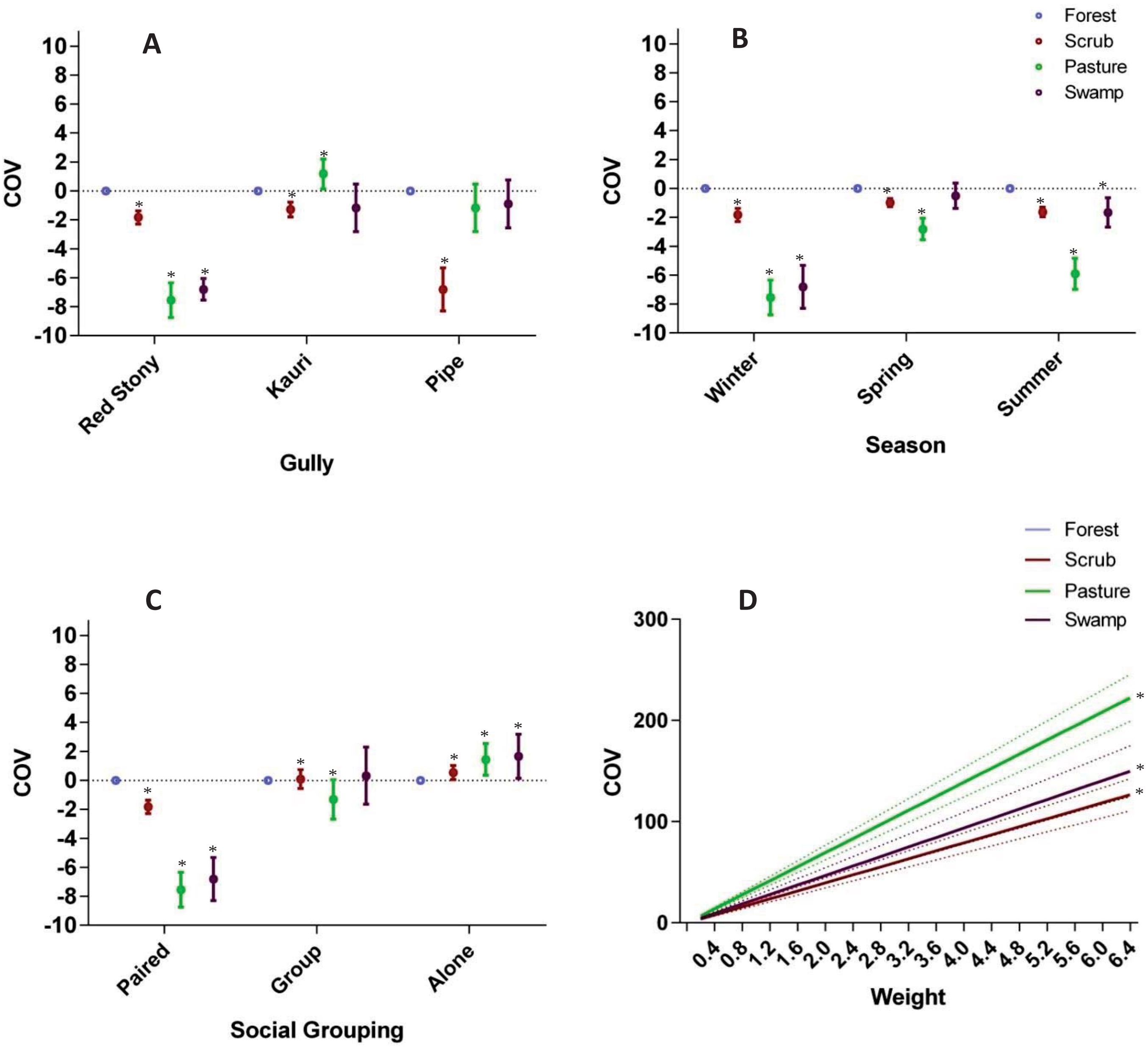


Figure 3.10 – Coefficient of variance (COV) with 2*SE for all factors included in the final model. Illustrates how each factor considered singularly impacts the likelihood of being found within a certain habitat type compared to being found within the reference category of forest. A) Gully, B) Season, C) Social grouping, D) Average weight of invertebrate content per pitfall.Positive COV scores represent increased likelihood, negative represent reduced likelihood. Asterisks mark P values less than 0.05.

3.4 Discussion

3.4.1 Nocturnal Habitat Utilisation

Brown kiwi on Ponui Island utilised habitat differently to predicted rates based on availability, selecting for forest habitat throughout the study over scrub, pasture and swamp. Habitat selection such as this is not unusual among avian species, with a range of other species exhibiting similar behaviours (Jones, 2001; Currie et al., 2005; Castillo-Guerrero et al., 2009). Different habitat types are thought to provide different benefits to avian species, related to fitness and survival (Block & Brennan, 1993; Jones, 2001; Dechant et al., 2002). If some habitats are more beneficial for brown kiwi than others, then selective habitat use should be expected (Taborsky & Taborsky, 1995). This suggests that forest habitat may provide major benefits to brown kiwi.

Birds in the study were located in forest habitat 31% above what would be expected based on habitat availability (25% more when Pipe Gully is excluded), accounting for over half of the total locations recorded. Both previous studies (Potter, 1989; Taborsky & Taborsky, 1995) to consider nocturnal habitat utilisation of adult brown kiwi found a similar result. This reinforces the long held opinion that brown kiwi are predominantly forest dwelling birds, perhaps unsurprising considering this was the dominant habitat type in New Zealand over the course of their evolution (Mills & Williams, 1979). Forest habitat provided reasonably high levels of invertebrate availability throughout the year, including several protein rich prey items favoured by brown kiwi (see Chapter 2). Forest litter is also an important foraging stratum for brown kiwi, with almost 20% of all prey captured in leaf litter (Cunningham & Castro, 2011). Denser forest habitat is often perceived to provide protection against predation (Gibbs & Clout, 2003), one of the most important drivers of habitat utilisation in another ground dwelling New Zealand bird, the takahe (Baber & Craig, 2003). Finally, forest habitat on Ponui Island contained the largest number of tree burrows, considered the most favourable roosting site (see Chapter 4). It is likely that a combination of these benefits were behind the higher rates of use of forest habitat by brown kiwi.

Scrub was the second most utilised habitat overall, accounting for over a third of the total locations recorded. The large numbers of birds recorded in scrub may reflect its position in the study site as an edge habitat, often bordering both pasture and forest. Ismail (1993) suggests that edge habitats are used more often by brown kiwi due to a greater relative availability of food resources, while still providing more safety than open pasture. Potter (1989) found that brown kiwi utilised edge habitats more frequently than expected, and Cunningham and Castro (2011) noted that brown kiwi on Ponui Island had higher foraging success in areas of edge between scrub, forest or swamp and pasture than in forest/scrub habitats alone. Increased use of edge habitats has also been documented in European Hedgehogs (*Europaeus erinaceus*) (Riber, 2006), a small nocturnal species of mammal which exploits a similar niche to brown kiwi. Despite high utilisation of scrub, birds were located within this type of habitat 13% less than expected based on its availability (8% less when pipe is excluded), reflecting the higher use of forest habitat. This contradicts the findings reported in both Potter (1989) and Taborsky and Taborsky (1995) which suggested that scrub habitat is a preferred habitat for brown kiwi.

Overall, pasture was utilised less than expected based on its availability. Birds were located relatively infrequently within pasture in total, 16% less than expected (still 16% less when pipe is excluded). This confirms the conclusions of both previous studies on brown kiwi adults (Potter, 1989; Taborsky & Taborsky, 1995), neither of which sampled pasture use comprehensively, that pasture may be used less than other habitats. An important consideration to note is that time spent within a habitat may not truly reflect habitat preference. Birds may have been located infrequently in pasture because it was rich in favoured invertebrates and thus they could meet their dietary needs quicker before heading to more sheltered habitat types (Bjørneraas et al., 2012). Previous studies have documented higher foraging success rates in pasture than within forest in a number of different species including brown kiwi (Cunningham & Castro, 2011), takahe (Baber & Craig, 2003) and rhea (Barri et al., 2012). Results of the dietary analysis (chapter 2) indicate that pasture was an important source of food, especially over summer and autumn. This suggests that while not utilised as often, pasture habitat might still prove an important habitat for brown kiwi at night at certain times of the year. This might help to explain the spatial and temporal variations in pasture utilisation, explored later in the discussion.

Swamp habitat was barely utilised by brown kiwi on Ponui Island over the course of this study, with only 2% of all locations recorded within this habitat type. This reflects the small amount of swamp habitat within the study site (4%), and in each of our banded bird's home range. Birds were located in swamp 2% less than expected (1% less when pipe is excluded). Errors in the triangulation technique, whereby points are only accurate to within a certain radius, could explain this discrepancy. Birds which were active within the often small and narrow areas of swamp might have instead been triangulated to be within neighbouring forest, pasture or scrub habitat due to slight errors in accuracy. Alternatively, swamp habitat may have been actively avoided by birds, resulting in the lower utilisation rates.

Further exploration of how utilisation may vary with a number of potential driving factors is required to better understand what might be driving these spatial patterns in habitat selection.

Spatial variation

Differences in nocturnal habitat utilisation between gullies suggest that brown kiwi change their spatial behaviour dependant on the area they reside in, a notion shared by several other authors (Potter, 1989; Ziesemann, 2011).

Variation in spatial behaviour between sites has previously been linked to differences in the characteristics of each site in both possums (Adams et al., 2013), and two species of migrating sea bird (Castillo-Guerrero et al., 2009). It is likely that gully characteristics are responsible for some of the spatial variation in my study. Pipe was found to possess dissimilar proportions of available habitat compared to the two other gullies, with an increased amount of forest and swamp habitat, and less pasture. In this regard Pipe gully is more alike to the gullies directly north of the study site which were not sampled in this study. Pipe birds were found to utilise forest habitat much more than its availability, exceeding rates documented in the other gullies. In comparison, scrub appears to be used significantly less often in Pipe gully, with the lowest utilisation compared to availability. This suggests that when access to pasture is reduced, birds will choose forest over scrub habitat.

Each habitat can provide different benefits to an animal relating to fitness and survival (Block & Brennan, 1993; Dechant et al., 2002), and as a result many species occur across a range of habitats (e.g. Currie 2005). The use of multiple habitats by brown kiwi has previously been linked to an increased likelihood of survival (Gibbs, 2000). This could help explain some of the spatial variation seen here. Pipe birds measured in April 2013 by Castro *et al* (in prep) were found lower in weight than birds from other gullies. Additionally Pipe gully had the lowest incubation success rate over my study, with only 50% of incubated eggs hatching compared to 67% and 60% in Red Stony and Kauri respectively. This suggests that

Pipe gully may represent less ideal habitat for brown kiwi, to the extent that it is impacting their ability to breed and maintain body weight. This may be due to a distinct lack of available pasture habitat.

Temporal variation

There was evidence of seasonal changes in brown kiwi habitat utilisation on Ponui Island, though each season still followed the same overall trends. This variation was particularly visible when Pipe gully was excluded from the analyses, with forest used increasingly over winter, and pasture during summer. Attention has recently been given to the importance of seasonal factors in avian community organisation, with growing empirical evidence of seasonal differences in spatial behaviour across a number of avian ecological guilds (Rice, Ohmart, & Anderson, 1983). Seasonal variation in habitat use has been reported in a number of other flightless bird’s endemic to New Zealand, including the takahe (Baber & Craig, 2003) and kakapo (Atkinson & Merton, 2006). The larger scale and time frame of this study enables us to confirm the suggestions of several other authors (Potter, 1989; Gibbs, 2000; Cunningham & Castro, 2011) that brown kiwi show seasonal habitat utilisation trends.

The reasons behind this seasonal change in habitat utilisation may be partially explained by the foraging behaviour of brown kiwi. Results from Chapter 2 of this thesis indicate that both the availability of invertebrates, as well as which invertebrates brown kiwi choose to exploit, follow similar seasonal trend, with pasture invertebrates favoured over summer and forest invertebrates in winter. This helps to explain the higher rate of pasture use over this time. Similar patterns are present in a range of other ground dwelling species in New Zealand, including the avian takahe (Baber & Craig, 2003) and mammalian hedgehog (Riber, 2006), ship rat (Latham, 2006) and possum (Whyte, Ross, & Blackie, 2013). Variations in climate throughout the year within preferred habitats of the hedgehog will influence the availability of their ground invertebrate prey, which has in turn resulted in the adoption of a very flexible foraging strategy (Riber, 2006). This flexible diet is a trait shared by brown kiwi, suggesting that diet could be driving the seasonal trends recorded.

Seasonal variation may also be related to social interactions surrounding courtship and breeding, as birds are often seen to prefer certain habitats for reproductive purposes (Mazur, Frith, & James, 1998; Vogl et al., 2004; Atkinson & Merton, 2006). During the breeding season over winter and spring, brown kiwi (particularly males) are less likely to travel large distances away from nest sites. In my study, 85% of the nest sites used by monitored birds were found within forest habitat. However, over summer these restrictions are reduced and birds are more likely to travel greater distances in search of food and mates for when the breeding season begins anew. Direct social and courtship interactions are observed only rarely in brown kiwi (Taborsky & Taborsky, 1992; Cunningham & Castro, 2011), perhaps in order to reduce competition for food resources when foraging at night (Beauchamp, 2007). Despite this, paired birds in my study were located in the same area as each other a large percentage of the time. These anecdotal interactions between brown kiwi on Ponui Island were reported in more detail by Ziesemann (2011). She theorised the high-density of birds on the island may increase social contact. In my study, focal birds were not seen to use large areas which were occupied by un-banded birds, though many banded birds had overlapping in home ranges. This suggests that the study birds may be sharing home ranges, indicating that sociality may also play a role on the habitat utilisation of brown kiwi on Ponui Island, as seen in Great Spotted Kiwi (Keye, 2008).

Rates of habitat utilisation in brown kiwi remained the same over the course of the night. This suggests that once birds leave their day time burrows they will head fairly quickly to their favoured foraging areas. Indeed, the majority of birds appeared to spend up to one hour in and around the area of their burrow at the start and end of the night, with most of the night spent in a single area usually consisting of one or two habitat types. The area favoured was subject to change throughout the study. As spatial behaviour appears relatively consistent throughout the night, sampling can occur at whichever time suits the researcher without considerably impacting the results gained.

Demographic variation

Despite figure 3.9A showing similar habitat utilisation between sexes, males and females were statistically found to utilise habitat slightly differently to one another, possibly as a reflection of their biology and behaviour. Brown kiwi show reversed sexual size dimorphism, with females up to 25% larger than males (Reid & Williams, 1975). Females have larger home range sizes than males, possibly due to their higher nutritional needs (Ziesemann, 2011), meaning they will travel further each night. Variation in habitat selection between sexes was also documented in another avian species that exhibits reverse sexual size dimorphism, the critically endangered Bengal florican (*Houbaropsis bengalensi)* (Gray et al., 2009). Sexual differences in this study were attributed to variation in breeding behaviour, another potential driver of habitat selection in brown kiwi. In a reversal of conventional sex roles, male brown kiwi undertake the entirety of incubation of the egg (Cockburn, 2006). Therefore, males are limited to a smaller area surrounding the nest while females have unrestricted movement throughout the year, free to travel further from the nest site while foraging or searching for mates during the breeding season.

Minor differences in habitat utilisation were apparent between birds within the three age groups. Young birds (age one to five) spent less time in pasture than adults, instead favouring scrub and forest habitat. This contradicts both previous utilisation studies focused on brown kiwi juveniles (Chan, 1999; Gibbs, 2000) where birds avoided forest habitat, instead utilising pasture and scrub habitats the most. However, these studies only focused on brown kiwi under one year old, while the youngest bird in my study was two years old, making comparison difficult. It is likely that younger birds in my study may feel the least vulnerable within dense scrub habitat, be unable to utilise the food resources of other areas as well as adults due to their reduced bill length, or may be excluded from the seasonally favourable forest and pasture habitats by the larger adults, as hypothesized by Gibbs and Clout (2003).

Behavioural variation

Though all birds followed the same overall trend, habitat utilisation varied between brown kiwi of different social groupings. Paired birds spent marginally more time within forest habitat than other groups. This is likely to again be a reflection of breeding behaviour, whereby paired males, and increasingly paired females (see Wilson, 2013), will remain close to their nest site during incubation. Incubating birds were most prevalent within forest habitat, and were rarely found within pasture. The majority of nest sites in my study were located within forest habitat. As breeding occurs any time between late June and early February (Reid & Williams, 1975), covering almost the entirety of my sampling period, this might explain much of the behavioural variation. Brown kiwi living in groups were the most likely to be found in pasture habitat at night. This may be a reflection of reduced requirement to remain close to the nest due to the occurrence of cooperative incubation of brown kiwi on Ponui Island (Ziesemann, 2011). Single birds were found slightly more often in scrub and swamp habitat rather than the more important foraging areas of forest and pasture (see Chapter 2). These single birds may have been pushed out of the vicinity of nest sites by paired males to ensure paternity of eggs. Alternatively, single birds may be less able to maintain and defend the more favourable forest home ranges. This interspecific competition limits the ability of an animal to exploit ideal habitat, forcing it to survive within its ‘realised’ niche (Szaro, Brawn, & Balda, 1990; Sinclair, Fryxell, & Caughley, 2006). Social factors including competition might have a large affect on brown kiwi spatial behaviour; however this needs further exploration.

3.4.2 Habitat Utilisation Drivers

Prior to this study, little was known about the drivers behind habitat utilisation in brown kiwi. Though previous research has suggested several potential drivers, including spatial, temporal, environmental and behavioural factors, these have never been explored in depth. This study is the first to develop a model which assesses the effects of ten probable drivers of brown kiwi habitat utilisation, in order to identify which have the biggest influence on their spatial behaviour at night.

Major driving factors

Invertebrate availability (measured in weight per pitfall trap) was considered the single most important driver of habitat utilisation. As the biomass of invertebrate content within a habitat increased, the likelihood of brown kiwi being found in that habitat instead of the reference category of forest also increased. This driving factor generated an extremely high positive coefficient of variance for all three habitat types, compared to the coefficients of other driving factors. This suggests that invertebrate availability has the largest effect on where brown kiwi are found at night.

The close link between foraging behaviour and spatial behaviour shown in this study is common among many other animal species that exploit a similar niche to brown kiwi. Ship rats on Ponui Island alter their foraging behaviour significantly dependant on invertebrate food resources (Latham, 2006), while diet was also found to be the main driver of habitat choice for takahe (Baber & Craig, 2003), hedgehogs (Riber, 2006) and possums (Whyte, Ross, & Blackie, 2013). Changes in food availability are now considered to drive many observed changes in the distribution and behaviour of insectivorous bird species (Razeng & Watson, 2015). Therefore, it is no surprise that this has a large impact on brown kiwi spatial behaviour, especially considering they spend the majority (75%) of their time at night foraging (Cunningham & Castro, 2011).

Invertebrate availability also helps to explain much of the variation between seasons and locations. The increased amount of favoured invertebrate food in forest over the wetter seasons and pasture over the drier seasons (as shown in Chapter 2) correlates with increases in nocturnal utilisation of forest over winter and pasture during summer. The habitat selection of takahe on an offshore island was similarly influenced by the availability of seasonally obtainable food resources (Baber & Craig, 2003). Lower pasture utilisation rates in Pipe gully match the lower levels of invertebrate availability. Pasture shows the steepest coefficient gradient and thus the most pronounced relationship between invertebrate availability and habitat utilisation. This again mirrors the results of chapter 2, where pasture showed the most pronounced seasonal trends for diet. This indicates that pasture might be particularly important in the habitat utilisation of brown kiwi, and supports the findings of Watt (1971) that brown kiwi are successfully adapting to the novel environments introduced by humans.

Season was considered the next most important driver of habitat utilisation in the model. While the generated coefficient of variance scores were smaller than those for invertebrate availability, season still helps to explain some of the habitat utilisation patterns.

Once the effects of individuality and the three other fixed effects are taken into account, the model shows that in winter, birds are more likely to be found in forest than all other habitat types. This was evident when exploring the seasonal variation in recorded locations previously in the chapter, and reinforces the important role forest plays for brown kiwi over this time of year for both diet and behaviour. In summer, birds have reduced likelihood to be found in pasture than forest compared to in spring and only slightly more chance than in winter. This in fact shows an opposite trend to the spatial behaviours documented in my study, indicating that the increase in pasture utilisation over summer is mostly explained by factors other than season, likely invertebrate availability.

There is increasing empirical evidence that avian community organisation may vary significantly between seasons (Rice, Ohmart, & Anderson, 1983). In this study, both food availability and social/behavioural factors were identified as potential drivers for the recorded seasonal variation in habitat utilisation. However, isolating these complex behaviours from one another can be difficult (Rosenzweig, 1991).

Gully was the third most important driver of brown kiwi habitat utilisation in this study. Although the coefficient of variance scores for this factor are much smaller than invertebrate availability, the gully that a bird inhabits still helps explain some of the spatial behaviours exhibited.

Once the effects of individuality and the three other fixed effects are taken into account, the model predicts that Red Stony birds are less likely to be found within pasture and swamp habitat than forest, reflecting the partiality of Red Stony birds for forest habitat. In Kauri, birds are more likely to be found within pasture than forest, a result which mirrors the increased availability and utilisation of pasture in this location. Likewise in Pipe gully, much of the reduced likelihood of being located in scrub habitat is explained by its location, reflecting the different habitat availability of that gully. As each habitat can provide different benefits to an animal relating to fitness and survival (Block & Brennan, 1993; Dechant et al., 2002), the makeup of habitat within a gully appears to be one of the main drivers of brown kiwi habitat utilisation.

Social grouping was the fourth significant driver of habitat utilisation by brown kiwi in this study, despite the fact that social interactions of brown kiwi are traditionally thought to occur only occasionally (Taborsky & Taborsky, 1992). Once the effects of individuality and the three other fixed effects are taken into account, the factor of social grouping in the model explains that paired birds are less likely to be found in pasture and swamp habitats than in forest. This reflects the increased amount of paired birds that are located in forest habitat due to breeding behaviour. Birds living alone are slightly more likely to be found in non-forest habitat types, following the trends seen in the utilisation data.

The last factor considered in the final model was the random effect of Individual. Individuality can have a large effect on the spatial behaviour of studied birds (Rosenzweig, 1991), as results can be skewed by individuals that are constrained to certain areas within their realised niche (Stephens & Krebs, 1986). Although each individual brown kiwi on Ponui

Island appeared to utilise the habitat available to them slightly differently (see Appendix C), the large sample population and number of locations recorded per individual appears to have reduced individual impact on the overall results. The Hausman Test results suggest that the random effect of ID does not add anything to the model to help explain variation in the data. Though individuality may still have some effect on the habitat used by brown kiwi, the fixed effect variables (invertebrate availability, season, gully, social grouping) are thought to offer a better explanation of the data by themselves.

Minor driving factors

Demographic factors of age and sex, the behavioural factor of breeding status, environmental factors including rainfall and temperature and the temporal factor of shift were all removed from the overall model, with none appearing to explain significant variation in the data. This is despite many of these drivers showing significant within-factor variation in utilisation rates. It is likely that any variation found within these factors is encompassed by one of the major driving factors, despite not being significantly correlated with one another. Variation in breeding status might be explained better by season or social grouping, whilst variation in environmental variables is probably included in season. These factors were all added to the model in two or three way interactions, however none were significant, nor impacted the significance of any of the major driving factors.

3.4.3 Effectiveness of Technique

The triangulation technique used in this study proved effective for studying the nocturnal spatial behaviour of this difficult to monitor species. It is inevitable that any telemetry study will have some inherent error, so caution should always be taken when drawing conclusions from the data (Saltz, 1994). The level of error in this study, estimated by a beacon study to be less than 50m in over two thirds of locations, was considered acceptable for studying habitat utilisation at the larger macrohabitat scale with a large sample size.

This technique solved many of the problems inherent in previous studies that used different methods. The large number of samples collected for each bird was also seen to reduce the impact of individuality. A well-defined methodology resulted in minimal pseudo-replication, although ensuring sample birds were spatially representative was more difficult and might have had some impact on the results. Future studies should attempt to ensure their sample population is as spatially representative as possible.

In total, only 8% of all bearings taken were discarded for error. This is far less than the 37% of signals removed due to signal ‘bouncing’ in Lee et al. (1985). However, reaching this level of accuracy required much time and effort. To ensure accuracy the researcher must be extremely familiar with the topography of the study site and have relatively advanced telemetry experience. This took over six months of practise to develop on Ponui Island. So while this methodology proved an effective tool for the investigation of brown kiwi spatial behaviour, time and effort requirements may limit its practical use.

3.5 Summary

Objective 1: Document habitat availability within my study site on Ponui Island.

