Comparison of human modified and native forest habitats in the Hunua Ranges, Auckland

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

Doctor of Philosophy in Ecology

at Massey University, Auckland, New Zealand

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2010

Acknowledgements

Without the enthusiasm and guidance of my primary supervisor Assoc Prof Dianne Brunton this project would not have taken place.

Thanks also to Dr Russell Death for supervision.

This study was planned with advice from: Assoc Prof Dianne Brunton, Dr Jacqueline Beggs, Dr Jocelyn Berry, Dr Louise Malone, Dr Tim Lovegrove, Dr Matt Baber, and Dr Graham Ussher.

The thesis was improved by comments and discussion provided by Dianne Brunton, and proofread by Dr Mark Seabrook-Davison and John Steemson.

This research was carried out with permission from: Auckland Regional Council, Massey University Animal Ethics Committee, Department of Conservation, Te Waka Totara Trust, The Ngati Paoa Trust, and The Ngati Paoa Whanau Trust Board. I am particularly grateful for the support from Hariata Gordon, David Gray, and James Brown.

Field sites and laboratory facilities were accessed with assistance from and kind permission of: Auckland Regional Council, Waytemore Forests Ltd, Department of Conservation, The University of Auckland, and Manaaki Whenua - Landcare Research. Especial thanks to Fred Fairbrother, Richard Harwood, Rosemary Gatland, Hazel Speed, Anne Tomlinson, Imogen Bassett, Shane Boustead, Jacqueline Beggs, Joanna Barr, and Steve Simpson.

Invertebrate identification and laboratory work training was aided by: Stephen Thorpe, Grace Hall, Dianne Brunton, and Jocelyn Berry.

Stable isotope sample preparation was undertaken under advisement of Stefania Mambelli and Sarah Bury who also carried out the final processing of stable isotope samples.

Fieldwork was assisted by: Michael Anderson, Marleen Baling, Paul Barnett, Dianne Brunton, Jane Dudley, Morag & Simon Fordham, Elisabeth Fraser, Melinda Habgood, Marine Hubert, Barbara Hughes, Kendra Koch, Pauline Kroef, Todd Landers, Daniel Lim, Nick McIntosh, Jasmin Popovic, Luis Ortiz Catedral, Jennifer Rickett, James Russell, Clare & Mark Seabrook-Davison, John Steemson, Dylan Storey, Monique Jansen van Rensburg, and Jenny Waite.

Laboratory work was aided by: John Steemson, Marine Hubert, Adrienne Verburg & Wim, and Ticiana Fettermann.

This project was funded by: Foundation for Research Science & Technology and Massey University.

Additional financial assistance was awarded by: Claude McCarthy Fellowship, New Zealand Federation for Graduate Women (North Shore Branch), Coombs Memorial Bursary, International Ornithological Committee, and Australasian Society of the Study of Animal Behaviour.

Throughout my PhD the time I spent in the Ecology & Conservation Group building was extensive. It would not have been as enjoyable without the humour and support of my labmates. In particular I would like to thank: Michael Anderson, Shauna Baillie, Marleen Baling, M. E. Ball, Manuela Barry, Anne-Sophie Boyer, Nicolas de la Brosse, Dianne Brunton, Anna Gsell, David Gudex-Cross, Weihong Ji, Brigitte Kreigenhofer, Emmanuelle Martinez, Gabriel Machovsky Capuska, Luis Ortiz Catedral, Kevin Parker, Jennifer Rickett, Mark Seabrook-Davison, Idan Shapira, Karen Stockin, Monique Jansen van Rensburg, Dylan van Winkel Sarah Wells, Cheeho Wong, and Birgit Ziesemann.

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General abstract

Understanding the trophic structure of a habitat is vital to understanding the species composition and interactions of species and individuals within that habitat. It dictates which organisms may survive, their abundance, and biotic interactions. Pine (*Pinus radiata*) (hereafter pine) plantations in New Zealand are the most common type of silviculture, and, although primarily a commercial forestry enterprise, they are recognised as an ecosystem able to provide habitat for some native species. It is therefore pertinent to evaluate the ecological value of this habitat while keeping in mind its lack of permanence. New Zealand's native forests are a natural comparison for mature pine plantation, and I have tracked the diet and behaviour of selected species across both habitats and their contiguous boundary. This study utilised multiple techniques and collected two years of behavioural and prey availability data to compare the habitats of interest on a variety of trophic levels (TLs) and temporal scales.

Research was conducted in the Hunua Ranges, New Zealand, between March 2006 and June 2009 and considered three habitats (pine plantation, native forest, and the contiguous boundary of these habitats). Vegetation samples from leaf litter (hereafter vegetation), Lepidopteran larvae (hereafter caterpillars), predacious adult Coleoptera (hereafter beetles), rats (*Rattus rattus*) (hereafter rats), house mice (*Mus musculus*) (hereafter mice), and North Island tomtits (*Petroica macrocephala toitoi*) (hereafter tomtits) were analysed in terms of $\delta\ ^{13}C$, and $\delta\ ^{15}N$ values. Comparisons between habitats, taxa, seasons, and sexes were conducted. Stable isotope analyses showed samples from native habitat had the lowest $\delta\ ^{15}N$ levels within taxa, with boundary samples usually showing an intermediate value, and pine plantation samples commonly having the highest $\delta\ ^{15}N$ levels. This suggests that the native forest provides a lesser amount of available nitrogen to the fauna inhabiting it, whereas the pine plantation (potentially due to fertilisation) contains a higher level of available nitrogen. Significant separation of taxa was seen between habitats for $\delta\ ^{13}C$ values of rat and tomtit samples, and for $\delta\ ^{15}N$ values of vegetation, rat, and tomtit samples. Within habitats, taxa were distinctly separated for both $\delta\ ^{13}C$ and $\delta\ ^{15}N$, and their foraging ranges spanned three to four TLs. The caterpillar and mouse samples collected did not show significant seasonal fluctuations in $\delta\ ^{13}C$ or $\delta\ ^{15}N$ values, and ship rats showed seasonal differences

only for $\delta^{13}C$ values. Seasonal difference in ship rat isotope signatures may indicate season related foraging locations with variation occurring between summer and autumn compared to winter and spring. Stomach content analyses for rats and mice did not show separation by habitat within species, but did show significant differences between rat and mouse diet in the boundary habitat. The volume of invertebrates, vertebrate remains, and vegetation in rat stomachs showed significant differences between seasons with a greater proportion of vegetation found during winter; however no evidence of this was seen for mice. Neither technique showed evidence of intersexual dietary differences for rodents, and isotopic values were also similar between tomtit sexes within each major habitat type. The use of stable isotope and stomach content analyses to assess rodent diet was a valuable combination as it clarified this aspect better than either method alone.

Tomtit sexes differed in foraging behaviour, with males observed foraging more frequently on the ground than females and females using vegetation (in particular substrates between 0 - 3 m) more than males. Foraging by both sexes varied between breeding and non-breeding season in 2006, with more ground use occurring in the non-breeding season and more vegetation use (males: 3 - 6 m; females: 0 - 3 m) in the breeding season. Tomtit foraging behaviour in three habitats (pine plantation, native forest, and the contiguous boundary of these habitats) was compared. Overall, tomtit foraging in native forest occurred more frequently in vegetation 3 - 6 m compared to the use of this strata in either pine or boundary habitat. Males showed inter-annual differences in foraging, using the ground significantly more in 2006 than 2007. The research described tomtit foraging and habitat use, illustrating the complexity of foraging behaviour and the difficulty of understanding sex, habitat, and season associated foraging variation.

The availability of the ground-prey items for tomtits differed most widely between habitats. Annual and seasonal differences were also found within pine and native forest habitat. Prey availability varied between seasons within pine (spring versus summer), native (winter versus spring), and boundary (winter versus summer) habitats. No differences between prey availability were found for male and female tomtits.

However, male foraging samples showed annual separation in the pine and native habitats, and between some seasons within the pine (winter versus summer) and native (winter versus spring) forests. No significant seasonal differences were found for female comparisons. Through comparison of habitat and temporal prey availability for tomtits I have begun to determine the role that pine plantation invertebrates play in the diet of insectivorous native birds. Many questions have been raised by this study, and there is much scope for future research into the trophic structure of pine versus native forest.

General introduction

Trophic structure is of utmost importance in an ecosystem, as it dictates which organisms occur, their numbers, and their biotic interactions within a habitat (Pascual & Dunne, 2006). The trophic links within food webs fluctuate temporally (Pimm, 2002; Pascual & Dunne, 2006), and different habitats may be largely distinct, or interact extensively with large amounts of resource exchange occurring (Pimm, 2002; Winemiller, 2007). The degree of trophic separation is largely a function of the scale of examination and the ecosystem of interest. Trophic structure research spans many different scales (Mitsch & Day, 2004), and investigates ecosystems ranging from marine (e.g. Tsagarakis *et al.*, 2010), to temperate terrestrial (e.g. Boyer *et al.*, 2003), polar (e.g. Brockerhoff *et al.*, 2002), and tropical systems (e.g. Kupfer *et al.*, 2006). The system complexity addressed extends from tri-trophic parasitoid-based interactions (e.g. Schädler *et al.*, 2010), to the extremely diverse food webs of tropical rainforest (e.g. Villanueva *et al.*, 2006), and studies utilising decades of data (e.g. Hutchings *et al.*, 2009).

The formulation of questions regarding habitat diversity is fundamental to considerations of the natural world, and heavily associated with the study of the trophic structure of a habitat. Since Darwin's considerations of an "entangled bank", researchers have been investigating the interactions between species and the associated energy and nutrient fluxes (Berlow *et al.*, 2009). From these initially formulated observations the theories of ecological niche were formed, including maximum niche overlap and the ideas surrounding this theory regarding interspecific competition, which relates directly to Gause's competitive exclusion principle (Vandermeer, 2007). Researchers such as Hairston *et al*. (1960) and MacArthur & Levins (1967) then continued with this framework when writing about community structure and species divergence, and these paradigms are still the basis of much research into trophic structure undertaken.

Foraging niche, interspecific niche overlap, and interspecific competition for food resources have been the focus of many researchers. Ulfstrand (1977) studied the

interactions of individuals of multiple *Parus* species forming a guild in Swedish forests to investigate niche size and overlap through time. In contrast, Hanson & Leggett (1986) studied intra- and interspecific competition in terms of freshwater fish foraging by examining stomach contents. Studies into resource portioning continue today with research taking advantage of technological advances and utilising methods such radiotelemetry (Frere *et al.*, 2008), and stable isotope analyses (York & Billings, 2009), to track resource use of individuals. These interactions between individuals and species within an ecosystem ultimately control the flow of energy and nutrients through predator-prey interactions and food resource partitioning. To investigate these aspects, observations of tomtit foraging and assessment of rodent diet were carried out to allow comparison of sexes and species and lead to evaluation of competition and niche overlap in the future.

The concept of energy flow through ecosystems from producers to consumers is key to the understanding of trophic structures. Odum & Odum (1955) studied producers and consumers inhabiting a coral reef (Marshall Islands) to investigate the productivity, energetic efficiency, standing crop structure, and steady state equilibrium of this tropical marine ecosystem. Their study largely utilised a variety of survey and chemical analyses to obtain measures of biomass, energy transfer efficiency, and equilibrium estimates. It is interesting to note that very similar questions are still being asked within this field of ecology today at larger scales and utilising technological advances. For example Gilmanov *et al*. (2010) examined the productivity and standing stock of grassland and agro-ecosystems using flux-tower measurements. Similarly, Davis *et al*. (2010) assessed the efficiency of energy transfer to predators and the influence of enrichment on the trophic stability of a stream ecosystem through experimental enrichment of the water system over a five year period.

There are a wide variety of techniques available to monitor trophic structure, from standard methods that clarify individual foraging, to general techniques that can be used to elucidate habitat and species-level trophic interactions. All methods vary in terms of difficulty and accuracy depending on the research question and the species of interest. Direct observation is utilised in this study to track tomtit foraging behaviour and can

determine a lot about spatial, temporal, and strategic foraging considerations (Faria & Rodrigues, 2009; Maldonado-Coelho, 2009; Puckett *et al.*, 2009). Feeding collars (Dyrcz & Flinks, 2003; Török *et al.*, 2004; Grim, 2006), stomach flushing (Sánchez-Bayo *et al.*, 1999; Fraser & Lalas, 2004; Denoël & Demars, 2008), and analysis of regurgitate (Cardiff & Goodman, 2008; González-Acuña *et al.*, 2009; Lesiński *et al.*, 2009), stomach content (this study; Kok & Louw, 2000; Lathiya *et al.*, 2008; Wilson & Lee, 2010), or faecal content (Eeva *et al.*, 2009; Ottoni *et al.*, 2009; Vernes & McGrath, 2009), are standard methods used to ascertain diet. More recently, molecular techniques have also become available, such as the use of DNA analysis of stomach contents (Sheppard & Harwood, 2005; Dunshea, 2009; Carreon-Martinez & Heath, 2010), evaluation of fatty acids in the blood (Tierney *et al.*, 2008; Jacobs *et al.*, 2009; Williams & Buck, 2010), tracking the accumulation of toxins within tissues (Eason *et al.*, 2002; Dowding *et al.*, 2006; Hoare *et al.*, 2007), and stable isotope analyses (this study; Carlton & Hodder, 2003; Harper, 2007; Nakagawa *et al.*, 2007).

Utilising the same technique across different habitats allows comparison of trophic structure between habitats, and the first aim of my research was to investigate trophic structures in pine plantation, native forest, and their contiguous boundary using both standard ecological and stable isotope techniques. Pine plantations in New Zealand are the most common type of silviculture (Withers & Keena, 2001; Brockerhoff *et al.*, 2003; Denyer *et al.*, 2006), with plantations covering approximately 1.7 million ha (Brockerhoff *et al.*, 2002). Although not as diverse as native forest, pine plantations are utilised by many species of native invertebrates and birds (Jackson, 1971; Clout & Gaze, 1984; Robertson *et al.*, 2007; Minor, 2008). Unfortunately, they also provide an environment suitable for a number of invasive species, e.g. mice (Badan, 1986), and rats (Clout, 1980). Although primarily a commercial forestry enterprise, pine plantations in New Zealand are becoming recognised as an ecosystem able to provide habitat to native, and even endangered animal species (Collier & Halliday, 2000; Brockerhoff *et al.*, 2005; Pawson *et al.*, 2010). It must be kept in mind however, that pine plantations are not the equivalent of native forest. Although they are capable of providing good quality habitat for native species, this habitat is not permanent, and the vast majority of species will not be able to survive through the felling regime. It is

therefore pertinent to evaluate the ecological value of this habitat while keeping in mind its lack of permanence.

In New Zealand, research into pine plantation as a habitat supporting both native and introduced species has been conducted utilising a variety of methods to clarify food chain interactions. The species present have been studied using standard survey techniques to investigate the occurrence of taxa including invertebrates (Pawson *et al.*, 2009; Pawson & Sky, 2009; Quinn *et al.*, 2009), birds (Clout & Gaze, 1984; Ledgard, 1995; Seaton *et al.*, 2010), and mammals (Jacometti *et al.*, 2007; Borkin & Parsons, 2009), which then allows trophic relationships to be ascertained. Additionally, stomach content analyses have been conducted on certain species inhabiting pine plantations, such as rats (Clout, 1980), mice (Badan, 1986), and fallow deer (*Dama dama*) (Nugent, 1990). Internationally, bird foraging has been investigated through direct observation in pine habitat (Kleintjes & Dahlsten, 1994), and terrestrial invertebrate food webs in *Pinus* spp. forest have been investigated using stable isotope techniques (Erdmann *et al.*, 2007; Robinson *et al.*, 2008; Abd El-Wakeil, 2009). This study adds to past research by considering pine plantation trophic structure using multiple techniques and comparing it to native forest.

New Zealand's native forests are a natural comparison for mature pine plantation and I have been able to track the behaviour of selected species, common to both habitats, in order to compare these habitats without the confounding factors of different species or substantial geographic distance. Native forests in New Zealand provide habitat for 159 bird species (Robertson *et al.*, 2007), and a large number of invertebrate species (the total number of insects alone in New Zealand has been estimated at over 20,000 species (Emberson, 1995)). However, there are very few locations, even within native forest, that have not been impacted by introduced species. Invasive species remain a paramount threat to native biodiversity in New Zealand (Brockerhoff *et al.*, 2010), and much research conducted in native forest is due to efforts of pest control and the study of impacted systems (Sweetapple & Nugent, 2007; Wilson *et al.*, 2007; Beggs *et al.*, 2008). Research into the trophic structure of native forest has utilised a variety of approaches from standard surveys and observations (Burns & Lake, 2009; Boulton *et*

al., 2010; Michel *et al.*, 2010), to DNA analysis of stomach contents (McQueen & Lawrence, 2008), and stable isotope techniques (Harper, 2006; Hawke & Holdaway, 2009; Najera-Hillman *et al.*, 2009). Mice, rats, and tomtits were investigated in this project to compare diet across habitats using standard observation, stable isotope, and stomach content analyses.

Each year both pine and native forest in New Zealand undergo resource fluctuations at a variety of temporal scales, and this research investigated the effects of seasonal and annual changes. Climatic changes and their flow-on effects have been shown to impact upon reproductive timing for birds and mammals (Bourgault *et al.*, 2006; Shine & Brown, 2008; Bourgault *et al.*, 2010), and are key triggers for invertebrate breeding and development (Raimondo *et al.*, 2004; Kobayashi & Kato, 2007). Additionally, seasonal climatic fluctuations cause resource changes in vegetation by cueing flower production, fruit ripening, and seed germination (Burrows, 1994; Richardson *et al.*, 2005; García-Mozo *et al.*, 2010). Each of these processes has large effects on resource availability, abundance, and quality, with ramifications throughout the trophic structure of the habitat. For instance, invertebrate biomass has a large impact on the nutrient flow of forest ecosystems as invertebrates are responsible for processes such as vegetation breakdown (Garrett *et al.*, 2007), and form a mainstay of many vertebrate diets (Gill & Whitaker, 2001; Heather & Robertson, 2005; King, 2005). Therefore seasonal fluctuations have marked influence on nutrient release and insectivore diet. By collecting data across seasons and years, temporal comparisons within and between habitats, taxa, and sexes were made, and are necessary to understand the scope of food chain variation across these temporal scales.

Temporal resource fluctuations can be tracked through community and individual level responses. For example beetle communities inhabiting New Zealand pine plantation stands of different ages have been tracked through time to compare spatial and temporal components of this invertebrate order (Hutcheson & Jones, 1999). In contrast, Barbour *et al*. (2002) used stable isotopes to track fluctuations of pine cellulose levels in ^{13}C and ^{18}O over the course of seasons. Studies conducted within New Zealand native forest have also traced beetle seasonality to ascertain abundance, activity, and reproductive

timing (Hutchison, 2007). The seasonal production of honeydew and mast seeding events in New Zealand beech (*Nothofagus*) are both well researched examples of seasonal nutrient pulses in indigenous, but invasive-species impacted, ecosystems (Harris, 1991; Fitzgerald *et al.*, 1996; Alley *et al.*, 2001; Richardson *et al.*, 2005; Beggs *et al.*, 2008; McQueen & Lawrence, 2008).

When trophic considerations are investigated at an individual level influences such as the sex of the animal become important. Competition occurs both between and within species and resources are partitioned to alleviate this in a variety of ways (Naoki, 2003; Minderman *et al.*, 2006). Within species, intersexual competition may be decreased by each sex utilising different resources (Recher & Holmes, 2000). These differences can be maintained through anatomical dimorphism that ensures each sex is physically limited as to which resources can be efficiently utilised (Temeles *et al.*, 2010), or they may be maintained behaviourally with the more aggressive sex dominating the most preferred resource (Stenberg & Hogstad, 2004; Temeles *et al.*, 2005; Franzreb, 2010). Obviously the level of competition is dependent on the availability of the required resource. Therefore, intersexual differences in foraging can sometimes be observed only at certain times of the year when resources become limited, or when it is advantageous to make use of a wider range of food sources (Ligon, 1973; Recher & Holmes, 2000; Morrissey *et al.*, 2010).

Intersexual niche differences have been widely studied with a variety of techniques utilised to determine their presence and degree (Hobson *et al.*, 1999; Perkins & Speakman, 2001; Nassar *et al.*, 2003; Ben-David *et al.*, 2004; Forero *et al.*, 2005; Bearhop *et al.*, 2006; Hedd & Montevecchi, 2006; Lewis *et al.*, 2006; Kurle, 2009; Morrissey *et al.*, 2010). Many earlier studies focused on behavioural observation or stomach content analysis alone to clarify foraging differences between males and females (Berry, 1968; Jackson, 1970; Ligon, 1973; Austin, 1976; Clout, 1980; Peters Wm & Grubb Jr, 1983; Badan, 1986). Recent studies have used a combination of more traditional methods with techniques such as stable isotope analysis to investigate both behavioural and nutritive aspects of intersexual foraging differences (Woo *et al.*, 2008; Kohler *et al.*, 2009; Morrissey *et al.*, 2010). These differences are important when

considering individual resource requirements. This research compared male versus female foraging and dietary differences for mice, rats, and tomtits using combinations of stable isotope and stomach content analyses, behavioural observation, and prey availability assessment.

My research combines investigation of disturbed and relatively undisturbed forest habitat with a comparison of native and invasive species common to both. In each habitat, stable isotope samples were collected from vegetation, leaf litter inhabiting invertebrates, rodents, and tomtits to allow comparison between taxa and habitats in addition to seasonal comparisons. Male and female rodents and tomtits were also contrasted within each species. Stomach content analyses of rodents were carried out permitting a comparison of this method versus stable isotope analyses. Foraging observations of tomtits and collection of invertebrates from tomtit ground foraging points allowed a thorough evaluation of the foraging and prey availability of this species between habitats, years, seasons, and sexes. Through consideration of multiple taxa and use of a variety of techniques to investigate the two years of data collected, this research aims to evaluate and compare the trophic structure of pine plantation, native forest, and their boundary habitat in the Hunua Ranges, New Zealand.

1.1 Thesis plan

In this thesis I investigated the trophic structure of three habitats (pine plantation, native forest, and their contiguous boundary) in the Hunua Ranges (New Zealand). I examined whether vegetation, caterpillars, beetles, rats, mice, and tomtits inhabiting the different habitats vary in isotopic signature between habitats, and whether vegetation, herbivores, and predators differ in their $\delta\ ^{15}N$ values within each habitat. Seasonal comparisons of the habitats were carried out for caterpillars, rats, and mice, and intersexual differences examined for rats, mice, and tomtits. The results of stable isotope and stomach content analyses of rodent diet were compared to evaluate their differences and similarities. Tomtit foraging behaviour was investigated to determine whether foraging substrate, height, and strategy differs between sexes, seasons, years, and habitats. The

invertebrate availability at tomtit ground foraging sites was outlined to test the predictions that prey availability differs between habitats, seasons, years, and sexes.

The aims of my thesis are addressed in the following chapters.

Chapter One provided a general introduction to trophic structure and foraging ecology.

Chapter Two addressed the trophic structure of pine plantation, native forest, and the contiguous boundary of these habitats in the Hunua Ranges (New Zealand). The questions of whether samples collected for each taxon inhabiting the different habitats vary in isotopic signature between habitats, and whether vegetation, herbivores, and predators differed in their $\delta\ ^{15}N$ values within each habitat were posed. Seasonal comparisons of the habitats were carried out and intersexual differences within species examined. I also evaluated the results of stable isotope and stomach content analyses of rodent diet.

Chapter Three investigated the foraging behaviour of tomtits, it asked whether foraging substrate, height, and strategy differed between sexes, seasons, years, and habitats.

Chapter Four outlined the availability of invertebrates at ground-foraging sites of tomtits, and then tests the predictions that prey availability differed between habitats, seasons, years, and sexes.

Chapter Five summarised the main findings of this research and discussed future lines of research stemming from this project.

This research was conducted under Massey University Animal Ethics Committee (05/126 & 06/34) and Department of Conservation permission (NHS-02-28, AK-17685-RES & banding permit 2008/33).

Comparison of trophic structures between human modified and native forest habitats

Abstract

The trophic structures of three different habitats (pine plantation, native forest, and the contiguous boundary of these habitats) in the Hunua Ranges, New Zealand, were compared using stable isotope analyses of biological samples representing different TLs, and stomach content analyses of rodents. Vegetation, caterpillars, beetles, rats, mice, and tomtits were analysed in terms of $\delta^{13}C$, and $\delta^{15}N$ values. Comparisons between habitats, taxa, seasons, and sexes were conducted. Stable isotope analyses showed samples from native habitat had the lowest $\delta^{15}N$ levels within taxa, with boundary samples usually showing an intermediate value, and pine plantation samples commonly having the highest $\delta^{15}N$ levels. Significant separation of taxa was seen between habitats for $\delta^{13}C$ values of rat and tomtit samples, and for $\delta^{15}N$ values of vegetation, rat, and tomtit samples. Within habitats, taxa were distinctly separated for both $\delta^{13}C$ and $\delta^{15}N$, and their foraging ranges spanned three to four TLs. The caterpillar and mouse samples did not show significant seasonal fluctuations in $\delta^{13}C$ or $\delta^{15}N$ values, and rats showed seasonal differences only for $\delta^{13}C$ values. Seasonal differences in rat isotope signatures may indicate season-related foraging locations with variation occurring between summer and autumn compared to winter and spring. Stomach content analyses for rats and mice did not show separation by habitat within species, but did show significant differences between rat and mouse diet in the boundary habitat. The volume of invertebrates, vertebrate remains, and vegetation in rat stomachs showed significant differences between seasons with a greater proportion of vegetation found during winter; however no evidence of this was seen for mice. Neither technique showed evidence of intersexual dietary differences for rodents, and isotopic values were also similar between tomtit sexes within each major habitat type. Using stomach content analyses in conjunction with stable isotope analyses allowed me to investigate the question of diet at the level of prey items, in addition to carbon and nitrogen signatures, and clarified the results of each technique.