Scrub habitat was the most prevalent, followed by pasture, forest and swamp. Habitat availability differed between the three gullies and some habitat was not used at all.

Objective 2: Assess habitat utilisation rates of brown kiwi at night, including how this may vary with a range of spatial, temporal, demographic and behavioural factors.

Brown kiwi adults on Ponui Island did not utilise habitat in line with its availability at night. As observed in the past, forest habitat was utilised far above rates predicted by availability. Scrub, pasture and swamp habitat were utilised at rates lower than expected. While overall trends remained consistent across all birds, patterns of habitat use showed slight variation within a range of factors. Brown kiwi utilised habitat at different rates depending on their gully location, choosing forest habitat over scrub when the availability of pasture was reduced. Reduced access to a wider range of habitat types was seen anecdotally to have an effect on the health and survival of brown kiwi. Seasonal trends were also evident, characterised by a shift from forest during winter to increased pasture use over summer. Sex, age, social grouping and breeding status all had a small effect on utilisation rates. Reproduction and diet were both suggested as potential drivers of this variation.

Objective 3: Explore potential driving factors and identify those which best explain the observed patterns of brown kiwi habitat utilisation at night.

Four factors were identified as the main drivers of habitat utilisation, encompassing spatial, temporal, behavioural and environmental influences. The most important of these was the availability of invertebrate food. Linking the foraging behaviour of brown kiwi on Ponui Island to their use of habitat helped to explain seasonal trends in habitat use. Birds spent more time at night within habitats that contained the highest availability of favoured food items. Other important driving factors identified included season, gully and social grouping, though the vast majority of variation was explained by the first factor. Individuality was taken into account in the model, however was judged to be less important than the four fixed effect factors.

CHAPTER FOUR

Diurnal Utilisation of Shelters by Brown Kiwi

Plate 4.1 - Male brown kiwi Mauro resting during the day inside a surface burrow in the middle of a clump of reeds in pasture. Photo by author.

4.1 Introduction

The way an animal interacts with its environment can be influenced by, and in turn influence many aspects of its ecology including foraging, breeding and social behaviours. By increasing our understanding of an animal's spatial behaviour we can improve management and conservation initiatives (White & Garrott, 1990), helping to ensure that available habitat can meet all the requirements of a managed species. However, this requires in-depth knowledge of habitat preference. Habitat utilisation (or use) is often studied to assess habitat preference, and compares the frequency at which an animal uses a particular habitat with the availability of that habitat. By identifying how often particular habitats are used, we can discover areas that might be important to the animal in its fundamental (realised) niche to aid in fitness or survival (Block & Brennan, 1993). A species may select multiple habitats to reap the different benefits each can provide, including protection from predation, provision of shelter and nest sites, availability of food, and levels of both inter and intra specific interaction (Jones, 2001; Dechant et al., 2002).

Detailed investigation into habitat selection can often prove challenging (MacFaden & Capen, 2002). This is because the spatial patterns of animals are influenced by many different factors, encompassing aspects of biology and behaviour (Schoener, 1971), as well as the characteristics of its habitat (Adams et al., 2013). Often forming complex relationships, these driving factors change over time and from place to place and can be difficult for researchers to unravel (Rosenzweig, 1991). Investigations into habitat utilisation should aim to consider a wide range of ecological factors, including demographic factors such as density (Manly et al., 2002), sex and age ratio (Harris et al., 1990); environmental factors such as habitat structure (MacFaden & Capen, 2002), climate (Stevens, Bayne, & Wellicome, 2011), seasonality (Rice, Ohmart, & Anderson, 1983), resource availability (Rosenzweig, 1991) and levels of competition or predation (Hughes, Ward, & Perrin, 1994); as well as behavioural factors such as territoriality, individuality and reproductive or foraging strategies (Robinson & Holmes, 1982; Bjørneraas et al., 2012; Adams et al., 2013).

Roosting habitat is considered important to birds, as individuals can spend up to two-thirds of their time taking shelter at roost sites (D'Amico & Hemery, 2007). The availability of good shelters can influence the likelihood of an animal settling and surviving in an area (Souter, Bull, & Hutchinson, 2004), and can serve to reduce potential predation danger (Tiddeman &

Flavel, 1987) and aid in thermoregulation (Walsberg, 1986). When birds roost together there can be added social benefits; assisting in mate acquisition, breeding, and information transfer between individuals (Marzluff, Heinrich, & Marzluff, 1996; Blanco & Tella, 1999).

Despite its status as New Zealand's most iconic species, much remains unknown about the ecology of the kiwi (*Apteryx* spp.). With all five species classed as either threatened or at risk of extinction (Robertson et al., 2013), time is running short to fully understand their ecology. For the most common species, the brown kiwi (*Apteryx mantelli*), only an estimated 25,000 individuals remain, with numbers continuing to decline despite extensive management (Holzapfel et al., 2008). This decline highlights the importance of learning more about the spatial systems of brown kiwi in order to improve our management of these remaining birds.

Brown kiwi show considerable flexibility with regard to habitat use, with populations found roosting and foraging in many different habitat types. If some habitat types are more beneficial for brown kiwi than others, selective use of habitat would be expected (Taborsky & Taborsky, 1995). Brown kiwi spend a large proportion of their time roosting in day-time shelters (Jamieson et al., In Prep), utilising many different shelter types, including hollow logs, natural cavities, excavated burrows, swamp or grass plantings, man-made structures, and under surface vegetation (McLennan, Rudge, & Potter, 1987; Potter, 1990; Taborsky & Taborsky, 1995; Forbes, 2009). The type of shelter used appears highly dependent on macrohabitat type (Miles, Potter, & Fordham, 1997; Forbes, 2009), with surface sites used more often in pasture and scrub habitat than in native forest, where burrows and holes are more commonly used. In general brown kiwi are thought to prefer forested habitat for roosting over other areas, utilising native forest and scrub habitat more than expected based on its availability (Jamieson et al., In Prep). However, the habitat and type of shelter chosen by brown kiwi is not consistent, with variation seen between sexes (Miles, 1995; Forbes, 2009), seasons (Potter, 1989; Miles, Potter, & Fordham, 1997; Forbes, 2009), age classes (Gibbs & Clout, 2003; Shapiro, 2005; Forbes, 2009; Wilson, 2014), individuals (Potter, 1989), and in the presence or absence of a mate (Potter, 1989; Ziesemann, 2011). Roost choice might be influenced by specific feeding or shelter requirements, social influences such as pair bond maintenance, or simply the characteristics of the site itself, such as roost microclimate, density of birds or protection from predation and disturbance (Potter, 1989; Taborsky & Taborsky, 1995; Gibbs & Clout, 2003; Forbes, 2009). What is driving the selection of shelter sites in brown kiwi remains unclear, while the interaction between diurnal and nocturnal habitat utilisation has never been explicitly explored.

Unlike their nocturnal habitat utilisation (explored in Chapter 3), a considerable amount of prior research has investigated the spatial behaviour of brown kiwi during the day in both adults (McLennan, Rudge, & Potter, 1987; Potter, 1989; Miles, 1995; Taborsky & Taborsky, 1995; Forbes, 2009; Ziesemann, 2011; Jamieson et al., In Prep) and juveniles (Chan, 1999; Gibbs, 2000; Shapiro, 2005; Forbes, 2009; Wilson, 2014). Despite this, specific details of their roosting behaviours and roost selection remain limited, and a complete picture of brown kiwi roosting ecology has yet to be given. Many of these studies were limited in time or scale, while differences in tracking methodologies, location, population density, time of year, length of study and a whole host of other site-specific attributes between each study makes comparison difficult.

This chapter will develop a comprehensive understanding of diurnal habitat and roost selection in a high-density population of brown kiwi adults. Building upon a substantial body of previous work that was often limited in accuracy by small sample sizes or reduced scale, this chapter will better our understanding of brown kiwi behaviour by elucidating the roles of food availability, social/reproductive cues and shelter benefits on habitat and roost selection. By considering the diurnal spatial behaviour of brown kiwi at a large scale, we can investigate how this behaviour changes both spatially and temporally, and how behaviour and population demographics might affect habitat and roost choice. Significantly, for the first time we can compare how brown kiwi interact with their habitat while roosting during the day and while active at night. Identifying these spatial interactions and patterns is critical to better understand brown kiwi ecology, and may prove important to the future survival of the species, leading to an improved ability to manage current and future populations in the wild. The objectives for this chapter are outlined below, and hypotheses suggested based upon the knowledge gathered in previous studies.

Objective 1: Assess habitat utilisation rates of Ponui Island brown kiwi while roosting, including how this may vary with spatial, temporal, demographic and behavioural factors.

- *Hypothesis 1.1) Brown kiwi do not utilise habitat while roosting at rates predicted by availability, instead selecting to use forest more than other habitats.*
- *Hypothesis 1.2) Brown kiwi roosting behaviour varies between seasons and in different gullies, with birds utilising habitat at different rates.*
- *Hypothesis 1.3) Brown kiwi of different sex, age and social grouping utilise habitat for roosting at differing rates.*

Objective 2: Assess shelter selection of brown kiwi on Ponui Island while roosting, including how this may vary with a range of spatial, temporal, demographic and behavioural factors.

- *Hypothesis 2.1) Brown kiwi do not utilise the shelter sites available to them equally, instead favouring more structural burrows.*
- *Hypothesis 2.2) Brown kiwi roosting behaviour varies between seasons and in different gullies, with birds utilising shelter types at slightly different rates.*
- *Hypothesis 2.3) Brown kiwi of different sex, age or social grouping utilise shelter types for roosting at differing rates.*
- *Hypothesis 2.4) Shelter type selected by brown kiwi is dependent upon habitat type.*

Objective 3: Explore the relationship between diurnal roost choice and nocturnal habitat utilisation of brown kiwi on Ponui Island.

- *Hypothesis 3.1) Brown kiwi select shelters closer on average to favourable habitats, following seasonal trends in foraging behaviour.*
- *Hypothesis 3.2) Brown kiwi select shelters closer on average to favourable habitat if that habitat type is available within their home range.*
- *Hypothesis 3.3) Brown kiwi roosting behaviour and foraging behaviour are independent of one another.*

4.2 Methods

General information regarding the study site and species is given in Chapter 1. Daytime roosting locations of brown kiwi were observed over a twelve month period on Ponui Island from March 2013 to February 2014. Sampling periods were split into four seasons as follows; autumn (March - May) winter (June - August), spring (September - November) and summer (December - February).

4.2.1 Sample Population

In March 2013, as part of the Ponui Kiwi Research Programme, 49 adult brown kiwi were fitted with radio transmitters (WildTech Ltd., Havelock North, NZ) following the protocols described in the Kiwi Best Practise Manual (Robertson et al., 2003). Chapter 3 section 3.2.1 outlines this process in more detail. Forty six of the birds were already banded from previous years as part of the ongoing research programme. Therefore, most birds have a known history including pairing status, home range and social interactions. Three new birds (Adriana, Vaughan and Leigh) were found within burrows and added to the study population to replace birds which were lost from the study the year before through transmitter failure. Each transmitter had its own radio frequency; ensuring birds could be individually identified. Birds were sexed using DNA analysis of feather samples, and classed into three different age groups based on their estimated age (less than five, between five and ten, and more than ten years).

4.2.2 Habitat Analysis

Habitats within the 1.2km^2 study site were classed as one of four broad macrohabitat types consisting of forest, scrub, pasture and swamp, and plotted onto a map using Arc GIS (Fig. 4.1). Chapter 3, section 3.2.2 outlines this process in more detail. The area (in km^2) covered by each habitat type within the study site and within each individual gully was measured using the calculator function in Arc GIS. The relative proportion of each habitat type was then calculated to determine their availability to brown kiwi within the study site.

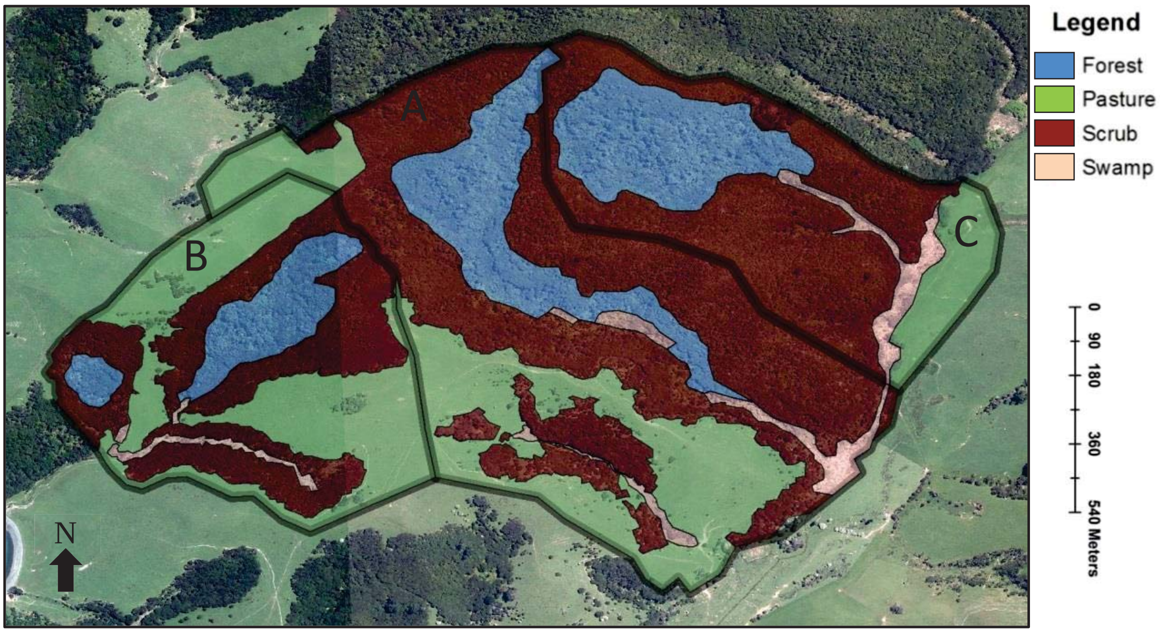


Figure 4.1 – Habitat map of the study site on Ponui Island. Showing the area of Forest, Pasture, Scrub and Swamp habitat within each of the three gullies. (A=Red Stony, B=Kauri, C=Pipe). Photograph from LINZ.

4.2.3 Collecting Brown Kiwi Location Data

Forty seven of the 49 banded brown kiwi adults were tracked using a Telonics TR4 receiver and Yagi three element antenna to detect transmitter signals. These included 26 males and 21 females spread across all three gullies (see Appendix I).

Up to thirty birds were located each day, with sampling focused on one or two selected gullies. It was ensured that any birds which were to be tracked during their nocturnal activity phase were located during the day before and the day after. This guaranteed that we had at least four daytime roosting locations per month for all 47 tracked birds. For the two months prior to the start of nocturnal sampling in May, all birds were located during the day only two times per month.

Birds were located using the 'homing in' telemetry technique, where the observer moves in the direction of the strongest signal until the bird is either visible or a strong signal is detected without the use of the antenna. GPS coordinates were recorded at each roosting location using a Garmin GPS (eTrex® H), as well as a description of the shelter site, the gully it was found in, and number of brown kiwi present (if possible to sight the birds). Birds located just outside of the study site were classed within the closest of the three main gullies, while those which strayed large distances were excluded from the analyses.

Shelters were described as one of four types: tree burrows, soil burrows, swamp sites, and surface sites. Tree burrows included either natural or excavated holes in trees or tree root systems that were alive, dead or fallen. Soil burrows were limited to excavated holes in the ground while swamp sites included any tunnels or shelters formed by vegetation occurring in swamp habitat. Any time a bird was not located in a burrow its location was classified as a surface site. Birds were found at surface sites most frequently under fallen or low-lying vegetation, or shrubs and sedge clumps in pasture, and were often visible to the researcher. All permanent burrow and nest locations were marked with flagging tape and given an identification number. Surface sites were not marked, but detailed descriptions along with coordinates were taken each time.

To minimise any impact on their spatial behaviour, effort was made to reduce disturbance to birds when locating them. Birds roosting on the surface were quietly approached to within a distance of 10m, stopping as soon as they could be sighted and GPS coordinates taken. To reduce the chance of nest abandonment, males known or suspected to be nesting were never sighted, instead relying solely on the strength of the telemetry signal without the antenna plugged in. If a bird was handled for re-banding (only outside of the breeding season) or for any other reason, it was not tracked for at least two days to avoid further disturbance.

All GPS coordinates of brown kiwi roost locations were mapped in Arc GIS version 10.2.2, and layered onto the previously produced habitat map. Using the Editor Toolbar, locations were then assigned a habitat type based on the habitat polygon each GPS point was contained in.

The month, season, gully (Red Stony, Kauri, Pipe or Other), sex (Male or Female), age (1-5, 6-10, <10) and social grouping (paired, group, alone), were all also recorded with each brown kiwi location.

4.2.4 Radio Telemetry Error

The homing technique used in this chapter has less inherent bias than the triangulation methodology typically used at night, as locations are not estimated or calculated, but actually known (Keye, 2008). As a result there was no impact of signal error. Homing is especially useful when birds are at a roost as presence of the researcher will not change their behaviour. Locating brown kiwi using the homing in method can take a long time, as only a single bird can be tracked at once. As brown kiwi remain in their shelter site throughout the entire day each bird was only located once per day and thus unlike the previous chapter pseudo-replication error is reduced.

Ensuring bird locations were spatially representative was difficult because I worked with only a sample of selected birds. Historically, birds that only used the large swamp areas at the bottom of each gully were released from the study population, and therefore some areas of the study site did not include any home ranges of marked birds. Additionally, in the past birds found close to other banded brown kiwi were often selected to aid in the study of social interactions between study birds.

4.2.5 Distance to Habitat

To assess the interaction between nocturnal habitat utilisation and diurnal roosting behaviour, the distance from each roost location to both forest and pasture habitats was measured. These two habitats were chosen based on the results of Chapter 3 which suggested that forest and pasture habitat are most important for brown kiwi adults on Ponui Island. Distance was measured in google maps by plotting the location and then recording the straight line distance from the roost to the border of the closest pasture and forest habitats. If a roost was located within one of these habitats then it was given a measurement of zero metres for that habitat type.

4.2.6 Statistical Analyses

All multivariate statistical analyses were performed using SPSS 20. Microsoft Excel 2010 and Graph Pad Prism 6 were used to generate further graphs and tables. A probability of ≤ 0.05 was deemed statistically significant.

The frequency of brown kiwi locations within each habitat type over the entire study was compared to predicted habitat use based on the availability of each habitat within the study site. A one-sample chi squared test was used to determine if apparent differences between actual habitat use and the expected habitat use were significant, with the expected values entered into the matrix by hand. Variation in habitat utilisation and shelter type utilisation rates between groups within a range of temporal, spatial, demographic and behavioural factors was also assessed using additional Pearson chi squared tests. Due to the large number of variables tested for both habitat and shelter type datasets (5), probability was corrected for using Holm-Bonferroni Sequential Correction (see Holm, 1979). This method presents a less conservative correction than the standard Bonferroni, and is used frequently in Ecological studies (Nakagawa, 2004). Corrected P values are presented in the results.

Variation in the distance to pasture and distance to forest were separately compared across seasons and gullies in a series of independent sample Kruskal Wallis tests. The Kruskal-Wallis H test is a rank-based nonparametric test used to identify statistically significant differences between two or more groups of a continuous or ordinal independent variable, such as distance (Field, 2013).

4.3 Results

4.3.1 Habitat Availability

The four habitats considered in this study were available in differing proportions within the study site (Table 4.1). Scrub was the most prevalent habitat type, covering almost half of the available area. Pasture and forest habitat covered a large proportion of what remained, with swamp only sparsely available. Each gully had a different overall distribution of habitat types, though this difference was most pronounced between Pipe and the other two gullies, with less forest and more swamp habitat available. Some areas of the study site were never used by the sample of brown kiwi tracked on Ponui Island (Fig. 4.2), given that they were not part of their home range. These areas were included in the availability analysis because I did not have home range data available and calculating it was outside the scope of my study. An attempt was made to remove these areas anecdotally; however this had a very small effect on results (changes of 2% on average). Given the non-robust approach, and small impact this would have had on results, the entire area was included.

Table 4.1 – Total area and proportions of the study site on Ponui Island covered by each of the four main habitat types.

Habitat	Area (Km^2)	Proportion of Study Site
Forest	0.21	19%
Scrub	0.54	48%
Pasture	0.33	29%
Swamp	0.05	4%

4.3.2 Habitat Utilisation

Tagged brown kiwi were located roosting a total of 2130 times over the twelve months of the study. In total, 172 different permanent shelters were utilised including both nests and burrows (Fig. 4.3). Birds were found roosting 259 times on the surface, usually under vegetation. Permanent sites were almost always used multiple times, with many containing a tagged bird more than 50 times during the study, and one frequented 76 times in total.

Data collection was evenly spread, with similar numbers of location fixes recorded for each season, gully, shift and sex. Samples were also spread evenly across the 47 tracked birds

(Appendix I), with an average of 45 diurnal locations per bird (± 1.27 SE). All birds were located in forest at least once, with six found exclusively in this habitat. 15 birds occurred in three different habitats, and six were found in all four over the course of the study (Appendix N). Individuals reused certain shelters many times over the course of the study and would often remain in one place for several weeks or even months. Brown kiwi were found roosting throughout the majority of the study site in all habitat types, although certain areas of the study site appeared to be used more often than others (Fig. 4.2).

Brown kiwi were located within each habitat type at differing proportions (Table 4.2). Birds were predominantly located within forest habitat, with much fewer found roosting in scrub, swamp or pasture. Habitat utilisation rates differed significantly from the expected rates based on habitat availability (one sample chi squared test; X^2=4404.251, df=3, P<0.001) (Appendix O). Overall, brown kiwi on Ponui Island were located within forest and swamp habitats more often and in scrub and pasture habitats less often than the availability of these habitats would suggest (Fig. 4.3).

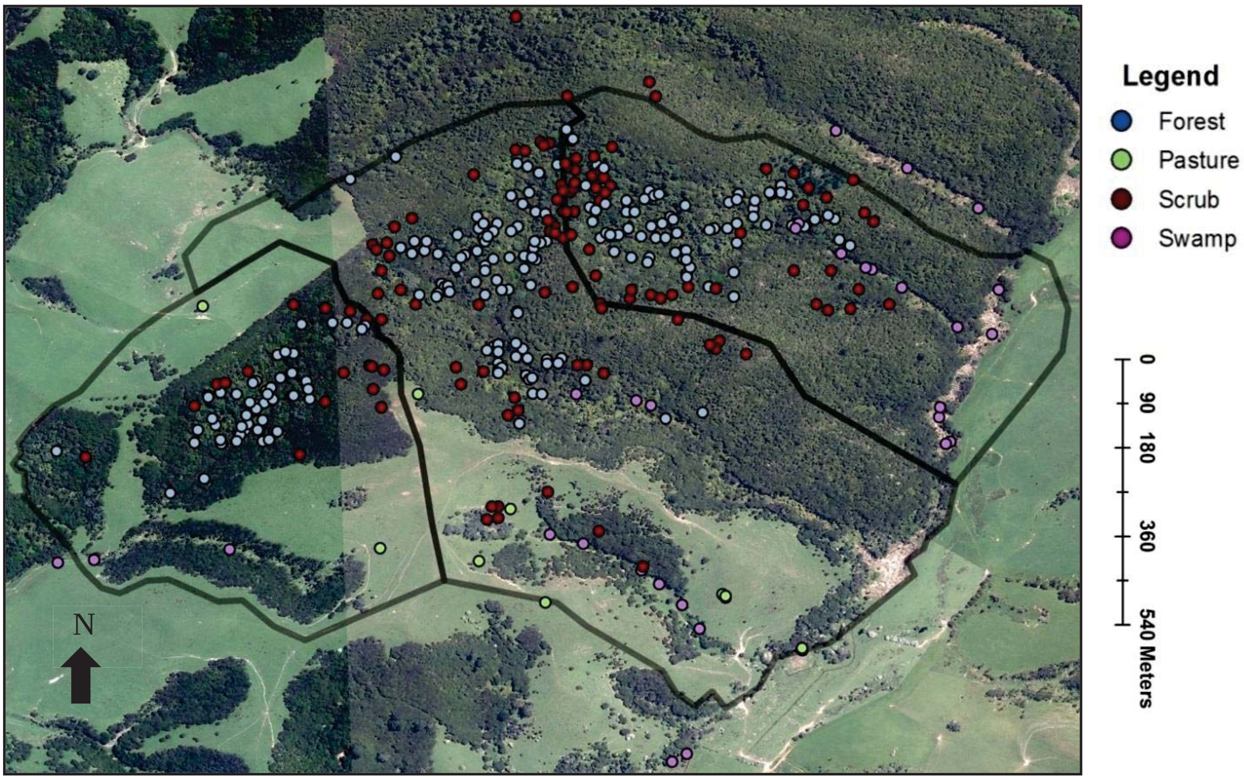


Figure 4.2 - GIS map illustrating the location of all 455 different diurnal roosting sites of brown kiwi on Ponui Island over the course of the study, with the corresponding habitat type for each point identified by colour. Photograph from LINZ.

Table 4.2 – Total number and proportions of diurnal roosting locations of brown kiwi on Ponui Island over the course of the study between each of the four main habitat types.

Habitat	# Locations	Proportion of Total Locations
Forest	1195	74%
Scrub	825	17%
Pasture	315	2%
Swamp	42	7%

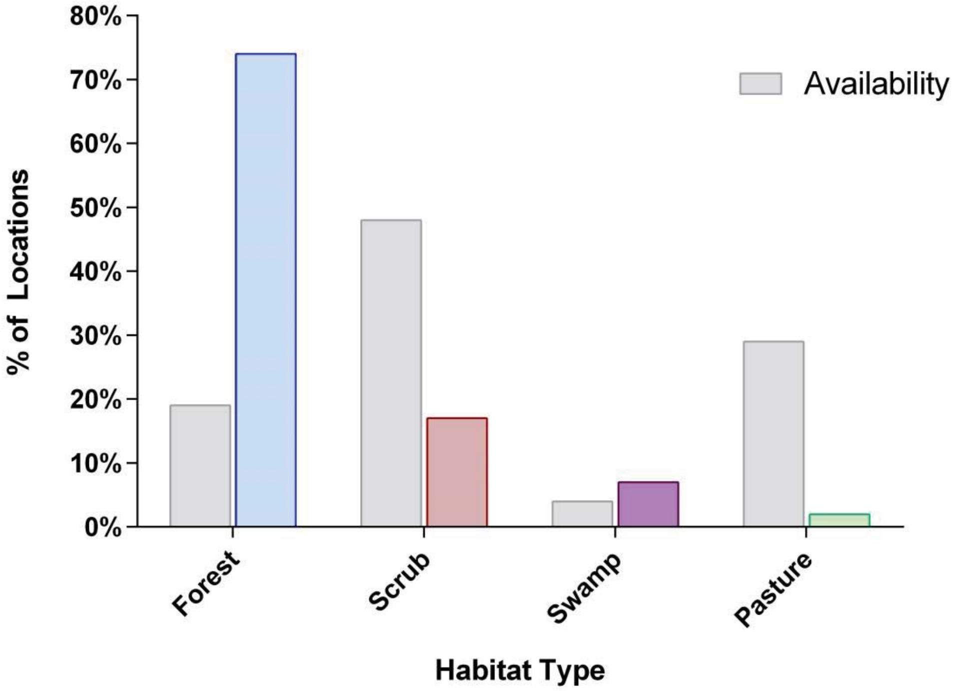


Figure 4.3 – Percentage of diurnal roosting locations of brown kiwi found within each of the four main habitat types over the course of the study, compared to the expected utilisation rates based on habitat availability.

Temporal Variation

The habitat used for roosting differed between seasons (Pearson chi square test; Chi Square=196.724, df=9, P<0.001) (Appendix O). Each of the four seasons followed the same overall trend, with forest habitat preferred, followed by scrub, swamp and then pasture (Fig. 4.4A). However, birds were found roosting in forest habitat slightly more often during winter and spring and in other habitats slightly more often in summer and autumn.

Spatial Variation

Habitat utilisation rates of brown kiwi roosting in the study site differed between gullies (Chi Square=822.029, df=9, P<0.001) (Appendix O). Birds roosted predominantly within forest habitat in all three of the study site gullies, with Kauri gully birds using this habitat particularly frequently (Fig. 4.4B). Rates of scrub and swamp habitat use were consistent between Red Stony and Pipe gullies, while Kauri birds were less likely to be found roosting in these habitats. Red Stony was the only gully in which brown kiwi were found within pasture.

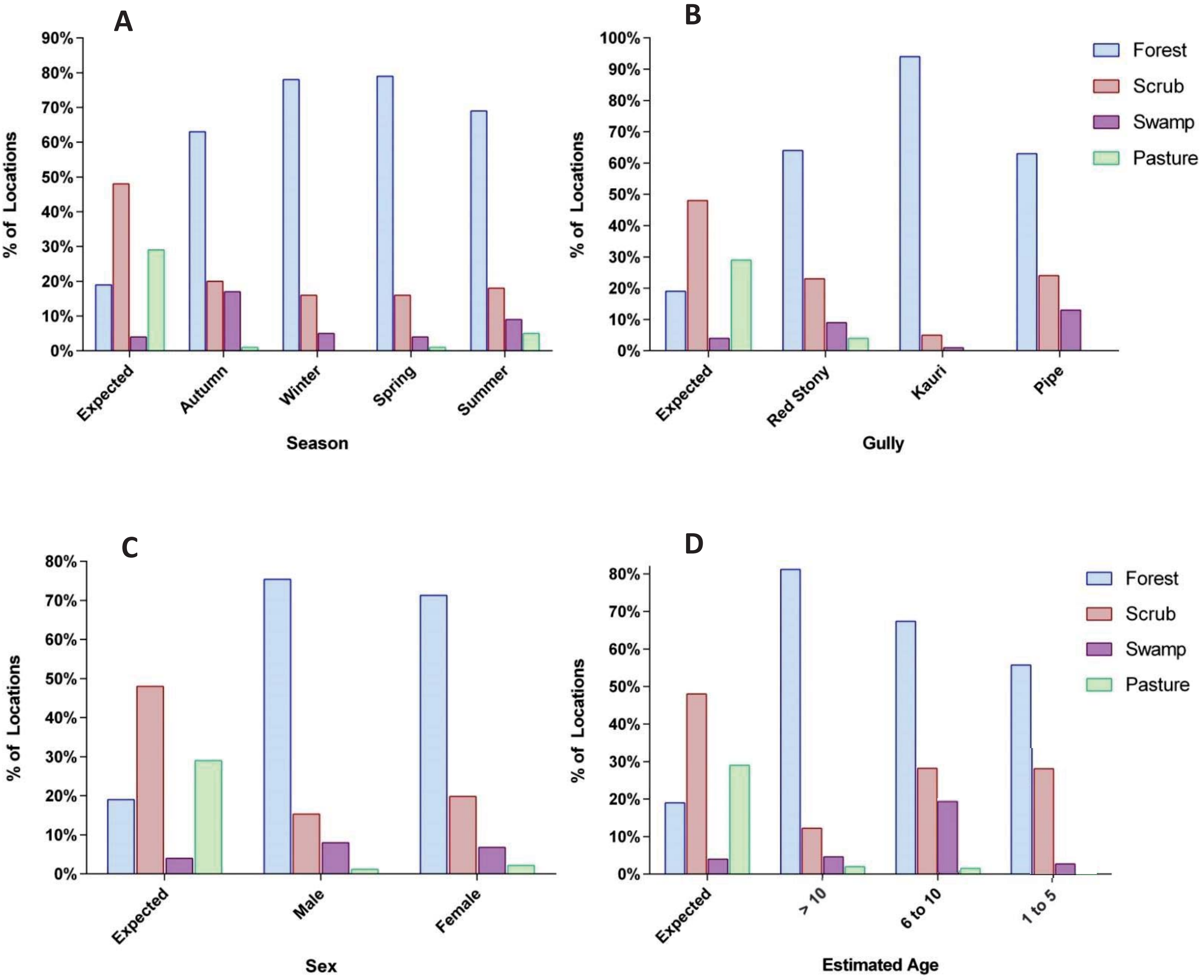
Demographic Variation

Males and females used roosting habitats differently (Chi Square=11.442, df=3, P=0.01) (Appendix O), although these differences were slight. Both sexes utilised forest habitat significantly more, with fewer found in other habitats (Fig. 4.4C). Males were located more frequently in forest and swamp habitats than females, while females were slightly more likely to be found within scrub and pasture.

Habitat utilisation rates of brown kiwi when roosting also differed between birds of different age groups (Chi Square=95.311, df=6, P<0.001) (Appendix O). All birds followed a similar trend, with forest habitat used the most, followed by scrub, swamp and then pasture (Fig. 4.4D). However, birds between one and five years old were located less often in forest habitat and more often within scrub than other age groups. Birds in this age group were very rarely found roosting in pasture or swamp habitat. Birds between the ages of six and ten were found roosting within swamp habitat more often than other age groups, while birds over the age of ten were found more often within forest habitat.

Behavioural Variation

Roosting habitat was affected by a bird’s social grouping (Chi Square=202.349, df=6, P<0.001) (Appendix O). While all birds were found most often within forest habitat, those which were alone or in a group were more likely to use other habitat types for roosting than paired birds (Fig. 4.4E). Those which sheltered alone were found more frequently in swamp habitat and were the least likely to roost in forest. Those which were part of a group had marginally higher rates of scrub utilisation than other social groupings.



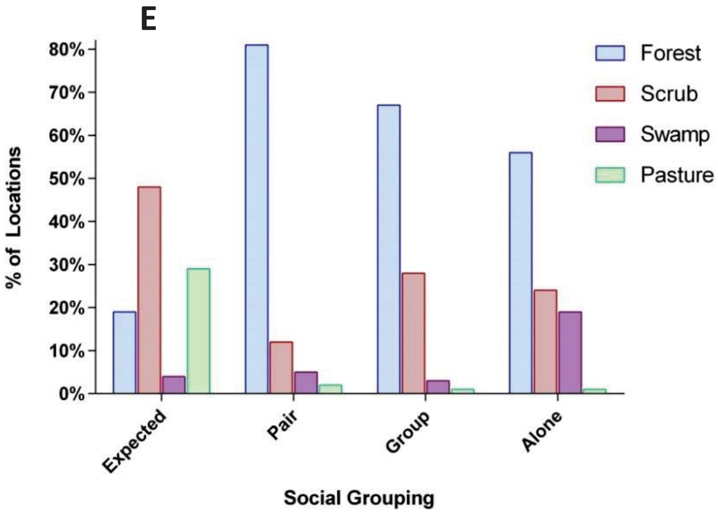


Figure 4.4 - Variation in diurnal habitat utilisation rates of brown kiwi in four habitat types while roosting on Ponui Island compared to expected rates based on habitat availability, across a number of potential driving factors:

A = Percentage of roosting locations of brown kiwi found in each habitat type over four seasons.

B = Percentage of roosting locations of brown kiwi found in each habitat type within three study gullies.

C = Percentage of roosting locations of male and female brown kiwi found in each habitat type.

D = Percentage of roosting locations of brown kiwi in three age groups found in each habitat type.

E = Percentage of roosting locations of brown kiwi in three social groupings found in each habitat type.

4.3.3 Shelter Utilisation

Brown kiwi were located within four different types of shelters over the course of the study (Fig. 4.5). Shelter types were utilised in differing proportions, with tree and soil burrows used more often, followed by surface and then swamp roost sites (Table 4.3).

Figure 4.5 - GIS map illustrating the location of all 455 different diurnal roosting sites of brown kiwi on Ponui Island over the course of the study, with the corresponding roost type for each point identified by colour. Photograph from LINZ.

Table 4.3 – Total number and proportions of diurnal roosting locations of brown kiwi on Ponui Island over the course of the study between each of the four different shelter types.

Habitat	# Locations	Proportion of Total Locations
Tree Burrow	1051	49%
Soil Burrow	695	33%
Surface	259	12%
Swamp Burrow	125	6%

Temporal Variation

Tree burrows were the most frequently used shelter site for brown kiwi throughout the year, with relatively consistent rates between seasons (Fig. 4.7A). However, there was a difference overall in the way brown kiwi used the four different shelters between seasons (Pearson chi squared test; Chi Square=190.057, df=9, P<0.001) (Appendix P). Soil burrows were the next most frequently used shelter type, with rates of use increasing in spring and decreasing significantly over autumn. The number of locations in surface and swamp roost types peaked over autumn and to a lesser extent in summer.

Spatial Variation

The rate at which different shelter types were used by brown kiwi in the study site differed between gullies (Chi Square=297.405, df=9, P=<0.001) (Appendix P). Red Stony and Pipe gullies exhibited almost identical patterns, with tree and soil burrows utilised evenly, followed by surface and then swamp sites (Fig. 4.7B). However, Kauri birds were found roosting predominantly in tree burrows, with lower utilisation of all other shelters compared to the other two gullies.

Demographic Variation

Male and female brown kiwi appeared to utilise shelters differently (Chi Square=41.726, df=3, P<0.001) (Appendix P). Both sexes were found predominantly within tree burrows, followed by soil burrows, surface sites and swamp sites (Fig. 4.7C). However females were more likely to be located on the surface than male birds, which were found slightly more frequently in soil burrows.

Brown kiwi of different age groups also showed variation in shelter utilisation (Chi Square=25.137, df=6, P<0.001) (Appendix P), despite following similar trends. Tree burrows were used more often across all age groups, followed by soil burrows and then surface and swamp sites (Fig. 4.7D). However, birds between the age of one and five were located roosting in soil burrows and on the surface more often than birds of other age groups, and less often in tree or swamp sites. Birds over ten were more likely to be found roosting in tree burrows and less likely to be found in surface roosts compared to younger birds.

Behavioural Variation

The type of shelter utilised by brown kiwi on Ponui Island differed according to social grouping (Chi Square=239.821, df=6, P<0.001) (Appendix P). Birds not part of a pair or group were located far less frequently in tree burrows and instead were found more frequently in all other habitat types (Fig. 4.7E). They were also located far more often in swamp sites than other social groups. Birds which were part of a pair or group had similar rates of utilisation for all shelter types with the exception of soil burrows, which were used more frequently by paired birds.

The Impact of Habitat

Brown kiwi on Ponui Island chose different shelters depending on the habitat type they were roosting in (Chi Square=2051.007, df=9, P=<0.001) (Appendix P). Birds roosting in forest habitat were found more often in tree burrows, but were also found roosting in soil burrows and very infrequently on the surface (Fig. 4.6). Birds in scrub habitat were found mostly within soil burrows or on the surface, with some also located in tree burrows. In pasture habitat, birds were found mostly within soil burrows, with a large percentage also found to use surface roosts. Swamp habitat was the only habitat in which brown kiwi were found within swamp sites, though birds were also found in soil burrows.

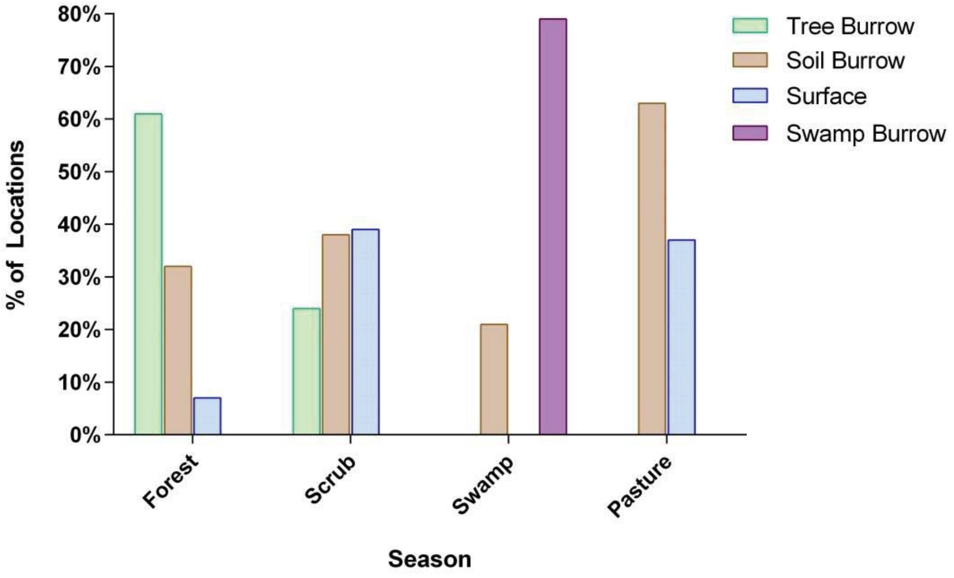


Figure 4.6 - Proportion of brown kiwi diurnal roosting locations recorded for each shelter type within four different types of habitat over the course of the study.

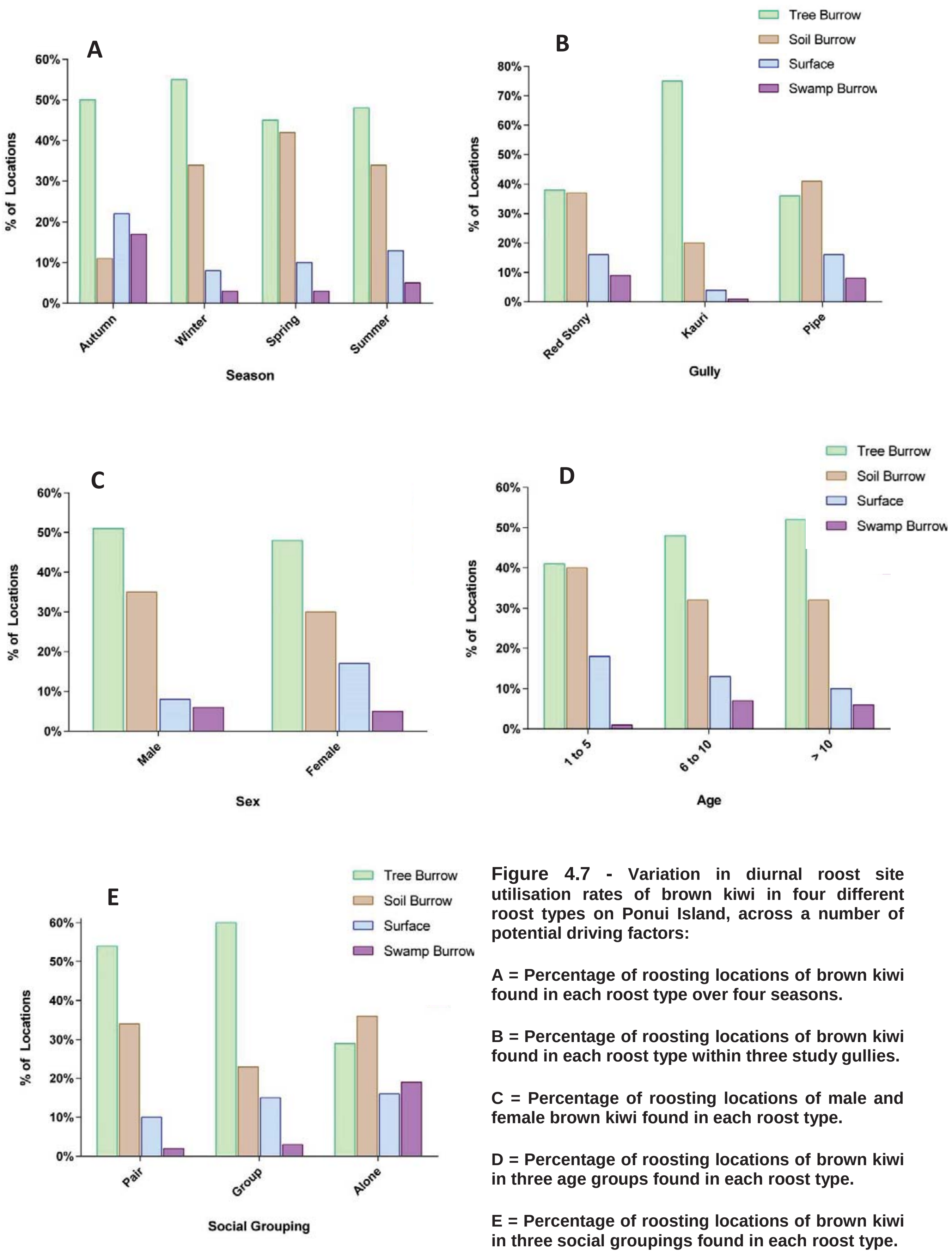


Figure 4.7 - Variation in diurnal roost site utilisation rates of brown kiwi in four different roost types on Ponui Island, across a number of potential driving factors:

A = Percentage of roosting locations of brown kiwi found in each roost type over four seasons.

B = Percentage of roosting locations of brown kiwi found in each roost type within three study gullies.

C = Percentage of roosting locations of male and female brown kiwi found in each roost type.

D = Percentage of roosting locations of brown kiwi in three age groups found in each roost type.

E = Percentage of roosting locations of brown kiwi in three social groupings found in each roost type.

4.3.4 Distance of Roost to Favourable Habitat

Over the course of the study brown kiwi were found roosting in sites located an average of 193 metres away from pasture, and 20 metres away from the closest forest habitat. This result suggests that birds prefer to roost close to or within forest habitat. However, these values varied significantly, with deviations of ±135 metres for pasture and ±62 metres for forest.

Temporal Variation

The distance between roosts used by brown kiwi on Ponui island and favourable nocturnal habitat varied between seasons for both pasture (Kruskal Wallis Test: Chi Square=73.959, df=3, P=<0.001) and forest (Chi Square=64.172, df=3, P<0.001) (Appendix Q). The distance from roost sites to pasture habitat decreased on average over autumn and summer, and increased during winter and spring (Fig. 4.8). Conversely, the distance from roost sites to forest habitat increased over autumn and summer, and decreased during winter and spring.

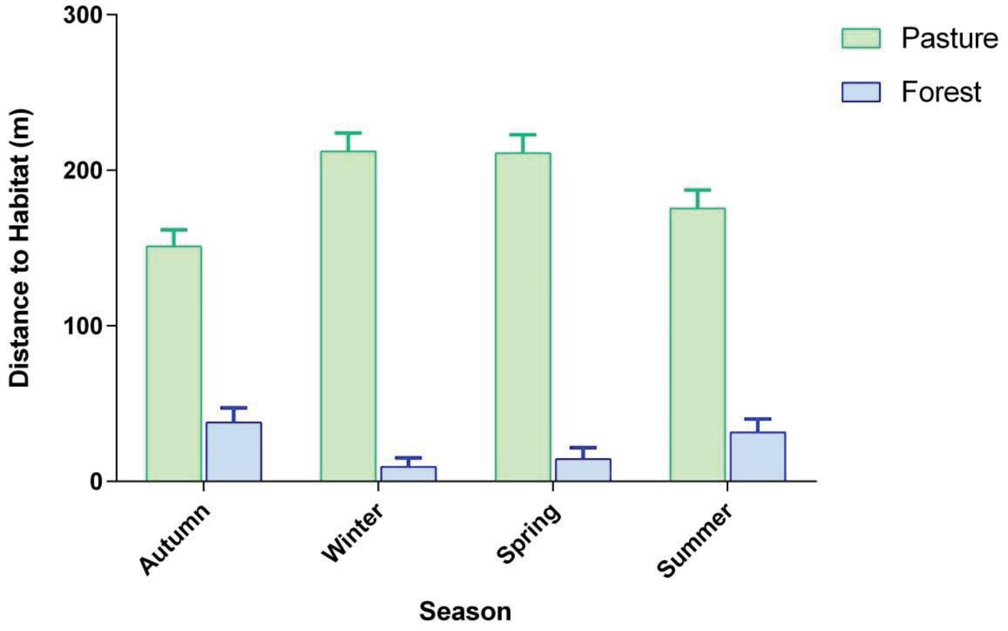


Figure 4.8 – Means and Standard Error for the distance between roost sites and pasture or forest habitat over the four seasons sampled over the course of the study.

Spatial Variation

The distance between roosts used by brown kiwi on Ponui island and favourable nocturnal habitats varied between gullies for both pasture (Chi Square=1153.793, df=3, P=<0.001) and forest (Chi Square=201.690, df=3, P<0.001) (Appendix Q). Birds in Kauri gully were found roosting nearest to both pasture and forest on average compared to other gullies, while Red Stony birds roosted slightly further away (Fig. 4.9). Birds in Pipe were found roosting much further from pasture than the other gullies, while birds located in other gullies were the furthest away from forest on average.