2.1 Introduction

One defining feature of New Zealand's terrestrial ecosystems is their degree of isolation from other such ecosystems, and the barrier to species movement this isolation creates (Murphy, 1951; Glasby, 1986; Halkett, 1991). New Zealand's ecosystems and the species within them have developed largely without external influence until human colonisation, and this lack of external influence has resulted in high levels of endemism, and some species being representatives of primitive lineages (Murphy, 1951; Glasby, 1986; Halkett, 1991). Terrestrial vertebrates are dominated by birds, with bats the only mammals until human colonisation, very few amphibians, and reptiles represented by tuatara (*Sphenodon* sp.) and lizards; empty niches have been filled by avian and invertebrate species (Murphy, 1951; Glasby, 1986; Halkett, 1991). Due to this, New Zealand's terrestrial ecosystems may be thought of as more simple than that of many other countries. Although other southern land masses started off with a similar Gondwanan species compliment, their subsequent contact with other terrestrial ecosystems has changed the ancient lineages more dramatically than in New Zealand, and often the Gondwanan species have been replaced through predation or competition with other species (Halkett, 1991). This process, in addition to that of human modification of landscapes at a habitat level, (e.g. the introduction of radiata pine for forestry), is now of concern in New Zealand as well, though a relatively recent one.

Nutrient flow within ecosystems

Within an ecosystem, species interact through trophic links that facilitate the transfer of energy and nutrients, and, when considered as an interlinking group, constitute a food web (Post, 2002; Woodward *et al.*, 2005). Each species within a food web will largely function in a certain role, e.g. detritivore, herbivore, or predator (Woodward *et al.*, 2005). The linearity of food chains, with interacting producers, herbivores, and carnivores is a central concept of community ecology (Fretwell, 1987), although there are few truly linear food chains (DeAngelis, 1992; Pimm, 2002; Post, 2002). At every transitional TL in a food chain there is nutrient transfer both "up" and "down" the system (Hunter & Price, 1992). Energy passes from the first TL, (producers e.g. pine), to the second level, (herbivores or primary consumers, e.g. caterpillars), to the third level, (carnivores or secondary consumers, e.g. tomtit), to the fourth level, (top

carnivores or tertiary consumers, e.g. stoat (*Mustela erminea*)) (Pimm, 2002). There are also species that feed at more than one level of the food chain (omnivores), e.g. rats and mice (Pimm & Lawton, 1978).

The length of food chains is a well-studied phenomenon but relies heavily on definition. When food chain length is considered to be the modal number of TLs that energy passes through to get to the top predators in a food web then the most common food chain length is three or four, although as stated previously, simple, linear food chains do not exist naturally (Pimm, 2002). The number of levels in a food chain may be limited by the amount of nutrient available to producers (DeAngelis, 1992). Although primary production in different ecosystems does not appear to affect food chain length it is likely that below certain production levels the length of food chains must be constrained (Pimm, 2002). For example, native habitats are often more heterogeneous and species rich than those that are highly modified (Robinson & Sutherland, 2002; Loyn *et al.*, 2007; Robertson *et al.*, 2007); therefore, native habitats would be expected to have longer food chains and more intricate food webs.

The range of producers available for herbivores to exploit is at least partly a product of the amount of nutrients within a system (Cadenasso *et al.*, 2004), and dictates herbivore diversity and quality as a food resource for predators (Hunter & Price, 1992). For example, the fitness of insectivorous birds has been linked to the abundance and quality of their prey, which varies with forest fragment size (Burke & Nol, 1998; Zanette *et al.*, 2000). However, the number and quality of producers within a food web may also be controlled by their own predators such as pathogens and herbivores (Hunter & Price, 1992). Hence the often debated "top-down" (e.g. predator pressure), or "bottom-up" (e.g. nutrient availability), control of community resource dynamics is a mix of both pressures in concert acting with differing levels of force over time (Hunter & Price, 1992).

Due to disturbance (e.g. introduction of invasive species or extinctions), species and their associated trophic links may be lost or added to a food web (DeAngelis, 1992; Ripple & Beschta, 2003; Woodward *et al.*, 2005). These changes may affect the

presence, density or behaviour of a species and have far reaching effects on other TLs due to their interlinked nature (Ripple & Beschta, 2003; Schmitz *et al.*, 2004; Woodward *et al.*, 2005). If species with similar food resource requirements partition these temporally or spatially, then they effectively have separate food webs (Pimm, 2002). The idea of separate food webs can be further explored by looking at what constitutes a habitat for each species and therefore what food resources are available to it (Pimm, 2002). These mechanisms often evolve over time and massive food chain disruptions may be caused when human introduced species have resource requirements that overlap with native species (DSIR, 1987). Introduced rodents frequently become invasive, damaging natural ecosystems and agro-ecosystems alike, partially due to their plastic diet (Cassaing *et al.*, 2007). Rats are widespread and of major conservation concern in New Zealand, because of the threats they pose to wildlife through predation of animals and seeds, and they have been implicated in the decline of many bird species (e.g. robin (*Petroica australis*)) (Innes, 2005; McQueen & Lawrence, 2008).

Central to the understanding of food webs are nutrient cycles. In this thesis, I focus on the carbon and nitrogen cycles. Carbon is fixed by producers from atmospheric CO_2, and from there three processes are possible: the carbon may be released again through respiration, it may be taken up by consumers if the vegetative material is eaten by herbivores, or taken up by decomposers when the producer, or parts of the producer die (Socolow, 1999; Kasparl *et al*., 2009). In contrast, most nitrogen enters the ecosystem through fixation of atmospheric nitrogen by bacteria, although it may also be fixed by lightening, and in anthropogenically influenced environments, nitrogen can also enter ecosystems as fertiliser (Wang *et al.*, 2004; Socolow, 1999). Once fixed into the tissues of an organism nitrogen is transferred through the ecosystem by standard food web links, and released again into the atmosphere through the action of denitrifying bacteria (Socolow, 1999). These cycles are impacted whenever habitat modification takes place (e.g. forest clearance), which is a drastic and often large-scale disturbance and has rapid and far reaching effects on the food web present (DeAngelis, 1992). After forest clearance, nutrient cycles are impacted due to increased losses to run off, as opposed to being recycled through vegetation uptake (Vitousek & Melillo, 1979). Changes in break down rates of nutrients are also increased, further limiting the remaining nutrient pools (Matson & Vitousek, 1981).

Total amounts of nutrients within soil and vegetation can be used to investigate relative productivity and nutrient enrichment of a habitat (Awiti *et al.*, 2008), with water and soil nutrient content influencing plant dynamics (Wang *et al.*, 2008). As a rule, soils which are cropped, and therefore have a low nutrient input, will tend to have higher $\delta^{15}N$ values (Awiti *et al.*, 2008). Conversely, if soil is collected from a naturally forested habitat, the $\delta^{15}N$ value tends to be low due to the closed nitrogen cycle (Awiti *et al.*, 2008). Organic carbon and total nitrogen in the soil under pine (*Pinus taeda*) plantations was compared with adjacent pasture in southern Brazil by Wiesmeier *et al*. (2009). They found both carbon and nitrogen components decreased under *P. taeda* that had been planted eight years previously versus pasture, and was even lower under *P. taeda* after 30 years. This result was largely due to the reduced breakdown of leaf litter under *Pinus* spp. versus grasses, the incorporation of nitrogen into trees, and the lack of nitrogen-fixing legumes in the plantations (Wiesmeier *et al.*, 2009). Depleted organic carbon and total nitrogen in addition to higher $\delta^{13}C$ and $\delta^{15}N$ values from soils in cultivated versus naturally forested sites have also been found (Beets *et al.*, 2002; Awiti *et al.*, 2008). This was due to higher soil nutrient loads in cultivated habitats resulting in increased photosynthesis rates, less intercellular CO_2, and therefore greater $\delta^{13}C$ values for foliage (Ma *et al.*, 2007). Unsurprisingly, treatment of plants with fertiliser will also increase percentage nitrogen in the foliage (Wang *et al.*, 2004; Oleksyn *et al.*, 2007). However, limited CO_2 uptake and assimilation will also occur in plants growing in nitrogen deficient soils (Oleksyn *et al.*, 2007).

The nutrient content of vegetation is affected by many factors in addition to the nutrient content of the soil, including phylogenetic relationships, seasonal variation (Swift *et al.*, 1979; DeAngelis, 1992; Wardle, 2002), and additional nutrient inputs into the community (Polis *et al.*, 1997; Wang *et al.*, 2004; Oleksyn *et al.*, 2007). Nutrient availability to producers is highly influenced by the environment due to its impact on decomposer activity (Swift *et al.*, 1979); in addition, marked influence can come from outside the ecosystem or habitat type (Swift *et al.*, 1979; Polis *et al.*, 1997; Cadenasso *et al.*, 2004; Holt, 2004). This influence may be in terms of nutrients from detritus, plants, or animals, and may enter the food web at any TL, causing major impacts on

food web dynamics (Polis *et al.*, 1997; Cadenasso *et al.*, 2004; Holt, 2004), such as seabird guano on offshore islands (Markwell & Daugherty, 2002).

Landscape level nutrient exchanges (e.g. nutrients carried by rainfall, detrital leaf litter input, and decomposition rates), are influenced by the composition of the habitat edges they cross, or through edge influence on animal behaviour (DeAngelis, 1992; Baudry & Burel, 2004; Cadenasso *et al.*, 2004). The agents that carry nutrients across habitat boundaries are wind, water, flying and terrestrial animals, and anthropogenic affects (Forman, 1997). The boundary itself acts as a kind of filter with some agents passing easily through and others hardly ever crossing the edge (Forman, 1997). The penetration of the compounds transported into different habitats are also affected by this phenomenon (Forman, 1997). There are many aspects influencing the permeability of boundaries including population density of species, vegetation structure, the sharpness of the boundary, source and sink pool dynamics, receiving habitat suitability, and the position of the boundary to a natural boundary (e.g. a territory edge) (Buechner, 1987; Stamps *et al.*, 1987a; Stamps *et al.*, 1987b). With small habitat fragments the majority of the habitat will be edge, but this edge will differ in width depending on a multitude of features and the variable of interest (Forman, 1997). The width of the edge is determined by many aspects and may differ between sides of a habitat according to sun exposure (Matlack, 1994), age of edge, prevailing wind direction (Forman, 1997), and intensity of slope. The amount of exchange between habitats is due to the number of factors in contact with both habitats (e.g., the number of shared species) (Forman, 1997). It could be said that the native sub-canopy present beneath the pine plantation of the Hunua Ranges is an example of a wide edge, or of an edge that if left free of human intervention would expand further due to colonisation of disturbed areas.

Stable isotope applications

The ecological applications of stable isotope analyses are based around transference of stable isotopes between dietary items and consumers (Harding & Stevens, 2001; Bennett & Hobson, 2009). Trophic levels can be estimated using $\delta\ ^{15}N$ values because this isotope increases by 1.46 - 5‰ between TLs (Gannes *et al.*, 1998; Harding & Stevens, 2001; Caut *et al.*, 2008b). In contrast $\delta\ ^{13}C$ shows less trophic discrimination but is indicative of carbon source from producers (Harding & Stevens, 2001; Caut *et*

al., 2008a) and hence relative productivity (Cook & Dawes-Gromadzki, 2005). Despite that, differences of -8.79 - 2.7‰ between TLs for carbon do occur and can be interpreted in a foraging context (DeNiro & Epstein, 1978; Fry *et al.*, 1978b; Caut *et al.*, 2008b). Stable isotope applications in ecological systems are gaining popularity as a way of discerning diet, trophic interactions, and patterns of habitat use (Harding & Stevens, 2001).

The proportion of stable isotopes found in a tissue sample is a relatively good estimate of the proportions of stable isotopes taken up from the environment (Jardine *et al.*, 2003; Schindler & Lubetkin, 2004). But as energy is transferred, variation of isotope proportions occurs between the initial source and the tissues due to biofractionation, which is a change in isotope ratios due to the slight variations between isotopes that give them different kinetic properties (Jardine *et al.*, 2003; Schindler & Lubetkin, 2004). Biofractionation also occurs within organisms as nutrients are processed, and so different tissues may show varied isotope signatures (Schindler & Lubetkin, 2004). Due to the uptake of nutrients from different sources within an organism's environment, and the variable distribution of nutrients to tissues, stable isotope ratios may not directly indicate separate resource contribution to an organism (Gannes *et al.*, 1997; Hart & Lovvorn, 2002). There are also concerns regarding the amount of variation that may occur between individuals and sites due to environmental factors in addition to variation through time (Lancaster & Waldron, 2001; Jardine *et al.*, 2003; Ma *et al.*, 2007). Therefore accuracy relies on samples being collected from an adequate number of tissues and individuals (Jardine *et al.*, 2003).

Using stable isotopes to elucidate food chain dynamics and a species' diet overcomes some of the common short falls of alternate techniques. If food items are easily digested there may be little evidence of them in the stomach or faeces, however, isotope analysis can show their dietary importance and origin if they are isotopically distinct (Harding & Stevens, 2001; Stapp & Polis, 2003; Caut *et al.*, 2008a; Hawke & Holdaway, 2009). It also overcomes the problem of looking at a snapshot of an animal's last meal which may not be generally representative of diet, or parts of the diet that are assimilated (Romanek *et al.*, 2000; Stapp, 2002; Bennett & Hobson, 2009). Even direct

observations may be biased due to ease of observation of certain dietary items and foraging behaviours (Caut *et al.*, 2008a; b). Isotopic ratios may change during the year, reflecting changes in food resources (Stapp, 2002; Kupfer *et al.*, 2006), and nutrient availability, however care must be taken that an appropriate tissue is used to reflect the time period of interest. Stable isotope analysis can clarify unexpected results that would not be detectable through other means. For instance, using stable isotope ratios Bodey *et al*. (2010) were able to show a shift in foraging habitat for mink (*Neovison vison*) to marine influenced resources on the Outer Hebrides (Scotland), as control measures for this invasive species were implemented.

However, stable isotope analyses do not necessarily provide the level of precision needed in terms of detailed and specific dietary analysis, and caution must be used in interpreting isotope values. Isotopic analysis is limited in showing specific trophic interactions due to dietary items overlapping in signature (Carreon-Martinez & Heath, 2010). For example, Herrera *et al*. (2003) found that stable isotopes enabled them to distinguish between animal and plant matter consumed by birds, and the relative importance of each dietary source, but could not determine the finer taxonomy of dietary items. Traditional methods such as gut and faecal content analyses, together with direct observation, are much better for finer taxonomic identification (Hobson *et al.*, 1999; Caut *et al.*, 2008a), and to detect prey changes that do not constitute a change in dietary stable isotope composition (Dalerum & Angerbjörn, 2005). Due to differential rates of fractionation within tissues, between individuals of the same species in different physiological states, and the potential for tissues to contain elements that were stored (e.g. as fat), and then mobilised to form the tissue of interest, comparisons using stable isotopes do need to be interpreted with care (Dalerum & Angerbjörn, 2005; Kurle, 2009).

The resources of a habitat will determine the species and density of individuals it can support, with habitat differences impacting across many levels of the food chain, from nutrient levels and individual foraging variation, to population and community level impacts. In theory, habitats that undergo regular and intense disturbances should have shorter food chains than more stable habitats, although the length of a food chain is also

controlled by a variety of other factors (e.g. ecosystem size) (Post, 2002). Stable isotope signatures often vary across habitats, with leaves collected from temperate forests having significantly lower average for $\delta\ ^{15}N$ values than those from tropical forests (Martinelli *et al.*, 1999). Delta ^{13}C and $\delta\ ^{15}N$ values differ between habitats and species for earthworms (Neilson *et al.*, 2000), and rodents (Harper, 2006). Birds also show diverse isotopic signatures depending on what forest type they inhabit (Fujita & Koike, 2009). Therefore, to understand ecosystems at a food chain level, it is useful to compare stable isotopes across habitats using common species.

Rodents within food chains

Rat diet in beech (*Nothofagus* spp.) forests in New Zealand has been found to be comprised of plant matter, invertebrates, rodents, and birds (McQueen & Lawrence, 2008). However, in pine plantations only trace amounts of vertebrate remains have been found in rat stomachs, and fewer stomachs were found to contain plant matter for the same season (Clout, 1980). Mice living in New Zealand beech forest also forage on plants, fungal matter, and invertebrates (Fitzgerald *et al.*, 1996). But when mice from pine plantation were compared (for the same season) to those from beech forest, the lack of fungus in their stomachs was a marked exception (Badan, 1986). However, Badan's (1986) comparison of mouse diet between pine and native forest showed general similarities between the two habitats, as well as some marked differences between invertebrate and seed species. It is likely that resource availability differences associated with habitat are responsible for these variations. When rodent species within the same habitat were compared, mice were found to lack vertebrate remains while this prey group was present in rats (Badan, 1986; McQueen & Lawrence, 2008).

Within most ecosystems, seasonal fluctuations in resources are observed due to interactions between changing climatic conditions and the organisms present. These changes may be predictable and occur annually at a relatively fixed time (e.g. bud burst and animal migration (Glendinning & Brower, 1990; Murakami, 1998)), or they may occur less predictably (e.g. mast seeding (Fitzgerald *et al.*, 1996)). Regardless of timing these seasonal variations have marked impacts on the species present, and are associated with individual, population, and community level consequences (Glendinning & Brower, 1990; Fitzgerald *et al.*, 1996; Stapp, 2002). The example

provided by Glendinning & Brower's (1990) research illustrates these impacts well. Each winter, monarch butterfly (*Danaus plexippus*) aggregations formed in Mexico constitute a superabundant seasonal food resource for mouse species (Glendinning & Brower, 1990). Not all species of mice in the area make use of this resource, and it was also utilised differently between the sexes of *Peromyscus melanotis* that do forage from monarch butterfly aggregations (Glendinning & Brower, 1990). The number of female *P. melanotis* increased between two and five times within aggregations, as opposed to smaller increases in numbers of males, with the males potentially limited from more extensive immigration by the larger females (Glendinning & Brower, 1990). Female *P. melanotis* that eat the lipid-rich monarch butterflies, breed successfully, and wean significantly more young than female *P. melanotis* outside of the monarch butterfly aggregations, and females of other mouse species within aggregations, due to this food resource (Glendinning & Brower, 1990).

Seasonal dietary fluctuations are common for mammals and birds (Dalerum & Angerbjörn, 2005; Hedd & Montevecchi, 2006), and rats are especially plastic in both their breadth and capacity for temporal diet shifts (Cassaing *et al.*, 2007). Past research on the hair of rats inhabiting islands in the Hyéres and Riou archipelagos have found evidence for seasonal stable isotope fluctuations occurring between winter and summer (Cassaing *et al.*, 2007). Studies on rats and Norway rats (*Rattus norvegicus*) have also taken advantage of the longer term record of certain tissues. For example, Stapp (2002) was able to show seasonal rat reliance by rats for seabird eggs and chicks on Shiant Island through stable isotope analyses of rat tissues with different rates of nutrient turnover. Stapp's (2002) investigation also included stomach content analysis on the same animals, and he found no evidence of this predation or scavenging, as the sampling took place after the seabird breeding season. He noted that even if stomach sampling had been concurrent with seabird breeding the highly digestible nature of the eggs and chicks would have made them difficult to observe. Research conducted on Norway rats on Langara Island, Canada, by Hobson *et al*. (1999) found similar stable isotope results.

Large, seasonal changes in diet composition, in terms of invertebrates versus vegetation volume, and different vegetation components, have been recorded for rats from the Ogasawara Islands (Yabe *et al.*, 2010). In particular, twig cutting was evident only in certain months (March - April), and corresponded to times when other foods were low in availability (Yabe *et al.*, 2010). In New Zealand beech forest, Fitzgerald *et al*. (1996) recorded seasonal shifts in mouse diet, although they noted that the shifts were not large; more mouse stomachs examined during May and August contained vegetation, and more stomachs in November and February contained invertebrates. Habitats such as New Zealand's beech forests experience pulsed inputs into their food webs through mast seeding years, which may alter trophic relationships drastically (DSIR, 1987; Fitzgerald *et al.*, 1996; Sears *et al.*, 2004). Pulses like this may even increase the number of species present (DeAngelis, 1992). Generalist feeders like rodents often irrupt during mast seeding events and then switch food resources once the resource pulse is over (DSIR, 1987). The increase in rodents can lead to an increase in rodent predators which also switch prey once rodent numbers begin to decrease (DSIR, 1987; Ostfeld & Keesing, 2000). These circumstances have dire consequences for rodent competitors as well as alternative predator food sources such as birds (Norbury & Heyward, 2008).

Within New Zealand ecosystems, tomtits are one of the native species at risk of rat predation with nest failure commonly due to rats, and breeding success higher in areas with mammalian predator control (Knegtmans & Powlesland, 1999; Powlesland *et al.*, 2000). Tomtits make use of both native forest and pine plantations (Clout & Gaze, 1984; DSIR, 1987; Heather & Robertson, 2005), but show a clear preference for native forest, and young pine plantings appear to be unsuitable for breeding population establishment (Clout & Gaze, 1984). They primarily feed on forest floor and plant living invertebrates (Skinner, 1978; Moeed & Fitzgerald, 1982; Kelly, 2005), with commonly taken prey items including Amphipoda, Annelida, Araneida, Coleoptera, adult Diptera, Hemiptera, Hymenoptera, Lepidopteran adults, caterpillars, and Orthoptera (Moeed & Fitzgerald, 1982; Spurr & Powlesland, 2000; Heather & Robertson, 2005). The South Island tomtit subspecies (*P. m. macrocephala*) is also almost solely insectivorous, spending the majority of foraging time scanning substrates

to locate invertebrates before gleaning prey (O'Donnell & Dilks, 1994; Heather & Robertson, 2005).

Intersexual differences in avian and mammalian diets, and correspondingly stable isotope signatures, are commonly found (Perkins & Speakman, 2001; Nassar *et al.*, 2003; Ben-David *et al.*, 2004; Forero *et al.*, 2005; Bearhop *et al.*, 2006; Lewis *et al.*, 2006; Morrissey *et al.*, 2010). Nassar *et al*. (2003) established that males and females of the Venezuelan nectar-feeding bat species, *Leptonycteris curasoae* and *Glossophaga longirostris*, showed intersexual differences in $\delta^{15}N$, with males having higher values than females. This may have been due to males foraging more on insects or C_3 plants which both showed elevated $\delta^{15}N$ in comparison to the crassulacean acid metabolism (CAM) plants sampled. Variation in $\delta^{13}C$ between male and female Eurasian dippers (*Cinclus cinclus*) during the pre-breeding and laying period has also been found, and was explained by female diet shifts between invertebrate orders (Morrissey *et al.*, 2010). However, intersexual differences in diet are not universal (Hobson *et al.*, 1999; Bearhop *et al.*, 2006; Hedd & Montevecchi, 2006; Kurle, 2009; Morrissey *et al.*, 2010). The significant difference between Eurasian dipper sexes found by Morrissey *et al*. (2010) is only apparent for $\delta^{13}C$, with no corresponding $\delta^{15}N$ difference. Similarly, no differences in $\delta^{13}C$ or $\delta^{15}N$ were found between wild male and female Norway rats (Hobson *et al.*, 1999), and Kurle (2009) found only slight differences between males and females for laboratory Norway rats, although she suggested these may not be biologically significant.

This study aims to detect habitat-based differences in the trophic structure of three habitats (pine plantation, native forest, and the contiguous boundary of these habitats) in addition to investigating seasonal and sexual differences in diet of rats, mice, and tomtits. Isotopic data from six taxa were compared: vegetation, caterpillars, and beetles inhabiting the leaf litter, rats, mice, and tomtits. Stomach content data was also collected from rats and mice. I test the general hypotheses that: 1) samples collected for each taxa inhabiting the different habitats will differ in isotopic signature between habitats, 2) vegetation, herbivores, and predators will differ in their $\delta^{15}N$ values within each habitat due to their differing positions in the food chain

(vegetation<caterpillars<beetles<mice<rats<tomtits). Seasonal comparisons were made for three taxa: caterpillars, rats, and mice. For these taxa I test the hypothesis that 3) samples collected for each taxa will differ between seasons in terms of $\delta^{13}C$ and $\delta^{15}N$ values and the stomach contents of rodents. Intersexual comparisons were also made for rats, mice, and tomtits to test the hypothesis that 4) samples for males and females would differ in terms of $\delta^{13}C$ and $\delta^{15}N$ values and the stomach contents of rodents. Finally, I tested the hypothesis that 5) stable isotope and stomach content analyses conducted for the rodents will vary in their separation of the diet of these species.

2.2 Methods

2.2.1 Study site

The Hunua Ranges Regional Park, New Zealand (37º 08' S, 175º 13' E) (Figure 2.1), is located in the south-eastern Auckland Region and administered by the Auckland Regional Council (ARC). Encompassing an area of 24,800 ha (Badan, 1986), the Hunua Ranges contains three distinct habitat types (pine plantation, native forest, and the boundary where these two habitats meet (from the intercept of the pine and native forest 50 m into each)). Sites within each habitat were chosen to be as similar as possible; all had achieved canopy closure, and had the same level of pest control. Original pine plantings began in 1960 (Barton, 1978), and by 1993, an area 2,350 ha had been planted (ARC, 1993). The pine plantation is second rotation, and in the areas used for this study (planted between 14 - 23 years previously), had reached canopy closure with a well developed understory of either native or exotic vegetation in places. The native forest of the Hunua Ranges is representative of remnant native vegetation with the common tree species being kauri (*Agathis australis*), tawa (*Beilschmedia tawa*), taraire (*B. tarairi*), karaka (*Corynocarpus laevigatus*), rimu (*Dacrydium cupressinum*), kahikatea, (*Dacrycarpus dacrydioides*), kawaka (*Libocedrus plumosa*), mangeao (*Litsea calicaris*), northern rata (*Metrosideros robusta*), hard beech (*Nothofagus truncata*), tanekaha (*Phyllocladus trichomanoides*), totara (*Podocarpus totara*), matai (*Po. spicatus*), puriri (*Vitex lucens*), and towai (*Weinmannia sylvocola*) (Barton, 1978; ARC, 1993). This native forest contains species of high conservation

value including North Island kokako (*Callaeas cinerea wilsoni*) and Hochstetter's frog (*Leiopelma hochstetteri*) (Barton, 1978; ARC, 1993; Pryde & Cocklin, 1998).

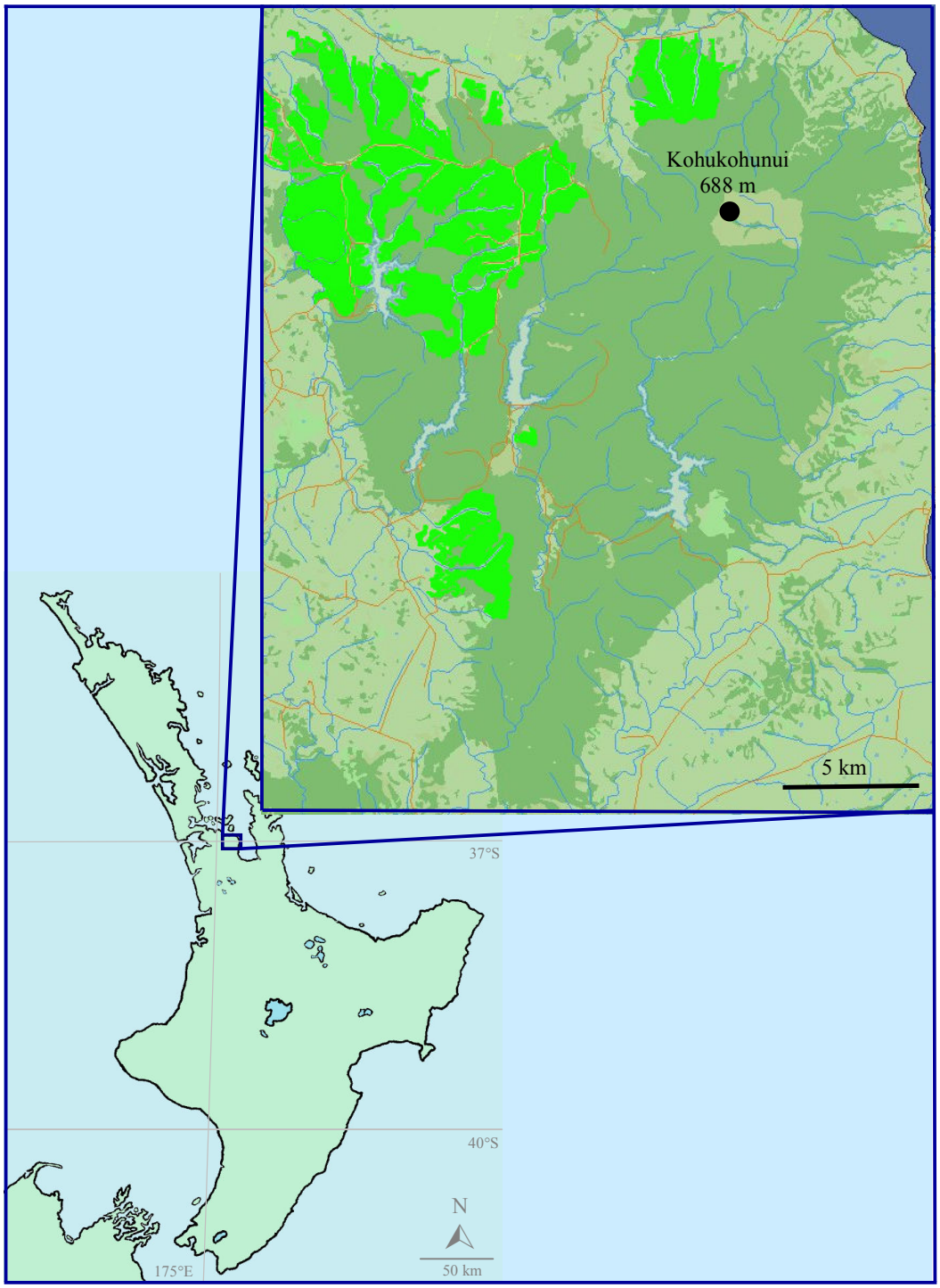

Figure 2.1. Location of study site (North Island, New Zealand) (Eagle Technology Group, 2000). Enlarged map of study site indicated by frame. Within frame: ■ = native forest, ■ = pine forest, ▬ = roads. (DoC, 2000).

2.2.2 Study species

Pine and native broadleaf species

Radiata pine is a native of coastal California (USA), Mexico, and Guadalupe Island where it grows in local stands and is a small component of the vegetation of the area (Sutton, 1999; Lev-Yadun & Sederoff, 2000). It has been introduced on a global scale, and, although it is only widely grown in temperate, coastal areas, dominates the planted production forests of New Zealand, Chile, and Australia, making it the most widely planted pine in the southern hemisphere (Raffa, 1989; Sutton, 1999). In New Zealand, pine plantations are planted across approximately 1.7 million ha (Brockerhoff *et al.*, 2002). Stands of pine are even-aged monocultures on an average rotation of 20 - 30 years with some locations, that have been used for multiple rotations, showing no notable productivity loss (Sutton, 1999).

Native forest and scrub originally covered approximately 85% of the area of New Zealand (Meurk, 1995), with native forests containing around 23% of the 2,300 native vascular plant species (Wardle, 2002). The most common native tree species present in the Hunua Ranges native forest were listed in the previous section. Although leaf litter samples contained leaves from various species, those analysed from broadleaf trees in the native and boundary habitats were from rewarewa (*Knightia excelsa*), lancewood (*Pseudopanax crassifolias*), or *Coprosma* spp.

Invertebrates: caterpillars and beetles

Two groups were chosen to represent two TLs within the invertebrates, with caterpillars representing herbivores, and beetles representing the primarily predacious families (Carabidae and Staphylinidae (Klimaszewski & Watt, 1997)).

There are more than 1,760 species of Lepidopterans in New Zealand, many (>89%) of them endemic, and collectively spanning all biotopes except caves (Dugdale, 1988). Of the species occupying the leaf litter there are two main types of caterpillar: those that are litter-feeding, and those that feed elsewhere before dropping to the ground to pupate

(Dugdale, 1996). Litter-feeding caterpillars consume leaves, flowers, fruits, and twigs and are well represented in New Zealand (12 - 19% species) (Dugdale, 1996). There are a number of caterpillars known to feed on pine in New Zealand, some of which (e.g. light brown apple moth (*Epiphyas postvittana*)), are widely recognised as horticultural pests (Danthanarayana, 1975; Brockerhoff *et al.*, 2002). The abundance and species of Lepidopterans present in pine stands vary according to the degree of canopy closure and growth of other species under the pine (Hosking & Hutcheson, 1987).

Over 5,570 species of Coleoptera are recognised in New Zealand with the majority of species endemic (>90%) and associated with native forest (Klimaszewski & Watt, 1997). Carabids may be diurnal or nocturnal and utilise a large variety of habitats from forests to tussock, and riparian to coastal ecosystems (Klimaszewski & Watt, 1997). Staphylinids are also wide ranging in terms of habitat and use the majority of terrestrial habitats available (Klimaszewski & Watt, 1997). Like carabid beetles, most of the known species of staphylinids are predators, and prey on Acarina, Collembola, and Nematoda (Klimaszewski & Watt, 1997). Coleoptera present in Kaingaroa (New Zealand) pine forest have shown community level differences between different aged pine stands, with up to (80%) of species being native (Hutcheson & Jones, 1999). The Kaingaroa survey found the majority of Coleoptera species in the pine plantation were detritivores, reflecting the large vegetation resources available from past rotations, thinning, and pruning in that plantation (Hutcheson & Jones, 1999).

Rats

Rats are widespread throughout the mainland of New Zealand, inhabiting forests in addition to a wide variety of other habitats from coastal to treeline areas (Innes, 2005). They feed on both vegetation and animals, varying the proportion of each consumed according to season (Innes, 2005). Rats caught during winter in a pine forest in Tokoroa, New Zealand and analysed for stomach content had eaten little vegetation. Instead, invertebrates constituted the majority of prey, and evidence of bird predation or scavenging was also found (Clout, 1980). Rats caught in native forest in the Dart Valley, New Zealand during winter and spring, and analysed in the same way showed that vegetation, invertebrate, and vertebrate remains from other rodents and birds had been consumed (McQueen & Lawrence, 2008).

Mice

Mice occupy a range of habitats from pine and native forests to buildings and rubbish tips (Badan, 1986; Ruscoe & Murphy, 2005). Like rats, they feed on both vegetation and animals with caterpillars, Araneida, Coleoptera adults, and Orthoptera the most common invertebrate prey (Ruscoe & Murphy, 2005). Stomach contents of mice caught in pine plantation (Woodhill Forest, New Zealand) revealed that vegetation and invertebrates were eaten throughout the year, although seasonal differences in the proportion of these components, and the identity of the invertebrate species were found (Badan, 1986). In a parallel study conducted in the native forest of the Hunua Ranges, Badan (1986) found similar results in terms of vegetation and animal material, but caterpillars composed a smaller percentage of the diet, while Lepidopteran pupae and Annelida were absent. Fitzgerald *et al*. (1996) examined mouse stomachs from a New Zealand native beech forest and found both vegetation and invertebrates to be common dietary items, with caterpillars again the invertebrate consumed most often. Seasonal fluctuations in proportion and species of vegetation and invertebrates eaten were also found for the native forest (Badan, 1986; Fitzgerald *et al.*, 1996).

North Island Tomtits

Tomtits are small birds (20 g) found throughout the North Island and on larger offshore islands (Heather & Robertson, 2005). Tomtits are territorial throughout the year (Skinner, 1978; Heather & Robertson, 2005; Kelly, 2005), holding territories of approximately 1.2 - 2.5 hectares in size (Skinner, 1978). They breed from October through to March producing a modal clutch size of four eggs which are incubated by the female for approximately 15 days (Knegtmans & Powlesland, 1999; Heather & Robertson, 2005). During the incubation period courtship feeding occurs (Knegtmans & Powlesland, 1999; Powlesland *et al.*, 2000; Heather & Robertson, 2005), and the male also helps the female feed the nestlings (Knegtmans & Powlesland, 1999; Heather & Robertson, 2005; Kelly, 2005).

2.2.3 Stable isotope sample collection and pre-treatment

Biological samples were collected between May 2006 and June 2009 with representatives of each of the six taxa (vegetation, caterpillars, beetles, mice, rats, and

tomtits) collected from each habitat when possible. The seasons were regarded as autumn (March - May), winter (June - August), spring (September - November), and summer (December - February). See Table 2.1 for details of stable isotope sample sizes and Table I in the Appendix for New Zealand map grid co-ordinates of vegetation, caterpillar, beetle, mouse, rat, and tomtit sample collection locations. Samples sizes were chosen through consideration of the material collected, the time and expense taken to prepare and analyse samples, and the likelihood of finding significant differences given the results of past research. The results of this research (Section 2.3.1) show that these sample sizes were big enough to detect significant differences in some cases.

Vegetation: pine and native broadleaf species

Leaf litter samples were chosen to span the largest area within each habitat possible, with samples selected from the most northerly, southerly, westerly, and easterly locations in each habitat, and contained the necessary invertebrate taxa. Leaf litter samples were collected from March 2006 - February 2008 at ground foraging points of tomtits, with no individual tomtits re-sampled within a two month period. Individual birds were not banded because tomtit mist-netting is commonly undertaken after a period of training birds to forage on mealworms (see Section 2.2.3), which may have altered their foraging behaviour in the presence of humans. In addition, attempts to lure birds into mist-nets using calls were unsuccessful. Instead, individuals were identified using a combination of sex, maturity, and territorial location. This was considered a reliable way to identify individuals within a given two month period as tomtits are widely recorded as tightly pair-bonded (Wilkinson, 1927; Knegtmans & Powlesland, 1999; Heather & Robertson, 2005), and territorial year round (Wilkinson, 1927; Skinner, 1978; Heather & Robertson, 2005). The assumption that they will remain on their territories has also been used as a monitoring technique by past authors (Powlesland *et al.*, 2000; Westbrooke *et al.*, 2003; Michaux, 2009).

Table 2.1. The number of stable isotope samples analysed from each habitat. Totals for taxa compared between seasons and sexes are indicated: A = autumn, W = winter, Sp = spring, Su = summer, M = male, F = female. Bracketed amounts indicate samples that only gave carbon values.

	Pine								**Native**								**Boundary**								**Totals**
Vegetation	5 (10)								1 (10)								6 (10)								**12 (30)**
Beetles	4								3								3								**10**
Caterpillars (habitat)	10								6								10								**26**
Caterpillars (season)	A 0		W 2		Sp 4		Su 4		A 2		W 3		Sp 0		Su 1		A 1		W 4		Sp 4		Su 1		
Rats (habitat)	20								31								25								**76**
Rats (season)	A 7		W 8		Sp 4		Su 1		A 9		W 9		Sp 7		Su 6		A 7		W 7		Sp 9		Su 2		
Rats (sex)	M 3	F 4	M 3	F 5	M 3	F 1	M 1	F 0	M 4	F 5	M 5	F 4	M 4	F 3	M 1	F 5	M 5	F 2	M 2	F 5	M 4	F 5	M 1	F 1	
Mice (habitat)	2								0								14								**16**
Mice (season)	A 0		W 2		Sp 0		Su 0		A 0		W 0		Sp 0		Su 0		A 6		W 8		Sp 0		Su 0		
Mice (sex)	M 0	F 0	M 1	F 1	M 0	F 0	M 0	F 0	M 0	F 0	M 0	F 0	M 0	F 0	M 0	F 0	M 3	F 3	M 4	F 4	M 0	F 0	M 0	F 0	
Tomtits (habitat)	5								5								0								**10**
Tomtits (sex)	M 4				F 1				M 4				F 1				M 0				F 0				
Totals	**46 (51)**								**46 (55)**								**58 (62)**								**150 (168)**

All the leaf litter, including rotted leaves, within a 50 x 50 cm area was collected with the depth varying from 1 - 50 mm (due to litter compaction) to reflect the potential depth of tomtit foraging at the site. Litter was placed in *Burlese* funnels that ran until the vegetation was dry. Individual leaves in the leaf litter samples ranged from fresh to decayed. However, those picked from dried leaf litter samples were all intact and identifiable to genus level. Leaves were picked out after invertebrate extraction and soaked for 24 hrs in distilled water with occasional gentle agitation to remove dirt prior to drying in an incubator for 48 hrs at 50 °C. Individual leaves were then ground to a fine powder using a mortar and pestle, weighed (2.9 - 7.6 mg), and packed into tin capsules.

Invertebrates: caterpillars and beetles

Invertebrates were extracted from the leaf litter using *Burlese* funnels run until the vegetation was dry, then all insects >1.5 mm were identified to order, and other invertebrates >1.5 mm identified to order (Acarina, Araneida, Isopoda, Opiliones, Pseudoscorpiones), class (Chilopoda, Diplopoda, Gastropoda), or phylum (Annelida, Nematoda, Onychophora, Platyhelminthes). Adult and larval stages of Coleoptera, Diptera, and Lepidoptera were separated, and adult Coleoptera were sorted to family. After sorting, invertebrates were stored in 70% ethanol until pre-treatment. For stable isotope analyses, the invertebrates were soaked for 24 hrs in distilled water with occasional gentle agitation prior to drying in an incubator for 48 hrs at 50 °C. Invertebrates were cut into pieces and, if necessary, individuals from within a leaf litter sample pooled together, weighed (1.4 - 2 mg), and packed into tin capsules.

Rodents: rats and mice

Rodents were caught using rodent snap traps set in four grids (one in pine, two in native, and one in boundary habitat) and frozen until dissection and hair removal. Grids were set out with five lines of snap traps placed at 25 m intervals in the pine and native habitat (DSIR, 1987; Brown, 1994), and six lines of four traps placed at 25 m intervals in the boundary habitat to accommodate the shape of this habitat. At each trapping station one mouse and one rat trap were set and baited with peanut butter and rolled oat mix, and a metal cover was fixed over each trap to exclude other species and protect the

bait during wet weather (Fitzgerald *et al.*, 1981; Brown, 1994; Choquenot & Ruscoe, 2000). Traps were installed at least eighteen days prior to setting, and trapping was conducted for three nights in April 2007 (autumn), July 2007 (winter), October 2007 (spring), and January 2008 (summer).

Rodent hair samples were used for stable isotope analyses. Hair was clipped from the head of rats and mice and stored in vials prior to cleaning. Rodent hair was cleaned by soaking in 2:1 chloroform:methanol solution for a minimum of 30 mins, rinsed by soaking in distilled water for a minimum of 30 mins, and dried in an incubator for 48 hrs at 50 °C. Once dry, the hair was weighed (1.5 - 2.5 mg), and packed into tin capsules.

Tomtits

Prior to mist-netting, tomtits were trained to approach future capture sites by feeding *Tenebrio molitor* larvae (mealworms) for six weeks (May - June 2009) in conjunction with hand clapping to create an association between the sound and feeding. Once captured, half of the two central tail feathers were clipped, and stored in paper envelopes prior to processing. Although mist-netting was undertaken in the boundary habitat to capture tomtits, none were caught.

Feathers were used for stable isotope analyses of tomtits. Tomtit feathers were cleaned by soaking in 2:1 chloroform:methanol solution for a minimum of 30 mins, rinsed by soaking in distilled water for a minimum of 30 mins, and dried in an incubator for 48 hrs at 50 °C. Tomtit feathers were cut into small sections prior to packaging, weighed (0.4 - 1.6 mg), and packaged into tin capsules.

2.2.4 Analyses

Stable isotope analyses

Samples were analysed for ^{13}C and ^{15}N isotopes and percentage carbon and nitrogen using mass spectrometers in two specialised laboratories that use the same standards to calibrate the machines used. Isotope analyses of vegetation, invertebrates, and rodent

hair was carried out by the Center for Stable Isotope Biogeochemistry, University of California, USA. At this laboratory samples were analysed via elemental analyser/continuous flow isotope ratio mass spectrometry (ANCA/SL elemental analyzer (*Sercon*, Cheshire, United Kingdom) coupled with a Finnigan MAT Delta^{Plus} XL mass spectrometer (*Thermo Scientific*, Bremen, Germany). The standard for carbon was V-PDB, and the standard for nitrogen was air, with the reference material NIST SMR 1547 used as a calibration standard. Five duplicate samples were run and showed a range of difference for $\delta\ ^{13}C$ values of 0.02 - 0.14‰, and a range of difference for $\delta\ ^{15}N$ values of 0.01 - 0.44‰.

Isotope analyses of tomtit feathers were carried out by NIWA (National Institute of Water and Atmospheric Research), Wellington, New Zealand. At this laboratory analyses were carried out on a Delta^{Plus} (*Thermo-Finnigan*, Bremen, Germany) continuous flow, isotope ratio mass spectrometer. Tin boats were combusted in an NA 1500N (*Fisons Instruments*, Rodano, Italy) elemental analyser combustion furnace at 1020 °C in a flow of oxygen and Helium carrier gas. Oxides of nitrogen were converted to N_2 gas in a reduction furnace at 640 °C. Nitrogen and CO_2 gases were separated on a Porapak Q gas chromatograph column before being introduced to the mass spectrometer detector via an open split Conflo II interface (*Thermo-Finnigan*, Bremen, Germany). Caron dioxide and N_2 reference gas standards were introduced to the mass spectrometer with each sample analysis. ISODAT (*Thermo-Finnigan*) software was used to calculate $\delta\ ^{15}N$ values against atmospheric air, and $\delta\ ^{13}C$ values against the CO_2 reference gas relative to PDB, correcting for ^{17}O. Percent C and N values were calculated relative to a solid laboratory reference standard of urea (*Elemental Microanalysis*, U.K.) at the beginning of each run. Internal standards were routinely checked against National Institute of Standards and Technology (NIST) standards. Three duplicate samples were run and showed a range of difference for $\delta\ ^{13}C$ values of 0.01 - 0.69‰, and a range of difference for $\delta\ ^{15}N$ values of 0 - 0.31‰.

Rodent stomach content analyses

Eighty five rats and 16 mice were caught for stomach content analyses (see Table I in Appendix for New Zealand map grid co-ordinates of rodent capture locations). Each individual was dissected to remove the stomach, the contents were then sieved (1 mm^2)

under running water, and emptied into Petri dishes for examination. Stomach contents were quantified in two ways. The volume of invertebrate and vertebrate remains, parasites, vegetation, and unknown material was estimated to 5%. Then the invertebrate portion was examined under a binocular microscope to determine the minimum number of representatives of each order as calculated from identifiable remains.

Statistics

The δ values for ^{13}C and ^{15}N, and total C and N were compared between habitats, taxa, seasons, and sexes using one and two way ANOVAs (analysis of variance), t-tests for independent samples, Kruskal-Wallis ANOVAs, and Mann-Whitney U tests (StatSoft, 2001). Tests were applied as appropriate given data adherence to the normal distribution and homogeneous variances. Comparisons for vegetation, caterpillar, and beetle stable isotope samples consider material collected during both years of the study. This was due to insufficient sample sizes to test for annual differences within each habitat or season or to run these comparisons for each year separately.

Stomach content data were not transformed prior to analysis using Bray-Curtis similarity. They were then graphed, with ten restarts, using MDS (Multi Dimensional Scaling) analysis (PRIMER-E, 2002). MDS analysis shows each sample as a point so that the relative distance between each sample is the same rank order as the relative dissimilarities of the samples and allows the data to be visually assessed. The stress value given by MDS analysis indicates the level of reliability of ordination achieved (<0.05 = excellent, <0.1 = good, <0.2 = useful, <0.3 = almost arbitrary). One-way ANOSIM (analysis of similarity), with a maximum 999 permutations, was then used to test the null hypothesis that there were no differences between groups of samples.

2.3 Results

2.3.1 Stable isotope analyses

Vegetation, caterpillars, rats, mice, and tomtits collected from native forest had the lowest δ ^{15}N values within their respective taxa, followed by boundary, and then pine

habitat (Figure 2.2). Within the pine plantation, δ ^{15}N values were lowest for vegetation followed by caterpillars, beetles, rats, mice, then tomtits. The pattern was the same for native forest except that no mice were caught in this habitat. The boundary habitat showed slight variation from this trend with δ ^{15}N values lowest for vegetation followed by caterpillars, rats, beetles, then mice.