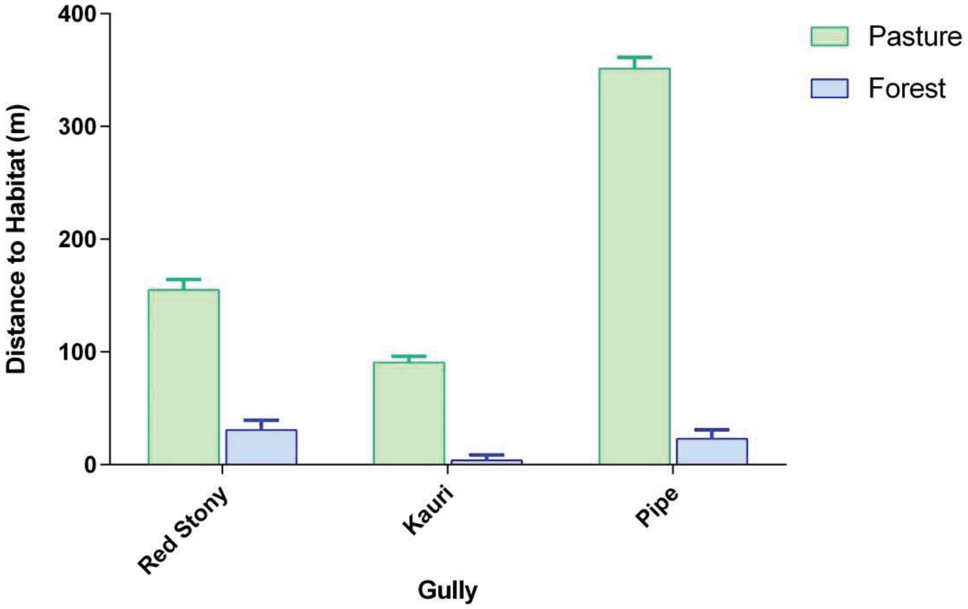


Figure 4.9 - Means and Standard Deviation for the distance between roost sites and pasture or forest habitat in each of the four locations sampled over the course of the study.

4.4 Discussion

4.4.1 Roost Selection

Brown kiwi on Ponui Island selected for forest, roosting in this habitat significantly more often than expected based on habitat availability. Forest habitat accounted for nearly three quarters of the total locations recorded. Six birds were found roosting exclusively within this habitat type over the entire study, while forest was utilised less than 40% of the time by only six birds. The higher selection of forest habitat for roosting matches the conclusions of recent studies of brown kiwi adults both on Ponui Island (Jamieson et al., In Prep) and in other locations (Forbes, 2009). Brown kiwi on Ponui Island also appeared to favour structural shelter types, actively selecting for tree burrows and soil burrows most often. The same result was found by (Jamieson et al., In Prep) on Ponui Island, though this differs from research in other locations. Both McLennan, Rudge, and Potter (1987) and (Forbes, 2009) observed that brown kiwi adults were found more often on the surface than in burrows. This inconsistency could be due to differences in habitat availability and structure between study sites, or the time of the year that sampling took place.

Strong predilection toward one habitat over others is common among avian species (Jones, 2001). In some cases the habitat most selected for will provide everything required for reproduction and survival. Generally however, constraints such as competition will limit the areas that can be exploited by each individual, forcing a bird into its realised niche (Szaro, Brawn, & Balda, 1990; Sinclair, Fryxell, & Caughley, 2006).

Foraging and breeding behaviours might help to explain this habitat selection. Forest habitat was identified as an important source of invertebrate food throughout the year (see Chapter 2), and was also where the majority of nest sites were used by tagged birds for incubation over the course of the study. The majority of male birds which incubated an egg during my study did so within soil burrows, perhaps due to thermoregulatory benefits. The selection of certain habitats for egg laying has been documented in a number of other birds including the barred owl (Mazur, Frith, & James, 1998), cuckoo (Vogl et al., 2004) and kakapo (Atkinson & Merton, 2006).

Tree burrow and soil burrow shelters are also the most structurally sound of the four roosts available, and provide the most protection from the elements (Coombs, Bowman, & Garroway, 2010). Burrows may also deter predators by preventing scent from drifting as far via wind, and by having a small hole entrance which is more easily defended by brown kiwi (Forbes, 2009).

There was a clear relationship between the habitat and type of shelter utilised by brown kiwi during the day on Ponui Island. This relationship has been identified before by many different authors (Taborsky & Taborsky, 1995; Miles, Potter, & Fordham, 1997; Beck & Jennings, 2003; Forbes, 2009). Each habitat is structured differently and thus provides different shelters for brown kiwi to exploit. The density of favourable roost sites can also differ between habitats (e.g. Beck, 2003). Birds in forest habitat were found roosting in tree and soil burrow sites almost exclusively in my study, as forest provided the largest and oldest trees more suitable for the development of the more commonly used tree burrows. Additionally, the majority of the gully floor in each gully was made up by forest habitat, and these areas possessed moister soil perhaps more conducive for digging soil burrows.

Scrub was the second most used habitat overall with 17% of all brown kiwi roosting locations found within this habitat. Scrub provides increased shelter to brown kiwi compared to other habitat types, and helps to reduce the impact of aerial predators (Potter, 1989). Additionally, the position of scrub habitat on Ponui Island acts as a buffer between forest and pasture, giving birds roosting in scrub quick access to both of these habitats considered especially important for foraging (see Chapter 2). Birds roosting in scrub used a combination of shelter types, but were found within surface sites and soil burrows more often. Relative to its availability, scrub was actually the least utilised habitat type. This is likely due to a reduction in favourable roosting sites, with far fewer tree burrows available, and soil with lower levels of penetrability, making the construction of soil burrows more difficult. Birds which roosted alone were more likely to be found in scrub, however there were few of these birds in our study sample, perhaps reducing scrub utilisation.

The majority of birds (82%) roosted within both forest and scrub habitat over the course of the study. Utilising multiple habitats for roosting may ultimately increase survival as each can play a different role in protection from predators, weather and provision of warmth and food (Jones, 2001). Currie et al. (2005) found that of 51 avian species studied in the Bahamas, almost all used a range of habitats. This reflects the important role that each habitat can play for different functions related to fitness and survival (Dechant et al., 2002). Other ground dwelling bird species endemic to New Zealand also utilise multiple habitat and vegetation types, with takahe exploiting both covered forest habitat and open pasture (Baber & Craig, 2003), and kakapo using both low growing vegetation and beech forest (Atkinson & Merton, 2006).

Swamp habitat was used by brown kiwi on Ponui Island for roosting slightly more than expected based on its availability. However, swamp habitat accounted for only 7.5% of all locations. Swamp sites shelter types were used equally little, with only 6% of locations recorded for this type of shelter. Swamp sites are limited entirely to swamp habitat, so both values likely reflect the very small amount of swamp habitat available in the study site (4%). Potential bias in the spatial representativeness of the sample birds may have compounded this, as many swamp birds have been historically removed from the study due to difficulty of access. This result is contrary to Taborsky and Taborsky (1995), who concluded that swamp and scrub were the most preferred habitats for roosting. It is possible that the warmer climate of their study site in Northland may reduce the reliance of brown kiwi on permanent burrows for thermoregulation, thus increasing their use of more open sites within swamp. The risk of more permanent structures like soil burrows flooding, as well as lack of trees help to explain the roosting choices of birds within this habitat.

Brown kiwi on Ponui Island did not choose pasture for roosting very frequently, utilising this habitat significantly less than expected based on its availability. This is probably due to a reduction in the availability of appropriate shelter sites, with pasture largely unsuitable for excavating new burrows and containing few natural cavities (Ziesemann, 2011). Brown kiwi that roosted in pasture were found either in soil burrows or else roosting on the surface under clumps of shrub or reeds. Surface sites are less preferable than soil or tree burrows that provide increased protection from potential predators and the strong, often cold winds that occur regularly at the study site (Jamieson et al., In Prep), as well as reduced disturbance from cattle and sheep. While the cryptic colouration of brown kiwi would have provided protection from historical aerial predators when roosting on the surface under shrubs or grasses, this is less effective against mammalian predators that primarily use smell to find their prey (King, 1990). The underutilisation of pasture for roosting reinforces the importance of more structural burrows to brown kiwi when roosting.

Temporal variation

Despite the overall trends remaining very similar throughout the year, brown kiwi roost choice varied slightly between seasons. Forest habitat was used by brown kiwi while roosting more often during the colder winter and spring seasons. Over this time tree burrows were also used more often, reinforcing the link between habitat and roost type choice. During the warmer summer and autumn months, more birds were found roosting in habitats other than forest, particularly swamp and pasture habitats. Birds were also found increasingly roosting in surface or swamp sites over this time. This confirms the suggestions of several authors (Potter, 1989; Miles, Potter, & Fordham, 1997; Forbes, 2009) that the roosting behaviour of brown kiwi changes throughout the year. Seasonal variation in shelter habitat has been reported in numerous other animals, including the reptilian gila monster (Beck & Jennings, 2003), and avian kakapo (Atkinson & Merton, 2006), found to shelter in the open more frequently when it is warmer.

The seasonal trends in habitat utilisation for roosting mirrors those seen in both the foraging behaviour of brown kiwi (see Chapter 2) and their use of habitat during the night (see Chapter 3). As the availability of invertebrate food increases in pasture over summer and autumn, birds appear to move from the mostly forested gully floor into other habitat types located closer to pasture to make the most of higher foraging success in this habitat over this time. Diet has been reported as a key driver of habitat use in many other species that exploit a similar niche, including the takahe (Baber & Craig, 2003), possum (Whyte, Ross, & Blackie, 2013), hedgehog (Riber, 2006) and ship rat (Latham, 2006). Foraging behaviour should therefore be considered an important driver of brown kiwi roost selection.

Breeding behaviour could also play a significant role in this temporal variation, as birds often favour certain habitats for reproductive purposes (Mazur, Frith, & James, 1998; Vogl et al., 2004; Atkinson & Merton, 2006). During the breeding season, which occurs mostly over winter and spring, birds may be more likely to be found within forest due to the large number of nest sites in this habitat type. An increase in soil burrow use over spring may also be linked to breeding, with soil burrows used for the majority of tagged brown kiwi nests during the study.

The structure of forest habitats, mostly present in the gully floor of the study site, might also be preferable for excavating burrows over winter, with moister soil and more cliffs and overhanging sites surrounding stream channels to dig burrows into. Additionally, the increased number of enclosed tree and soil burrows in this habitat might aid in thermoregulation, keeping birds warmer. In contrast over the warmer seasons surface roosts may serve the opposite purpose, keeping the birds cooler during the heat of the day.

Spatial variation

Utilisation rates of brown kiwi during the day for both habitat and roost type differed between gullies, suggesting that brown kiwi will alter their roost selection behaviour depending on the area they reside within.

Red Stony and Pipe gullies had very similar rates of both habitat utilisation and shelter type choice, selecting for forest most often followed by scrub and then swamp, with tree and soil burrows used equally. Both of these gullies are large and contain extensive forest habitat. The distinct lack of pasture available to Pipe gully birds had little bearing on the results due to the avoidance of this habitat for roosting by brown kiwi overall. In fact Red Stony was the only gully in which birds were found roosting within pasture at all, mostly due to a few individuals that roosted in Pasture relatively frequently, such as Mauro, Ken and Amanda.

Birds in Kauri gully selected forest habitat and tree burrows most often during the day, with less roosting in scrub and swamp habitats and soil burrow sites. Compared to the other gullies Kauri is small, with little distance between each of the habitat types. As such it is likely that Kauri birds were less inclined to move out of preferable roost sites in forest and tree burrows to move closer to pasture habitat when it was temporally favoured at night, due to its closer proximity.

Demographic variation

Males and females varied in their use of habitat and shelter types during the day, although these differences were small. Males were found roosting in forest habitat slightly more often than females, a result shared with both Miles, Potter, and Fordham (1997) and Forbes (2009). Males were also more likely to be found within trees and soil burrows than females. This is likely due to the requirements of incubation for males, restricting them to nest sites, which were predominantly located in forest during the study and were limited to soil burrow or tree burrow sites only. Females are less impacted by this requirement and as such were able to utilise different types of shelters more often and could roost further from forest habitat in scrub and pasture. These results support the findings of Forbes (2009) of brown kiwi in the Coromandel, but are opposite to trends seen by Miles, Potter, and Fordham (1997) in the central North Island. This difference may be due to variation in habitat availability, as Ponui Island possesses a significantly more fragmented habitat.

Differences in roost choice were apparent between three distinct age groups. Young birds used forest habitat the least out of all three age groups and were found roosting very infrequently in swamp and never in pasture. Instead birds in this age group were the most likely out of all age groups to be found in scrub. This has also been documented in other studies focused on brown kiwi juveniles (Gibbs & Clout, 2003; Wilson, 2014; Shapiro, Castro, & Colbourne, In Prep) and is thought to be due to this more densely covered habitat being perceived as safer from predation (Gibbs & Clout, 2003). Younger birds were found less within tree burrows than older birds, instead using soil and surface roost sites, both of which were common within scrub habitat. Protection from predation was one of the most important drivers of habitat utilisation in another ground dwelling New Zealand bird, the takahe (Baber & Craig, 2003). The inexperience or else small size of young birds may also have resulted in them being outcompeted and forced away from the more favourable roosting habitat in forest and tree burrows by older, more experienced birds. This explains why birds over ten years old were the most likely to be found roosting within tree burrows. Birds in the two older group’s shared similar patterns of roost choice, suggesting that roost selection remains similar after a certain age is reached.

Behavioural variation

Despite following similar trends, brown kiwi of different social groupings exhibited slightly varied roost choice behaviour. Birds which were part of a pair or group were found more often roosting within forest habitat in the more favourable structural tree and soil burrows. This is likely due to breeding, where the male will remain roosting in a single nesting site while incubating, occurring any time between late June and early February. The female is increasingly thought to remain closer to the nest over this time as well.

Alternatively, birds which were not part of a pair or a group were the least likely to be found in roosting in forest, and instead frequented swamp and scrub habitats within swamp or surface roosts. This suggests that birds which are forced to utilise sub-par habitat are less likely to form a pair or a group as their territory is considered unfavourable to potential suitors. These birds may be inferior or else inexperienced and thus lack the abilities required to obtain and defend a superior territory. This suggests that those birds which are able to find a mate and form a pair or a group are likely to out-compete those which cannot, gaining the most sought after shelters for roosting. Likewise, birds which are forced to utilise sub-par habitat are less likely to form a pair or a group due to their unfavourable territories, and as such are left by themselves with the less favourable swamp and surface sites.

4.4.2 Nocturnal and Diurnal Interaction

Recent research by Jamieson et al. (In Prep) suggested that the close proximity of different habitat on Ponui Island is such that brown kiwi would likely make independent foraging and roosting decisions. With habitat destruction reducing brown kiwi to increasingly fragmented and varied habitats (Potter, 1990), understanding the interaction between these two behaviours is increasingly important. However, until now this relationship has never been implicitly assessed in any brown kiwi population.

Results from my study suggest that the spatial behaviour of brown kiwi when roosting during the day is in fact impacted by their spatial behaviour during the night (Chapter 3), and thus foraging and roosting behaviours are not independent of one another.

A link between roosting and foraging behaviour will benefit the animal, allowing it to respond better to fluctuations in resource availability (Paprocki et al., 2015) and thus maximise its net intake of energy (Stephens & Krebs, 1986). An extreme example of this can be seen in those birds which migrate to different continents in order to make the most of changing resource availability.

The use of habitat recorded in both diurnal and nocturnal brown kiwi locations follow identical seasonal trends. Over the colder winter and spring seasons forest is utilised at an increased rate during the night due in large part to an increase in availability of favoured invertebrates over these seasons (See Chapters 2 + 3). During this time brown kiwi appear to select roost sites located closer to forest habitat. Alternatively, in the warmer summer and autumn, brown kiwi show higher utilisation of pasture habitats when foraging at night. Birds appear to alter their roosting behaviour as a result, selecting those roost sites which are closer to pasture, leading to an increase in the use of habitats other than forest for roosting over this time.

A similar interaction in nocturnal and diurnal habitat use was found between gullies. Birds within Kauri and Red Stony were located in pasture at night much more often than those from Pipe gully. Similarly, birds in Red Stony and Kauri gullies were seen to roost much closer to pasture on average than birds from Pipe. This suggests that brown kiwi will roost closer to the habitats they are utilising. This also reflects the constraints faced by Pipe birds, which would have to cross a larger distance and thus larger number of home ranges in order to reach pasture habitat.

4.5 Summary

Objective 1: Assess habitat utilisation rates of Ponui Island brown kiwi while roosting, including how this may vary with spatial, temporal, demographic and behavioural factors.

Brown kiwi adults on Ponui Island did not utilise habitat in line with its availability when roosting, selecting for forest habitat most often. Scrub, pasture and swamp habitat were utilised at rates lower than expected. These trends remained consistent across birds, with only a few birds roosting predominantly in pasture and swamp habitats. Habitat selection varied slightly between seasons and locations and across demographics and behaviours. Birds appear to choose their roost dependent on the presence of favoured food resources nearby or the availability of appropriate nest sites for incubation.

Objective 2: Assess shelter selection of brown kiwi on Ponui Island while roosting, including how this may vary with a range of spatial, temporal, demographic and behavioural factors.

Like habitat, brown kiwi adults do not utilise shelter types evenly, favouring the more structural tree burrow and soil burrow sites over less structural surface and swamp roosts. The type of shelter used was found to be heavily dependent on the habitat selected, as certain shelters occur more often in some habitat types than others. While largely following the overall trend, shelter selection varied slightly between seasons, locations, and in different demographic and social groups, likely due to similar driving factors as habitat selection. Although not measured, it was suggested that benefits gained from roost sites, including the reduction of predation risk and regulation of temperature, may also effect roost selection.

Objective 3: Explore the relationship between diurnal roost choice and nocturnal habitat utilisation of brown kiwi on Ponui Island.

The foraging and roosting behaviours of brown kiwi are not independent of one another, contrary to the suspicions of Jamieson et al. (2015). Birds chose roosting sites which were closer to whichever habitat was most beneficial for foraging during that time of the year. Roost selection varied between gullies, however when distance to favourable habitat exceeds a certain amount brown kiwi will not attempt to utilise this habitat for roosting, potentially due to the requirement of crossing many conspecific home ranges.

CHAPTER FIVE

Patterns in Brown Kiwi Spatial Behaviour - Conclusions

Plate 5.1 – Male brown kiwi Mauro rests in the arms of a researcher prior to re-banding. Photo by author.

5.1 Synopsis

Despite the number of studies exploring avian habitat selection, surprisingly little research has been undertaken in this field looking at New Zealand's most iconic species, the kiwi (*Apteryx* spp.). As a result, much remains unknown about the unusual behaviour and ecology of this nocturnal flightless insectivore. The few studies to have explored this topic have suggested that forest and scrub habitat are favoured by brown kiwi, with pasture used only sparingly (Potter, 1989; Taborsky & Taborsky, 1995). This spatial behaviour is thought to vary between seasons and locations (Potter, 1989; Gibbs, 2000; Cunningham & Castro, 2011), with foraging behaviour, breeding and sociality acting as potential driving factors (Taborsky & Taborsky, 1992; Cunningham & Castro, 2011). Equally little research has focused on the diet of brown kiwi, with only a handful of previous studies, most limited in scale and sample size. With numbers of brown kiwi continuing to decline despite extensive management (Holzapfel et al., 2008), learning more about the spatial behaviour and diet of brown kiwi is vital to improve our management of the remaining populations.

This study set out to assess how brown kiwi on Ponui Island utilise the habitat around them while foraging at night and roosting during the day, including how this habitat utilisation may vary and what might be driving this selection. This study also examined Kiwi diet and foraging behaviour in more detail than attempted before. Building upon the work of previous authors as well as investigating unexplored aspects of brown kiwi spatial ecology and diet, this study represents the most comprehensive analysis to date of brown kiwi spatial behaviour within a high-density population, giving rise to several management suggestions and recommendations for future research.

Chapter 2 provided the first broad analysis of brown kiwi diet over a twelve month period, assessing both the availability and exploitation of invertebrate prey. We were able to confirm suggestions of previous authors that brown kiwi are selectively opportunistic in their foraging, favouring several invertebrate groups. Brown kiwi also showed considerable flexibility in diet, with foraging strategies changing temporally and spatially, likely based upon their increased consumption of invertebrates which provide the highest protein input. Differences were particularly obvious between winter and summer, with mostly soil dwelling invertebrates favoured during winter and mostly surface dwelling invertebrates over summer. This was driven largely by a combination of invertebrate lifecycles and changing environmental conditions. Pasture habitat provided huge nutritional value and was important to brown kiwi diet, particularly over summer and autumn. This suggests that brown kiwi may temporally utilise pasture for foraging more than traditionally assumed. The similarities between these results and previous results at other locations indicate that a typical diet does exist for brown kiwi, suggesting applicability to other managed sites. Bias inherent in the methodology meant several important invertebrate taxa may have been underestimated in both availability and exploitation; however this was accounted for in the discussion.

Chapter 3 assessed the use of habitat by brown kiwi during their nocturnal activity phase, investigating how habitat selection varies with a range of factors, and with the use of statistical modelling, what may be driving this spatial behaviour. Similar to previous studies of brown kiwi, our birds did not utilise habitat according to its availability and instead were found most often within forest habitat. Other habitats were utilised less than expected based on availability. Rates varied with spatial, temporal, demographic and behavioural factors with reproduction and diet considered important. Four factors were identified as the main drivers of habitat utilisation in the model, encompassing spatial, temporal, behavioural and environmental influences. The most important of these was the availability of invertebrate food. As brown kiwi spend the majority of their time foraging while active at night, food is thought to play an important role in their spatial behaviour. This was confirmed in my study as birds spent more time at night within habitats that contained the highest availability of preferred food items. Other important driving factors identified in the model included season, gully and social grouping, though the vast majority of variation was explained by the first factor. Individuality was taken into account in the model, however was considered to play less of a role on habitat utilisation than the four fixed effect factors. Pasture proved to be a seasonally important habitat type, with birds utilising this habitat more often during summer and autumn. This is another indication that pasture habitat may indeed be a seasonally important resource for brown kiwi. Triangulation proved an effective method to track large numbers of birds throughout a vast and varied landscape with manageable levels of error.

Chapter 4 produced a comprehensive description of habitat and shelter selection of Brown kiwi while roosting, while investigating the relationship between their use of habitat at night and during the day. Brown kiwi adults on Ponui Island used a diversity of habitat while roosting, but selected strongly for forest habitat, utilising it at rates far exceeding its availability. Birds also favoured tree and soil burrow sites over the less enclosed surface and swamp roosts. Similar to previous work, the location and type of roost chosen varied slightly with spatial, temporal, demographical and behavioural factors. Birds appear to choose roosts dependent on the availability of favoured food resources nearby or the availability of appropriate nest sites for incubation. Although not measured, the provision of benefits in reduction of predation risk and regulation of temperature may also have impacted roost selection. A unique insight of this research is the link between diurnal and nocturnal spatial behaviour. Birds chose roosting sites which were closer to whichever habitat was most utilised for foraging during that time of the year. When distance to favourable habitat exceeds a certain amount brown kiwi will not attempt to utilise this habitat for roosting, potentially due to the requirement of crossing many conspecific home ranges.

5.2 Synthesis

The ways in which brown kiwi interacted with the habitat available to them, both at night and during the day, appear to be closely linked to the availability of invertebrate food resources. An increase in nocturnal pasture use over summer corresponded with a switch in foraging strategy. Over the same time, on average birds were choosing to roost closer to pasture, reducing their use of the more favourable structural burrows to enable better access to pasture habitat. In contrast, during winter and spring brown kiwi clearly used forest habitat the most often for both foraging and roosting, also selecting sheltered soil and tree burrows over other sites. These patterns correspond directly with higher availability during this time of favoured invertebrates within the soil column in forest. Interestingly, nutrition appears to be the instigator of these patterns, with birds favouring those invertebrates that contain the highest levels of protein and fat, changing their foraging behaviour in order to find and exploit these food items.

Forest was chosen by brown kiwi most often throughout the year for both roosting and foraging. Different habitats will often provide different benefits to the animal, helping to increase fitness and survival (Dechant et al., 2002). Denser habitat such as forest and scrub is often perceived to be safer from predation (Gibbs & Clout, 2003), and in this study also contained the largest number of more structured shelter sites such as tree and soil burrows, providing additional thermal and social benefits (Walsberg, 1986; Tiddeman & Flavel, 1987). Forest habitat was considered especially important for brown kiwi breeding and social behaviour in this study, utilised at higher rates by birds which were breeding, or were part of a pair or group. Pasture habitat was identified as temporally important to the spatial behaviour of brown kiwi, utilised to a greater extent during warmer seasons for foraging, when pasture invertebrates were consumed in significant numbers. The high levels of deforestation of New Zealand since the arrival of humans is such that brown kiwi would have accessed little pasture habitat over the course of their evolution. The fact that brown kiwi now appear to exploit this habitat suggests that they are successfully adapting to the novel environments and species introduced by humans.

Brown kiwi on Ponui Island showed generalist foraging and roosting behaviour, utilising a range of different invertebrates, habitats and shelter types. This enabled birds to alter their behaviours between seasons or locations in response to changes in resource availability or changes in social and/or dietary requirements. Different habitat types can provide different benefits to avian species, including availability of food, protection from predation, provision of shelter and nest sites, and levels of inter and intra specific interaction (Jones, 2001). Birds which were limited in their fundamental niche and had reduced access to multiple habitat types, especially pasture, appeared to struggle to maintain bodyweight and successfully reproduce, though this should be explored in more detail.