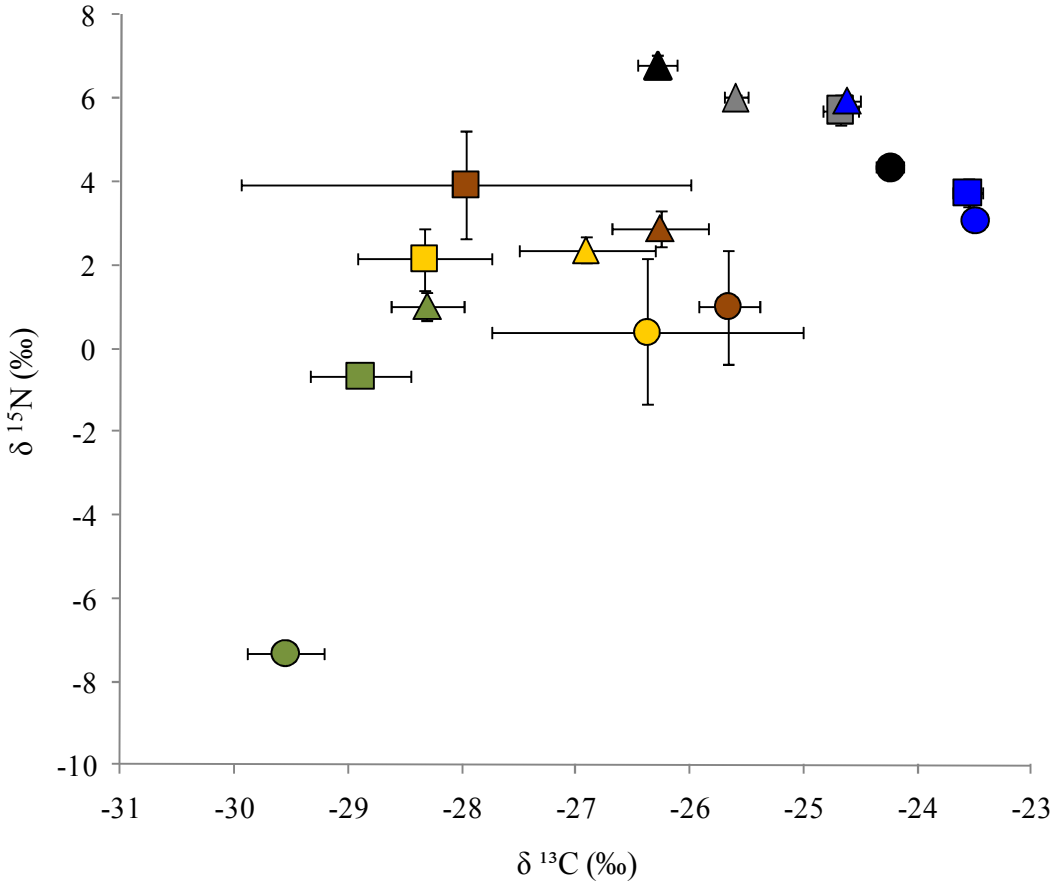

Figure 2.2. Mean isotopic values (± standard error) of taxa sampled. ▲ = pine vegetation, ● = native vegetation, ■ = boundary vegetation, △ = caterpillar pine, ○ = caterpillar native, □ = caterpillar boundary, ▲ = beetle pine, ● = beetle native, ■ = beetle boundary, ▲ = mouse pine, ■ = mouse boundary, ▲ = rat pine, ● = rat native, ■ = rat boundary, ▲ = tomtit pine, ● tomtit native.

All vegetation samples overlapped in δ ^{13}C values, but showed significant separation in terms of δ ^{15}N values (Table 2.2, Figure 2.2). Unfortunately, only one sample of native vegetation was successfully analysed for nitrogen so comparison could only be made between vegetation nitrogen for boundary and pine habitats. Caterpillars from the different habitats showed incomplete separation on the δ ^{13}C axis, but also in terms of δ

^{15}N values (Table 2.2). Beetles showed a similar pattern to the caterpillars, with no significant separation between habitats for δ ^{13}C, or δ ^{15}N (Table 2.2). However, it was interesting to note that for beetles the mean values for the boundary habitat had a higher δ ^{15}N level than the pine. Rats were captured in sufficient numbers during autumn, winter, and spring to allow analysis of habitat and season effects simultaneously, and showed highly significant differences for both δ ^{13}C and δ ^{15}N between habitats, but only for δ ^{13}C between seasons (Table 2.2, Figure 2.3). The interaction effect was not significant. Only two mice were collected in the pine habitat precluding statistical comparison between habitats. Tomtits were highly significantly different between habitats for their δ ^{13}C and δ ^{15}N values (Table 2.2). No tomtits were caught in the boundary habitat so no information regarding tomtit isotopic signatures was obtained for this habitat.

Table 2.2. Summary of between habitat and season stable isotope comparisons.

	Carbon			Nitrogen		
	n	Statistical value	*P*	n	Statistical value	*P*
Vegetation	30	$F_{2, 27} = 2.721$	0.083	10	$t_9 = 4.117$	0.002
Caterpillars (habitat)	26	$F_{2, 23} = 1.677$	0.208	26	H = 1.121	0.570
Caterpillars (season)	26	$F_{22} = 0.960$	0.960	26	$F_{22} = 1.016$	0.404
Beetles	10	$F_{2, 7} = 1.169$	0.364	10	$F_{2, 7} = 1.942$	0.213
Rats (habitat)	67	$F_{2, 58} = 27.000$	<0.001	67	$F_{2, 58} = 25.201$	<0.001
Rats (season)	67	$F_{2, 58} = 6.000$	<0.001	67	$F_{2, 58} = 0.746$	0.478
Mice (season)	13	$F_{11} = 0.100$	0.756	13	$F_{11} = 0.576$	0.463
Tomtits	10	$t_8 = 9.661$	<0.001	10	$t_8 = -9.176$	<0.001

Taxa sampled within the three habitats show significant differences for both δ ^{13}C and δ ^{15}N (Table 2.3). Differences between taxa large enough to constitute an increase in TL occurred in all habitats (Table 2.4). Total carbon and nitrogen content did not differ significantly between habitats for any taxa (Table 2.4 & Appendix I, Table II).

Table 2.3. Summary of within habitat taxa stable isotope comparisons.

	Carbon			Nitrogen		
	n	Statistical value	*P*	n	Statistical value	*P*
Pine	51	H = 36.457	<0.001	44	H = 35.48	<0.001
Native	55	$F_{4, 50} = 47.570$	<0.001	45	H = 12.76	0.005
Boundary	61	H = 48.838	<0.001	57	H = 26.27	<0.001

Delta ^{13}C and $\delta^{15}N$ values for caterpillars were pooled across habitats due to the lack of significant differences found between habitats for this taxon, and sample sizes precluded two-way analysis of habitat and season concurrently. Caterpillars showed no difference between seasons (Table 2.2). Delta ^{13}C and $\delta^{15}N$ values for mice in the boundary habitat (insufficient numbers of mice were caught in the native or pine forest to allow seasonal comparisons) showed no seasonal differentiation (Table 2.2).

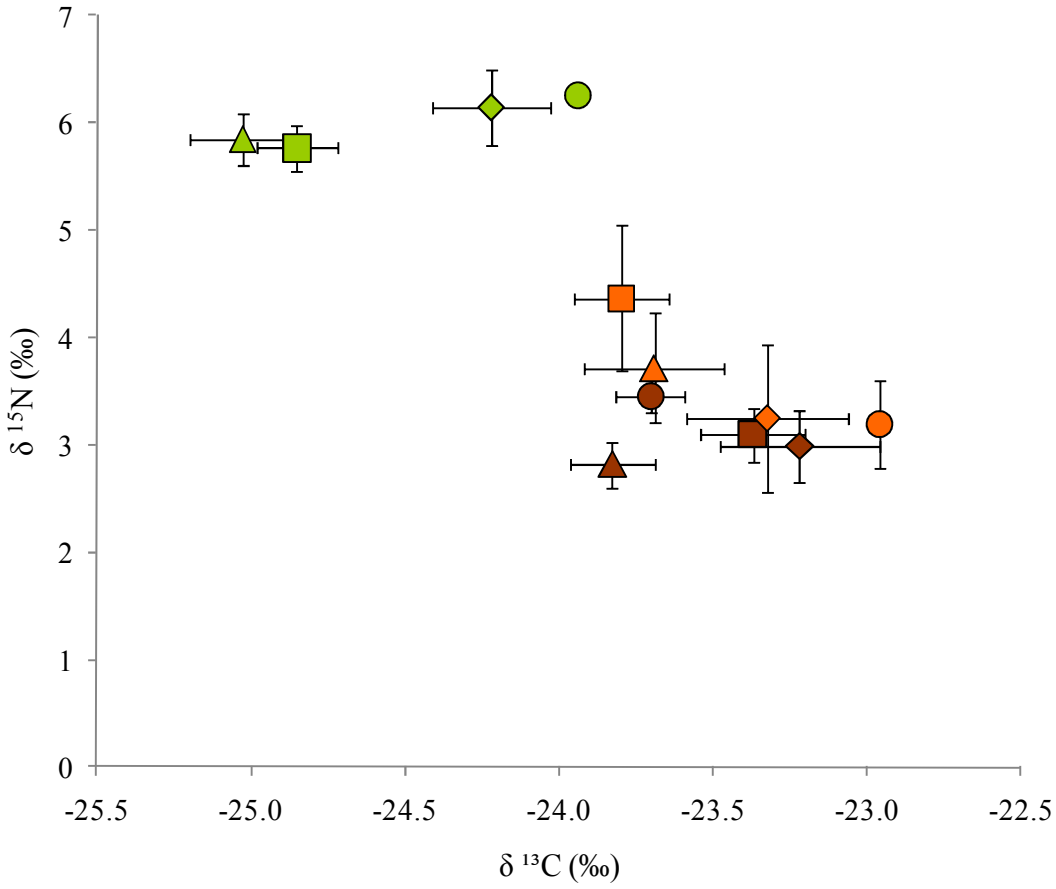

Figure 2.3. Mean isotopic values (± standard error) of rats. ◇ = pine autumn, ◆ = native autumn, ◇ = boundary autumn, □ = pine winter, ■ = native winter, □ = boundary winter, △ = pine spring, ▲ = native spring, ▲ = boundary spring, ○ = pine summer, ● = native summer, ○ = boundary summer. NB there was only one rat sampled in the pine during the summer and therefore no error bars are shown.

Table 2.4. TL partitioning within pine plantation, native forest, and boundary habitats as apparent from mean (± standard error) δ ^{13}C and δ ^{15}N and minimum-maximum percentage total carbon and nitrogen values for each set of samples. Veg = vegetation, Cater = caterpillars. NB nitrogen values for vegetation in the native habit are represented by one value.

	Pine				Native				Boundary			
TL	**δ ^{13}C**	**Total C**	**δ ^{15}N**	**Total N**	**δ ^{13}C**	**Total C**	**δ ^{15}N**	**Total N**	**δ ^{13}C**	**Total C**	**δ ^{15}N**	**Total N**
One	Veg	Veg	Veg	Veg	Veg	Veg	Veg	Veg	Veg	Veg	Veg	Veg
	-28.31	44.97	1.00	0.40	-29.56	31.78	-7.31	1.27	-28.90	42.34	-0.67	0.33
	±0.32	-49.54	±0.34	-1.64	±0.33	-51.93			±0.43	-50.66	±0.23	-1.85
Two	Cater	Cater	Cater	Cater	Cater	Cater	Cater	Cater	Cater	Cater	Cater	Cater
	-26.90	44.77	2.36	8.81	-26.37	42.63	0.39	9.99	-28.33	42.24	2.14	6.67
	±0.59	-53.11	±0.30	-13.13	±1.36	-50.09	±1.74	-12.55	±0.58	-57.39	±0.73	-13.12
	Beetles	Beetles	Beetles	Beetles	Beetles	Beetles	Beetles	Beetles	Beetles	Beetles		
	-26.26	47.57	2.87	10.53	-25.66	45.83	1.00	10.58	-27.96	48.96		
	±0.42	-49.97	±0.44	-11.69	±0.26	-63.48	±1.36	-15.10	±1.97	-64.03		
	Tomtits	Tomtits										
	-26.28	44.74										
	±0.17	-46.08										
	Mice	Mice										
	-25.59	43.65										
	±0.10	-45.27										
Three	Rats	Rats	Rats	Rats	Tomtits	Tomtits	Rats	Rats	Mice	Mice	Rats	Beetles
	-24.61	41.68	5.94	13.47	-24.24	44.18	3.07	13.38	-24.68	40.43	3.72	5.98
	±0.12	-46.63	±0.15	-14.78	±0.11	-45.67	±0.13	-15.23	±0.15	-46.04	±0.32	-17.63
			Mice	Mice	Rats	Rats	Tomtits	Tomtits	Rats	Rats	Beetles	Rats
			6.02	13.60	-23.49	41.03	4.35	12.70	-23.56	41.96	3.93	13.54
			±0.08	-13.98	±0.10	-47.79	±0.09	-13.98	±0.12	-47.16	±1.31	-15.28
			Tomtits	Tomtits								
			6.78	12.10								
			±0.24	-13.30								
Four											Mice	Mice
											5.72	13.26
											±0.36	-14.90

Rodents were also compared for intersexual differences in δ ^{13}C and δ ^{15}N values when caught in sufficient numbers; low sample sizes prevented examination of habitat, season, and sex effects together. Neither rats, nor mice showed separation between the sexes (Table 2.5). No large differences were found between the stable isotope signatures of male and female tomtits within the same habitat (Figure 2.4), however, the sample sizes (for females especially) were too small for statistical analyses.

Table 2.5. Summary of intersexual stable isotope comparisons.

				Carbon			**Nitrogen**	
			n	Statistical value	*P*	n	Statistical value	*P*
Rat	**Pine**	**Autumn**	7	$t_5 = 0.015$	0.885	7	$t_5 = 0.460$	0.664
		Winter	8	$t_6 = -1.921$	0.103	8	U = 3.000	0.179
	Native	**Autumn**	9	$t_7 = -0.014$	0.989	9	$t_7 = 0.808$	0.445
		Spring	7	$t_5 = 0.286$	0.786	7	$t_5 = 0.142$	0.892
		Winter	9	$t_7 = 0.650$	0.536	9	$t_7 = 0.025$	0.980
	Boundary	**Spring**	9	$t_7 = -0.064$	0.950	9	$t_7 = -0.681$	0.517
Mice	**Boundary**		14	$t_{12} = -0.450$	0.660	14	$t_{12} = 0.375$	0.713

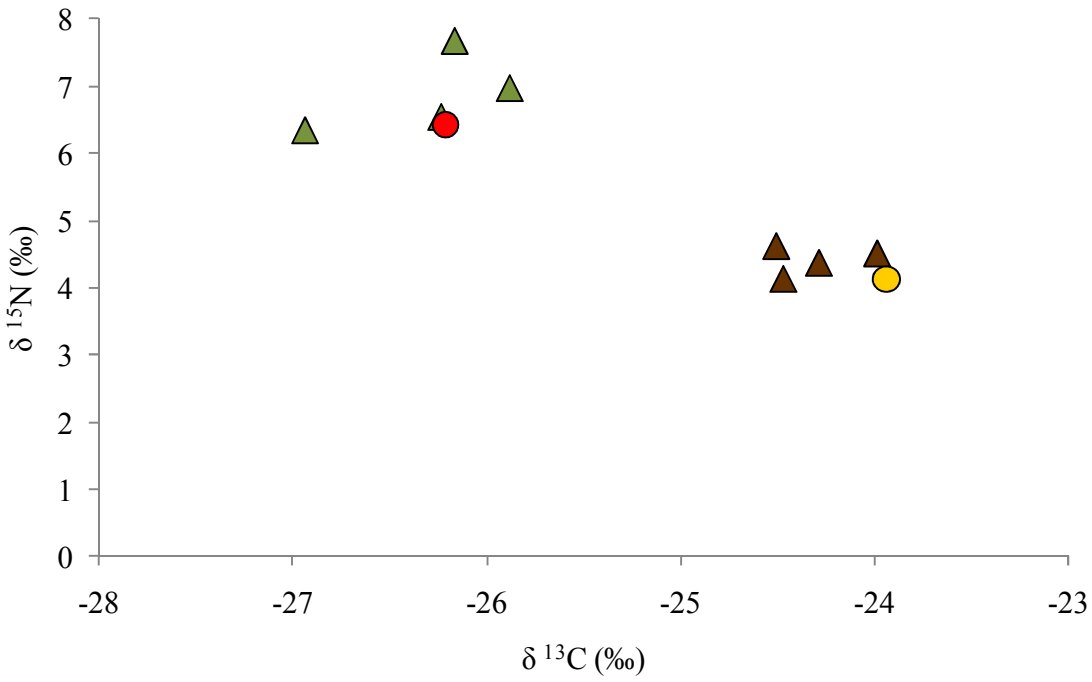

Figure 2.4. Mean isotopic values of tomtit feathers. ▲ = pine males, ● = pine female, ▲ = native males, ● = native female.

2.3.2 Stomach content analyses

Rodent stomachs contained vegetative material, vertebrate and invertebrate remains. In general, rat diet was comprised mostly of invertebrates (remains in 74 out of 85 stomachs) and seeds (present in 24 stomachs). Seventeen invertebrate orders were identified from rat stomachs with the most common invertebrate component being caterpillars (20% of the identified invertebrate individuals), Araneida (19%), adult Coleoptera (19%), and Orthoptera (19%). Invertebrates comprised the most frequent item in the diet of mice (remains in 6 out of 14 stomachs); in particular, caterpillars and Araneida made up 42% and 36%, respectively, of the identified invertebrate individuals in the mouse stomachs.

In contrast to the analyses of stable isotope values, MDS analysis of stomach contents showed no separation for the estimated volume of identified dietary items (invertebrates, vertebrate remains, and vegetation) in rat (stress = 0.06) or mouse (stress = 0) stomachs between habitats. This result was supported by ANOSIM (rats: R = 0.019, P = 0.215; mice: R = 0.22, P = 0.5). When these data were simplified to presence/absence of known items the result was similar (MDS: rats - stress = 0; mice - stress = 0. ANOSIM: rats - R = 0.035, P = 0.074; mice - R = 0, P = 1). When invertebrates per identifiable order were considered the results were similar whether considered as minimum number per order (MDS: rats - stress = 0.2; mice - stress = 0. ANOSIM: rats - R = 0.034, P = 0.086; mice - R = -0.332, P = 1), or presence/absence of each order (MDS: rats - stress = 0.14; mice - stress = 0. ANOSIM: rats - R = 0.013, P = 0.292; mice - R = -0.344, P = 1).

Comparison of the estimated volume of known items between rodent species in the boundary habitat showed no separation (MDS: stress = 0.05; ANOSIM: R = -0.031; P = 0.543). A similar result was seen when the data were transformed to presence/absence of known items (MDS: stress = 0; ANOSIM: R = -0.136, P = 1). However, when boundary habitat data were considered as the minimum number of invertebrates per identifiable order, a highly significant difference was seen between rat and mouse stomach contents (ANOSIM: R = 0.278, P = 0.001), although this was not clearly shown by the MDS plot (Figure 2.5). This difference persists when these data were

treated as presence/absence of each order (MDS: stress = 0.09; ANOSIM: R = 0.31, *P* = 0.001). When a comparison of rat and mouse isotopic signatures within the boundary habitat was made there was also support for this significant difference in diet between the species (δ ^{13}C: n = 38, t_{36} = 5.438, *P* <0.001; δ ^{15}N: n = 38, U = 64, *P* = 0.002).

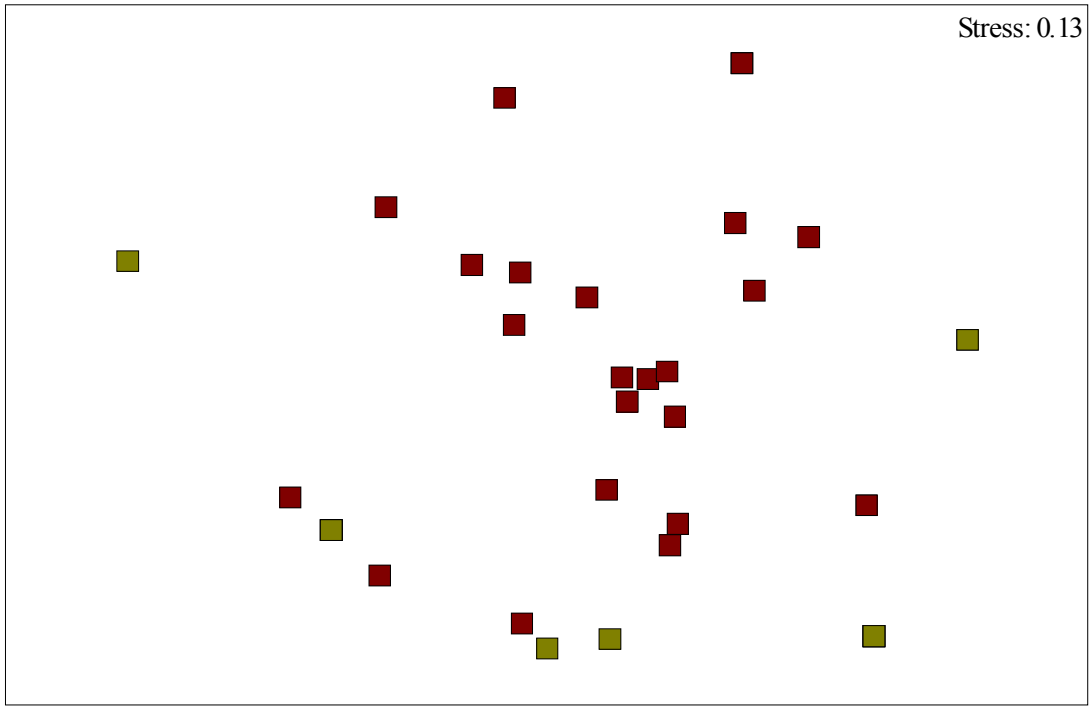

Figure 2.5. MDS plot showing boundary habitat rodent stomach content data as minimum number of invertebrates per identifiable order per individual. ■ = rat stomachs, ■ = mouse stomachs.

The estimated volume of known dietary items in the stomach contents were compared between seasons for rats and mice. MDS analysis showed no clear separation for rat diet between seasons (stress = 0.06) (Figure 2.6). However, ANOSIM results showed significant separation between seasons overall (R = 0.196, *P* = 0.001), and for three of the seasonal pairwise comparisons (autumn, winter R = 0.317, *P* = 0.001; autumn, spring R = 0.241, *P* = 0.002; autumn, summer R = 0.177, *P* = 0.063; winter, spring R = 0.133, *P* = 0.007; winter, summer R = 0.05, *P* = 0.244; spring, summer R = -0.085; *P* = 0.803) (Figure 2.7). No seasonal differences were found for mice (MDS: stress = 0; ANOSIM: R = -0.34, *P* = 1). Presence/absence of identified dietary items were then analysed for rats and mice between seasons. MDS did not show clear separation for rat diet between seasons (stress = 0), although ANOSIM found overall significant

differences (R = 0.108, *P* = 0.003) and for three of the pairwise comparisons (autumn, winter R = 0.207, *P* = 0.002; autumn, spring R = -0.023, *P* = 0.729; autumn, summer R = -0.107, *P* = 1; winter, spring R = 0.223, *P* = 0.003; winter, summer R = 0.126, *P* = 0.014; spring, summer R = -0.039, *P* = 1). No seasonal differences were found for mice (MDS: stress = 0; ANOSIM: R = 0, *P* = 1).

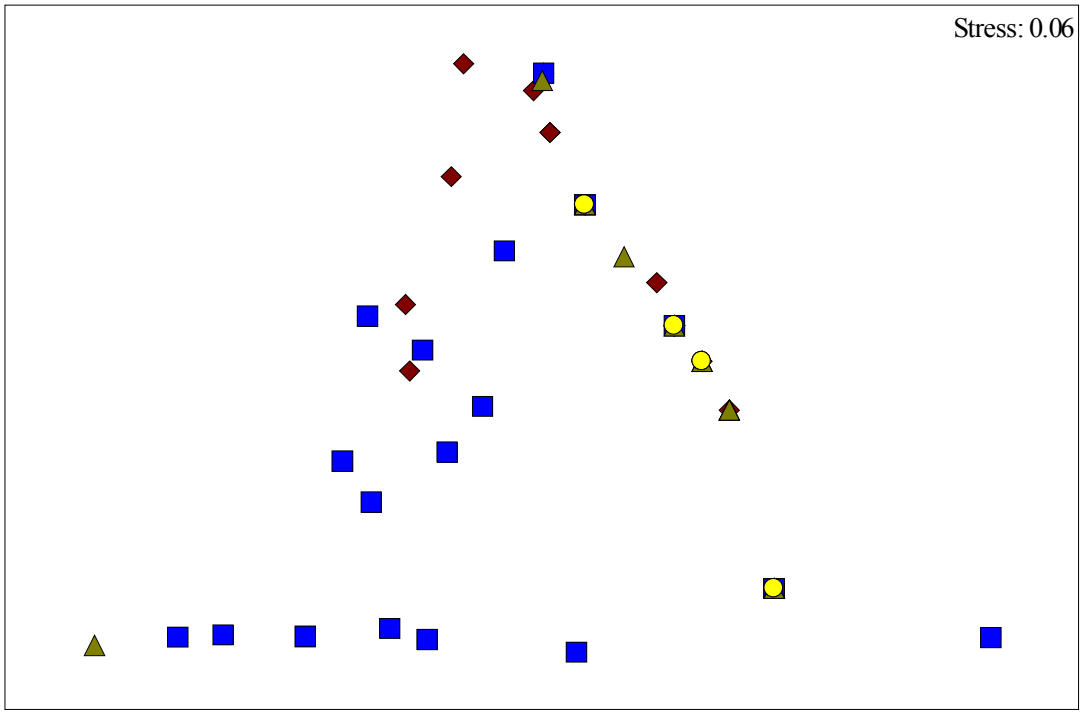

Figure 2.6. MDS plot showing rat stomach content data as estimated volume of identified dietary items. ◆ = autumn, ■ = winter, ▲ = spring, ● = summer.

Stomach contents were then analysed as the minimum number of identifiable invertebrates per order. Neither rats (MDS: stress = 0.2; ANOSIM: R = 0.011, *P* = 0.37), nor mice (MDS: stress = 0; ANOSIM: R = 0.011, *P* = 0.376) showed seasonal differences. When these data were transformed to presence/absence of invertebrate orders the result was the same (rats - MDS: stress = 0.14; ANOSIM: R = 0.006, *P* = 0.377; mice - MDS: stress = 0; ANOSIM: R = 0.018, *P* = 0.321).

When sexes of each species were compared their diets were very similar. Comparisons between the estimated volume of identified dietary items in the stomach contents of male and female rats (MDS: stress = 0.06; ANOSIM: R = -0.018, *P* = 0.735), and mice

(MDS: stress = 0; ANOSIM: R = 0.54, *P* = 0.267) did not reveal any intersexual differences. Assessment of the presence/absence of identified dietary items for male and female rats (MDS: stress = 0; ANOSIM: R = -0.017, *P* = 0.728), and mice (MDS: stress = 0; ANOSIM: R = 0, *P* = 1) gave a similar result. When these data were analysed as minimum number of invertebrates per order the result was the same (rats - MDS: stress = 0.2; ANOSIM: R = -0.02, *P* = 0.81; mice - MDS: stress = 0; ANOSIM: R = -0.1, *P* = 0.745). Once again comparison of the presence/absence of orders eaten by males and females of each species showed that similar invertebrate orders were consumed regardless of sex (rat - MDS: stress = 0.14; ANOSIM: R = -0.022, *P* = 0.86; mice - MDS: stress = 0; ANOSIM: R = -0.106, *P* = 0.83).

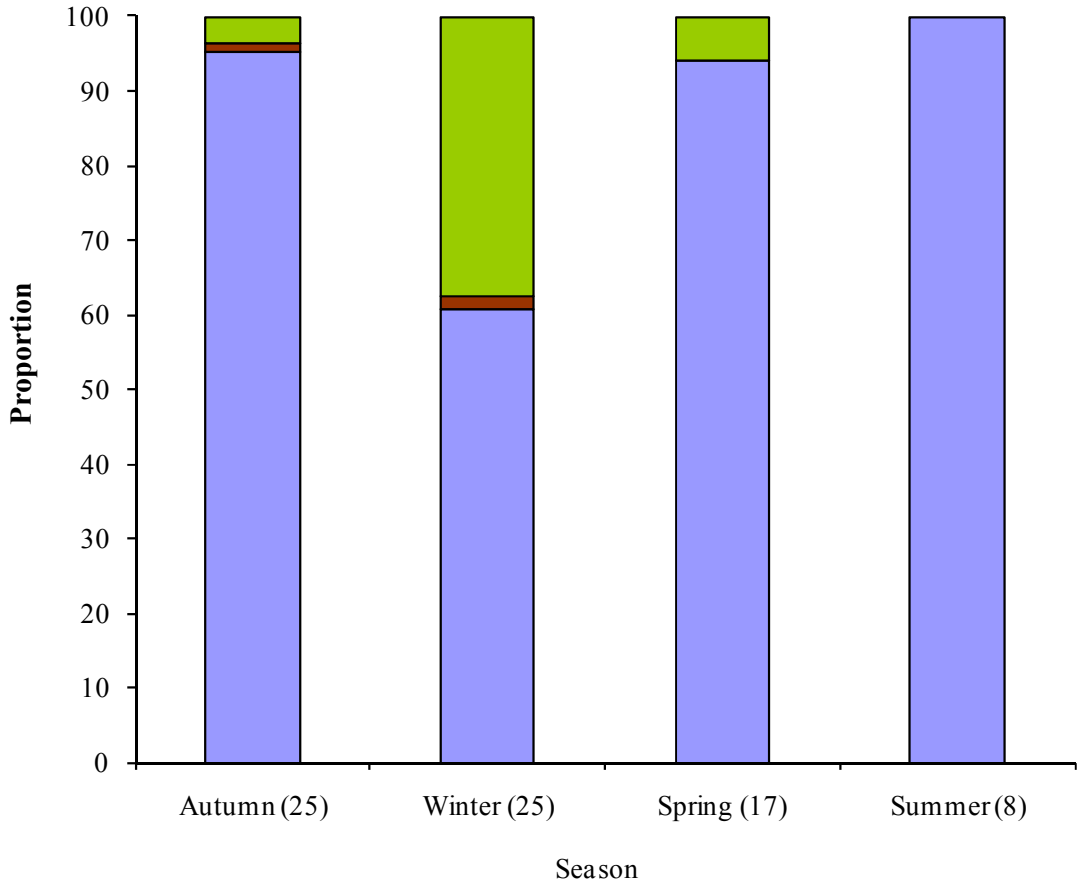

Figure 2.7. Seasonal proportion of each of the identifiable dietary components for rats. ■ = invertebrate remains, ■ = vertebrate remains, ■ = vegetation.

2.4 Discussion

It was hypothesised that stable isotope signatures would differ between habitats, and this was the result found, with native habitat having the lowest $\delta^{15}N$ levels within taxa, boundary samples usually having intermediate values, and pine plantation samples having the highest $\delta^{15}N$. This difference was significant for $\delta^{15}N$ values of vegetation, rat, and tomtit samples, and for $\delta^{13}C$ of rat and tomtit samples. It was anticipated that taxa would separate within each habitat, and this was also found, with significant differences for both isotopes analysed and two to four TLs displayed. However, the order of $\delta^{15}N$ signatures within each habitat did not necessarily reflect the predicted progression (vegetation<caterpillars<beetles<mice<rats<tomtits); in both pine and boundary habitats mice showed a slightly higher mean $\delta^{15}N$ than rats, and in the boundary habitat beetles also had a higher mean $\delta^{15}N$ than rats. Fluctuations in stable isotope values between seasons were only seen for rat $\delta^{13}C$ values, and may indicate seasonal foraging movements. Differences in stable isotope values were not found between sexes for rats, mice, or tomtits, and investigation of stomach contents for the rodents also showed very similar intersexual diets. In contrast to stable isotope results, the stomach content analyses undertaken for rodents did not show within species habitat separation, but revealed significant differences between rat and mouse diet in the boundary habitat. It was also found that the stable isotope and stomach content methods employed differed in their separation of seasonal diet for rats, although their findings agreed for mice. Between seasons rats showed significant variations in diet for vegetation and invertebrate proportions taken, and also the presence of vertebrate remains in autumn and winter.

Stable isotope analysis allows us to find unexpected trophic relationships, e.g. sources of allochthonous nutrient inputs, although at times this is achieved with a decrease in specific information regarding input due to overlapping isotope signatures (Carreon-Martinez & Heath, 2010; Moreno *et al.*, 2010). Therefore dietary studies utilising this technique often have to limit their results regarding prey items consumed and the temporal changes in diet (Bodey *et al.*, 2010). This is particularly noteworthy when the tissue examined does not have a high turnover rate as it will only reflect the stable isotope during the time of growth (Kelly, 2000). This temporal limitation is also placed

on stomach content analyses as they can only identify remains that have not been digested, which introduces bias into the dietary assessment (Kelly, 2000). Studies incorporating additional isotopes (e.g. $\delta\ ^{34}S$), have been successful in clarifying otherwise overlapping $\delta\ ^{13}C$ and $\delta\ ^{15}N$ signatures (Moreno *et al.*, 2010), and isotope studies can also make use of the differing temporal scales of tissue turnover within an organism in order to assess diet (Dalerum & Angerbjörn, 2005; Caut *et al.*, 2008b; Kurle, 2009). Stable isotope analysis can deliver information on trophic interactions with reduced sample sizes in comparison to more traditional methods such as stomach content analysis. For example, Abrantes and Sheaves (2010) found significant and strong trophic relationships despite potential losses in precision in their stable isotope analyses due to only eight of 34 organisms examined having three or more replicates. Previous research investigating a riparian zone in a native New Zealand forest (both aquatic and terrestrial elements) also found clear separation between different trophic elements with relatively limited sample sizes (Najera-Hillman *et al.*, 2009).

Vegetation, caterpillar, rat, mouse, and tomtit samples from native forest had the lowest mean $\delta\ ^{15}N$ values followed by boundary habitat and pine plantation. Although studying different habitats (grassland and marsh), Harding & Stevens (2001) also found vegetation differences for nitrogen and carbon between the plant species they investigated. The result that pine forest samples had the highest $\delta\ ^{15}N$ levels was not unexpected as the pine plantation has been fertilised which increases the availability of nitrogen to plants (Cassaing *et al.*, 2007; Oleksyn *et al.*, 2007; Göthe *et al.*, 2009). In addition, increasing soil depth can be paralleled by increased ^{15}N levels (Shearer *et al.*, 1978; Melillo *et al.*, 1989). Therefore, it is possible that soil disturbance associated with land clearance may have caused enriched soils to become available for plants and their consumers.

Large differences in vegetation $\delta\ ^{15}N$ values in this study have interesting impacts higher up the food chain. For example, caterpillars collected from the native forest have lower $\delta\ ^{15}N$ values than the vegetation of the pine plantation. However, $\delta\ ^{15}N$ results must be treated with caution as significant differences between the mean $\delta\ ^{13}C$ of taxa within the same habitat indicate that their main sources of carbon may vary. Rats within

a New Zealand native forest have also been shown to have the highest $\delta^{13}C$ values of the taxa sampled (Najera-Hillman *et al.*, 2009). In my study I also found this result within each habitat and past researchers have suggested that this indicates foraging on additional resources to those sampled (Najera-Hillman *et al.*, 2009). However, I can be confident that my results for habitat comparisons are indicative of habitat differences, as opposed to different basal soil types or rainfall regimes, as each sample collected was within an 8 km range.

Although mean $\delta^{15}N$ values for mice follow the trend (native<boundary<pine), they were very close (boundary $\delta^{15}N$ 5.72‰, pine $\delta^{15}N$ 6.02‰). This may be due to 11 of the 14 mice in the boundary being caught on the pine side of the trapping grid and hence potentially more representative of pine habitat than a mix of the two habitats. Not all taxa displayed the trend of native<boundary<pine, however, with the mean $\delta^{15}N$ value for pine beetle samples being lower than that from boundary habitat. It is important not to overlook the influence of adjacent habitats on each other, as they can have a marked impact in terms of isotopic signature (Harding & Stevens, 2001). Harding & Stevens (2001) were able to discern between vole (*Microtus californicus*) prey items in raptor diet from a habitat mosaic of salt marsh and grassland covering less than 500 m, even though the isotopic signatures were a continuum between the two habitats. Beetle boundary samples were all collected within 5 m of grassed roads and nutrients and other windborne compounds may be carried as gas or fine particles that deposit on edge vegetation (DeAngelis, 1992; Forman, 1997). For example, nitrogen input from the atmosphere has been found to be almost twice as high at the edge versus the interior of forest (Cadenasso *et al.*, 2004). Therefore $\delta^{15}N$ levels may be elevated due to increased deposition on vegetation fringing the road, or run off from surrounding pine. Litter input may be greater in the edge habitat due to larger amounts of vegetation being present there (Forman, 1997), and the quality of this litter may be better due to higher nutrient inputs to the edge (Weathers *et al.*, 2001). However, given that the boundary vegetation and caterpillar samples were collected within 20 m of roads but do not show this effect, this explanation seems unlikely. Conversely, the native beetle sample has a notably low $\delta^{15}N$ value (0.4 ±1.363‰) when compared to the $\delta^{15}N$ from a beetle caught in native forest on Stewart Island, New Zealand (Harper, 2006).

However, all beetles collected in my study were representatives of the same families, and consequently the effect of taxonomic influence can be ruled out.

Vegetation δ ^{13}C values found were relatively similar (mean range: -29.56 - -28.31‰) suggesting producers were utilising relatively similar carbon sources and experiencing similar environmental conditions. This was not unexpected given the proximity of all samples collected, and therefore the highly similar environmental regimes plants would have experienced. My values are also similar to the pine cellulose and native leaf litter δ ^{13}C values reported by Barbour *et al*. (2002) and Najera-Hillman *et al*. (2009) respectively for other New Zealand stable isotope studies (Table 2.6). Lower values have been found for New Zealand native riparian vegetation (Najera-Hillman *et al.*, 2009), and plant material collected in other countries have been found (Fry *et al.*, 1978a; Duarte *et al.*, 2005; Wooller *et al.*, 2005; Kohzu *et al.*, 2009), but higher values are reported for Australian leaf litter (Cook & Dawes-Gromadzki, 2005) (Table 2.6). Such differences are due to the producers experiencing different growth conditions and carbon sources which then influence δ ^{13}C values. Delta ^{13}C depends on a variety of factors including level of aquatic nutrient input (Najera-Hillman *et al.*, 2009), intensity of sun exposure (Duarte *et al.*, 2005), degree of water stress, atmospheric carbon dioxide and vapour pressure deficit, and overall habitat productivity (Cook & Dawes-Gromadzki, 2005).

Conversely, vegetation δ ^{15}N values were significantly different between habitats, although collectively the values are consistent with those from other locations and plant species in New Zealand (Table 2.6). However, the native vegetation δ ^{15}N value (-7.31‰) was markedly lower than that reported by Martinelli *et al*. (1999) (-2.8 ±2‰) for temperate forest vegetation, and also lower than values found by Harper (2006) for leaves and fruit of New Zealand native plants. It is possible, for Harper's result at least, that the higher value was due to their samples being collected from a relatively small island, and therefore due to marine input. But it must also be kept in mind that my vegetation values are from leaves in the leaf litter, which may naturally be lower in nutrients than fresh leaves. My values are higher than those found by Tozer *et al*. (2005) for epiphytic plants and lichen sampled from locations with geothermal activity,

and the authors suggested their vegetation may have been taking up atmospheric ammonia which influenced the δ ^{15}N values. Higher δ ^{15}N values have been found for Australian plant material (Blüthgen *et al.*, 2003), and increased values may be associated with habitats that have higher nutrient availability (Cassaing *et al.*, 2007; Oleksyn *et al.*, 2007; Göthe *et al.*, 2009).

Table 2.6. Comparison of selected terrestrial vegetation δ ^{15}N and C_3 plant δ ^{13}C values.

Vegetation type (location)	δ ^{13}C (‰)	δ ^{15}N (‰)	Reference
Pine habitat leaf litter (NZ)[1]	-28.31 ±0.32	1.00 ±0.34	This study (see Chapter 2 for details)
Native habitat leaf litter (NZ)[1]	-29.56 ±0.33	-7.31	This study (see Chapter 2 for details)
Boundary habitat leaf litter (NZ)[1]	-28.90 ±0.43	-0.67 ±0.23	This study (see Chapter 2 for details)
Pine cellulose (NZ)[2]	-28.50 - -21.70		Barbour *et al*.(2002)
Native riparian leaf litter (NZ)[1]	-29.61 ±0.22	-3.19 ±0.61	Najera-Hillman *et al*. (2009)
Plant material (NZ)[2]	-34.55 - -29.39	-6.72 - -2.37	Najera-Hillman *et al*. (2009)
Epiphytes and lichens (NZ)[1]		-19.32 ±0.32	Tozer *et al*. (2005)
Plant material (NZ)[1]		0.44 ±0.18	Wang *et al*. (2004)
Plant material (Africa)[2]		-1.30 - 3.90	Ambrose (1991)
Plant material (Australia)[3]	-28.50 ±1.70	2.20 ±1.30	Blüthgen *et al*. (2003)
Leaf litter (Australia)[2]	-25.30 - -26.60	1.41 - 3.50	Cook & Dawes-Gromadzki (2005)
Plant material (Australia)[2]	-27.20 - -25.90	0.87 - 1.65	Cook & Dawes-Gromadzki (2005)
Plant material (Texas, USA)[4]	-30.00 - -22.80		Fry *et al*. (1978a)
Plant material (Brazil)[2]	-32.70 - -25.40	1.00 - 4.50	Duarte *et al*.(2005)
Plant material (Mongolia)[4]	- 30.50 - -23.00	-3.70 - 8.10	Kohzu *et al*.(2009)
Plant material (Alaska, USA)[2]		-7.72 - 0.84	Schulze *et al*.(1994)
Plant material (Australia)[4]	-35.00 - -21.00	-0.09 - 16.25	Wooller *et al*.(2005)

[1]Delta values expressed as mean ± standard error.

[2]Delta values expressed as range of mean values.

[3]Delta values expressed as mean ± standard deviation.

[4]Delta values expressed as range of reported values.

Mean values for rat δ ^{13}C and δ ^{15}N values differ in terms of their ranges (see Table 2.7) due to the fact they are different stable isotopes; they behave differently within organisms and indicate different processes in the environment (DeNiro & Epstein, 1978; Gannes *et al.*, 1998; Caut *et al.*, 2008b). The mean δ ^{13}C values observed for rats in this study ranged from -24.61 to -23.49‰, which are similar to those found for rats inhabiting the native forest of Pearl, Stewart, and Taukihepa Islands, and the Waitakere

Ranges, (New Zealand) (Harper, 2006; Harper, 2007; Najera-Hillman *et al.*, 2009) (Table 2.7). However, lower mean values were recorded from rats occupying areas where their diet has a larger marine-influenced component, such as the coastal habitat of Pearl Island (Harper, 2006), and the studies of Cassaing *et al*. (2007) and Quillfeldt *et al*. (2008), both of which investigated the stable isotope signatures of rats inhabiting small island ecosystems. When mean rat $\delta^{15}N$ values are considered, those from this study (3.07 - 5.94‰) are similar to values from rats inhabiting native forest on Pearl Island and the Waitakere Ranges (New Zealand) (Harper, 2006; Najera-Hillman *et al.*, 2009) (Table 2.7). Additionally, similar values were gained from research conducted on the French islands of Porquerolles and Port-Cros (Cassaing *et al.*, 2007). Once again, strong habitat-dependent differences are found between the forested habitats examined by this study and the coastal habitats investigated by other researchers, with coastal rats showing a diet more enriched in nitrogen (Harper, 2006; Cassaing *et al.*, 2007; Harper, 2007; Quillfeldt *et al.*, 2008). Nakagawa *et al*. (2007) found that rats in Lambir Hills National Park, Malaysia showed an increase in $\delta^{15}N$ values between primary and partially degraded habitats to highly degraded forests such as fallow areas and rubber plantations. This increase was suggested to be due to rats in degraded habitats eating greater proportions of invertebrates as opposed to vegetation. However, I can rule this out as stomach content analyses shows large proportions of invertebrates consumed regardless of habitat. This comparison suggests that the values I found in this study are similar to that expected based on the literature for forest-living rats, but much lower than expected for coastal rats.

Pine plantation vegetation samples had the lowest mean $\delta^{15}N$ value for taxa sampled within this habitat followed by caterpillars, beetles, rats, mice, and tomtits. This was largely expected as each step in the food chain is associated with an accumulation of ^{15}N. Lower $\delta^{15}N$ values for herbivorous insects, including caterpillars, relative to carnivorous insects, represented by my beetles, have also been found by previous researchers (Bennett & Hobson, 2009). It was predicted that rats (5.941‰) would have had a higher mean $\delta^{15}N$ value than mice (6.02‰) due to the amount of vegetative versus animal matter usually found in their respective diets, and although this was not the case, the values were extremely close. This may be due to the small sample size for

the mice, as only two were caught in the pine forest, or it may simply be that the prey taken by these rodents was highly similar in terms of TL.

Table 2.7. Comparison of selected rat mean δ ^{13}C and ^{15}N values (± standard error).

Sample type (location)	δ ^{13}C (‰)	δ ^{15}N (‰)	Reference
Hair (Pine plantation - Hunua Ranges, NZ)[1]	-24.61 ±0.12	5.94 ±0.15	This study
Hair (Native forest - Hunua Ranges, NZ)[1]	-23.49 ±0.10	3.07 ±0.13	This study
Hair (Boundary habitat - Hunua Ranges, NZ)[1]	-23.56 ±0.12	3.72 ±0.32	This study
Muscle (Native forest - Pearl Island, NZ)[1]	-23.70 ±0.10	3.85 ±0.75	Harper (2006)
Muscle (Coastal habitat - Pearl Island, NZ)[1]	-20.86 ±0.39	12.96 ±0.98	Harper (2006)
Muscle (Native forest - Stewart Island, NZ)[1]	-24.50 ±0.32	2.20 ±0.43	Harper (2006)
Muscle (Native forest - Taukihepa Island, NZ)[1]	-22.76 ±0.23	14.66 ±0.58	Harper (2007)
Muscle (Native forest - Waitakere Ranges, NZ)[1]	-24.11 ±0.26	5.80 ±0.60	Najera-Hillman *et al*. (2009)
Hair (Porquerolles Island, France)[1]	-21.12 ±0.80	2.84 ±1.34	Cassaing *et al*. (2007)
Hair (Port-Cros Island, France)[1]	-21.65 ±0.34	3.62 ±0.96	Cassaing *et al*. (2007)
Hair (Riou archipelago, France)[1]	-20.98 ±1.43	8.92 ±0.73	Cassaing *et al*. (2007)
Liver (Rookery tussac grass habitat - New Island, Falkland Islands)[1]	-21.20 ±0.40	32.20 ±1.20	Quillfeldt *et al*. (2008)
Muscle (Rookery tussac grass habitat - New Island, Falkland Islands)[1]	-21.80 ±0.20	32.60 ±0.90	Quillfeldt *et al*. (2008)
Liver (South End tussac grass habitat - New Island, Falkland Islands)[1]	-19.90 ±0.40	22.10 ±1.00	Quillfeldt *et al*. (2008)
Muscle (South End tussac grass habitat - New Island, Falkland Islands)[1]	-19.50 ±0.30	21.00 ±1.00	Quillfeldt *et al*. (2008)
Liver (Gorse - New Island, Falkland Islands)[1]	-20.00 ±0.40	16.90 ±0.20	Quillfeldt *et al*. (2008)
Muscle (Gorse - New Island, Falkland Islands)[1]	-20.20 ±0.40	16.80 ±0.20	Quillfeldt *et al*. (2008)
Liver (Open habitat - New Island, Falkland Islands)[1]	-18.60 ±0.20	17.10 ±1.30	Quillfeldt *et al*. (2008)
Muscle (Open habitat - New Island, Falkland Islands)[1]	-18.00 ±0.20	17.90 ±0.50	Quillfeldt *et al*. (2008)

Taxa sampled in the native forest also follow the expected trend with mean δ ^{15}N increasing (vegetation<caterpillars<beetles<rats<tomtits). Najera-Hillman *et al*. (2009) conducted a stable isotope study of a native New Zealand riparian ecosystem in the same region as this study, and found similar δ ^{13}C values (-29.83 to -29.39‰) for the leaf litter they sampled, and substantially higher δ ^{15}N values (-3.8 to -2.58‰). This suggests that the locations I sampled for leaf litter in the native habitat have significantly lower nitrogen input, which may be due to the vicinity of the stream they

based their study around. Water can carry nutrients (Forman, 1997), and the δ ^{15}N Najera-Hillman *et al*. (2009) found for an aquatic primary producer (-1.74‰) would suggest that their habitat may indeed be more enriched. Their study found clearer separation for terrestrial non-predatory and predatory invertebrates, potentially due to their choice of Araneida and Opiliones to represent the predatory group, as these invertebrates may be foraging at a higher trophic position (i.e. foraging proportionally less on detritivores) than the beetles I considered.

Delta ^{15}N results for boundary taxa were less straight forward (vegetation<caterpillars<rats<beetles<mice). It is important to note that the standard error for boundary beetles is quite large, and it could be that with a larger sample size the mean δ ^{15}N value found would drop lower than that of rats. The δ ^{13}C value of boundary beetles also showed markedly larger variation than other taxa. In part this is likely to be due to the restricted sample size (three samples), although both pine and native beetle samples have equivalent sample sizes and do not show this level of variation. Stomach content analyses carried out on the rodents suggests that there was significant separation between rats and mice in this habitat. Interestingly, the stable isotope mean δ ^{15}N values show that it may be due to rats foraging on items with a significantly lower δ ^{15}N signature than mice. However, the lower δ ^{15}N value might also be due to the numbers of rats caught on each side of the boundary as the number of individuals was more skewed towards the native side (16) of the boundary than the pine (9).

Within each habitat, enough separation occurred between mean δ ^{13}C and δ ^{15}N values to constitute between three and four TLs between taxa. This is consistent with the results of Najera-Hillman *et al*. (2009) who found three TLs for a stream running through native forest and four TLs for the terrestrial habitat adjacent to the stream. In general, stable isotope analyses showed different TLs for the vegetation, herbivores, and predators, although some predators (beetles and tomtits), showed the same TL as herbivores (caterpillars), for δ ^{13}C and δ ^{15}N values. For δ ^{15}N values in the pine and native habitats, with vegetation considered a basal value, the second TL consisted of the invertebrates and the third of the rodents and tomtits. This was anticipated as

caterpillars are primary consumers, however the beetles sampled were from predacious families, and would have been expected to separate from the caterpillars, which was not seen in these habitats. The grouping of invertebrates with tomtits and rodents was also unexpected as tomtits are almost solely insectivorous (Moeed & Fitzgerald, 1982; Spurr & Powlesland, 2000), and would be expected to be feeding higher up the food chain than beetles, whereas both rodent species are omnivores (Clout, 1980; Badan, 1986; Fitzgerald *et al.*, 1996; McQueen & Lawrence, 2008).