5.2.1 Conservation Implications

The high utilisation of forest habitat throughout the year, seasonal importance of pasture and increased utilisation of scrub by younger individuals suggests that a combination of habitats is beneficial to brown kiwi populations. This allows birds to respond to changes in resource availability by making use of different habitat types at different times of the year, life stage or with changing dietary or roost site requirements. This is supported by the reduction in breeding success and body size of birds in Pipe Gully which has significantly reduced access to pasture habitat, and also by the reduced survival of juveniles that used fewer habitats documented in Gibbs (2000). As a result, future translocations and management of brown kiwi should ensure there is a mix of available habitat, giving priority to fragmented landscapes which contain a significant area of mature native forest.

Pasture habitat was reported to be seasonally important for brown kiwi adults while foraging at night. With almost half of the total land mass of New Zealand converted into pasture since human colonisation (Blackwell, 2005), there are plenty of fragmented forest/pasture sites which previously were probably not considered suitable for translocation or management of brown kiwi. This knowledge could result in these sites being considered for management in the future.

Confirmation that brown kiwi select a large amount of pasture invertebrates in their diet, many of which are considered pests to farmers, could also prove useful for advocacy. If farmers are made aware of the potential benefits a healthy population of brown kiwi could have on their land, they may be more willing to undertake or fund future conservation initiatives. This knowledge raises new problems as well. Management of dogs within pasture where birds may be located should be targeted, particularly on farms with working dogs. Kiwi aversion training for farm dogs is recommended to help bring down the incidence of dog related mortality in fragmented areas with high brown kiwi density such as Northland.

The more structural tree and soil burrows were utilised more often by brown kiwi than surface and swamp roost sites. Current and future managed sites containing brown kiwi should ensure that these types of shelters are readily available, potentially making use of artificial shelters within captive enclosures or regenerating areas where there is little mature forest available. This would increase the number of burrow roosts available, helping to reduce the number of brown kiwi roosting above ground, thereby reducing their susceptibility to predators such as dogs.

A detailed analysis of brown kiwi diet can provide the means to develop more suitable diets for their captive management, and act as a checklist for important species that should be present in managed sites. The nutrient content of many artificial diets fed to captive brown kiwi has been found to differ significantly to the natural diet of wild kiwi, and to vary between captive sites (Potter et al., 2010). Often these diets were based loosely on recommendations in a kiwi husbandry manual (Johnson, 1996) which are based on a diet formulated forty years ago by Reid and Williams (1975). The identification that brown kiwi select high protein invertebrates over might lead to the development of more efficient diets for captive brown kiwi. Interestingly, quality of faecal sample was found to have no effect on exploitation results in this study. This suggests that no matter the condition of the sample it can be used for analysis.

The use of triangulation on a large scale appears to be an effective method for studying the spatial behaviours of brown kiwi, provided the researcher is suitably equipped and skilled. Time of night was also found to have no effect on the spatial behaviour of brown kiwi. This increases the effectiveness of this type of study, and could lead to more large scale spatial studies occurring in the future.

While this research is particularly relevant to high-density populations of brown kiwi in intensively managed or island sites, knowledge of how this species behaves at particularly high densities may prove vital for future management. As densities of brown kiwi begin to slowly increase in mainland New Zealand following incremental advances in the efficiency of pest eradication, egg rearing and dog advocacy programmes; studies of high-density populations such as this one will prove increasingly relevant.

5.3 Limitations

The most significant limitation to the overall study is that any inferences made on the diet and spatial behaviour of brown kiwi were based upon a single population of birds living at an extremely high-density compared to other sites on the mainland. Density has been shown to affect patterns of spatial use in a range of species (Baber & Craig, 2003; Latham, 2006; Whyte, Ross, & Buckley, 2014) including brown kiwi (Ziesemann, 2011), and therefore should be considered during any spatial analysis (Rosenzweig, 1991; Manly et al., 2002). It is likely that the density of brown kiwi on Ponui Island has impacted the documented spatial behaviours in this study. This makes comparison with other populations difficult, especially those in low density mainland sites. However, with a density similar to proposed pre-human colonisation levels (Reid & Williams, 1975; McLennan et al., 1996), Ponui Island may in fact be a more accurate reflection of true brown kiwi behaviour than other sites. As other more intensively managed populations of brown kiwi increase in density, the results of this study will prove increasingly relevant.

The fragmented landscape of Ponui Island may have also produced different habitat utilisation results to previous studies, of which three out of four occurred in relatively large areas of intact native and pine forest. However, as deforestation has left only 22% of the country's original forest cover remaining (Mills & Williams, 1979), the fragmented habitat found in my study site is actually a good representation of much of modern New Zealand (Potter, 1990), offering hope that many other managed sites might replicate the success of Ponui Island brown kiwi.

Comparisons with previous research are further confounded by the differing methodologies and scale of focus of each study, with most previous studies of brown kiwi occurring over a small time frame and using fewer samples. The mixed genetic heritage of brown kiwi on Ponui Island is another point of difference to other populations.

In addition, my findings are based off a sample of radio tagged birds, which may not represent the entire Ponui Island population. Given the large sample size (47), this impact was likely significantly reduced. Ensuring the sample population was spatially representative was difficult, as most of the birds were already selected to study social behaviour. In the past, birds that only used the main swamp, and those that exhibited no social interactions with other study birds were released from the study population. This has resulted in group of birds with shared and overlapping home ranges. Significantly however, only a few areas of the study site were not used by banded birds at all during the year for either roosting or foraging. Though these areas are definitely used by other birds, social restrictions on territory are likely to have made them unavailable to study birds.

Bias inherent in the methodology of both invertebrate availability and exploitation sampling meant that a number of invertebrate groups were likely underrepresented in samples. Additionally, when analysing samples at a coarse taxonomic level, Wolda (1990) suggests that care should be taken when interpreting the results. Another difficulty of dietary studies is the need to relate changes in foraging behaviour to changes in food resource. Lacking a bird's perception, we are often unaware of the relationships between itself and its prey, including what impact prey crypticity, inaccessibility, difficulty of capture or mechanical and chemical defences might have on foraging preference (Hutto, 1990). Although the patterns of utilisation by brown kiwi in this study appear to be directly linked to patterns in availability and nutrition, it is important that readers do not lose sight of the limitations surrounding dietary sampling.

The precision of triangulated locations recorded in a beacon study was considered to be acceptable for studying habitat utilisation at a large macrohabitat scale. Additionally, the use of triangulation allowed for a large sample size with minimal pseudo-replication. Despite this, use of this technique will clearly have resulted in the recorded rates of habitat utilisation differing to the actual spatial behaviour exhibited. As Springer (1979) pointed out, bearings determined by radio-tracking are only estimates, not exact locations. With a potential error of around 50m, birds which were active within the often small and narrow areas of swamp or on habitat borders might have instead been triangulated to be within neighbouring forest, pasture or scrub habitat, and vice versa. The large sample size and scale of this research will have reduced this impact, however care should still be when reporting this result.

Finally, there has been debate over whether habitat utilisation alone is a true indicator of habitat preference (White & Garrott, 1990; Perrins & Birkhead, 1993). Habitat studies assume that an animal will select and use areas that are best able to satisfy its life requirements, though this assumption is not always held true. Individuals are often constrained in their choice of habitat due to the presence of social factors like competition and territoriality, as well as restrictions in habitat availability (Bjørneraas et al., 2012). As a result not all individuals are able to settle in the most suitable habitat, and instead are limited to the composition of habitat within their individual home ranges. Many birds in Pipe gully for example would have to travel a large distance, likely through the home ranges of other birds, to reach pasture habitat. Nevertheless, habitat utilisation can still explain which habitat is preferred by animals under their realised (constrained) niche. In this thesis I have avoided the use of the word ‘preference’ because of these constraints.

5.4 Future Research

A number of key research gaps have been identified throughout duration of this study. To further understand the spatial behaviour and diet of brown kiwi and improve management of surviving populations, these gaps must be filled. I have outlined six possible study areas which will contribute to achieving this goal.

- Long term studies of diet should be attempted at other locations looking at both invertebrate availability and utilisation to confirm the foraging behaviour of brown kiwi on Ponui Island is similar to other populations across the North Island. Annual variation in invertebrate composition should also be investigated.

- The importance of nutrition should be further explored in brown kiwi, with particular focus on the development of diets for captive birds, and the capacity of brown kiwi to digest chitin.

- Further dietary research should further investigate the effect of habitat upon foraging behaviour and diet. These studies could make use of captive birds or a population within in a more controlled environment to further examine whether faecal samples contain invertebrates from a single type of habitat.

- Additional research exploring habitat utilisation of brown kiwi adults should be attempted within a population occurring at a lower density. This should aim to determine the effect of density upon brown kiwi spatial behaviours, and produce results more relevant to the majority of current low density populations.

- The lack of habitat selection studies of brown kiwi gives very few options for comparison between locations, methodologies, and conclusions. Habitat utilisation should be investigated at a large scale in other populations, with emphasis on driving factors, in order to confirm patterns in spatial behaviour identified in this study.

- Future spatial research should investigate the importance of social factors as potential drivers of brown kiwi spatial behaviour. Focus should be placed upon those factors which were not explicitly considered in this study, such as the effects of territoriality, competition, and social interaction.

Reference List

Adams, A. L., Recio, M. R., Robertson, B. C., Dickinson, K. J. M., & Van Heezik, Y. (2013). Understanding home range behaviour and resource selection of invasive common brushtail possums (*Trichosurus vulpecula*) in urban environments. *Biological Invasions, 16*, 1791-1804.

Anderson-Sprecher, R. (1994). Robust estimates of wildlife location using telemetry data. *Biometrics, 50*(2), 406-416.

Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. Plymouth: PRIMER-E Ltd.

Atkinson, I. A. E., & Merton, D. V. (2006). Habitat and diet of kakapo (*Strigops habroptilis*) in the Esperance Valley, Fiordland, New Zealand. *Notornis, 53*, 37-54.

Atkinson, I. A. E., & Millener, P. (1991). *An ornithological glimpse into New Zealand's pre-human past.* Paper presented at the Acta XX Congressus Internationalis Ornithologici.

Baber, M. J., & Craig, J. L. (2003). The relationship between foraging behaviour and habitat use by South Island Takahe (*Porphyrio hochstetteri*) on Tiritiri Matangi Island. *Notornis, 50*(2), 59-66.

Barker, D., Fitzpatrick, M. P., & Dierenfeld, E. S. (1998). Nutrient composition of selected whole invertebrates. *Zoo Biology, 17*, 123-134.

Barri, F. R., Roldan, N., Navarro, J. L., & Martella, M. B. (2012). Effects of group size, habitat and hunting risk on vigilance and foraging behaviour in the Lesser Rhea (*Rhea pennata pennata*). *Emu, 112*, 67-70.

Bassett, S. M., McLennan, J. A., & Blackwell, G. L. (2005). *The biology and conservation status of the Brown Kiwi.* Paper presented at the Proceedings of the 3rd International Ratite Science Symposium of the World's Poultry Science Association (WPSA) & 12th World Ostrich Congress, Madrid, Spain.

Beauchamp, G. (2007). Exploring the role of vision in social foraging: What happens to group size, vigilance, spacing, aggression and habitat use in birds and mammals that forage at night. *Biological Reviews, 82*, 511-525.

Beck, D. D., & Jennings, R. D. (2003). Habitat Use by Gila Monsters: The Importance of Shelters. *Herpetological Monographs, 17*, 111-129.

Bell, G. P. (1990). Birds and mammals on an insect diet: A primer on diet composition analysis in relation to ecological energetics. *Studies in Avian Biology, 13*, 416-422.

Bellingham, P. J. (1979). The birds of Ponui (Chamberlin's) Island, Hauraki Gulf, August 1978. *Tane, 25*, 17-21.

Benedict, L., & Krakauer, A. H. (2013). Kiwis to pewees: the value of studying bird calls. *Ibis, 155*, 225-228.

Berry, C. (1999). *Potential interactions of hedgehogs with North Island Brown Kiwi at Boundary Stream Mainland Island*. Department of Conservation, Wellington.

Bjørneraas, K., Herfindal, I., Solberg, E. J., Sæther, B. E., Van Moorter, B., & Rolandsen, C. M. (2012). Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. *Oecologia, 168*, 231-243.

Blackwell, G. L. (2005). Another World: The composition and consequences of the introduced mammal fauna of New Zealand. *Zoologist, 33*, 108-118.

Blanco, G., & Tella, J. (1999). Temporal, spatial and social segregation of red-billed choughs between two types of communal roost: a role for mating and territory acquisition. *Animal Behaviour, 57*, 1219-1227.

Blem, C. R. (1976). Patterns of lipid storage and utilisation in birds. *American Zoologist, 16*(4), 671-684.

Block, W. M., & Brennan, L. A. (1993). The habitat concept in ornithology: Theory and applications. *Current Ornithology, 11*, 35-91.

Boyd, S. (1993). Little Spotted Kiwi transfer to Tiritiri Matangi Island. *Auckland Conservancy Technical Report Series* (Vol. 6). Wellington, New Zealand: Department of Conservation.

Boyer, S., Wratten, S. D., Holyoake, A., Abdelkrim, J., & Cruickshank, R. H. (2013). Using next-generation sequencing to analyse the diet of a highly endangered land snail (*Powelliphanta augusta*) feeding on endemic earthworms *PLoS ONE, 8*(9), 1-25.

Brockerhoff, E. G., Barratt, B. I. P., Beggs, J. R., Fagan, L. L., Kay, M. K., Phillips, C. B., & Vink, C. J. (2010). Impact of exotic invertebrates on New Zealand's indigenous species and ecosystems. *New Zealand Journal of Ecology, 34*(1), 158-174.

Brown, E. A. (1979). Vegetation and flora of Ponui Island, Hauraki Gulf, New Zealand. *Tane, 25*, 5-16.

Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioural Ecology and Sociobiology, 22*, 37-47.

Bull, P. C. (1959). Stomach contents of a North Island Kiwi (*Apteryx australis mantelli*) from the Raetihi district. *Notornis, 8*(5), 143-144.

Buller, W. L. (1888). *A history of the birds of New Zealand* (2nd ed. Vol. 2). London, UK: The Author.

Burbidge, M. L., Colbourne, R. M., Robertson, H. A., & Baker, A. J. (2003). Molecular and other biological evidence supports the recognition of at least three species of Brown Kiwi. *Conservation Genetics, 4*, 167-177.

Calder, W. A. (1991). The Kiwi and its Egg. In E. Fuller (Ed.), *Kiwis: A monograph of the family Apterygidae*. Shrewsbury, England: Swan Hill Press.

Calder, W. A., Parr, C. R., & Karl, D. P. (1978). Energy content of eggs of Brown Kiwi *Apteryx australis* - extreme in avian evolution. *Comparative Biochemistry and Physiology, 60*, 177-179.

Castillo-Guerrero, J. A., Fernandez, G., Arellano, G., & Mellink, E. (2009). Diurnal abundance, foraging behavior and habitat use by non-breeding Marbled Godwits and Willets at Guerrero Negro, Baja California Sur, México. *Waterbirds, 32*(3), 400-407.

Castro, I., Cunningham, S. J., Gsell, A. C., Jaffe, K., Cabrera, A., & Liendo, C. (2010). Olfaction in birds: A closer look at the kiwi (*Apterygidae*). *Journal of Avian Biology, 41*, 213-218.

Castro, I., & *etal.* (2015). Title TBC. Manuscript in preperation.

Catry, A., Alves, J. A., Gill, J. A., Gunnarsson, T. G., & Granadeiro, J. P. (2014). Individual specialization in a shorebird population with narrow foraging niche. *Acta Oecologica, 56*, 56-65.

Chan, T. (1999). *Habitat selection by brown kiwi chicks (Apteryx mantelli) in Trounson Kauri Park, Northland.* (Unpublished MSc Thesis), Auckland University, Auckland, New Zealand.

Clarke, K. R., & Gorley, R. N. (2006). PRIMER v6: User Manual/Tutorial. Plymouth: PRIMER-E Ltd.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B-Biological Sciences, 273*, 1375-1383.

Cockrem, J. F., Potter, M. A., Barrett, D. P., & Candy, E. J. (2008). Corticosterone responses to capture and restraint in emperor and adelie penguins in Antarctica. *Zoological Science, 25*(3), 291-298.

Colbourne, R. (2002). Incubation behaviour and egg physiology of kiwi (*Apteryx spp.*) in natural habitats. *New Zealand Journal of Ecology, 26*(2), 129-138.

Colbourne, R., Baird, K., & Jolly, J. (1990). Relationship between invertebrates eaten by little spotted kiwi, *Apteryx owenii*, and their availability on Kapiti Island, New Zealand. *New Zealand Journal of Zoology, 17*, 533-542.

Colbourne, R., Bassett, S., Billing, T., McCormick, M., McLennan, J., Nelson, A., & Robertson, H. (2005). The development of Operation Nest Egg as a tool in the conservation management of kiwi. *Science for Conservation, 259*, 1-24.

Colbourne, R., & Kleinpaste, R. (1984). *A study of kiwis in an exotic forest*. Auckland, New Zealand: (Unpublished Report), New Zealand Forest Service.

Colbourne, R., & Kleinpaste, R. (1990). Kiwis in a pine forest habitat. In E. Fuller (Ed.), *Kiwis* (pp. 97-138). Auckland: SeTo Publishing Ltd.

Colbourne, R., & Powlesland, R. G. (1988). Diet of the Stewart Island Brown Kiwi (*Apteryx australis lawryi*) at Schollay's Flat, southern Stewart Island. *New Zealand Journal of Ecology, 11*, 99-104.

Coombs, A. B., Bowman, J., & Garroway, C. J. (2010). Thermal properties of tree cavities during winter in a northern hardwood forest. *The Journal of Wildlife Management, 74*, 1875-1881.

Cooper, R. J., & Whitmore, R. C. (1990). Arthropod sampling methods in ornithology. *Studies in Avian Biology, 13*, 29-37.

Corfield, J. (2009). *Evolution of the brain and sensory systems of the kiwi.* (Unpublished PhD Thesis), Auckland University, Auckland, New Zealand.

Corfield, J., Eisthen, H. L., Iwaniuk, A. N., & Parsons, S. (2014). Anatomical specializations for enhanced olfactory sensitivity in Kiwi, *Apteryx mantelli*. *Brain, Behaviour and Evolution, 84*(3), 214-226.

Corfield, J., Gillman, L., & Parsons, S. (2008). Vocalisations of the North Island Brown Kiwi (*Apteryx mantelli*). *The Auk, 125*(2), 326-335.

Corti, R., Larned, S. T., & Datry, T. (2013). A comparison of pitfall-trap and quadrat methods for sampling ground-dwelling invertebrates in dry riverbeds. *Hydrobiologica, 717*, 13-26.

Crowe, A. (2007). *Which New Zealand Spider?* Rosedale, New Zealand: Penguin Books Ltd.

Cunningham, S. (2006). *Foraging Sign, Prey Detection and Bill Morphology in the North Island Brown Kiwi (Apteryx mantelli).* (Unpublished Honours Thesis), Massey University, Palmerston North, New Zealand.

Cunningham, S., Alley, M. R., & Castro, I. (2011). Facial bristle feather histology and morphology in New Zealand birds: implications for function. *Journal of Morphology, 272*(1), 118-128.

Cunningham, S., & Castro, I. (2011). The secret life of wild brown kiwi: studying behaviour of a cryptic species by direct observation. *New Zealand Journal of Ecology, 35*(3), 209-219.

Cunningham, S., Castro, I., & Alley, M. (2007). A new prey-detection mechanism for kiwi (*Apteryx* spp.) suggests convergent evolution between paleognathous and neognathous birds. *Journal of Anatomy, 211*, 493-502.

Cunningham, S., Castro, I., & Potter, M. A. (2009). The relative importance of olfaction and remote touch in prey detection by North Island brown kiwis. *Animal Behaviour, 78*, 899-905.

Currie, D., Wunderle, J. M., Ewert, D. N., Anderson, M. R., Davis, A., & Turner, J. (2005). Habitat distribution of birds wintering in Central Andros, The Bahamas: Implications for management. *Caribbean Journal of Science, 41*(1), 75-87.

D'Amico, F., & Hemery, G. (2007). Time-activity budgets and energetics of Dipper *Cinclus cinclus* are dictated by temporal variability of river flow. *Molecular & integrative physiology, 148*(Part A), 811-820.

Deagle, B. E., Gales, N. J., Evans, K., Jarman, S. N., Robinson, S., Trebilco, R., & Hindell, M. A. (2007). Studying seabird diet through genetic analysis of faeces: A case study on Macaroni Penguins (*Eudyptes chrysolophus*). *PLoS ONE, 2*(9), 1-9.

Dechant, J. A., Sondreal, M. L., Johnson, D. H., Igl, L. D., Goldade, C. M., Rabie, P. A., & Euliss, B. R. (2002). *Effects of management practices on grassland birds: Burrowing owl.* Jamestown, ND: Northern Prairie Wildlife Research Center.

Denny, K. M. (2009). *The diet of moreporks (Ninox novaeseelandiae) in relation to prey availability, and their roost site characteristics and breeding success on Ponui Island, Hauraki Gulf, New Zealand.* (Unpublished MSc Thesis), Massey University, New Zealand, Albany.

Dickman, C. R., & Huang, C. (1988). The reliability of fecal analysis as a method for determining the diet of insectivorous mammals. *Journal of Mammalogy, 69*(1), 108-113.

Didham, R. K., Barker, G. M., Costall, J. A., Denmead, L. H., Floyd, C. G., & Watts, C. H. (2009). The interactive effects of livestock exclusion and mammalian pest control on the restoration of invertebrate communities in small forest remnants. *New Zealand Journal of Zoology, 36*, 135-163.

Digby, A., Towsey, M., Bell, B. D., & Teal, P. D. (2013). A practical comparison of manual and autonomous methods for acoustic monitoring. *Methods in Ecology and Evolution, 4*, 675-683.

Durst, S. L., Theimer, T. C., Paxton, E. H., & Sogge, M. K. (2003). Age, habitat, and yearly variation in the diet of a generalist insectivore, the Southwestern Willow Flycatcher. *The Condor, 110*(3), 514-525.

Fidgett, A. L., & Gardner, L. (2014). Advancing avian nutrition through best feeding practice. *International Zoo Yearbook, 48*, 116-127.

Field, A. (2013). *Discovering Statistics using IBM SPSS* (M. Carmichael Ed. 4th ed.). London, United Kingdom: Sage.

Finke, M. D. (2002). Complete nutrient composition of commercially raised invertebrates used as food for insectivores. *Zoo Biology, 21*, 269-285.

Finke, M. D. (2007). Estimate of chitin in raw whole insects. *Zoo Biology, 26*, 105-115.

Finke, M. D. (2013). Complete nutrient content of four species of feeder insects. *Zoo Biology, 32*, 27-36.

Forbes, Y. (2009). *Natal dispersal, Habitat Selection and Mortality of North Island Brown Kiwi (Apteryx mantelli) at the Moehau Kiwi Sanctuary, Coromandel.* (Unpublished MSc Thesis), Auckland University of Technology, Auckland, New Zealand.

Frye, G. G., Connelly, J. W., Musil, D. D., & Forbey, J. S. (2013). Phytochemistry predicts habitat selection by an avian herbivore at multiple spatial scales. *Ecology, 94*(2), 308-314.

Fuller, E. (1990). *Kiwis*. Auckland, New Zealand: SeTo Publishing Ltd.

Fuller, M. R., Millspaugh, J. J., Church, K. E., & Kenward, R. E. (2005). Wildlife radiotelemetry. In C. E. Braun (Ed.), *Techniques for wildlife investigations and management* (pp. 377-417). Bethesda, USA: The Wildlife Society.

Gerritson, A. F. C., & Vanheezik, Y. M. (1985). Substrate Preference and Substrate Related Foraging Behavior in 3 Calidris Species. *Netherlands Journal of Zoology, 35*, 671-692.

Gibbs, G. (2010). Do New Zealand invertebrates reflect the dominance of birds in their evolutionary history. *New Zealand Journal of Ecology, 34*(1), 152-157.

Gibbs, S. (2000). *Distribution, habitat use and survival of immature North Island brown kiwi (Apteryx australis mantelli) at Trounson Kauri Park.* (Unpublished MSc Thesis), Auckland University, Auckland, New Zealand.

Gibbs, S., & Clout, M. N. (2003). Behavioural vulnerability of juvenile Brown Kiwi: habitat use and overlap with predators. *DOC Science Internal Series* (Vol. 102, pp. 1-17). Wellington, New Zealand: Department of Conservation.

Gray, T. N. E., Chamnan, H., Collar, N. J., & Dolman, P. M. (2009). Sex-specific habitat use by a lekking bustard: Conservation implications for the critically endangered Bengal Florican (Houbaropsis bengalensis) in an intensifying agroecosystem. *The Auk, 126*(1), 112-122.

Gregory, R. D., Gibbons, D. W., & Donald, P. F. (2004). Bird Census and Survey Techniques *Bird Ecology and Conservation: A Handbook of Techniques* (pp. 17-55). Oxford, UK: Oxford Biology.

Gurr, L. (1952). Some food of the North Island Kiwi (*Apteryx australis*). *Notornis, 4*(8), 209-210.

Harris, R. J., & Reed, L. M. (2002). Behavioural barriers to non-migratory movements of birds. *Annual Zoological Fennici, 39*, 275-290.

Harris, S., Cresswell, W. J., Forde, P. G., Trewhella, W. J., Woollard, T., & Wray, S. (1990). Home-range analysis using radio-tracking data: A review of problems and techniques particularly as applied to the study of mammals. *Mammal Review, 20*(2/3), 97-123.

Harshman, J., Braun, E. L., Braun, M. J., Huddleston, C. J., Bowie, R. C. K., Chojnowski, J. L., Hackett, S. J., Han, K., Kimball, R. T., Marks, B. D., Miglia, K. J., Moore, W. S., Reddy, S., Sheldon, F. H., Steadman, D. W., Steppan, S. J., Witt, C. C., & Yuri, T. (2008). Phylogenomic evidence for multiple losses of flight in ratite birds. *PNAS, 105*(36), 13462-13467.

Hausman, J. A. (1978). Specification tests in econometrics. *Econometrica, 46*(6), 1251-1271.

Herbert, J., & Daugherty, C. H. (2002). Genetic variation, systematics and management of kiwi. In F. Overmars (Ed.), *Some early 1990s studies in kiwi (Apteryx spp.) genetics and management* (pp. 11-34). Wellington, New Zealand: Science & Research Internal Report 191, Department of Conservation.

Holm, S. (1979). A simple sequential rejective method procedure. *Scandinavian Journal of Statistics, 6*, 65-70.

Holzapfel, S., Robertson, H. A., McLennan, J. A., Sporle, W., Hackwell, K., & Impey, M. (2008). Kiwi (*Apteryx* spp.) recovery plan: 2008-2018. *Threatened Species Recovery Plan 60* (pp. 1-71). Wellington, New Zealand: Department of Conservation.

Hughes, J. J., Ward, D., & Perrin, M. R. (1994). Predation risk and competition affect habitat selection and activity of Namib desert gerbils. *Ecology, 75*, 1397-1405.

Hutto, R. L. (1990). Measuring the availability of food resources. *Studies in Avian Biology, 13*, 20-28.

Ismail, S. (1993). *The spatial analysis of North Island Brown Kiwi (Apteryx australis mantelli) food resources, Paerata Reserve.* (Unpublished MA geography Thesis), University of Auckland, Auckland, New Zealand.

James, B. (2001). Evaluation of kiwi advocacy programmes in Northland and Coromandel. *Science for Conservation, 161*, 1-52.

Jamieson, S. E., Castro, I., Jensen, T., Morrison, K. W., & Durrant, B. (In Prep). Roosting preferences of North Island brown kiwi.

Johnson, T. (1996). *Husbandry manual for North Island brown kiwi, Apteryx australis mantelli.* Rotorua, New Zealand: Rainbow and Fairy Springs.

Jones, J. (2001). Habitat selection studies in avian ecology: A critical review. *The Auk, 118*(2), 557-562.

Keye, C. (2008). *A study of home ranges, movement and activity patterns of Great Spotted Kiwi (Apteryx haastii) in the Hurunui Region, South Island, New Zealand.* (Unpublished MSc Thesis), Lincoln University, Christchurch, New Zealand.

King, C. M. (1990). *The Handbook of New Zealand Mammals*. Auckland, New Zealand: Oxford University Press.

Kleinpaste, R. (1990). Kiwis in a pine forest habitat. In E. Fuller (Ed.), *A monograph of the Apterygidae* (pp. 97-138). Shrewsbury, UK: Swan Hill.

Kleinpaste, R., & Colbourne, R. (1983). Kiwi food study. *New Zealand Journal of Ecology, 6*, 143-144.

Kristan, W. B. (2006). Sources and expectations for hierarchical structure in bird–habitat associations. *Condor, 108*, 5-12.

Kufeld, R. C., Bowden, D. C., & Siperek Jr, J. M. (1987). Evaluation of a telemetry system for measuring habitat usage in mountainous terrain. *Northwest Science, 61*(4), 249-416.

Labaque, M. C., Martella, M. B., Maestri, D. M., & Navarro, J. L. (2013). The influence of diet composition on egg and chick traits in captive Greater Rhea females. *British Poultry Science, 54*(3), 374-380.

Lack, D. (1933). Habitat selection in birds with special reference to the effects of afforestation on the Breckland avifauna. *Journal of Animal Ecology, 2*, 239-262.

Latham, J. (2006). *The ecology of ship rats (Rattus rattus) on Ponui Island: implications for North Island brown kiwi (Apteryx mantelli).* (Unpublished MSc Thesis), Auckland University, Auckland, New Zealand.

Lee, J. E., White, G. C., Garrott, R. A., Bartmann, R. M., & Alldredge, A. W. (1985). Assessing accuracy of a radio telemetry system for estimating animal locations. *Journal of Wildlife Management, 49*, 658-663.

Lindsay, K. J., Allen, A. P., & Major, R. E. (2015). Can spatial and temporal food variability explain the winter foraging movements of a threatened saltmarsh insectivore. *Austral Ecology, 40*, 160-169.

MacFaden, S. W., & Capen, D. E. (2002). Avian habitat relationships at multiple scales in a New England forest. *Forest Science, 48*(2), 243-253.

MacLeod, S. B., & Kerly, G. I. H. (1996). Habitat and diet of Bushbuck *Tragelaphus scriptus* in the woody cape nature reserve: Observations from faecal analysis. *South African Journal of Wildlife Research, 26*(1), 19-26.

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonals, T. L., & Erickson, W. P. (2002). *Resource selection by animals: statistical design and analysis for field studies*. Dordrecht, Netherlands: Kluwer Academic Publishers.

Martin, G. R., Wilson, K., Wild, J. M., Parsons, S., Kubke, M. F., & Corfield, J. (2007). Kiwi forego vision in the guidance of their nocturnal activities. *PLoS ONE, 198*(2), 1-6.

Marzluff, J. M., Heinrich, B., & Marzluff, C. S. (1996). Raven roosts are mobile information centres. *Animal Behaviour, 51*, 89-103.

Mazur, K. M., Frith, S. D., & James, P. C. (1998). Barred owl home range and habitat selection in the boreal forest of central Saskatchewan. *The Auk, 115*, 746-754.

McColl, H. P. (1981). *An illustrated guide to common soil animals.* Wellington, New Zealand: P.D. Hasselberg, Government Printer.

McLennan, J. A. (1992). Nationwide Monitoring of Kiwi Populations. *DSIR Land Resources Contract Report* (Vol. 92/21). Havelock North, New Zealand: DSIR.

McLennan, J. A., Dew, L., Miles, J., Gillingham, N., & Waiwai, R. (2004). Size matters: predation risk and juvenile growth in North Island brown kiwi (*Apteryx mantelli*). *New Zealand Journal of Ecology, 28*(2), 241-250.

McLennan, J. A., Potter, M. A., Robertson, H. A., Wake, G. C., Colbourne, R., Dew, L., Joyce, L., McCann, A. J., Miles, J., Miller, P. J., & Reid, J. (1996). Role of predation in the decline of Kiwi, *Apteryx* spp., in New Zealand. *New Zealand Journal of Ecology, 20*(1), 27-35.

McLennan, J. A., Rudge, M. R., & Potter, M. A. (1987). Range size and denning behaviour of Brown Kiwi, *Apteryx australis manteli*, in Hawkes Bay, New Zealand. *New Zealand Journal of Ecology, 10*, 97-107.

McNab, B. K. (1996). Metabolism and temperature regulation of Kiwis (Apterygidae). *The Auk, 113*(3), 687-692.

Michalski, M., Nadolski, J., Marciniak, B., Loga, B., & Bañbura, J. (2011). Faecal analysis as a method of nestling diet determination in insectivorous birds: A case study in Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major*. *Acta Ornithologica, 46*(2), 164-172.

Miles, D. B. (1990). The importance and consequences of temporal variation in avian foraging behaviour. *Studies in Avian Biology, 13*, 210-217.

Miles, J. (1995). *Comparative ecology of Northern Brown Kiwi (Apteryx australis mantelli) in Tongariro National Park and Tongariro Forest Park, central North Island.* (Unpublished MSc Thesis), Massey University, Palmerston North, New Zealand.

Miles, J., & Castro, I. (2000). Survey of Northern Brown Kiwi (*Apteryx mantelli*) on Ponui Island, Hauraki Gulf. Wellington, New Zealand: Department of Conservation.

Miles, J., Potter, M. A., & Fordham, R. A. (1997). Northern brown kiwi (*Apteryx australis mantelli*) in Tongariro National Park and Tongariro Forest - ecology and threats. *Science for Conservation, 51*, 1-22.

Miller, P. J., & Pierce, R. J. (1995). Distribution and decline of the North Island Brown Kiwi (Apteryx australis mantelli) in Northland. *Notornis, 42*, 203-211.

Mills, J. A., & Williams, G. R. (1979). The status of endangered New Zealand birds. In M. J. Tyler (Ed.), *The status of endangered Australasian wildlife*: Royal Zoological Society of South Australia.

Minson, C. (2013). *Diet related factors in the conservation of kiwi (Apteryx mantelli).* (Unpublished PhD Thesis), Massey University, Palmerston North, New Zealand.

Mitchell, K. J., Llamas, B., Soubrier, J., Rawlence, N. J., Worthy, T. H., Wood, J., Lee, M. S. Y., & Cooper, A. (2014). Ancient DNA reveals elephant birds and kiwi are sister taxa and clarifies ratite bird evolution. *Science, 344*(6186), 898-900.

Moeed, A., & Meads, M. J. (1985). Seasonality of pitfall trapped invertebrates in three types of native forest, Orongorongo Valley, New Zealand. *New Zealand Journal of Zoology, 12*, 17-53.

Morgan, D. K. J., & Castro, I. (2014). The impact of exotic and native predators on the abundance of ground dwelling invertebrates in a New Zealand forest. *In Print*.

Morrison, C., Osborne, T., Harlow, P. S., Thomas, N., Biciloa, P., & Niukula, J. (2007). Diet and habitat preferences of the Fijian crested iguana (Brachylophus vitiensis) on Yadua Taba, Fiji: implications for conservation. *Australian Journal of Zoology, 55*, 341-350.

Mulwa, R. K., Neuschulz, E. L., Böhning-Gaese, K., & Schleuning, M. (2014). Seasonal fluctuations of resource abundance and avian feeding guilds across forest–farmland boundaries in tropical Africa. *Oikos, 122*, 524-532.

Myles, H., Menz, M., Mosimann-Kampe, P., & Arlettaz, R. (2009). Foraging habitat selection in the last Ortolan Bunting *Emberiza hortulana* population in Switzerland: Final lessons before extinction. *Ardea, 97*(3), 323-333.

Nakagawa, S. (2004). A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioural Ecology, 15*(6), 1044-1045.

Naumann, J. D., Carne, P. B., Lawrence, J. F., Nielsen, E. S., Spradbery, J. P., Taylor, R. W., Whitten, M. J., & Littlejohn, M. J. (1991). *The Insects of Australia: A Textbook for Students and Research Workers* (2nd Edition ed.). CSIRO, Melbourne University Press: Melbourne, Australia.

O'Donnell, C. F. J., & Dilks, P. (1994). Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. *New Zealand Journal of Ecology, 18*(2), 87-107.

Paprocki, N., Glenn, N. F., Atkinson, E. C., Strickler, K. M., Watson, C., & Heath, J. A. (2015). Changing habitat use associated with distributional shifts of wintering raptors. *Journal of Wildlife Management, 79*(3), 402-412.

Pearce, J. L., Shuurman, D., Barber, K. N., Larrivee, M., Venier, L. A., McKee, J. E., & McKenney, D. W. (2005). Pitfall trap designs to maximize invertebrate captures and minimize captures of nontarget vertebrates. *The Canadian Entomologist, 137*, 233-250.

Peat, N. (2006). *Kiwi: The People's Bird*. Christchurch: Otago University Press.

Perrins, C. M., & Birkhead, T. R. (1993). *Avian Ecology*. London, UK: Blackie.

Petit, D. R., Petit, K. E., & Petit, L. J. (1990). Geographic variation in foraging ecology of North American insectivorous birds. *Studies in Avian Biology, 13*, 254-263.

Phillips, M. J., Gibb, G. C., Crimp, E. A., & Penny, D. (2010). Tinamous and Moa flock together: Mitochondrial genome sequence analysis reveals independant losses of flight among ratites. *Systematic Biology, 59*(1), 90-107.

Pierce, R. J., & Sporle, W. (1997). Causes of kiwi mortality in Northland. *Conservation Advisory Science Notes, 169*, 1-8.

Pierce, R. J., & Westbrooke, I. M. (2003). Call count responses of North Island brown kiwi to different levels of predator control in Northland, New Zealand. *Biological Conservation, 109*, 175-180.

Piggott, M. P., & Taylor, A. C. (2003). Remote collection of animal DNA and its applications in conservation management and understanding the population biology of rare and cryptic species. *Wildlife Research, 30*, 1-13.

Potter, M. A. (1989). *Ecology and Reproductive Biology of the North Island Brown Kiwi (Apteryx australis mantelli).* (Unpublished PhD Thesis), Massey University, Palmerston North, New Zealand.

Potter, M. A. (1990). Movement of North Island Brown Kiwi (*Apteryx australis mantelli*) between forest remnants. *New Zealand Journal of Ecology, 14*, 17-24.

Potter, M. A., Hendriks, W. H., Lentle, R. G., Thomas, D. V., Minson, C. J., & Pindur, N. B. (2010). An exploratory analysis of the suitability of diets fed to a flightless insectivore, the North Island Brown Kiwi (*Apteryx mantelli*), in New Zealand. *Zoo Biology, 29*, 537-550.

Potter, M. A., Lenthle, R. G., Minson, C. J., Birthles, M. J., Thomas, D., & Hendriks, W. H. (2006). Gastrointestinal tract of the Brown Kiwi (*Apteryx mantelli*). *Journal of Zoology, 270*, 429-436.

Poulin, B., Lefebvre, G., & McNeil, R. (1992). Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology, 73*(6), 2295-2309.

Prasifka, J. R., Lopez, M. D., Hellmich, R. L., Lewis, L. C., & Dively, G. P. (2007). Comparison of pitfall traps and litter bags for sampling ground-dwelling arthropods. *Journal of Applied Entomology, 131*(2), 115-120.

Prugh, L. R., Arthus, S. M., & Ritland, C. E. (2008). Use of faecal genotyping to determine individual diet. *Wildlife Biology, 14*, 318-330.

Raphael, M. G., & Maurer, B. A. (1990). Biological considerations for study design. *Studies in Avian Biology, 13*, 123-125.

Razeng, E., & Watson, D. M. (2015). Nutritional composition of the preferred prey of insectivorous birds: Popularity reflects quality. *Journal of Avian Biology, 46*, 89-96.

Reid, B., Ordish, R. G., & Harrison, M. (1982). An analysis of the gizzard contents of 50 North Island Brown Kiwis, *Apteryx australis mantelli*, and notes on feeding observations. *New Zealand Journal of Ecology, 5*, 76-85.

Reid, B. E., & Williams, G. R. (1975). The Kiwi. In G. Kuschel (Ed.), *Biogeography and ecology in New Zealand* (pp. 301-330). Holland: The Hague.

Rettie, W. J., & Messier, F. (2000). Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography, 23*, 466-478.

Riber, A. B. (2006). Habitat use and behaviour of European hedgehog *Erinaceus europaeus* in a Danish rural area. *Aeta Theriologica, 51*(4), 363-371.

Rice, J., Ohmart, R. D., & Anderson, B. W. (1983). Habitat selection attributes of an avian community: A discriminant analysis investigation. *Ecological Monographs, 53*(3), 263-290.

Richardson, B. A., Richardson, M. J., Gonzalez, G., Shiels, A. B., & Srivastava, D. S. (2010). A canopy trimming experiment in Puerto Rico: The response of litter invertebrate communities to canopy loss and debris deposition in a tropical forest subject to hurricanes. *Ecosytems, 13*(2), 286-301.

Ricklefs, R. E. (1979). Adaptation, constraint, and compromise in avian postnatal development. *Biological Reviews, 54*, 269-290.

Robel, R. J., Press, B. M., Henning, B. L., Johnson, K. W., Blocker, H. D., & Kemp, K. E. (1995). Nutrient and energetic characteristics of sweepnet-collected invertebrates. *Journal of Field Ornithology, 66*(1), 44-55.

Robertson, H. A. (2004). Research and monitoring plan for the kiwi sanctuaries. *Science for Conservation, 241*, 1-23.

Robertson, H. A., Colbourne, R., Castro, I., Miller, C., Cresswell, M., McLennan, J., Dew, L., Miles, J., Pierce, R., Olsen, D., Flux, I. I., & Potter, P. (2003). *Kiwi (Apteryx spp.) Best Practice Manual*. Wellington, New Zealand: Department of Conservation.

Robertson, H. A., Colbourne, R. M., Graham, P. J., Miller, P. J., & Pierce, R. J. (2011). Experimental management of Brown Kiwi *Apteryx mantelli* in central Northland, New Zealand. *Bird Conservation International, 21*, 207-220.

Robertson, H. A., Dowding, J. E., Elliot, G. P., Hitchmough, R. A., Miskelly, C. M., O'Donnell, C. F. J., Powlesland, R. G., Sagar, P. M., Scofield, R. P., & Taylor, G. A. (2013). Conservation status of New Zealand birds, 2012. *New Zealand Threat Classification Series, 4*.

Robertson, H. A., & Fraser, J. R. (2009). Use of trained dogs to determine the age structure and conservation status of kiwi (*Apteryx* spp.) populations. *Bird Conservation International, 19*(2), 121-129.

Robertson, H. A., & Monchy, P. J. M. (2012). Varied success from the landscapescale management of kiwi *Apteryx* spp. in five sanctuaries in New Zealand. *Bird Conservation International, 22*, 429-444.

Robertson, H. A., & Westbrooke, I. A. (2005). A practical guide to the management and analysis of suvivorship data from radio-tracking studies. *DOC Technical Series* (Vol. 31, pp. 5-16). Wellington, New Zealand: Department of Conservation.

Robinson, S. K., & Holmes, R. T. (1982). Foraging behavior of forest birds: The relationships among search tactics, diet, and habitat structure. *Ecology, 63*(6), 1918-1931.

Romanowski, J., & Mihorski, M. (2008). Effect of season, weather and habitat on diet variation of a feedingspecialist: a case study of the long-eared owl, *Asio otus* in Central Poland. *Folia Zoologica, 57*(4), 411-419.

Rosenberg, K. V., & Cooper, R. J. (1990). Approaches to avian diet analysis. *Studies in Avian Biology, 13*, 80-90.

Rosenzweig, M. L. (1991). Habitat selection and population interactions: The search for mechanism. *The American Naturalist, 137*, 5-28.

Sales, J. (2005). The endangered kiwi: a review. *Folia Zoologica, 54*(1-2), 1-20.

Sales, J. (2006a). Digestive physiology and nutrition of Ratites. *Avian and Poultry Biology Reviews, 17*(2), 41-55.

Sales, J. (2006b). Feeding of the captive kiwi. *Zoos' Print Journal, 21*(11), 2454-2458.

Saltz, D. (1994). Reporting error measures in radio location by triangulation: A review. *Journal of Wildlife Management, 58*(1), 181-184.

Schirmel, J., Buchholz, S., & Fartmann, T. (2010). Is pitfall trapping a valuable sampling method for grassland Orthoptera? *Journal of Insect Conservation, 14*, 289-296.

Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology, Evolution, and Systematics, 2*, 369-404.

Seldon, D. S., & Beggs, J. R. (2010). The efficacy of baited and live capture pitfall traps in collecting large-bodied forest carabids. *New Zealand Entomologist, 33*(1), 30-37.

Shapiro, L. M. (2005). *Diet overlap and potential competition between North Island brown kiwi chicks (Apteryx mantelli) and ship rats (Rattus rattus) for limited resources on Ponui Island, New Zealand.* (Unpublished MSc Thesis), Massey University, Palmerston North, New Zealand.

Shapiro, L. M., Castro, I., & Colbourne, R. (In Prep). High mortality, slow growth rates and the diet of North Island Brown kiwi chicks on Ponui Island: A population at K?

Sinclair, A. R., Fryxell, J. M., & Caughley, G. (2006). *Wildlife ecology, conservation, and management* (2nd ed. ed.). Oxford, UK: Blackwell Publishing Ltd.

Singleton, P. L., Boyes, M., & Addison, B. (2000). Effect of treading by dairy cattle on topsoil physical conditions for six contrasting soil types in Waikato and Northland, New Zealand, with implications for monitoring. *Journal of Agricultural Research, 43*, 559-567.

Smith, K. G., & Rotenbetty, J. T. (1990). Quantifying food resources in avian studies: Present problems and future needs. *Studies in Avian Biology, 13*, 3-5.

Souter, N. J., Bull, M. C., & Hutchinson, M. N. (2004). Adding burrows to enhance a population of the endangered pygmy blue tongue lizard,*Tiliqua adelaidensis*. *Biological Conservation, 116*, 403-408.

Spence, J. R., & Niemela, J. (1994). Sampling Carabid assemblages with pitfall traps: The madness and the method. *The Canadian Entomologist, 126*, 881-894.

Standen, V. (2000). The adequacy of collecting techniques for estimating species richness of grassland invertebrates. *Journal of Applied Ecology, 37*(5), 884-893.

Stephens, D. W. (1990). Foraging theory: Up, down and sideways. *Studies in Avian Biology, 13*, 444-454.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging Theory* (1st Edition ed.). New Jersey, USA: Princeton University Press.

Stevens, A. F. J., Bayne, E. M., & Wellicome, T. I. (2011). Soil and climate are better than biotic land cover for predicting home-range habitat selection by endangered burrowing owls across the Canadian Prairies. *Biological Conservation, 144*, 1526-1536.

Stevens, G., McGlone, M., McCulloch, B., Ward, V., & Coz, G. (1995). *Prehistoric New Zealand*. Birkenhead, Auckland: Reed Publishing.

Strang, K. (2013). *The weasel (Mustela nivalis vulgaris): Opportunist, pest, and foraging competitor of North Island brown kiwi (Apteryx mantelli).* (Unpublished Honours Thesis), Massey University, Palmerston North, New Zealand.

Straub, J., Forbes, N., Pees, M., & Krautwald-Junghanns, M. E. (2003). Effect of handling-induced stress on the results of spectral Doppler echocardiography in falcons. *Research in Veterinary Science, 74*(2), 119-122.

Sullivan, J. J., Kelly, D., & Ladley, J. J. (2010). Feathers to fur: the status of New Zealand ecological research in 2009. *New Zealand Journal of Ecology, 34*(1), 1-5.

Swanson, G. A., & Bartonek, J. C. (1970). Bias associated with food analysis in gizzards of Blue-winted Teal. *Journal of Wildlife Management, 34*, 739-746.

Swift, R. J., Heath, A. C. G., & Jamieson, S. E. (2015). The kiwi tick, Ixodes anatis Chilton, 1904 (Acari: Ixodidae): aspects of its biology and ecology. *Systematic & Applied Acarology, 20*(1), 1-12.

Szaro, R. C., Brawn, J. D., & Balda, R. P. (1990). Yearly variation in resource-use behaviour by ponderosa pine forest birds. *Studies in Avian Biology, 13*, 226-236.

Taborsky, B., & Taborsky, M. (1992). Spatial organization of the North Island Brown Kiwi (*Apteryx australis mantelli*): sex, pairing status and territoriality. *Ibis, 134*, 1-10.

Taborsky, B., & Taborsky, M. (1995). Habitat use and selectivity by the Brown Kiwi (*Apteryx australis mantelli*) in a patchy environment. *The Auk, 112*(3), 680-689.

Taylor, H. R., Nelson, N. J., & Ramstad, K. M. (2014). Chick Timer™ software proves an accurate disturbance minimising tool for monitoring hatching success in little spotted kiwi (*Apteryx owenii*). *New Zealand Journal of Zoology, 41*(2), 139-146.