The clumping of taxa which were expected to separate may suggest that they are more omnivorous than anticipated, are feeding largely from sources not analysed in this study, or feeding on prey relatively low in the food chain. For example, terrestrial detritivores are likely to be more nitrogen limited than herbivores (Alley *et al.*, 2001), and the beetles are likely to be feeding on detritivores present in the leaf litter. In contrast, the rodents potentially scavenge on carnivorous vertebrates remains and offset the lower nitrogen signatures for the vegetation they consume. When $\delta^{13}C$ values were examined for the pine plantation, caterpillars, beetles, tomtits, and mice all group together within the second TL. As this occurs for the $\delta^{13}C$ but not the $\delta^{15}N$ values, it is likely to be a reflection of similar carbon sources for the four taxa. The pattern of caterpillars and beetles grouping together was also observed for boundary $\delta^{13}C$ but the pattern was slightly altered when the boundary $\delta^{15}N$ was considered. In this case, the beetles separated out from the caterpillars, and the value gained for mice was different enough from that of the rats to suggest a fourth TL. When minimum and maximum carbon and nitrogen percentages were considered the results differ from those of $\delta^{13}C$ and $\delta^{15}N$, with similar mismatches also found by other researchers (Wang *et al.*, 2008), and no significant differences in total C or N seen between habitats.

The degree of seasonality in stable isotope values measured in this study varied between the taxa sampled. The caterpillars collected did not show significant seasonal fluctuations in $\delta^{13}C$ and $\delta^{15}N$ values, which may be due to the fact they were sourced from leaf litter samples and would most probably have been feeding on leaf litter year round. If they had been eating fresh vegetation they may have shown seasonal differences due to new leaf production, flowering, and fruiting, but the leaf litter

represents leaves from a variety of species shed at different times of the year (all habitats investigated were evergreen). Therefore, any seasonal fluctuations in caterpillar food sources were not large enough to be obvious in their tissues given the sample sizes examined. However, stable isotope analysis can deliver information on trophic interactions with reduced sample sizes, (e.g. Najera-Hillman *et al.*, 2009; Abrantes & Sheaves, 2010), in comparison to more traditional methods. Therefore if seasonal fluctuations were a strong effect for forest floor caterpillars in these habitats I would have anticipated detecting them. It is also notable that, although dealing with flying nocturnal insects, Herrera *et al*. (2001) did not detect seasonal fluctuations in their insect or plant stable isotope samples either.

Rats showed seasonal differences for $\delta\ ^{13}C$ but not $\delta\ ^{15}N$ values. Carbon signatures show less trophic discrimination but indicate carbon source from producers (Harding & Stevens, 2001; Caut *et al.*, 2008a). Therefore rats may be ranging widely within the habitats investigated, and consuming foods with different carbon signatures depending on season. Studies conducted on rats inhabiting Surprise Island, New Caledonia, compared rat $\delta\ ^{13}C$ and $\delta\ ^{15}N$ values over time (November and February) and found significant differences for both isotopes (Caut *et al.*, 2008a). Caut *et al.* (2008a) also discovered that rats moved to track readily available prey; during November the rats were present in higher numbers at the centre of the island where they preyed on eggs, whereas in February they moved to the coast where sea turtle (*Chelonia mydas*) hatchlings were abundant (Caut *et al.*, 2008a). A similar tracking of resources may be affecting the stable isotope signatures of my rats, with feeding occurring within the same habitat but on a resource with a different ^{13}C signature, potentially near the border or outside of the respective habitats. Harding & Stevens (2001) point out that the isotopic signature of a habitat may extend past its obvious boundary. This may be what has happened in my study, with rats concentrating their foraging seasonally in locations with different ^{13}C signatures, or dispersing into the trapping grid from these locations. A change in the diet of prey items, prey physiology, or the physiology of prey diet, as opposed to an actual diet shift by the rats, could also be responsible for the shift in $\delta\ ^{13}C$ values seen (Dalerum & Angerbjörn, 2005). Additionally, rat physiology and assimilation rates may also change seasonally and impact on the stable isotope values found (Dalerum & Angerbjörn, 2005).

There was no evidence for this seasonal shift in the stable isotope values for mice. It is possible that if the change in diet, or the time taken for the hair to grow is too brief then the stable isotope ratio will not reflect the shift of interest (Cassaing *et al.*, 2007). That may also be why significant changes were only found for rats in the pine plantation. If a tissue type with a higher nutrient turnover than hair had been chosen I might have found further evidence for seasonal dietary shifts. This is because stable isotope signatures reflect only the time when the tissue is being formed, which for rat hair is approximately 20 days (Caut *et al.*, 2008b). However, hair has been recommended by past researchers as appropriate to determine seasonal diet changes (Cassaing *et al.*, 2007).

Quillfeldt *et al*. (2008) sampled mice and rats from New Island, Falkland Islands, using stable isotopes, and found they had consistent diets maintained over a period of weeks. Although this study considers a larger time frame it may be presenting a similar result, with mice and rats (in native and boundary habitats) able to forage on relatively similar diets over extended periods. A lack of seasonality in diet composition was also found for deer mice (*Peromyscus maniculatus elusus*) inhabiting Santa Barbara Island, USA, in terms of this species not utilising a seasonally abundant potential food resource (Millus & Stapp, 2008). Millus & Stapp (2008) found no evidence of Xantus' murrelet (*Synthliboramphus hypoleuscus*) as a dietary item for deer mice when they examined both stable isotopes and stomach contents of this rodent. Their result was in spite of previous evidence that deer mice scavenge or prey on Xantus' murrelet during the breeding season.

Neither mice nor rats show any evidence, in terms of $\delta\ ^{13}C$ or $\delta\ ^{15}N$ values, to suggest that males and females forage on different prey items within each habitat. However, intersexual differences between male and female Norway rats have been found in laboratory based isotope studies by previous researchers. Kurle (2009) found higher $\delta\ ^{15}N$ values for kidney, muscle, plasma, and red blood cell samples for female versus male rats fed a control diet. When some rats had their diet changed, the intersexual $\delta\ ^{15}N$ difference was consistent for those tissues, with liver tissue also showing significantly higher in $\delta\ ^{15}N$ values for females (Kurle, 2009). However, she did not

find intersexual differences for hair samples. In terms of $\delta^{13}C$, values Kurle (2009) did not see intersexual differences for the control diet group, but found higher female values for kidney, liver, and red blood cells in the group that experienced a diet switch. Obviously, the circumstances for laboratory versus wild rats are very different, and Kurle (2009) cautions that the intersexual differences found were potentially too small to have biological significance for wild rats. She suggests that size differences, with females being smaller than males and therefore having higher metabolic rates, as the likely reason for the differences. The stable isotope analyses in this study did not show segregation of diet between male and female rats or mice, and this finding was backed up by the stomach content analyses.

No intersexual differences in stable isotope values were found for tomtits within habitats either. However, the research of Morrissey *et al*. (2010) raises a salient point as they found significant differences in male and female Eurasian dipper $\delta^{13}C$ values only at certain times of the year. Their study analysed red blood cells and plasma for comparison between the sexes, and this type of sample will reflect very recent diet. In contrast, my samples were collected during winter and were from feathers which will only reflect the stable isotope signatures of diet while they were being grown during the moult period in late summer. If a tissue with a higher nutrient turnover was sampled at different times of the year, evidence for dietary differences between the sexes of tomtits may be seen, especially in light of the striking differences in foraging that were found by this study (Section 3.3).

It is interesting to consider the lack of differentiation between habitats of the rodent stomach content analyses in light of the isotopic results. Although the nutritional content between habitats is significantly different for rodents, they seem to be able to locate similar prey when considered at the level of invertebrate order, and a similar proportion of invertebrates to vertebrate remains and vegetation. These findings also contrast with those of previous researchers who have noted dietary differences for this rat species captured in pine versus native forest in New Zealand (Clout, 1980; McQueen & Lawrence, 2008). Clout (1980) found rats inhabiting pine plantation showed a distinct lack of vegetation in their stomachs compared to those caught in

native forest in other studies, and noted a relative lack of fruit and seeds in pine forests during winter, when his rats were captured. This was corroborated by McQueen & Lawrence (2008) who found plant matter in at least half of all rat stomachs they examined from beech forest during each month of their study. Within the boundary habitat, comparison of the relative proportions of stomach contents showed no significant differences between rats and mice. However, when the invertebrate portion of the contents was considered, significant differences appear suggesting variation in the proportion and types of invertebrate taxa eaten by each species. Stomach samples examined for this research were collected during April, July, October, and January and the effects of season on diet in comparison to previous studies are discussed below.

The stomach contents of rats and mice were examined in four different ways to determine seasonal and intersexual differences. The volume of invertebrates, vertebrate remains, and vegetation in stomachs were also examined, with significant seasonal differences found for rats but not mice. Stomach content volumes differed between seasons for rats; in particular, autumn samples separate from winter and spring samples, and spring samples separate from winter samples. Across most of the year the diet was overwhelmingly comprised of invertebrates, although in both autumn and spring small amounts of vegetation were found, and during winter the proportion of vegetation increased. When rat diet is supplemented by vegetation over winter, individuals may travel to edge habitats to gain this plant material. Production of fruit can be higher in edge habitats (Zanette *et al.*, 2000), and even the distance that seeds penetrate into a habitat is partially a function of the edge structure (Cadenasso & Pickett, 2001). Many seeds and other windborne agents are deposited at edges due to a decrease in wind velocity (Willson & Crome, 1989), or when they come into contact with edge vegetation (Forman, 1997). This could be of particular importance in habitats with a native or exotic sub-canopy, such as a pine plantation, as they are anticipated to have less fruit and seed available than more diverse habitats.

Stomach contents from rats inhabiting pine plantations have been found to contain less vegetation (including fruit and seeds over winter) than those of rats in native forest (Clout, 1980). Clout (1980) captured 17 rats in a New Zealand pine plantation during

winter and found results similar to mine. All but one of the stomachs he examined contained invertebrates, 15 rats had consumed vegetation (plants or fungi), and one had eaten vertebrate remains. The reliance of rats on vegetation was corroborated by McQueen & Lawrence (2008) who found plant matter in at least half of all the rat stomachs they examined from New Zealand beech forest during each month of their study (June - December). McQueen & Lawrence (2008) also determined that, for rats trapped in native forest in winter and spring, vegetation, invertebrate and vertebrate remains were most often present.

Seasonal differences were seen even when the presence or absence of each food group was considered, so not only were rats differing in the proportion of each dietary component between seasons, they were also differing in terms of whether they ate a particular food type. Autumn samples differed from winter and spring samples because they contained less vegetation than found in winter, and included vertebrate remains not found in spring. The spring samples differed from winter samples due to smaller amounts of vegetation and the lack of vertebrate remains. Although the proportion of vertebrates preyed on or scavenged was low overall, they may constitute an important contribution at times. Caut (2008a) also found varying levels of vegetation eaten over the course of her study, with all rat stomachs containing plant matter in November, and 67% containing vegetation in February. The same study also found varying numbers of stomachs to contain vertebrate remains, while the presence of invertebrates was constant (Caut *et al.*, 2008a). This is a similar result, in terms of seasonal fluctuations of dietary items seen, to this study, with invertebrates providing a mainstay to the rats and being supplemented at times with vegetation and vertebrates.

When the minimum number of identifiable invertebrates per order were examined there was no evidence for seasonal diet variation, i.e., the proportion of each invertebrate order consumed was not found to differ significantly across seasons. The same result was found when the data was examined in terms of the presence or absence of each invertebrate order in the diet. This suggests that, regardless of season, both rats and mice were able to prey on invertebrates of the same order and relative proportion. This may be because they were able to find preferred prey items regardless of season, or

simply that there were always sufficient invertebrates suitable for rodent prey throughout the year. If dietary items had been identified to a lower taxonomic level seasonal fluctuations may well have been found. It has been suggested that by grouping species within higher taxa seasonal patterns may be lost as each species within an order may be responding differently to the seasons (Alley *et al.*, 2001). A similar effect may be occurring with the invertebrates preyed on by rodents in this study; they may find prey of the same order, but not necessarily the same species, to feed on at different times of the year.

When Badan (1986) looked at mouse stomachs he found invertebrates and vegetation (seed) present in the majority of stomachs each month. He also identified fluctuations in relative importance of some prey species across the seasons, which, for seed at least, was in keeping with their availability in the habitat. My analyses did not detect seasonal fluctuations in mouse diet, however, sample sizes were smaller (16 versus 260), and classified with a coarser scale of identification. To identify seasonal fluctuations the sample size would need to increase to at least match that of the rats examined (85). The difference may also be due to habitat, as Badan (1986) caught mice in three habitats (young and mature pine plantation, and native forest) and the animals caught in my study come almost exclusively (14 out of 16) from the boundary habitat. Although, as the boundary habitat represents both mature pine and native forest, it seems unlikely the lack of seasonality seen would be due to habitat differences. Fitzgerald *et al*. (1996) also found stronger seasonal stomach content fluctuations for certain elements of plant and invertebrate content for mice caught in New Zealand beech forest, but only slight seasonality for invertebrates and vegetation overall.

Conclusions

The hypothesis that stable isotope signatures would differ between habitats was proved correct, with native habitat having the lowest $\delta\ ^{15}N$ levels within taxa, boundary samples usually having intermediate values, and pine plantation samples having the highest $\delta\ ^{15}N$. This difference was significant for $\delta\ ^{15}N$ values of vegetation, rat, and tomtit samples, and for $\delta\ ^{13}C$ of rat and tomtit samples. The anticipated separation of

taxa within each habitat was also found, with significant differences for both isotopes analysed and two to four TLs displayed. However, the order of $\delta^{15}N$ signatures within each habitat did not necessarily reflect the predicted progression (vegetation<caterpillars<beetles<mice<rats<tomtits); in both pine and boundary habitats mice showed a slightly higher mean $\delta^{15}N$ than rats, and in the boundary habitat beetles also had a higher mean $\delta^{15}N$ than rats. Stable isotope fluctuations between seasons were only seen for rat $\delta^{13}C$ values, and may indicate seasonal foraging movements. No intersexual differences in stable isotope values were found for rats, mice, or tomtits, and investigation of stomach contents for the rodents also showed very similar diets for both sexes. In contrast to stable isotope results, the stomach content analyses undertaken for rodents did not show within species habitat separation, but revealed significant differences between rat and mouse diet in the boundary habitat. I also found that the stable isotope and stomach content methods employed differed in their separation of seasonal diet for rats, although their findings agreed for mice. Significant variations in diet for rats between seasons, in terms of vegetation and invertebrate proportions taken, and also the presence of vertebrate remains in autumn and winter, were found.

Use of stomach content analyses in conjunction with stable isotope analyses compliments the findings of each method allowing investigation of diet at the level of prey items in addition to isotopic signatures. In this instance I have been able to see that the rodents were feeding on similar types of prey in each habitat, however the $\delta^{15}N$ and $\delta^{13}C$ values were distinct for each habitat, so if only one technique had been applied very different conclusions would have been drawn. Stomach content analysis alone would have led me to conclude that prey items, and therefore presumably nutrient availability to the rodents, were the same in each habitat. In contrast, stable isotope analysis alone would have led me to conclude that the rodents were accessing widely differing nitrogen and carbon sources, and therefore presumably prey items, in each habitat. The need to couple different methodologies in order to gain a better understanding of diet at a temporal level was also highlighted. Stomach content analysis alone would not have detected seasonal shifts in diet for rats that suggested movement to source food. When stable isotope results were coupled with the information from stomach content analyses I found that, although the $\delta^{15}N$ values do

not vary between seasons for the rodents investigated, the overall composition and $\delta^{13}C$ value of the diet does.

Tomtit foraging behaviour: variation with sex, season, year, and habitat type

Abstract

Tomtit foraging behaviour was observed in the Hunua Ranges, New Zealand, between March 2006 and February 2008. Sexes differed in foraging behaviour, with males observed foraging more frequently on the ground than females and females using vegetation (in particular substrates between 0 - 3 m) more than males. Foraging by both sexes varied between breeding and non-breeding season in 2006, with more ground use occurring in the non-breeding season and more vegetation use (males: 3 - 6 m; females: 0 - 3 m) in the breeding season. Tomtit foraging behaviour in three habitats (pine plantation, native forest, and the contiguous boundary of these habitats) was compared. Overall, tomtit foraging in native forest occurred more frequently in vegetation 3 - 6 m compared to the use of this stratum in either pine or boundary habitat. Males showed inter-annual differences in foraging, using the ground significantly more in 2006 than 2007. This study clarifies some aspects of tomtit foraging and habitat use, and illustrates the complexity of foraging behaviour and the difficulty of understanding variation due to sex, habitat, and season.

3.1 Introduction

Many aspects of foraging that are important for the description and quantification of this fundamental behaviour, such as foraging substrate, height, and technique, have been found to differ between species of insectivorous forest birds (Airola & Barrett, 1985; Unno, 2002; Buckingham *et al.*, 2006). Research of such guilds has shown that certain species will utilise the different foraging heights available proportionally to their target prey biomass (Hino *et al.*, 2002). Inter-annual variation in bird foraging is also a fundamental, but rarely quantified, aspect of foraging ecology (Adamík & Korňan, 2004). When investigated, significant variation between years in terms of tree species

preferences (Adamík & Korňan, 2004), and microhabitat use (Craig & Beal, 2001), have been found.

Foraging differences can also occur intraspecifically between males and females, with variation between sexes reported widely for birds (Jackson, 1970; Austin, 1976; Peters Wm & Grubb Jr, 1983; VanderWerf, 1994; Olsson *et al.*, 2000; Temeles *et al.*, 2005; Burns & Steer, 2006), and sometimes manifesting in differing stable isotope signatures between sexes (Forero *et al.*, 2005; Morrissey *et al.*, 2010). Previous research concentrating on New Zealand robins (*Petroica australis*) found clear differences between sexes when birds were fed mealworms (*Tenebrio molitor* larvae) (Burns & Steer, 2006; Burns & van Horik, 2007; Steer & Burns, 2008). Males approached prey first and displaced females if they approached; these behaviours meant that males fed on more than twice the amount of mealworms than females (Burns & Steer, 2006; Burns & van Horik, 2007). New Zealand robins cache food, with males caching more frequently than females, with caching behaviour changing depending on whether birds were foraging alone or in a pair (Burns & Steer, 2006). Both sexes cached more when solo, and this behaviour increased markedly more for solo females than males (Burns & Steer, 2006). However, when foraging as a pair, male caches were more likely to be utilised (eaten or re-cached) by the attending female than the male (Burns & van Horik, 2007).

Differences between sexes can be consistent throughout the year or they may be seasonal, with prey, foraging substrate, height, and strategy found to change between seasons (Osborne & Green, 1992; Murakami, 2002). Intersexual seasonal foraging variation may be associated with egg production, which has been recorded for Eurasian dippers, where females switch to foraging on more abundant invertebrate orders than males during the egg-laying period (Morrissey *et al.*, 2010). Robinson (1992) found seasonal shifts in substrate type, height use, and foraging technique for the scarlet (*Petroica multicolor*) and flame robins (*P. phoenicea*) observed in the Southern Tablelands (Australia). Both robin species made more use of vegetation during summer, November to January, and autumn, February to April. This substrate shift was associated with foraging higher in the vegetation, and, for the scarlet robin, utilising

snatch and hawking strategies more often (Robinson, 1992). These seasonal shifts were ascribed to changes in the vegetation, such as flowering and bark shedding, in addition to varying levels of invertebrate abundance (Robinson, 1992).

Foraging patterns also show significant variation between years, and this is particularly noticeable when certain prey species reach extremely high numbers. Hogstad (2005) found increased use of mountain birch (*Betula pubescens* ssp. *czerepanovii*) canopy, as opposed to fields, by bluethroat (*Luscinia svecica*), brambling (*Fringilla montifringilla*), redpoll (*Carduelis flammea*), reed bunting (*Emberiza schoeniclus*), tree pipit (*Anthus trivialis*), and willow warbler (*Phylloscopus trochilus*) during years in which autumnal moth (*Epirrita autumnata*) numbers reached outbreak population levels. Additionally, Adamík and Korňan (2004) found significant differences in the amount of time treecreepers (*Certhia familiaris*) and nuthatch (*Sitta europaea*) spent foraging in beech (*Fagus sylvatica*) trees between years. The proportional use of sycamore (*Acer pseudoplatanus*) and snags also changed annually for treecreepers and nuthatch respectively, with the authors suggesting the birds could be utilising substrates opportunistically as resources varied (Adamík & Korňan, 2004).

Habitat differences impact on a range of bird foraging variables including strategy, number of attacks on prey, flight frequency, and flight distance (VanderWerf, 1994; Brotons *et al.*, 1998; Hartung & Brawn, 2005). Adamík *et al*. (2003) studied the effect of two distinct habitats (old-growth beech-fir (*Abies alba*) forest versus spruce (*Picea abies*) plantation) on bird guild foraging, and found a much less complex vertical stratification of foraging in the plantation due to the lower structural diversity of this habitat. Birds may also seek out habitats within a mosaic that offer the best foraging opportunities, for example lower tree and shrub density, greater native herb cover, and increased amounts of coarse woody debris have all been found to influence bird foraging (Antos *et al.*, 2008).

In New Zealand, pine plantations are emerging as a major component of the landscape, and an ecosystem requiring examination. As a forest ecosystem they provide habitat for a variety of native forest species, although they are less biodiverse and the species

inhabiting pine plantations do not necessarily reach the same levels of abundance as in native forests (Jackson, 1971; Clout & Gaze, 1984; Robertson *et al.*, 2007; Minor, 2008; Borkin & Parsons, 2009; Deconchat *et al.*, 2009). Regardless of this, pine plantations are becoming recognised as habitat for a number of native and even endangered animal species (Collier & Halliday, 2000; Brockerhoff *et al.*, 2005; Pawson *et al.*, 2010). This makes them a natural comparison for native forest when evaluating general habitat worth and the importance of native forest structure for species common to each. However, although pine plantations are capable of providing good quality habitat for native species they are not the equivalent of native forest. Pine plantations are not permanent, and the vast majority of species inhabiting them will not be able to survive through the felling regime.

Tomtits are an endemic New Zealand birds that make use of both native forest and pine plantation habitat (Clout & Gaze, 1984; Heather & Robertson, 2005; Deconchat *et al.*, 2009; Seaton *et al.*, 2010). Studies investigating tomtit abundance in native versus exotic forests have found lower abundance of this species in exotic forests, and state that young stands of pine may not be suitable for breeding (Clout & Gaze, 1984; Deconchat *et al.*, 2009). Tomtits do not rely on resources that may be lacking in pine plantations such as fruit or nectar, and do not require cavities for nesting which add to their ability to utilise this habitat (Clout & Gaze, 1984). They primarily feed on invertebrates inhabiting the forest floor and plant microhabitats (Skinner, 1978; Moeed & Fitzgerald, 1982; O'Donnell & Dilks, 1994). Both male and female adult tomtits are territorial (Fleming, 1950), with territorial behaviour occurring year round (Fleming, 1950; Skinner, 1978; Heather & Robertson, 2005). Tomtits breed from October through to March with both males and females feeding the chicks (Knegtmans & Powlesland, 1999) (see Section 2.2.2 for more details regarding this species).

This study investigated the foraging behaviour of tomtits with observations made in three habitats (pine plantation, native forest, and the contiguous boundary of these habitats). I test the hypotheses that: 1) foraging differences exist between sexes, 2) tomtits show seasonal variation in their foraging behaviour, 3) foraging varies between years, and 4) tomtits forage differently within different habitats.

3.2 Methods

Behavioural observations were made between March 2006 and February 2008 in the Hunua Ranges, New Zealand (37º 08' S, 175º 13' E), in three habitat types defined as pine plantation, native forest, and the boundary where these two habitats meet (from the intercept 50 m into each) (see Section 2.2.1 for more study site details). Replicate sites within each habitat were chosen based on their similarity, in terms of the same level of pest control and canopy closure. Observations took place throughout the day (06:55 to 19:30) as long as visibility allowed, with tomtits located through direct observation or finding calling birds. Events were recorded using a hand-held tape recorder. The sex, month, year, habitat, and territorial location of each individual was noted and the tomtit was followed for up to one hour (or until at least one foraging event was recorded) with behaviours continuously recorded. Each year began at the end of the tomtit's breeding season, so the years compared in this research were April 2006 - March 2007, and April 2007 - February 2008. Tomtits generally breed from October - March (Knegtmans & Powlesland, 1999), with the non-breeding season being the remainder of the year.

When a focal bird foraged the following data were collected: foraging substrate, height above ground, and foraging strategy utilised (Gill, 1980; Powlesland, 1981; Keast & Recher, 1997) (Table 3.1). A focal bird was defined as the bird being observed. Individual birds were not banded because tomtit mist-netting is commonly undertaken after a period of training birds to forage on mealworms (see Section 2.2.3), which may have altered their foraging behaviour in the presence of humans. In addition, attempts to lure birds into mist-nets using calls were unsuccessful. Instead, individuals were identified using a combination of sex, maturity, and territorial location. This was considered a reliable way to identify individuals within a given two month period as tomtits are widely recorded as tightly pair-bonded (Wilkinson, 1927; Knegtmans & Powlesland, 1999; Heather & Robertson, 2005), and territorial year round (Wilkinson, 1927; Skinner, 1978; Heather & Robertson, 2005). The assumption that they will remain on their territories has also been used as a monitoring technique by past authors (Powlesland *et al.*, 2000; Westbrooke *et al.*, 2003; Michaux, 2009).

Table 3.1. Foraging definitions and variables measured for each foraging event.