Tennyson, A. J. D. (2010). The origin and history of New Zealand's terrestrial vertebrates. *New Zealand Journal of Ecology, 34*, 6-27.

Tiddeman, C. R., & Flavel, S. C. (1987). Factors affecting choice of diurnal roost site by tree-hole bats (*Microchiroptera*) in south-eastern Australia. *Australian Wildlife Research, 14*, 459-473.

Van Tuinen, M., Sibley, C. G., & Hedges, S. B. (1998). Phylogeny and biogeography of ratite birds inferred from DNA sequences of the mitochondrial ribosomal genes. *Molecular Biology and Evolution, 15*, 370-376.

Vogl, W., Taborsky, B., Taborsky, M., Teuschl, Y., & Honza, M. (2004). Habitat and space use of European Cuckoo females during the egg laying period. *Behaviour, 141*, 881-898.

Walker, A. (2000). *The Reed Handbook of Common New Zealand Insects*. Auckland, New Zealand: Reed Books.

Walker, L. K., Armstrong, D. P., Brekke, P., Chauvenet, A. L. M., Kilner, R. M., & Ewen, J. G. (2013). Giving hihi a helping hand: assessment of alternative rearing diets in food supplemented populations of an endangered bird. *Animal Conservation, 16*, 538-545.

Walsberg, G. E. (1986). Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. *The Auk, 1*, 1-7.

Ward, D. F., New, T. R., & Yen, A. L. (2001). Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. *Journal of Insect Conservation, 5*, 47-53.

Watt, J. C. (1971). The North Island Kiwi: A predator of pasture insects. *New Zealand Entomologist, 5*(1), 25-27.

White, G. C., & Garrott, R. A. (1990). *Analysis of Wildlife Tracking Data*. California, USA: Academic Press, Inc.

Whyte, B. I., Ross, J. G., & Blackie, H. M. (2013). Differences in brushtail possum home-range characteristics among sites of varying habitat and population density. *Wildlife Research, 40*, 537-544.

Whyte, B. I., Ross, J. G., & Buckley, H. L. (2014). Changes in Australian brushtail possum (*Trichosurus vulpecula*) den site use following density reduction. *New Zealand Journal of Ecology, 38*(1), 147-151.

Wilson, A. (2014). *The triumphs, challenges and failures of young North Island brown kiwi (Apteryx mantelli): a study of behaviour, growth, dispersal and mortality.* (Unpublished MSc Thesis), Massey University, Palmerston North, New Zealand.

Wolda, H. (1990). Food availibility for an insectivore and how to measure it. *Studies in Avian Biology, 13*, 38-43.

Woo, K. J., Elliot, K. H., Davidson, M., Gaston, A. J., & Davoren, G. K. (2008). Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *Journal of Animal Ecology, 77*, 1082-1091.

Woolaver, L. G., Nichols, R. K., Morton, E. S., & Stutchbury, B. J. M. (2013). Feeding ecology and specialist diet of critically endangered Ridgway's Hawks. *Journal of Field Ornithology, 84*(2), 138-146.

Wroot, A. J. (1985). A quantitative method for estimating the amount of earthworm (*Lumbricus terrestris*) in animal diets. *Oikos, 44*, 239-242.

Ziesemann, B. (2011). *The social organisation and mating system of the Brown Kiwi (Apteryx mantelli).* (Unpublished PhD Thesis), Massey University, Auckland, New Zealand.

Ziesemann, B., Brunton, D. H., & Castro, I. C. (2011). Nesting success and breeding ecology in a high-density population of Brown Kiwi (*Apteryx mantelli*). *Emu, 111*, 148-154.

Appendices

Appendix A - Taxa/family classification and common names for all invertebrate groups identified over 12 months within pitfall traps and brown kiwi faecal samples on Ponui Island. Those in dark blue are groupings that were split further and identified at a lower level (those in light blue).

Amphipoda	Hoppers
Arachnida	Spiders, Harvestmen, Pseudoscorpians
Acari	Ticks and Mites
Blattodea	Cockroaches
Coleoptera	Beetles
Scarabaeidae	Scarab Beetles
Carabidae	Ground Beetles
Elateridae	Click Beetles
Staphylinidae	Rove Beetles
Oedemeridae	Blister Beetles
Cicindeliae	Tiger Beetles
Tenebrionidae	Darkling Beetles
Other	Other Beetles
Dermaptera	Earwigs
Diplopoda/Chilopoda	Millipede/Centipede
Diptera	Flies, Crane Flies
Gastropoda	Snails, Slugs
Hemiptera	True Bugs
Cicadae	Cicadas
Hymenoptera	Ants, Wasps, Ichneumonid Wasp
Isopoda	Slaters
Larvae	Unidentifiable Bug Larvae
Lepidoptera	Moths, Caterpillars
Oligochaeta	Earthworms
Orthoptera	Crickets, Weta
Formicidae	Crickets
Rhaphidophoridae	Weta
Phasmatodea	Stick Insect
Trichoptera	Caddisfly

Appendix B - Invertebrate availability abundance in grams of dry weight per pitfall for invertebrates caught over 12 months in pitfall traps on Ponui Island. Monthly measures of each of the 28 pitfall traps are given along with their gully location and habitat type.

#	Site	Habitat	Mar-13	Apr-13	May-13	Jun-13	Jul-13	Aug-13	Sep-13	Oct-13	Nov-13	Dec-13	Jan-14	Feb-14	Total
1	Red Stony	Forest	0.40	0.12	0.18	0.10	0.08	0.06	0.10	0.10	0.48	0.18	0.22	0.32	2.34
2	Red Stony	Forest	0.46	0.22	0.08	0.06	0.08	0.06	0.06	0.12	0.25	0.15	0.14	0.10	1.78
3	Red Stony	Forest	0.74	0.14	0.18	0.10	0.08	0.18	0.14	0.12	0.10	0.08	0.14	0.12	2.12
4	Red Stony	Scrub	0.14	0.14	0.24	0.22	0.06	0.10	0.16	0.14	0.22	0.14	0.32	0.16	2.04
5	Red Stony	Scrub	0.04	0.14	0.10	0.12	0.06	0.14	0.15	0.16	0.10	0.18	0.12	0.12	1.43
6	Red Stony	Scrub	0.16	0.24	0.12	0.12	0.06	0.08	0.10	0.10	0.14	0.18	0.26	0.40	1.96
7	Red Stony	Pasture	2.30	1.55	0.65	0.68	0.54	0.68	0.23	0.40	1.14	1.82	6.04	6.60	22.63
8	Red Stony	Pasture	2.98	1.00	1.68	2.00	0.94	1.13	0.78	0.82	0.96	1.80	4.72	6.02	24.82
9	Red Stony	Swamp	0.16	0.02	0.02	0.06	0.06	0.05	0.05	0.12	0.50	0.10	0.16	0.18	1.48
10	Red Stony	Swamp	0.10	0.06	0.10	0.06	0.06	0.03	0.06	0.08	0.10	0.06	0.08	0.06	0.84
11	Kauri	Forest	0.10	0.06	0.08	0.12	0.12	0.08	0.06	0.10	0.08	0.06	0.10	0.10	1.06
12	Kauri	Forest	0.32	0.04	0.20	0.04	0.08	0.10	0.08	0.16	0.30	0.20	0.46	0.18	2.16
13	Kauri	Scrub	0.18	0.16	0.20	0.10	0.14	0.18	0.16	0.22	0.16	0.10	0.12	0.16	1.88
14	Kauri	Scrub	0.10	0.22	0.56	0.32	0.40	0.20	0.28	0.16	0.34	0.28	0.56	0.46	3.88
15	Kauri	Pasture	3.32	2.03	0.23	0.24	0.10	0.10	0.24	0.20	0.48	0.28	1.78	6.62	15.61
16	Kauri	Pasture	3.72	0.64	0.23	0.22	0.10	0.18	0.38	1.10	0.52	0.80	5.00	4.74	17.62
17	Kauri	Swamp	0.14	0.08	0.06	0.14	0.12	0.06	0.47	1.23	0.90	0.58	0.64	0.42	4.84
18	Kauri	Swamp	0.27	0.22	0.10	0.10	0.12	0.12	0.20	0.32	0.35	0.45	2.35	1.62	6.22
19	Pipe	Forest	0.16	0.16	0.20	0.12	0.10	0.18	0.10	0.14	0.20	0.12	0.10	0.10	1.68
20	Pipe	Forest	0.06	0.06	0.12	0.10	0.06	0.06	0.05	0.12	0.06	0.08	0.06	0.10	0.93
21	Pipe	Forest	0.18	0.10	0.08	0.04	0.08	0.12	0.04	0.14	0.08	0.12	0.22	0.10	1.30
22	Pipe	Scrub	0.24	0.08	0.12	0.04	0.06	0.14	0.14	0.08	0.18	0.06	0.32	0.14	1.60
23	Pipe	Scrub	0.24	0.38	0.15	0.10	0.06	0.08	0.10	0.18	0.18	0.12	0.58	0.34	2.51
24	Pipe	Scrub	0.44	0.14	0.20	0.10	0.18	0.08	0.18	0.16	0.22	0.18	0.62	0.70	3.20
25	Pipe	Pasture	0.44	0.16	0.18	0.10	0.04	0.14	0.26	0.54	0.94	0.72	1.54	3.78	8.84
26	Pipe	Pasture	2.40	1.36	0.33	0.20	0.12	0.35	0.33	0.28	0.36	0.66	4.04	3.06	13.49
27	Pipe	Swamp	0.10	0.08	0.00	0.10	0.08	0.08	0.05	0.18	0.15	0.16	0.23	0.04	1.23
28	Pipe	Swamp	0.08	0.18	0.25	0.10	0.06	0.10	0.15	0.13	0.16	0.18	0.15	0.10	1.64
		Total	**19.97**	**9.77**	**6.63**	**5.80**	**4.04**	**4.84**	**5.09**	**7.59**	**9.64**	**9.84**	**31.07**	**36.84**	**151.09**
		Average	0.72	0.33	0.24	0.21	0.14	0.16	0.17	0.25	0.33	0.35	1.11	1.32	0.45

Appendix C - Invertebrate availability abundance in numbers of individual invertebrates of 16 different taxa caught over 12 months in pitfall traps on Ponui Island, sorted alphabetically. Measures of each month are given as the sum of all 28 pitfall traps.

Month	Amphipoda	Arachnida	Blattodea	Coleoptera	Collembola	Diplopoda/ Chilopoda	Diptera	Gastropoda	Hemiptera	Hymenoptera	Isopoda	Larvae	Lepidoptera	Oligochaeta	Orthoptera	Phasmatodea	Total
Mar-13	192	610	41	229	18	15	35	24	0	166	826	0	10	12	501	0	2679
Apr-13	130	327	37	185	16	10	54	78	0	155	555	0	3	7	284	3	1844
May-13	71	121	52	85	10	9	4	123	0	42	784	0	1	38	39	0	1379
Jun-13	65	102	36	85	0	2	2	81	1	17	1324	0	8	64	21	1	1809
Jul-13	75	117	19	40	0	12	10	64	2	8	745	3	3	26	13	0	1137
Aug-13	106	100	12	52	3	6	7	91	0	18	530	0	2	78	12	0	1017
Sep-13	165	121	18	84	10	16	11	152	0	45	599	7	7	84	16	0	1335
Oct-13	268	241	8	211	0	33	8	175	3	53	1213	32	11	79	35	0	2370
Nov-13	320	321	19	155	14	39	18	94	7	125	1887	53	34	17	62	0	3165
Dec-13	293	289	44	227	17	41	37	57	4	238	2136	27	19	22	304	0	3755
Jan-14	199	249	144	252	4	19	101	65	9	146	1208	0	13	9	1542	0	3960
Feb-14	220	248	134	163	8	19	178	38	7	110	1875	6	7	6	1077	0	4096
Total	2104	2846	564	1768	100	221	465	1042	33	1123	13682	128	118	442	3906	4	28546

Appendix D - ANOSIM test results table for invertebrate availability, including global and pairwise results.

Comparison	Observed R value	# of permutations	# simulated R ≥ observed R	P
One way (global): **Season**	0.137	999	0	0.001
Autumn x Winter	0.170	999	0	0.001
Autumn x Spring	0.075	999	0	0.001
Autumn x Summer	0.052	999	0	0.001
Winter x Spring	0.144	999	0	0.001
Winter x Summer	0.302	999	0	0.001
Spring x Summer	0.083	999	0	0.001
One way (global): **Habitat**	0.362	999	0	0.001
Forest x Scrub	0.208	999	0	0.001
Forest x Pasture	0.712	999	0	0.001
Forest x Swamp	0.156	999	0	0.001
Scrub x Pasture	0.571	999	0	0.001
Scrub x Swamp	0.211	999	0	0.001
Pasture x Swamp	0.368	999	0	0.001
One way (global): **Gully**	0.044	999	0	0.001
Red Stony x Kauri	0.068	999	0	0.001
Red Stony x Pipe	0.062	999	0	0.001
Kauri x Pipe	0.011	999	36	0.037
Two way cross (global): **Season x Habitat**	---	---	---	---
Season	0.246	999	0	0.001
Autumn x Winter	0.250	999	0	0.001
Autumn x Spring	0.199	999	0	0.001
Autumn x Summer	0.162	999	0	0.001
Winter x Spring	0.214	999	0	0.001
Winter x Summer	0.476	999	0	0.001
Spring x Summer	0.190	999	0	0.001
Habitat	0.455	999	0	0.001
Forest x Scrub	0.245	999	0	0.001
Forest x Pasture	0.814	999	0	0.001
Forest x Swamp	0.257	999	0	0.001
Scrub x Pasture	0.686	999	0	0.001
Scrub x Swamp	0.312	999	0	0.001
Pasture x Swamp	0.501	999	0	0.001

Appendix E - PERMDISP test results table for dispersion between groups in invertebrate availability (A) and utilisation (B), including ANOVA F statistic and Z scores.

A	F statistic	P (perm)
Season	3.9683	0.016
	Average Z score	**SE**
Autumn	36.318	1.0567
Winter	40.528	1.0826
Spring	13.092	1.0834
Summer	36.06	0.91696
Habitat	7.7808	0.001
	Average Z score	**SE**
Forest	30.761	0.92791
Scrub	35.095	0.85675
Pasture	36.371	1.0293
Swamp	37.171	1.4316
Gully	1.3681	0.344
	Average Z score	**SE**
Red Stony	39.656	0.98164
Kauri	37.377	0.93121
Pipe	38.971	0.95633

B	F statistic	P (perm)
Season	0.71804	0.616
	Average Z score	**SE**
Autumn	39.741	1.1951
Winter	40.045	1.2684
Spring	38.041	1.3177
Summer	38.102	1.2248
Habitat	1.5253	0.225
	Average Z score	**SE**
Forest	41.099	1.0773
Scrub	38.84	1.044
Pasture	41.073	1.0345
Poo Size	1.8164	0.18
	Average Z score	**SE**
Small	40.093	1.1259
Normal	40.512	0.83385
Large	36.735	1.5792
Poo Consistancy	1.4537	0.263
	Average Z score	**SE**
Dry	40.658	1.61
Normal	40.994	0.80714
Fresh	38.573	1.146

Appendix F - Invertebrate exploitation abundance in numbers of individual invertebrates of fifteen different taxa identified over 12 months in brown kiwi faecal samples collected on Ponui Island. Table also includes number and habitat of samples, as well as the number of fragments (Total, identifiable and unidentifiable).

Month	Number	Forest	Scrub	Pasture		# Fragments	ID'able	Un ID'able		Coleoptera	Adult	Larvae	Diptera	Hemiptera	Orthoptera	Acari	Arachnida	Blattodea	Chilopoda +Diplopoda	Hymenopter	Isopoda	Amphipoda	Trichoptera	Gastropoda	Dermaptera	Lepidoptera	Total
Mar-13	29	11	7	11		1515	1401	114		210	138	72	145	14	100	6	22	21	1	5	2	0	1	0	0	2	529
Apr-13	29	8	11	10		1551	1498	53		320	211	109	22	6	52	2	16	15	3	5	3	0	0	1	0	0	445
May-13	30	11	11	8		291	262	29		93	63	30	9	15	10	2	5	2	3	0	1	0	0	0	0	0	140
Jun-13	46	19	16	11		459	440	19		119	81	38	21	36	3	23	7	6	7	3	2	2	5	1	0	0	235
Jul-13	37	12	14	11		436	424	12		130	85	45	20	36	2	8	9	4	12	1	1	0	0	0	0	0	223
Aug-13	38	13	15	10		557	548	9		189	118	71	17	25	5	32	15	1	9	3	1	11	1	0	0	0	309
Sep-13	36	14	12	10		686	673	13		253	159	94	18	42	3	15	6	0	8	2	2	0	0	1	0	0	350
Oct-13	35	12	10	13		871	851	20		260	196	64	68	47	1	17	2	2	4	1	1	0	1	0	0	0	404
Nov-13	37	13	13	11		526	522	4		169	119	50	12	42	17	39	7	0	9	0	2	0	0	0	0	0	297
Dec-13	34	12	11	11		629	621	8		197	137	60	27	41	6	4	6	2	3	3	0	0	0	1	0	0	290
Jan-14	36	12	13	11		888	868	20		322	231	91	8	29	23	5	11	3	7	3	5	0	0	2	3	0	421
Feb-14	35	11	11	13		1287	1274	13		364	258	106	20	38	127	0	26	10	2	12	1	0	0	1	0	0	601
Total	422	148	144	130		9696	9382	314		2626	1796	830	387	371	349	153	132	66	68	38	21	13	8	7	3	2	4244

Appendix G - Invertebrate exploitation frequency of occurrence for fifteen different invertebrate taxa identified over 12 months in brown kiwi faecal samples collected on Ponui Island. Table also includes number and habitat of samples, as well as the number of fragments (Total, identifiable and unidentifiable).

Month	Number	Forest	Scrub	Pasture		# Fragments	ID'able	Un ID'able		Coleoptera	Adult	Larvae	Diptera	Hemiptera	Orthoptera	Acari	Arachnida	Blattodea	Chilopoda +Diplopoda	Hymenoptera	Isopoda	Amphipoda	Trichoptera	Gastropoda	Dermaptera	Lepidoptera	Total
Mar-13	29	11	7	11		1515	1401	114		1.00	1.00	0.69	0.69	0.31	0.66	0.17	0.66	0.48	0.03	0.10	0.03	0.00	0.03	0.00	0.00	0.03	0.35
Apr-13	29	8	11	10		1551	1498	53		0.97	0.93	0.83	0.41	0.21	0.48	0.07	0.41	0.38	0.10	0.10	0.07	0.00	0.00	0.03	0.00	0.00	0.29
May-13	30	11	11	8		291	262	29		0.87	0.77	0.53	0.30	0.33	0.20	0.03	0.17	0.07	0.10	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.20
Jun-13	46	19	16	11		459	440	19		0.78	0.72	0.52	0.41	0.52	0.07	0.22	0.15	0.13	0.11	0.04	0.04	0.02	0.02	0.02	0.00	0.00	0.22
Jul-13	37	12	14	11		436	424	12		0.89	0.65	0.70	0.49	0.51	0.05	0.16	0.22	0.11	0.19	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.24
Aug-13	38	13	15	10		557	548	9		0.87	0.76	0.61	0.45	0.47	0.11	0.21	0.37	0.03	0.21	0.08	0.03	0.03	0.03	0.00	0.00	0.00	0.25
Sep-13	36	14	12	10		686	673	13		0.89	0.75	0.75	0.50	0.61	0.08	0.17	0.17	0.00	0.17	0.06	0.06	0.00	0.00	0.03	0.00	0.00	0.25
Oct-13	35	12	10	13		871	851	20		0.91	0.91	0.71	0.54	0.66	0.03	0.17	0.06	0.06	0.11	0.03	0.03	0.00	0.03	0.00	0.00	0.00	0.25
Nov-13	37	13	13	11		526	522	4		0.84	0.70	0.65	0.32	0.59	0.14	0.16	0.14	0.00	0.24	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.23
Dec-13	34	12	11	11		629	621	8		0.91	0.82	0.56	0.47	0.59	0.15	0.09	0.18	0.06	0.09	0.09	0.00	0.00	0.00	0.03	0.00	0.00	0.24
Jan-14	36	12	13	11		888	868	20		0.86	0.81	0.72	0.22	0.56	0.44	0.14	0.22	0.06	0.17	0.08	0.06	0.00	0.00	0.06	0.06	0.00	0.26
Feb-14	35	11	11	13		1287	1274	13		1.00	0.94	0.83	0.51	0.54	0.77	0.00	0.46	0.17	0.06	0.06	0.03	0.00	0.00	0.03	0.00	0.00	0.32
Total	422	148	144	130		9696	9382	314		0.90	0.81	0.68	0.44	0.49	0.26	0.13	0.27	0.13	0.13	0.06	0.04	0.00	0.01	0.02	0.00	0.00	

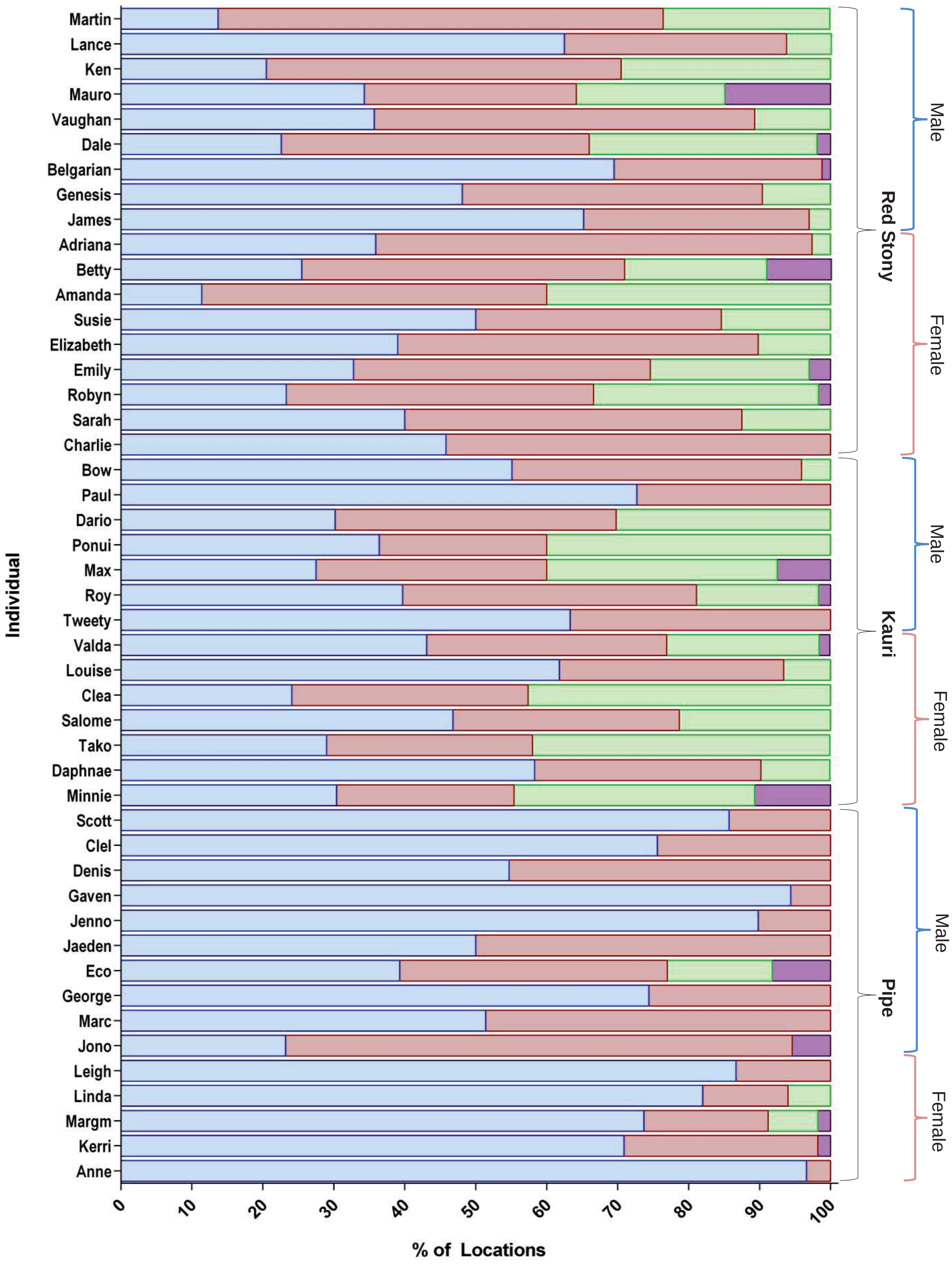
Appendix H - ANOSIM test results table for invertebrate exploitation, including global and pairwise results.

Comparison	Observed R value	# of permutations	# simulated R ≥ observed R	P
One way (global): **Season**	0.076	999	0	0.001
Autumn x Winter	0.111	999	0	0.001
Autumn x Spring	0.141	999	0	0.001
Autumn x Summer	0.045	999	0	0.001
Winter x Spring	0.011	999	61	0.062
Winter x Summer	0.097	999	0	0.001
Spring x Summer	0.067	999	0	0.001
One way (global): **Habitat**	0.009	999	27	0.028
Forest x Scrub	-0.002	999	672	0.673
Forest x Pasture	0.013	999	26	0.027
Scrub x Pasture	0.016	999	14	0.015
One way (global): **Poo Size**	0.015	999	171	0.172
Small x Normal	0.01	999	249	0.250
Small x Large	0.092	999	4	0.005
Normal x Large	-0.013	999	615	0.616
One way (global): **Poo Consistancy**	-0.006	999	595	0.596
Dry x Normal	0.025	999	212	0.213
Dry x Fresh	0.036	999	56	0.057
Normal x Fresh	-0.026	999	910	0.911
Two way cross (global): **Season x Habitat**	---	---	---	---
Season	0.094	999	0	0.001
Autumn x Winter	0.127	999	0	0.001
Autumn x Spring	0.209	999	0	0.001
Autumn x Summer	0.089	999	1	0.002
Winter x Spring	0.002	999	362	0.363
Winter x Summer	0.092	999	0	0.001
Spring x Summer	0.078	999	0	0.001
Habitat	0.030	999	2	0.003
Forest x Scrub	0.017	999	51	0.052
Forest x Pasture	0.033	999	6	0.007
Scrub x Pasture	0.041	999	3	0.004

Appendix I – Table of all 49 brown kiwi banded with transmitters on Ponui Island from March 2013 to March 2014. Includes transmitter number, sex, gully location, social grouping, estimated age, evidence of breeding and numbers of location fixes during the night and day in total and within each habitat type. M = male; F = female; # = transmitter frequency in TR4 receiver; F = forest, S = scrub, P = pasture, Sw = swamp.

#	Name	Sex	Gully	Social	Age	Breeding	Nocturnal Fixes	F	S	P	Sw	Diurnal Fixes	F	S	P	Sw
1	Tweety	M	Kauri	Group	6-10	Yes	60	38	22	0	0	36	35	1	0	0
3	Jono	M	Pipe	Alone	>10	No	56	13	40	0	3	36	6	20	0	10
5	Roy	M	Kauri	Pair	>10	Yes	58	23	24	10	1	51	49	1	0	1
7	Minnie	F	Kauri	Pair	>10	Pair	56	17	14	19	6	53	53	0	0	0
9	Anne	F	Pipe	Pair	>10	Pair	59	57	2	0	0	42	36	6	0	0
11	James	M	Red Stony	Pair	1-5	Yes	66	43	21	2	0	51	51	0	0	0
13	Sarah	F	Red Stony	Alone	1-5	-	40	16	19	5	0	30	14	15	0	1
15	Robyn	F	Red Stony	Group	6-10	Pair	60	14	26	19	1	43	7	31	3	2
17	Emily	F	Red Stony	Group	>10	Pair	67	22	28	15	2	50	28	14	2	6
19	Marc	M	Pipe	Alone	6-10	Yes	35	18	17	0	0	43	32	11	0	0
21	George	M	Pipe	Pair	6-10	Yes	43	32	11	0	0	45	26	1	0	18
23	Eco	M	Pipe	Alone	>10	No	61	24	23	9	5	47	18	6	0	23
25	Daphnae	F	Kauri	Pair	6-10	Pair	72	42	23	7	0	53	45	8	0	0
29	Elizabeth	F	Red Stony	Pair	>10	-	59	23	30	6	0	52	47	5	0	0
31	Kerri	F	Pipe	Pair	6-10	Pair	55	39	15	0	1	44	20	5	0	19
33	Max	M	Kauri	Pair	>10	Yes	40	11	13	13	3	54	54	0	0	0
35	Ponui	M	Kauri	Pair	6-10	Yes	55	20	13	22	0	55	55	0	0	0
37	Tako	F	Kauri	Alone	6-10	-	31	9	9	13	0	58	40	5	0	13
39	Genesis	M	Red Stony	Pair	>10	Yes	52	25	22	5	0	49	45	4	0	0
41	Jaeden	M	Pipe	Pair	1-5	Yes	30	15	15	0	0	42	13	29	0	0
43	Salome	F	Kauri	Pair	6-10	-	47	22	15	10	0	53	52	1	0	0
45	Susie	F	Red Stony	Pair	6-10	Pair	58	26	18	8	0	49	34	8	3	4
47	Amanda	F	Red Stony	Pair	6-10	-	35	4	17	14	0	49	36	2	11	0
49	Jenno	M	Pipe	Pair	>10	Yes	49	44	5	0	0	44	44	0	0	0
51	Belgarian	M	Red Stony	Alone	>10	No	82	57	24	0	1	49	42	5	0	2
53	Gaven	M	Pipe	Pair	6-10	Yes	54	51	3	0	0	44	31	8	0	5
55	Margm	F	Pipe	Pair	>10	Pair	57	42	10	4	1	45	34	2	0	9
57	Linda	F	Pipe	Pair	6-10	Pair	50	41	6	3	0	41	7	34	0	0
59	Dale	M	Red Stony	Group	6-10	Yes	53	12	23	17	1	48	12	35	0	1
61	Denis	M	Pipe	Alone	1-5	No	53	29	24	0	0	39	27	12	0	0
63	Vaughan	M	Red Stony	Pair	>10	Yes	28	10	15	3	0	36	29	7	0	0
65	Mauro	M	Red Stony	Alone	6-10	No	67	23	20	14	10	51	1	15	3	32
67	Clea	F	Kauri	Pair	>10	Pair	54	13	18	23	0	53	50	3	0	0
71	Ken	M	Red Stony	Pair	>10	No	44	9	22	13	0	44	33	0	11	0
73	Leigh	F	Pipe	Pair	6-10	Pair	60	52	8	0	0	36	29	7	0	0
75	Louise	F	Kauri	Group	6-10	Pair	76	47	24	5	0	51	48	2	0	1
77	Charlie	F	Roaming	Alone	1-5	-	24	11	13	0	0	30	15	15	0	0
79	Valda	F	Kauri	Pair	>10	Pair	65	28	22	14	1	45	41	0	0	4
81	Betty	F	Red Stony	Alone	6-10	-	55	14	25	11	5	51	38	7	0	6
83	Adriana	F	Red Stony	Pair	>10	Pair	39	14	24	1	0	45	20	22	2	1
85	Dario	M	Kauri	Pair	6-10	No	53	16	21	16	0	54	50	4	0	0
87	Clel	M	Pipe	Alone	>10	Yes	41	31	10	0	0	43	40	3	0	0
89	Paul	M	Kauri	Pair	>10	No	33	24	9	0	0	15	12	3	0	0
91	Lance	M	Red Stony	Alone	>10	No	16	10	5	1	0	20	9	10	0	1
95	Martin	M	Red Stony	Pair	>10	No	51	7	32	12	0	41	40	1	0	0
97	Bow	M	Kauri	Group	6-10	Yes	49	27	20	2	0	55	54	1	0	0
99	Scott	M	Pipe	Pair	>10	Yes	35	30	5	0	0	46	46	0	0	0
*27	Babe	F	Roaming	Alone	1-5	-	-	-	-	-	-	-	-	-	-	-
*69	Carla	F	Richards	Alone	>10	-	-	-	-	-	-	-	-	-	-	-

Appendix J – Graph showing the proportion of locations for each individual brown kiwi tracked on Ponui Island at night found within each of the four main habitat types. Gullies and sexes marked in brackets. Average N of 51 locations per individual.



Appendix K – Results of all Chi Squared analyses, including statistical outputs of the test as well as the expected and observed numbers of each habitat type for each grouping. P values are corrected for multiple comparisons.

Cross Tabulation

Availability*Utilisation	Chi Square		df	P
	1570.747		3	<0.001
	Forest	Scrub	Pasture	Swamp
Expected	448	1135	699	95
Observed	1195	825	315	42

Availability*Utilisation PIPE EXCLUDED	Chi Square		df	P
	835.681		3	<0.001
	Forest	Scrub	Pasture	Swamp
Expected	256	770	564	54
Observed	674	636	302	32

Gully*Habitat	Chi Square		df	P
	249.576		6	0.007
Red Stony	Forest	Scrub	Pasture	Swamp
Expected	446	308	118	16
Observed	337	388	142	21
Kauri	Forest	Scrub	Pasture	Swamp
Expected	380	263	100	13
Observed	337	248	160	11
Pipe	Forest	Scrub	Pasture	Swamp
Expected	369	254	97	13
Observed	521	189	13	10

Season*Habitat	Chi Square		df	P
	35.871		6	0.007
Winter	Forest	Scrub	Pasture	Swamp
Expected	407	281	108	14
Observed	409	309	80	12
Spring	Forest	Scrub	Pasture	Swamp
Expected	371	256	98	13
Observed	394	247	81	16
Summer	Forest	Scrub	Pasture	Swamp
Expected	417	288	110	14
Observed	392	269	154	14

Sex*Habitat	Chi Square		df	P
	16.237		3	0.007
Male	Forest	Scrub	Pasture	Swamp
Expected	631	436	166	22
Observed	641	455	134	25
Female	Forest	Scrub	Pasture	Swamp
Expected	564	389	149	20
Observed	554	370	181	17

Cross Tabulation

Shift*Habitat	Chi Square		df	P
	9.377		6	0.153
Start	Forest	Scrub	Pasture	Swamp
Expected	429	296	113	15
Observed	436	293	102	22
Middle	Forest	Scrub	Pasture	Swamp
Expected	387	267	102	13
Observed	368	281	110	10
End	Forest	Scrub	Pasture	Swamp
Expected	380	262	100	13
Observed	391	251	103	10

Age*Habitat	Chi Square		df	P
	34.091		6	0.007
1 to 5	Forest	Scrub	Pasture	Swamp
Expected	107	74	28	4
Observed	114	92	7	0
6 to 10	Forest	Scrub	Pasture	Swamp
Expected	542	375	143	19
Observed	554	341	166	18
>10	Forest	Scrub	Pasture	Swamp
Expected	545	377	144	19
Observed	527	392	142	24

Social Group*Habitat	Chi Square		df	P
	58.862		6	0.007
Pair	Forest	Scrub	Pasture	Swamp
Expected	737	509	194	26
Observed	795	458	199	14
Group	Forest	Scrub	Pasture	Swamp
Expected	184	127	49	6
Observed	160	143	59	4
Alone	Forest	Scrub	Pasture	Swamp
Expected	274	189	72	10
Observed	240	224	57	24

BreedingStatus*Habitat	Chi Square		df	P
	19.336		3	0.007
Incubating	Forest	Scrub	Pasture	Swamp
Expected	79	55	21	3
Observed	102	48	8	0
Not Incubating	Forest	Scrub	Pasture	Swamp
Expected	1116	770	294	39
Observed	1093	777	307	42

Appendix L – Results of the final GLMM, coefficients of variance, SE, 2*SE and t values for each grouping of all four factors included in the final model, comparing between all four habitat types. Coefficient of variance scores shaded grey are significant to P<0.05.

Gully	Red Stony				Kauri				Pipe			
	Coefficient	SE	t	2*SE	Coefficient	SE	t	2*SE	Coefficient	SE	t	2*SE
Forest	0	0	0	0	0	0	0	0	0	0	0	0
Scrub	-1.821	0.232	-7.855	0.464	-1.282	0.256	-4.998	0.512	-1.128	0.246	-4.588	0.492
Pasture	-7.543	0.607	-12.417	1.214	1.183	0.524	2.257	1.048	-1.275	0.795	-1.603	1.59
Swamp	-6.803	0.742	-9.168	1.484	-1.173	0.821	-1.428	1.642	-0.897	0.825	-1.087	1.65

Grouping	Paired				Group				Alone			
	Coefficient	SE	t	2*SE	Coefficient	SE	t	2*SE	Coefficient	SE	t	2*SE
Forest	0	0	0	0	0	0	0	0	0	0		0
Scrub	-1.821	0.232	-7.855	0.464	0.092	0.327	0.281	0.654	0.544	0.249	2.183	0.498
Pasture	-7.543	0.607	-12.417	1.214	-1.315	0.68	-1.935	1.36	1.44	0.548	2.627	1.096
Swamp	-6.803	0.742	-9.168	1.484	0.324	0.984	0.329	1.968	1.672	0.761	2.2	1.522

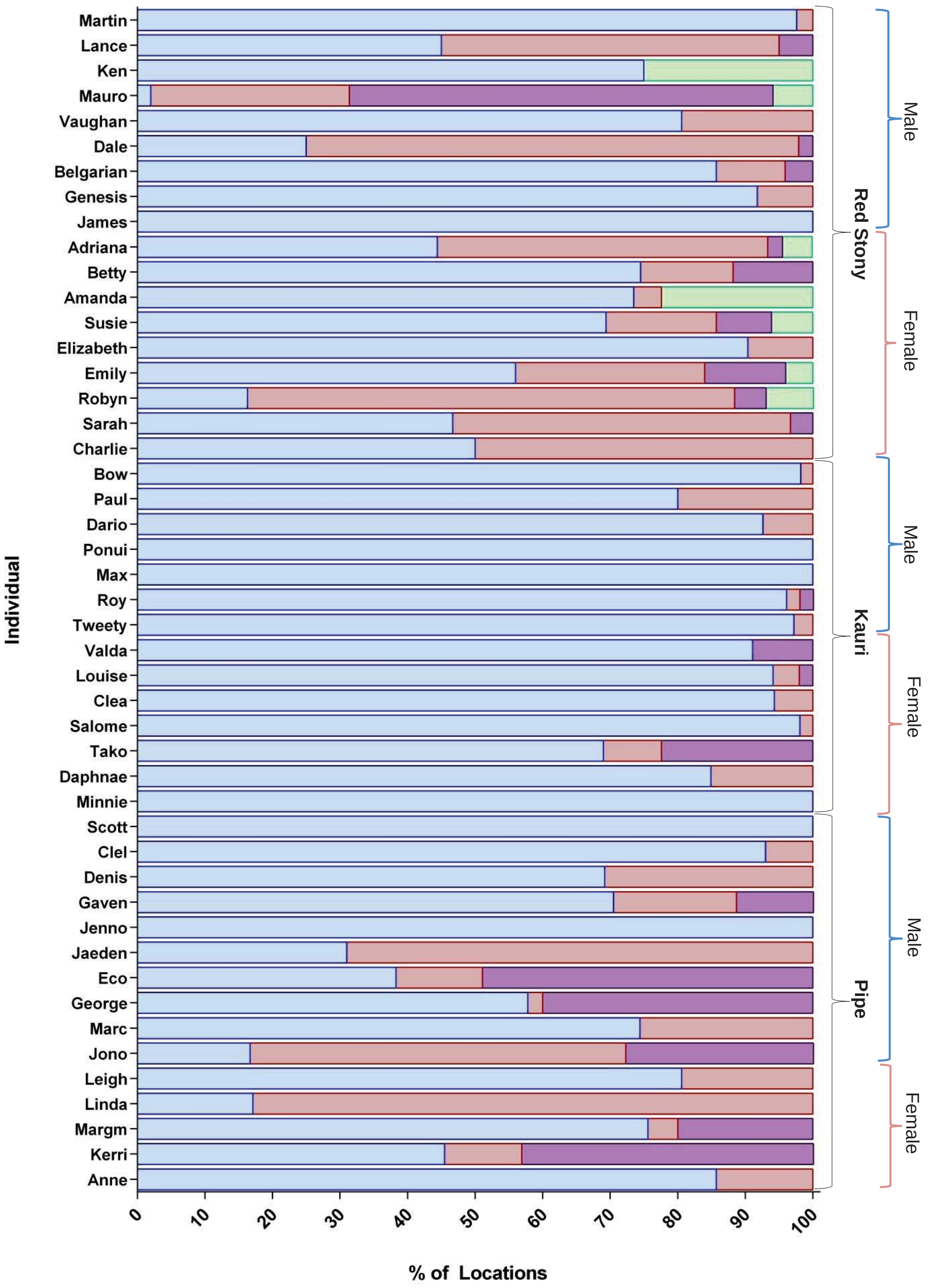
Season	Winter				Spring				Summer			
	Coefficient	SE	t	2*SE	Coefficient	SE	t	2*SE	Coefficient	SE	t	2*SE
Forest	0	0	0	0	0	0	0	0	0	0	0	0
Scrub	-1.821	0.232	-7.855	0.464	-0.982	0.139	-7.085	0.278	-1.629	0.164	-9.907	0.328
Pasture	-7.543	0.607	-12.417	1.214	-2.81	0.37	-7.598	0.74	-5.902	0.536	-11.021	1.072
Swamp	-6.803	0.742	-9.168	1.484	-0.505	0.439	-1.152	0.878	-1.663	0.504	-3.291	1.008

Weight	Coefficient	SE	t	2*SE
Forest	0	0	0	0
Scrub	19.805	1.242	15.944	2.484
Pasture	34.771	1.817	19.137	3.634
Swamp	23.458	1.944	12.067	3.888

Appendix M – Table showing the number and percentage of nocturnal brown kiwi locations for four important factors, indicating an even spread of sampling.

	# Locations	Percentage
Season		
Winter	810	34%
Spring	738	31%
Summer	829	35%
Gully		
Red Stony	888	37%
Kauri	756	32%
Pipe	733	31%
Shift		
Start	853	36%
Middle	769	32%
End	755	32%
Sex		
Male	1255	53%
Female	1122	47%

Appendix N – Graph showing the proportion of roosting locations for each individual brown kiwi tracked on Ponui Island found within each of the four main habitat types. Gullies and sex marked in brackets. Average N of 45 locations per individual.



Appendix O – Results of all Chi Squared analyses for habitat, including statistical outputs of the test as well as the expected and observed numbers of each habitat type for each grouping. P values are corrected for multiple comparisons.

Habitat Type Cross Tabulation				
Availability*Utilisation	Chi Square		df	P
	4404.251		3	<0.001
	Forest	Scrub	Pasture	Swamp
Expected	402	1018	625	85
Observed	1566	370	35	159

Season*Habitat	Chi Square		df	P
	196.724		9	0.005
Autumn	Forest	Scrub	Pasture	Swamp
Expected	250	59	6	25
Observed	214	66	3	57
Winter	Forest	Scrub	Pasture	Swamp
Expected	487	115	11	49
Observed	517	110	1	34
Spring	Forest	Scrub	Pasture	Swamp
Expected	459	108	10	47
Observed	492	100	8	24
Summer	Forest	Scrub	Pasture	Swamp
Expected	370	88	8	38
Observed	343	94	23	44

Gully*Habitat	Chi Square		df	P
	822.029		9	0.005
Red Stony	Forest	Scrub	Pasture	Swamp
Expected	548	136	30	60
Observed	497	179	32	66
Kauri	Forest	Scrub	Pasture	Swamp
Expected	511	123	11	52
Observed	653	34	1	9
Pipe	Forest	Scrub	Pasture	Swamp
Expected	476	122	13	48
Observed	416	157	2	84

Habitat Type Cross Tabulation				
Sex*Habitat	Chi Square		df	P
	11.442		3	0.01
Male	Forest	Scrub	Pasture	Swamp
Expected	850	201	19	86
Observed	872	177	93	14
Female	Forest	Scrub	Pasture	Swamp
Expected	716	169	16	73
Observed	694	193	66	21

Age*Habitat	Chi Square		df	P
	95.311		6	0.005
1 to 5	Forest	Scrub	Pasture	Swamp
Expected	134	32	3	13
Observed	114	66	2	0
6 to 10	Forest	Scrub	Pasture	Swamp
Expected	718	170	16	73
Observed	670	186	101	20
>10	Forest	Scrub	Pasture	Swamp
Expected	714	169	16	72
Observed	782	118	56	15

Social Group*Habitat	Chi Square		df	P
	202.349		6	0.005
Pair	Forest	Scrub	Pasture	Swamp
Expected	979	231	22	100
Observed	1082	162	27	61
Group	Forest	Scrub	Pasture	Swamp
Expected	250	59	6	25
Observed	229	96	5	10
Alone	Forest	Scrub	Pasture	Swamp
Expected	337	80	7	34
Observed	255	112	3	88

Appendix P – Results of all Chi Squared analyses for shelter type, including statistical outputs of the test as well as the expected and observed numbers of each habitat type for each grouping. P values are corrected for multiple comparisons.

Roost Type Cross Tabulation

Season*RoostType	Chi Square		df	P
	190.057		9	0.005
Autumn	Tree	Soil	Surface	Swamp
Expected	168	111	41	20
Observed	169	39	75	57
Winter	Tree	Soil	Surface	Swamp
Expected	327	216	80	39
Observed	361	223	56	22
Spring	Tree	Soil	Surface	Swamp
Expected	308	204	76	36
Observed	280	260	63	21
Summer	Tree	Soil	Surface	Swamp
Expected	249	164	61	39
Observed	241	173	65	25

Gully*RoostType	Chi Square		df	P
	297.405		9	0.005
Red Stony	Tree	Soil	Surface	Swamp
Expected	379	262	90	43
Observed	293	289	126	66
Kauri	Tree	Soil	Surface	Swamp
Expected	343	227	86	41
Observed	521	137	30	9
Pipe	Tree	Soil	Surface	Swamp
Expected	319	218	84	38
Observed	237	269	103	50

Cross Tabulation

Roost Type*Habitat	Chi Square		df	P
	2051.007		9	<0.001
Tree Burrow	Forest	Scrub	Pasture	Swamp
Expected	773	183	17	78
Observed	963	88	0	0
Soil Burrow	Forest	Scrub	Pasture	Swamp
Expected	511	121	11	52
Observed	500	139	22	34
Surface	Forest	Scrub	Pasture	Swamp
Expected	191	45	4	19
Observed	103	143	13	0
Swamp Burrow	Forest	Scrub	Pasture	Swamp
Expected	92	22	2	9
Observed	0	0	0	125

Roost Type Cross Tabulation

Sex*RoostType	Chi Square		df	P
	41.726		3	0.005
Male	Tree	Soil	Surface	Swamp
Expected	570	377	141	68
Observed	584	404	93	75
Female	Tree	Soil	Surface	Swamp
Expected	481	318	118	57
Observed	467	291	166	50

Age*RoostType	Chi Square		df	P
	25.137		6	0.005
1 to 5	Tree	Soil	Surface	Swamp
Expected	90	59	22	11
Observed	75	73	32	2
6 to 10	Tree	Soil	Surface	Swamp
Expected	482	319	119	57
Observed	467	315	126	69
>10	Tree	Soil	Surface	Swamp
Expected	479	317	118	57
Observed	509	307	101	54

Social Group*RoostType	Chi Square		df	P
	239.821		6	0.005
Pair	Tree	Soil	Surface	Swamp
Expected	657	435	162	78
Observed	714	453	136	29
Group	Tree	Soil	Surface	Swamp
Expected	168	111	41	20
Observed	203	77	50	10
Alone	Tree	Soil	Surface	Swamp
Expected	226	149	56	27
Observed	134	165	73	86

Appendix Q – Results of all Kruskal Wallis Tests for distance to habitat, including statistical outputs as well as number of samples, mean, standard deviation and standard error between seasons or gullies.

Distance to Habitat Kruskal Wallis Tests

Pasture*Season	Chi Square		df	P
	73.959		3	<0.001
	N	Mean	Std Dev	Std Error
Autumn	340	151.02	114.76	6.22
Winter	662	212.19	136.54	5.31
Spring	624	211.06	137.60	5.51
Summer	504	175.51	137.58	6.13
Total	2130	193.41	135.87	2.94

Distance to Habitat Kruskal Wallis Tests

Forest*Season	Chi Square		df	P
	64.172		3	<0.001
	N	Mean	Std Dev	Std Error
Autumn	340	37.96	85.65	4.65
Winter	662	9.26	34.73	1.35
Spring	624	14.41	52.92	2.12
Summer	504	31.48	76.36	3.40
Total	2130	20.61	62.19	1.35

Pasture*Gully	Chi Square		df	P
	1153.793		3	<0.001
	N	Mean	Std Dev	Std Error
Red Stony	774	155.09	86.15	3.17
Kauri	697	90.67	29.39	1.12
Pipe	659	351.28	98.58	3.88
Total	2130	193.41	135.87	2.94

Forest*Gully	Chi Square		df	P
	201.690		3	<0.001
	N	Mean	Std Dev	Std Error
Red Stony	774	30.64	76.45	2.81
Kauri	697	3.9	21.62	0.82
Pipe	659	22.84	66.65	2.62
Total	2130	20.61	62.19	1.35