Category	Sub-category	Description
Substrate	Ground	Ground layer of habitat including leaf litter, bare ground, etc.
	Vegetation	Any component of vegetation including leaves, branches, trunks, etc.
	Air	The air either below or above the canopy
Height	Ground	Ground layer of habitat including leaf litter, bare ground, etc.
	0 - 3 m	Any substrate occurring above the ground to a height of 3 m
	3 - 6 m	Any substrate occurring above 3 m up to a height of 6 m
	>6 m	Any substrate occurring above 6 m
Strategy	Gleaning	Perched on the ground or vegetation attempting to capture food from a substrate other than the air
	Snatch	In flight and attempting to capture food from a substrate other than the air while flying past
	Hover	In hovering flight and attempting to capture food from a substrate other than the air
	Hawk	In flight and attempting to capture food from the air

To describe general tomtit foraging and compare between sexes, seasons, years, and habitats, the observation with the most foraging events recorded per individual was kept for each two month period starting March 2006. Each observation is counted as the time from the first sighting of an individual until it can no longer be observed; each observation can therefore contain a number of foraging events. The observation with the most foraging events recorded per individual was the observation chosen because it was assumed to be the most indicative of the individual's general foraging behaviour. To avoid pseudoreplication only the first foraging event within each observation was considered in descriptions and analyses. Birds described as paired were those observed with an adult tomtit of the opposite sex on their territory within one calendar month of the foraging event considered. All comparisons were made using Chi square tests and carried out in Microsoft Excel (Microsoft Corporation, 2007).

3.3 Results

Tomtits utilised vegetation (62%) most often as a foraging substrate, ground use was also important (35%), but aerial foraging was rarely used (3%) (n = 294). When foraging events were broken down into height categories the ground (38%) was the most important, then the lower (0 - 3 m) substrates (32%), followed by those 3 - 6 m (25%), with few foraging events observed at >6 m (5%) (n = 290). In terms of foraging

strategy, gleaning was most often utilised (52%). Both snatch and hover strategies were used to a similar degree (22%), and hawking was used very little (4%) (n = 232).

Females appeared to prefer to forage on vegetation more (74%) (n = 85), and the ground less (25%) (n = 85) than males (53% and 45% respectively) (n = 178) (Table 3.2). When paired versus non-paired birds were compared there were no significant differences between substrate utilisation for males or females (Table 3.2). Use of the different height categories also varied significantly between sexes, with males using the ground more, and the substrates between 0 - 3 m less, than females (Figure 3.1). Again, this difference in usage was not associated with the presence of another bird. No significant differences between foraging strategies were observed between sexes regardless of whether birds were paired or non-paired.

Table 3.2. Foraging comparisons between male and female and paired and non-paired tomtits.

Comparison		χ^2	df	n	*P*
Males vs females:	substrate	10.865	2	263	0.004
	height	9.822	3	260	0.020
	strategy	5.748	3	201	0.124
Paired vs non-paired males:	substrate	1.415	2	214	0.492
	height	3.553	3	207	0.313
	strategy	1.550	3	142	0.670
Paired vs non-paired females:	substrate	2.787	2	95	0.248
	height	4.358	3	94	0.225
	strategy	4.936	3	70	0.176

Breeding and non-breeding season observations were compared between males and females for each year. In both the breeding and the non-breeding season of 2006, males utilised the ground significantly more for foraging than females (Table 3.3). When foraging height was considered, the results were consistent with those for foraging substrate; males showed more ground use than females during the non-breeding season, and during the breeding season utilised this height significantly more than females. In contrast, the foraging strategies used were not significantly different between the sexes in both the breeding and non-breeding season of 2006 - 07. Finally, in 2007 - 08, there were no significant differences between the sexes in foraging substrate, height, or strategy used regardless of season.

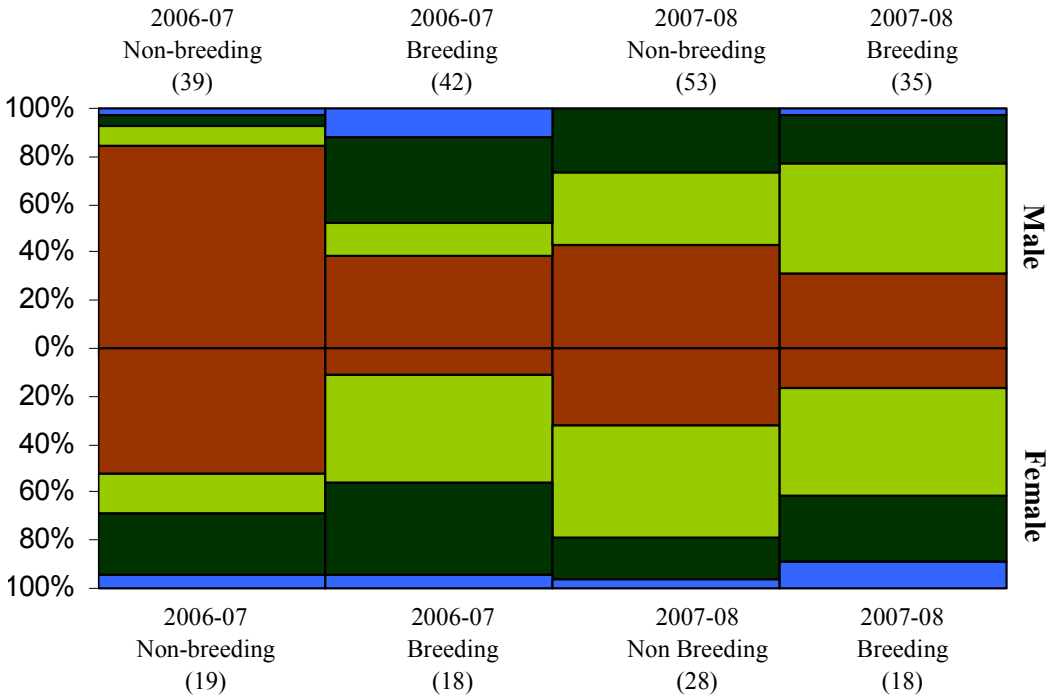

Figure 3.1. Proportional foraging height category utilisation by males (top part of the graph) and females (bottom part of the graph) for each season of observation (March 2006 - February 2008). Bracketed number denotes sample size. = >6 m, = 3 - 6 m, = 0 - 3 m, = ground.

Differences between seasons were also compared within sexes. In 2006 - 07, males showed significant differences in the choice of foraging substrate used between the breeding and non-breeding season, with more ground use seen within the non-breeding season and more vegetation use seen in the breeding season (Table 3.3). When foraging height was examined for males in 2006 - 07, a highly significant difference was seen between seasons. The vast majority of foraging events occurred on the ground in the non-breeding season, but almost equal proportions occurred on the ground and 3 - 6 m in the breeding season (Figure 3.1). A significant difference was also seen for females during this period, with more foraging events observed on the ground during the non-breeding season, and more taking place 0 - 3 m in the breeding season. No significant differences between seasons were found within either sex for foraging strategy in 2006 - 07. For 2007 - 08 data, no significant differences between seasons occurred within either sex when foraging substrate, height, or strategy were considered.

Table 3.3. Foraging comparisons between breeding and non-breeding seasons within and between sexes. Conventions as Table 3.1.

Comparison		χ2	df	n	*P*
2006 - 07 non-breeding season males vs females:	substrate[1]	4.442	1	58	0.035
	height	7.594	3	58	0.055
	strategy	4.725	3	27	0.193
2006 - 07 breeding season males vs females:	substrate	5.820	2	60	0.054
	height	8.512	1	60	0.036
	strategy	6.191	3	47	0.102
2007 - 08 non-breeding season males vs females:	substrate	2.710	2	82	0.257
	height	4.401	3	81	0.221
	strategy	0.702	3	67	0.872
2007 - 08 breeding season males vs females:	substrate	1.353	2	54	0.508
	height	2.733	3	53	0.434
	strategy	0.530	3	52	0.912
2006 - 07 non-breeding vs breeding season males:	substrate	11.424	2	81	0.003
	height	19.421	3	81	<0.001
	strategy	5.868	3	49	0.118
2006 - 07 non-breeding vs breeding season females:	substrate[1]	3.067	1	37	0.079
	height	7.918	3	37	0.047
	strategy[2]	2.939	2	25	0.230
2007 - 08 non-breeding vs breeding season males:	substrate	0.997	2	90	0.607
	height	4.050	3	88	0.255
	strategy	2.221	3	79	0.527
2007 - 08 non-breeding vs breeding season females:	substrate	1.916	2	46	0.383
	height	2.466	3	46	0.481
	strategy	2.044	3	40	0.563

[1]Comparison between ground and vegetation substrates as no use of air as a foraging substrate seen.

[2]Comparison between glean, snatch, and hover strategies as no hawking foraging strategy observed.

Differences in foraging behaviour between years (2006 - 07 vs 2007 - 08) was compared for males and females. Males foraged significantly more often on the ground, and utilised substrates in the 0 - 3 m category significantly less during 2006 - 07 as opposed to 2007 - 08 (Table 3.4). No significant differences in foraging strategy use were found for males between the two years, or for any female foraging variables between years.

Table 3.4. Foraging comparisons for each sex between years. Conventions as Table 3.1.

Comparison		χ^2	df	n	*P*
Males 2006 - 07 vs 2007 - 08:	substrate	6.350	2	171	0.040
	height	14.210	3	179	0.003
	strategy	5.468	3	128	0.140
Females 2006 - 07 vs 2007 - 08:	substrate	1.068	2	83	0.585
	height	2.817	3	83	0.420
	strategy	1.264	3	65	0.737

Finally, for a general comparison of tomtit foraging within habitats, sexes and seasons were pooled but years separated. In 2007 - 08, there was a trend towards greater vegetation use, and significantly more foraging events in the 3 - 6 m category in the native forest (Table 3.5). Foraging strategy showed no effect of habitat in either year, however, and in 2006 - 07 no significant effects of habitat on either foraging substrate or height were found. When foraging behaviour used within each habitat was compared between male and female tomtits the patterns were consistent with general habitat results (Table 3.5). In 2006 - 07, there was a trend towards greater use of the ground as a foraging substrate by males in the pine plantation, and this foraging height by males in the native forest. No difference between male and female foraging substrate use was found in native or boundary habitats, or for foraging height in the pine or boundary habitat for 2006 - 07. However, the results for strategy use in 2006 - 07 between the sexes were not consistent with previous findings; in the pine plantation there was a trend ($P = 0.070$) towards different foraging strategies for each sex, although this may be due to a small female sample size (n = 8). A significant difference between sexes was found for foraging strategy used in the boundary habitat. Again, the sample size for females was small (n = 6), so the difference may be due to the absence of snatch foraging observed. No differences were found between male and female strategy in the native forest for 2006 - 07, and in 2007 - 08 no comparisons between sexes within habitats were significantly different.

Table 3.5. Foraging comparisons between habitats and within habitats between sexes. Conventions as Table 3.1.

Comparison		χ^2	df	n	*P*
2006 - 07 pine vs native vs boundary:	substrate	5.900	4	119	0.206
	height	4.013	6	118	0.674
	strategy	8.158	6	74	0.226
2007 - 08 pine vs native vs boundary:	substrate	8.970	4	136	0.062
	height	22.460	6	133	0.001
	strategy	4.784	6	118	0.571
2006 - 07 pine males vs females:	substrate	5.260	2	41	0.072
	height	6.191	3	41	0.102
	strategy	7.030	3	28	0.070
2006 - 07 native males vs females:	substrate[1]	0.809	1	41	0.368
	height	7.360	3	40	0.061
	strategy[2]	2.761	2	26	0.251
2006 - 07 boundary males vs females:	substrate[1]	1.363	1	37	0.242
	height	3.890	3	37	0.273
	strategy[2]	6.428	2	20	0.040
2007 - 08 pine males vs females:	substrate	0.959	2	47	0.619
	height	5.712	3	46	0.126
	strategy	1.023	3	40	0.795
2007 - 08 native males vs females:	substrate	2.397	2	57	0.301
	height[3]	1.016	2	55	0.601
	strategy	0.746	3	48	0.862
2007 - 08 boundary males vs females:	substrate[1]	0.120	1	32	0.728
	height[3]	2.530	2	32	0.282
	strategy[2]	0.809	2	30	0.667

[1]Comparison between ground and vegetation substrates as no use of air as a foraging substrate seen.

[2]Comparison between glean, snatch, and hover strategies as no hawking foraging strategy observed.

[3]Comparison between ground, 0 - 3 m, and 3 - 6 m height categories as no foraging over >6 m recorded.

3.4 Discussion

Tomtits predominantly utilised vegetation as a foraging substrate, an unsurprising result given the dominance of this substrate in the habitats examined. However, the ground was obviously also very important, being used in over one third of foraging events. The breakdown of foraging by height category allowed determination of the substrate levels most used. The forest floor was the most important strata (38%), with ground cover and lower vegetation (0 - 3 m), closely followed by sub-canopy (3 - 6 m), utilised 32% and 25%, respectively. This result is consistent with O'Donnell and Dilks (1994) who found most South Island tomtit foraging occurring in the understory. I believe the small number of foraging events observed in my study over 6 m accurately represents the use

of this stratum for foraging, as opposed to these events being missed, because territorial singing and preening were observed at this height regularly, and animals could be followed, but foraging was rarely observed. Over half the foraging events utilised gleaning (52%), although snatch and hover strategies were both used in 22% of the events considered. The latter are aerial strategies and used when birds target more distant prey, or prey on the undersides of leaves (Whelan, 2001), with the snatch strategy also targeting invertebrates on top of leaves and branches. Glean, snatch, and hover techniques are those associated with capture of low mobility invertebrates (Amano & Eguchi, 2002). As expected, given the general low occurrence of aerial foraging, hawking was a behaviour rarely seen. Previous *P. m. macrocephala* studies have also found a large majority of gleaning with smaller amounts of hovering and hawking utilised (O'Donnell & Dilks, 1994).

Significant differences between tomtit sexes were seen for both foraging substrate and height, with females utilising vegetation more, and the ground less than males, in addition to foraging more between 0 - 3 m. Both sexes are alike in morphology and neither appears to specialise in a particular foraging strategy. So it is possible that males dominated the richest foraging substrate, as suggested for *Dendrocopos scalaris* (Austin, 1976), and found for *Picoides pubescens* (Peters Wm & Grubb Jr, 1983). Evidence for male dominance of females during foraging has also been found in the closely related New Zealand robin, with behavioural changes evident between solo and paired birds (Burns & Steer, 2006; Burns & van Horik, 2007; Steer & Burns, 2008). If this was the case for tomtits, it was not reflected in nitrogen or carbon values from the stable isotope analyses carried out (Figure 2.4), and so did not equate to males utilising invertebrates with a different carbon signature, or from a higher or lower TL than females. It was also notable that when paired and non-paired tomtits were compared, no evidence of males or females changing their foraging behaviour in the presence of the opposite sex was observed.

An alternate explanation for differences in foraging is that females have a different nutritional requirement, potentially for egg production, supplied by vegetation-based prey, or that they may be more reluctant to forage far from their nest due to predation

risk. If this was the case, differences between the sexes within breeding and non-breeding seasons might be expected, and also for females but not males between seasons. When the 2006 - 07 data were considered, the same significant trend of males foraging on the ground more than females during both seasons was seen. Males show significant differences and females a trend towards seasonal differences, with relatively more ground use occurring in the non-breeding season and more vegetation use in the breeding season for both sexes. Foraging height also changed seasonally for males and females, with birds showing less dependence on the ground in the breeding season and relatively more utilisation of 3 - 6 m substrates for males, and 0 - 3 m for females. As both sexes switch their focus seasonally it is likely that they were simply following abundances of invertebrates to make use of emerged larval and adult stages feeding on the vegetation. However, mate guarding by the males is an alternate explanation.

Interestingly, this seasonal switch was observed only in 2006 - 07. When comparisons were made between years (seasons pooled) for each sex, significant foraging differences between years for males, but not for females, were found. Males forage more on the ground in 2006 - 07 than 2007 - 08. This is likely to be due to differences in prey availability between years, potentially driven by differing environmental conditions. Reductions of soil surface water can limit invertebrate availability (Peach *et al.*, 2004; Devereux *et al.*, 2006), and birds have been found to shift microhabitat use between years, most probably to make use of differing food availability (Craig & Beal, 2001). It is interesting to speculate as to why only male tomtits switched foraging behaviour between years, and again implies a potential for intersexual competition and differing nutritional requirements.

Habitat-related foraging differences were seen in 2007 - 08, with a trend for greater vegetation use in the native forest, as opposed to pine or boundary habitat. Considering structural differences between these habitats this is unsurprising; although sites were picked to be as similar as possible, the native forest often had more sub-canopy than pine plantation. Foraging differences between undisturbed and disturbed forest habitats for *Chasiempis sandwichensis* were due to fewer perches and lower foliage density in disturbed habitats (VanderWerf, 1994). A similar effect may be occurring between the

native and pine forest in this study. This was highlighted in this study as greater numbers of foraging events in the native forest occurred in the 3 - 6 m height category. Strong selection for certain vegetation types and structure has been found for other insectivorous forest birds as well (Airola & Barrett, 1985; Virkkala, 1988). However, it is interesting to note that Kleintjes and Dahlsten (1994), who studied *Parus rufescens* foraging behaviour in a pine plantation in the USA, found individuals preferentially foraging from pines during the breeding season. Again, a marked difference between the two years of my study was seen with no significant differences between habitats found for 2006 - 07. When sexes were compared within each habitat the same trend seen previously for 2006 - 07 was found again; greater ground use by males than females in pine and native forests. It has been noted that birds will concentrate their foraging efforts on tree species with the most available or numerous prey (Holmes & Robinson, 1981), so it is probable tomtits concentrate their foraging on the most profitable substrates within each season, year, and habitat.

In New Zealand, pine plantations are the most common form of plantation forest and cover approximately 1.7 million ha (Brockerhoff *et al.*, 2002). Pine plantations form a valuable ecosystem for a variety of species that inhabit open, scrub, and forest habitats as they transition through these broad habitat stages from planting to harvest over a period of 20 - 30 years (Sutton, 1999). The comparison of tomtit foraging between habitats highlighted the importance of habitat structure to birds. Previous research such as that of Loyn *et al*. (2007) who investigated the impacts of eucalypt (*Eucalyptus* spp.) plantations versus other habitat types in Australia, has also found this to be an important consideration when regarding both broad and microhabitat scale changes in the landscape. Pine plantations are a significant ecosystem in New Zealand and provide habitat to a wide variety of native species (Robertson *et al.*, 2007; Pawson *et al.*, 2008; Borkin & Parsons, 2009). Ongoing investigation of this habitat is required throughout the rotational cycle to ascertain its worth to different taxa through time and the effect of felling on the species inhabiting this habitat as a forest.

Summary

I found that male and female tomtits differed in foraging substrate and height utilisation with males using the ground more than females, and females using vegetation (in

particular between 0 - 3 m) more than males. However, large differences within pine and native forest were not seen when $\delta^{13}C$ and $\delta^{15}N$ values were compared between sexes (Figure 2.5). Both sexes differed between breeding and non-breeding seasons in 2006 - 07, with relatively more ground use occurring in the non-breeding season, and more vegetation use (males: 3 - 6 m; females: 0 - 3 m) in the breeding season. Males also showed annual differences in foraging, using the ground significantly more in 2006 - 07 than 2007 - 08, but no annual differences were found for females. The three forest habitats were utilised differently by the birds, with vegetation as a substrate and the 3 - 6 m height category used more frequently in the native forest than the pine or boundary habitat. This study allowed in-depth comparison of many aspects of tomtit foraging, and provides intriguing results regarding tomtit use of their habitat. It also poses some questions for the future, in particular regarding the foraging differences between sexes.

Comparison of invertebrate availability at tomtit ground foraging sites between habitats, years, and sexes

Abstract

Three habitats (pine plantation, native forest, and the contiguous boundary of these habitats) within the Hunua Ranges, New Zealand were compared for invertebrate prey availability from March 2006 to February 2008. Ground foraging habitat (leaf litter) of Tomtits was sampled within two hours of focal birds foraging and invertebrate availability ascertained. Highly significant dissimilarities between habitats were evident, with the greatest differences occurring between pine and native forests. Annual and seasonal differences were also found within pine and native forest habitat. Prey availability varied between seasons within pine (spring versus summer), native (winter versus spring), and boundary (winter versus summer) habitats. No differences between prey availability were found for male and female tomtits. However, male foraging samples showed annual separation in the pine and native habitats, and between some seasons within the pine (winter versus summer) and native (winter versus spring) forests. No significant seasonal differences were found for female comparisons. Through comparison of habitat and temporal prey availability for this native bird I have begun to clarify the role that pine plantation invertebrates play in the diet of insectivorous native birds.

4.1 Introduction

One challenge facing researchers is to comprehend and forecast interactions within food chains in heterogeneous environments (Hunter & Price, 1992). Prey availability responds to a myriad of environmental influences ranging from temperature-mediated activity levels (Low *et al.*, 2008; Tulp & Schekkerman, 2008), to habitat and nutrient availability (Evans *et al.*, 2003), and anthropogenic influence, e.g. the response of invertebrate prey to introduced predators (Gibbs, 2009). The availability of prey can

have far reaching impacts on populations of forest birds, affecting species in terms of number, breeding success, and behaviour, especially when prey numbers reach high levels (Hockey, 2000; Komdeur, 2002; Strong *et al.*, 2004). Implications of prey type, abundance, and availability extend from landscape and species level effects (Patten & Burger, 1998; Taft & Haig, 2006), to impacts on proportional tree species and foraging substrate use and foraging strategy (Holmes & Schultz, 1988; Strode, 2009). The true availability of a specific prey item relies on several factors; the prey must be abundant enough to be located efficiently by the predator, the season must be correct to allow emergence, development, and metamorphosis, and the prey must occupy a microhabitat accessible to the predator.

Variation between sites in terms of invertebrate abundance have been noted by past researchers (Poulin & Lefebvre, 1997; Doxon & Carroll, 2010), and are anticipated given habitat and geographic variation. Doxon and Carroll (2010) found that the amount of bare ground made a difference to prey availability for game bird chicks (ring-necked pheasants (*Phasianus colchicus*) and northern bobwhite (*Colinus virginianus*)), where higher mobility and foraging rates were achieved in habitats with increased amounts of bare ground. So in that instance, the structural differences in the habitat and not the invertebrate abundance itself were responsible for the differing availability. Vegetation structure may also affect bird foraging by increasing the production of some resources. For example, production of fruit and nectar can be higher in edge habitats (Zanette *et al.*, 2000). Conversely, it may decrease the availability of others, such as the visibility of invertebrates under ground cover (Buckingham *et al.*, 2006). For example, dead wood can reach high volumes within unmanaged native forests in New Zealand (Harmon & Hua, 1991; Stewart & Burrows, 1994; Allen *et al.*, 1997) and although trimmed branches are left for the short term in pine plantations the majority of all living and dead vegetation is ultimately removed. This resource constitutes an important nutrient source especially for invertebrates (Swift *et al.*, 1979) and may influence food webs, especially those below-ground (Hutcheson & Jones, 1999; Durst *et al.*, 2008). The invertebrates present on native plants may be different to those on exotics, and if bird species require certain invertebrate prey species, then their occurrence may be limited to a certain extent by the amount of native vegetation, e.g.

the bird species grey warbler (*Gerygone igata*) may possibly be influenced this way by invertebrates (Day, 1995).

Invertebrate prey abundance can vary across years (Holmes & Schultz, 1988; Tulp & Schekkerman, 2008; Champlin *et al.*, 2009), which may be due to environmental (Durst *et al.*, 2008; Tulp & Schekkerman, 2008), or biotic factors (Fitzgerald *et al.*, 1996). Colder weather can lead to increased invertebrate mortality or decreased emergence, and may also decrease general invertebrate activity, which has the same effect of decreasing availability (Tulp & Schekkerman, 2008). Durst *et al*. (2008) found differences between both adult and nestling diet between years due to fluctuations in invertebrate availability. In contrast, other authors have noted fledging success or adult survival differing between years, and suggested these impacts were because of variations in available prey biomass (Eeva *et al.*, 2000; Kèrbiriou & Julliard, 2007).

Unsurprisingly, invertebrate abundance, type, and availability vary between seasons (Holmes & Schultz, 1988; Eeva *et al.*, 2000; Hockey, 2000). Abundance may change due to presence of resources that invertebrates themselves utilise as food, e.g. caterpillars that require palatable freshly grown leaves (Murakami, 1998; Eeva *et al.*, 2000). The availability of certain types of invertebrate is obviously seasonal, with larval stages often limited by temperature and food resource availability (Eeva *et al.*, 2000). Murakami (1998) found that narcissus flycatchers (*Ficedula narcissina*) fed on caterpillars in the canopy after bud burst until caterpillar abundance dropped due to migration to the forest floor. The birds then switched foraging substrate to follow the prey, switching back to their preferred substrate and alternate invertebrate prey in the canopy once caterpillar abundance on the forest floor had also decreased. Similar results in terms of foraging substrate shift associated with varying prey availability were observed by Eeva *et al*. (2000).

Invertebrate availability can even vary intraspecifically with sexes often partitioning food resources (Jackson, 1970; Morales *et al.*, 2008; Franzreb, 2010). Differences in invertebrate availability between sexes emerge due to competition for the same resources (Austin, 1976), and are often mediated by each sex using different foraging

substrates (Austin, 1976; Peters Wm & Grubb Jr, 1983; Franzreb, 2010) (see also Chapter 3). Foraging strategies may also differ between sexes sufficiently to partition food resources (Austin, 1976; Franzreb, 2010). Intersexual foraging differences may be constant throughout the year or themselves change seasonally, with one sex shifting foraging concentration during times when food resources are limited, (e.g. winter), or demand is higher, (e.g. breeding season) (Jackson, 1970). Both sexes may specialise to achieve the separation in foraging niche, or one may specialise within the broader foraging niche shown by the other either in terms of substrate (Jackson, 1970; Austin, 1976; Franzreb, 2010), or foraging strategy (Jackson, 1970; Franzreb, 2010). This partitioning of resources can be maintained through aggressive behaviours that result in displacement of the subordinate sex from the more favourable resource (Austin, 1976; Peters Wm & Grubb Jr, 1983; Franzreb, 2010).

Tomtits commonly utilise the ground for foraging (see Chapter 3). This study tracked tomtit forest floor prey availability across two years and in three different habitats, to ascertain prey availability differences for sexes within each habitat between years and seasons. I predicted that prey availability would differ between habitats, years, and seasons for birds of both sexes.

4.2 Methods

Samples were collected between March 2006 and February 2008 in the Hunua Ranges, New Zealand (37º 08' S, 175º 13' E) in three habitat types (pine plantation, native forest, and the boundary, ±50 m, where these two habitats meet. See Section 2.2 for study site and species details, and Appendix I Table I for New Zealand map grid co-ordinates of leaf litter sample collection locations.

Tomtit observations took place throughout the day as long as visibility allowed. The year, month, habitat, sex, and territorial location of each individual was recorded. Each year began at the end of the tomtit's breeding season, so the years compared in this research were March 2006 - February 2007 and March 2007 - February 2008. The

seasons were regarded as autumn (March - May), winter (June - August), spring (September - November), and summer (December - February). When a focal individual foraged on the ground the exact point was marked and a 50 cm x 50 cm leaf litter sample centred on the foraging point was collected. All the leaf litter, including rotted leaves, within the area were collected with the depth varying from 1 - 50 mm (due to litter compaction) to reflect the potential depth of tomtit foraging at the site. The depth of collection was ascertained by observing the tomtit forage at that site (and previous sites) prior to leaf litter collection. The substrate to be assessed for prey availability was decided during a pilot study conducted from February to March 2006 with the majority of foraging events observed occurring on the ground.

The aim was to collect representative samples for five different birds per habitat every two months; however this number was not always achieved and in total 133 samples containing invertebrates were collected (Table 4.1). Invertebrates were extracted from the litter using Burlese funnels run until the vegetation was dry, then all insects >1.5 mm were identified to order, and other invertebrates identified to order (Acarina, Araneida, Isopoda, Opiliones, Pseudoscorpiones), class (Chilopoda, Diplopoda, Gastropoda), or phylum (Annelida, Nematoda, Onychophora, Platyhelminthes). Adult and larval stages of Coleoptera, Diptera, and Lepidoptera were also separated.

Table 4.1. The number of samples collected by variable: year, habitat, and sex of foraging bird.

	Pine		**Native**		**Boundary**		**Total**
	Male	**Female**	**Male**	**Female**	**Male**	**Female**	
2006	24	5	17	5	11	5	67
2007	22	6	14	6	15	3	66
Total	**46**	**11**	**31**	**11**	**26**	**8**	**133**

The 1.5 mm cut off was decided on after analysis of tomtit scat, collected during observations, by Stephen Thorpe (Manaaki Whenua - Landcare Research) during which he ascertained that the smallest identifiable prey taken was a minimum length of 1.5 mm. Throughout tomtit observations identifiable prey captured by the birds were noted, however as these prey items were usually larger >5 mm and easy to identify, therefore these observations were not considered a reliable way of including or excluding

invertebrates from the above list of potential prey items available in the leaf litter where tomtits foraged.

Invertebrate data were considered as counts or presence/absence and analysed using Bray-Curtis similarity (no transformation) and then MDS (non-metric Multi Dimensional Scaling) analysis (with ten restarts) (PRIMER-E, 2002). One-way ANOSIM (analysis of similarity) was then run to assess assemblage differences (maximum 999 permutations) (PRIMER-E, 2002). These tests were used to compare samples from the different habitats (pine, native, and boundary), years (2006 and 2007), seasons (autumn, winter, spring, and summer), and sexes (male and female). Seasonal comparisons consider invertebrates collected during both years of the study due to insufficient sample sizes to test for annual differences within each season or to run seasonal comparisons for each year separately.

4.3 Results

A total of 16,077 invertebrates were identified from the leaf litter samples collected. MDS (stress = 0.17) conducted on count data found that prey availability was consistent between habitats, years, and seasons (Figure 4.1). However, ANOSIM results show a highly significant result for dissimilarity between habitats, revealing significant differences between all habitat pairs, with the greatest difference occurring between pine and native forests (Table 4.2). The most striking variation between the proportion of individuals from each invertebrate group were a smaller proportion of Amphipoda (6%), and greater numbers of adult Coleoptera (16%) and Diptera larvae (37%) in the native habitat (Figure 4.2). The pine plantation samples had a larger proportion of Collembola (20%) and smaller numbers of Diptera larvae (8%) than either of the other two habitats. When these data were analysed as presence/absence of each invertebrate order, the MDS (stress = 0.15) result was the same, showing no separation. ANOSIM once again reveals significant dissimilarity even at this coarse level between habitats, although the difference was only significant between pine and native, and pine and boundary habitats (Table 4.2). The differences between pine and native forests at the level of order were due to the lack of Archaeognatha, Dermaptera,

and Neuroptera in the pine plantation. A similar pattern of variation was seen between pine and boundary habitats with the boundary habitat supporting Archaeognatha, Blattodea, Neuroptera, and Onychophora, but lacking Nematoda which were found in the pine plantation. Comparison of native and boundary habitats does not show a significant difference (Table 4.2).

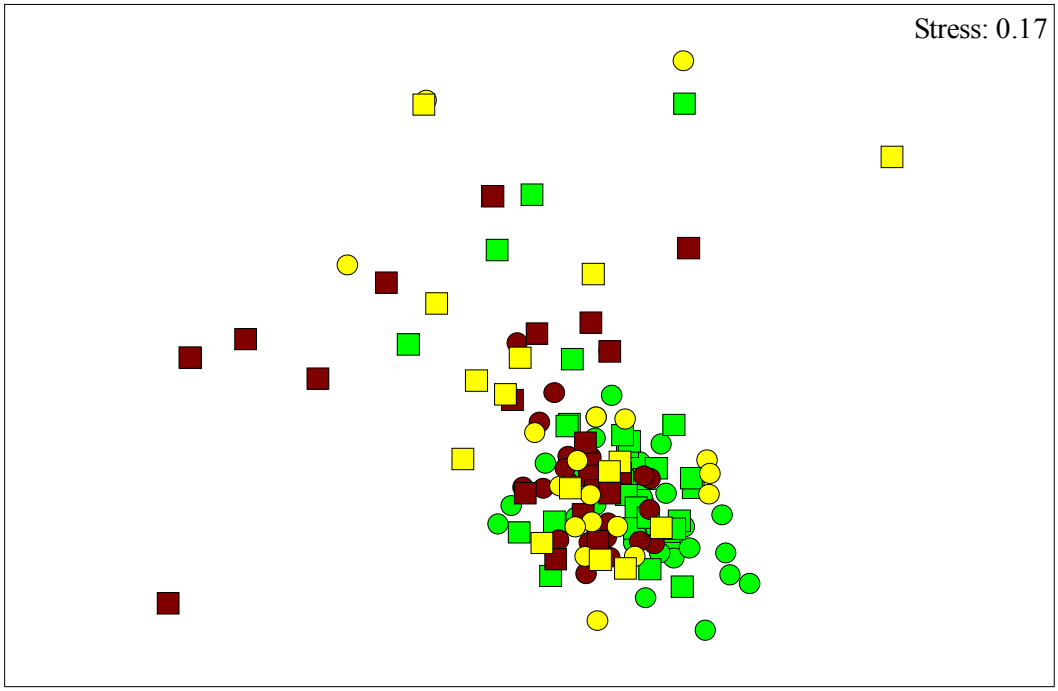

Figure 4.1. MDS plot showing invertebrate samples from different habitats and years. ● = pine 2006, ■ = pine 2007, ● = native 2006, ■ = native 2007, ● = boundary 2006, ■ = boundary 2007.

Table 4.2. Summary of invertebrate sample habitat comparisons conducted using ANOSIM. Count data values are shaded.

Habitat		**Pine**		**Native**		**Boundary**		**All**	
		P	R	*P*	R	*P*	R	*P*	R
Pine		-	-	0.001	0.143	0.003	0.131	-	-
Native		0.003	0.098	-	-	0.023	0.058	-	-
Boundary		0.015	0.107	NS	0.037	-	-	-	-
All	**Count**	-	-	-	-	-	-	0.001	0.118
All	**Pres/Abs**	-	-	-	-	-	-	0.003	0.088

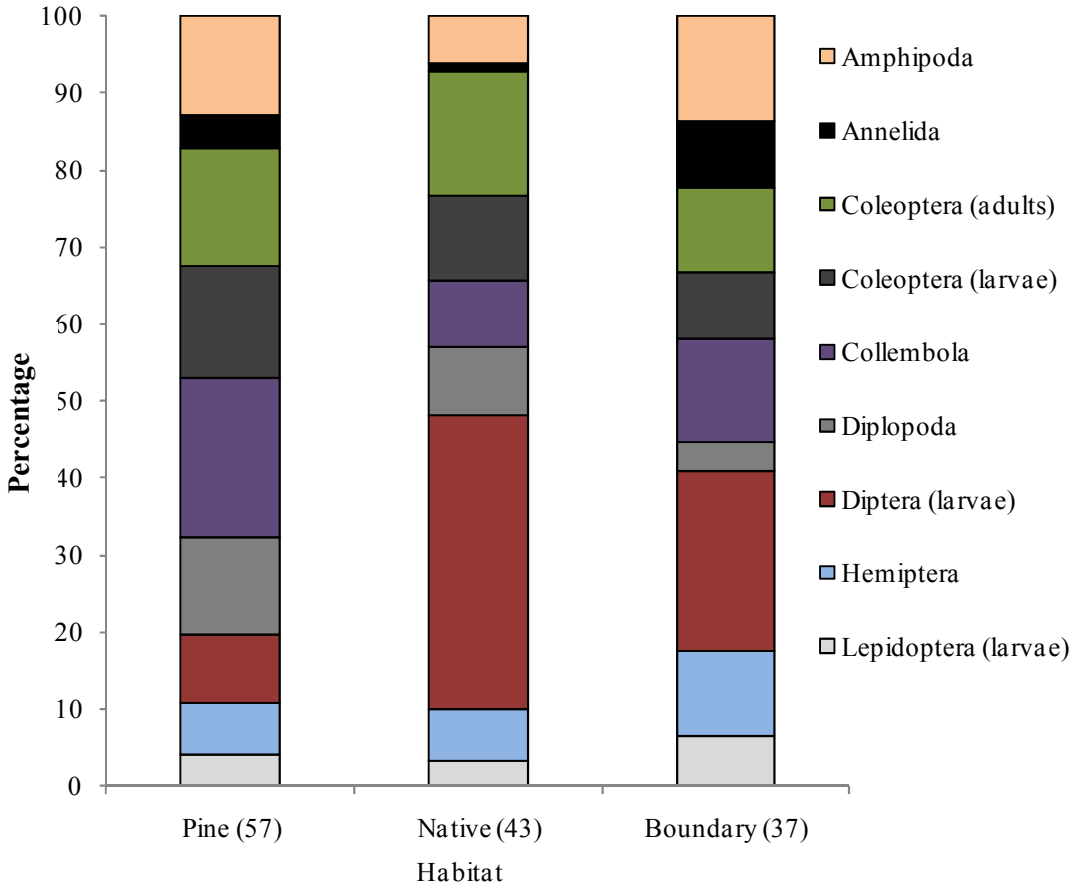

Figure 4.2. Proportion of invertebrate orders comprising >5% of invertebrates for at least one habitat's samples. Bracketed number denotes number of samples from each habitat.

Data were analysed for differences between years within each habitat because habitats were found to be significantly different. Samples taken from the pine habitat did not separate visually when analysed using MDS for count (stress = 0.17) or presence/absence data (stress = 0.14) between years. However, ANOSIM does show significant differences between 2006 and 2007 for count, and presence/absence data (Table 4.3, pg 85). The differences in count data were due to larger proportions of Amphipoda (14%), adult (16%) and larval (15%) Coleoptera, and Collembola (23%), and smaller proportions of adult (1%) and larval Diptera (7%), and Hemiptera (4%) being sampled in 2006 (Figure 4.3). Nematoda, Orthoptera, and Platyhelminthes were present in 2006 samples but not in 2007. Similar to results from pine plantation samples, native forest samples showed no clear separation between years when considered using MDS for either count (stress = 0.13) or presence/absence data (stress

= 0.14). Once again ANOSIM reveals highly significant differences for this habitat between 2006 and 2007 for both count and presence/absence data (Table 4.3). The count data differences were due to more adult Coleoptera (18%) and Diptera (5%) being present in 2007 versus 2006 (Figure 4.3). Significant separation of the two years based on the presence/absence of orders was due to Archaeognatha, adult Lepidoptera, and Neuroptera being present, but Dermaptera and Nematoda were absent in 2006 samples. Boundary samples were not differentiated by year when analysed with MDS as count (stress = 0.13) or presence/absence data (stress = 0.1), and ANOSIM also shows a lack of difference between years for this habitat (Table 4.3).

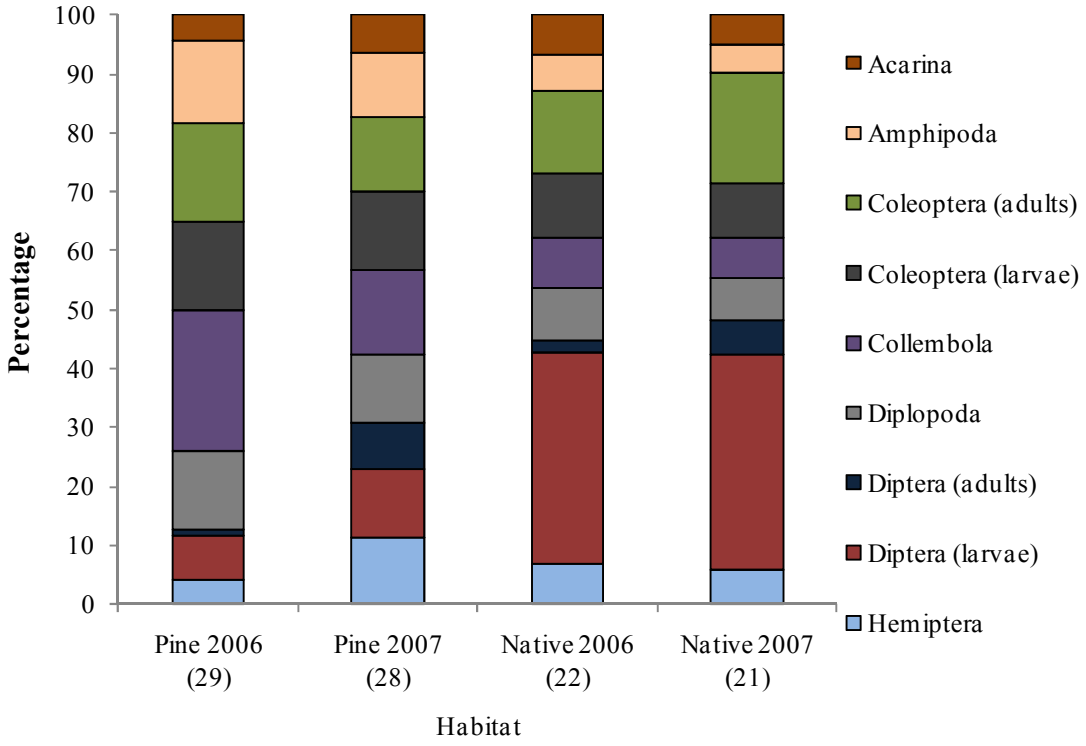

Figure 4.3. Proportion of invertebrate orders comprising >5% of invertebrates for at least one habitat and year's samples. Bracketed number denotes number of samples from each habitat and year.

Samples were also compared between seasons within each habitat. Pine samples did not separate visually when analysed using MDS for count data (stress = 0.17) or presence/absence data (stress = 0.14). ANOSIM did not find global significance for either count or presence/absence data from pine plantation, but pairwise comparisons for count data showed significant differences between samples collected in spring

versus summer (Table 4.4). The differences between spring and summer were due to spring samples having smaller proportions of Amphipoda (12% versus 18%), adult Coleoptera (12% versus 9%), larval Diptera (6% versus 11%), and Hemiptera (1% versus 12%), and larger proportions of Collembola (25% versus 9%), adult Diplopoda (13% versus 7%), and Diptera (8% versus 2%) than summer samples. These seasonal differences disappear when the data were considered as presence/absence, indicating that the seasonal differences were due to proportional invertebrate abundance and not order changes. No seasonal differences were found for native samples using MDS for either count (stress = 0.13) or presence/absence data (stress = 0.14), and ANOSIM found significant differences only for the presence/absence data between winter and spring (Table 4.5). There were six groups of invertebrates (Annelida, Gastropoda, adult Lepidoptera, Platyhelminthes, Symphyla, and Thysanoptera) present during spring that were absent from winter samples, the exception was Nematoda that was present during winter but not spring. Boundary samples were not differentiated by season when analysed with MDS as count (stress = 0.13) or presence/absence data (stress = 0.1). ANOSIM also showed a lack of difference between most seasons within the boundary samples; with the exception of the winter versus summer comparison using presence/absence data (Table 4.6). These seasonal differences in the boundary habitat were due to the absence of Archaeognatha, Blattodea, Neuroptera, Orthoptera, and Symphyla, and the presence of Platyhelminthes and Psocoptera in winter versus summer samples.

Table 4.4. Summary of invertebrate sample seasonal comparisons for pine habitat conducted using ANOSIM. Conventions as for Table 4.2.

Season	**Autumn**		**Winter**		**Spring**		**Summer**		**All**	
	P	R	*P*	R	*P*	R	*P*	R	*P*	R
Autumn	**-**	-	NS	-0.006	NS	0.068	NS	-0.022	-	**-**
Winter	NS	-0.025	-	-	NS	-0.051	NS	0.095	-	**-**
Spring	NS	0.014	NS	0.090	-	-	0.026	0.101	-	**-**
Summer	NS	-0.026	NS	0.027	NS	0.018	-	-	-	**-**
All Count	**-**	-	-	-	-	-	-	-	NS	0.031
All Pres/Abs	**-**	-	-	-	-	-	-	-	NS	-0.011

Table 4.5. Summary of invertebrate sample seasonal comparisons for native habitat conducted using ANOSIM. Conventions as for Table 4.2.

Season	Autumn		Winter		Spring		Summer		All	
	P	R	*P*	R	*P*	R	*P*	R	*P*	R
Autumn	-	-	NS	-0.042	NS	-0.085	NS	0.025	-	-
Winter	NS	-0.029	-	-	NS	0.017	NS	0.000	-	-
Spring	NS	-0.103	0.022	0.160	-	-	NS	-0.012	-	-
Summer	NS	-0.002	NS	-0.039	NS	-0.002	-	-	-	-
All Count	-	-	-	-	-	-	-	-	NS	-0.024
All Pres/Abs	-	-	-	-	-	-	-	-	NS	-0.024

Table 4.6. Summary of invertebrate sample seasonal comparisons for boundary habitat conducted using ANOSIM. Conventions as for Table 4.2.

Season	Autumn		Winter		Spring		Summer		All	
	P	R	*P*	R	*P*	R	*P*	R	*P*	R
Autumn	-	-	NS	-0.165	NS	-0.166	NS	-0.194	-	-
Winter	NS	-0.365	-	-	NS	-0.005	NS	0.196	-	-
Spring	NS	-0.284	NS	0.067	-	-	NS	0.025	-	-
Summer	NS	-0.284	0.034	0.257	NS	0.041	-	-	-	-
All Count	-	-	-	-	-	-	-	-	NS	0.034
All Pres/Abs	-	-	-	-	-	-	-	-	NS	0.049

Because the leaf litter samples were taken from observed foraging sites it was possible to allocate a sex category to the sample and compare the prey availability for male and female tomtits. Because prey availability was different for tomtits between habitats, comparisons of prey availability between and within sexes was restricted to samples from each habitat. No differences between male and female prey availability were found in any habitat regardless of data treatment or analysis (MDS - count data: pine stress = 0.17, native stress = 0.13, boundary stress = 0.13; presence/absence data: pine stress = 0.14, native stress = 0.13, boundary stress = 0.1) (Appendix II, Table I - II).

When year comparisons of prey available were made separately for each sex, no evidence of annual or seasonal separation for males or females was found for any habitat or data treatment using MDS (male count data: pine stress = 0.16, native stress = 0.11, boundary stress = 0.11; male presence/absence data: pine stress = 0.13, native stress = 0.11, boundary stress = 0.11; female count data: pine stress = 0.05, native stress = 0.05, boundary stress = 0.01; female presence/absence data: pine stress = 0.14, native stress = 0.01, boundary stress = 0.01). However, separation of season and year was found for males using ANOSIM count data for native habitat samples, and for the pine

and native habitats using presence/absence data (Table 4.7 & 4.8, & see Appendix II, Table II for boundary habitat results). The count data analysis for males was affected by the larger numbers of larval Coleoptera (9% versus 6%) and Diptera (37% versus 25%), and smaller numbers of Araneida (5% versus 8%) and adult Coleoptera (10% versus 23%) found in 2006 versus 2007 (Table 4.2 & Appendix II, Table III). The presence/absence data for the native habitat was significantly different between 2006 and 2007 because Archaeognatha, adult Lepidoptera, Neuroptera, and Platyhelminthes were present in 2006, whereas Dermaptera and Nematoda were absent. The annual differences for male prey availability in the pine habitat were less pronounced; Nematoda and Platyhelminthes were present in 2006 while Psocoptera were absent in 2006 versus 2007. The same set of ANOSIM comparisons of female prey availability samples between years within each habitat does not show any significant degree of dissimilarity (Appendix II, Table II & IV).

Seasonal data for each sex was also analysed for each habitat. Count data for the males showed a significant level of dissimilarity between pine samples collected in winter versus summer (Table 4.8). These differences were characterised by increased numbers of adult Coleoptera (26% versus 13%), larval Diptera (8% versus 6%), Hemiptera (7% versus 1%), and fewer Collembola (15% versus 27%) and adult Diptera (1% versus 9%) in winter than summer (Appendix II, Table V). In contrast, presence/absence data for males in the native habitat picked up substantial sample differences between winter versus spring due to the lack of Annelida, Gastropoda, adult Lepidoptera, and Symphyla, and the presence of Nematoda in the winter samples (Table 4.9). No significant differences were found between male boundary samples collected during different seasons, or any of the seasonal comparisons of female foraging samples (Appendix II, Table II, V, & VI).

Table 4.3. Summary of invertebrate sample annual comparisons conducted using ANOSIM. Conventions as for Table 4.2.

Year		2006						2007					
	Habitat	Pine		Native		Boundary		Pine		Native		Boundary	
		P	R	*P*	R	*P*	R	*P*	R	*P*	R	*P*	R
2006	Pine	-	-	-	-	-	-	0.044	0.038	-	-	-	-
	Native	-	-	-	-	-	-	-	-	0.001	0.121	-	-
	Boundary	-	-	-	-	-	-	-	-	-	-	NS	-0.01
2007	Pine	0.032	0.04	-	-	-	-	-	-	-	-	-	-
	Native	-	-	0.003	0.102	-	-	-	-	-	-	-	-
	Boundary	-	-	-	-	NS	0.011	-	-	-	-	-	-

Table 4.7. Summary of invertebrate sample annual comparisons for male tomtits conducted using ANOSIM. Conventions as for Table 4.2.

Year		2006						2007					
	Habitat	Pine		Native		Boundary		Pine		Native		Boundary	
		P	R	*P*	R	*P*	R	*P*	R	*P*	R	*P*	R
2006	Pine	-	-	-	-	-	-	NS	0.029	-	-	-	-
	Native	-	-	-	-	-	-	-	-	0.004	0.152	-	-
	Boundary	-	-	-	-	-	-	-	-	-	-	NS	-0.002
2007	Pine	0.013	0.061	-	-	-	-	-	-	-	-	-	-
	Native	-	-	0.004	0.135	-	-	-	-	-	-	-	-
	Boundary	-	-	-	-	NS	-0.009	-	-	-	-	-	-

Table 4.8. Summary of invertebrate sample seasonal comparisons for male tomtits in the pine habitat conducted using ANOSIM. Conventions as for Table 4.2.

Season		Autumn		Winter		Spring		Summer		All	
		P	R	*P*	R	*P*	R	*P*	R	*P*	R
Autumn		-	-	NS	-0.075	NS	0.002	NS	- 0.055	-	-
Winter		NS	-0.068	-	-	NS	-0.084	0.043	0.117	-	-
Spring		NS	-0.025	NS	-0.120	-	-	NS	0.080	-	-
Summer		NS	-0.063	NS	0.002	NS	-0.054	-	-	-	-
All	**Count**	-	-	-	-	-	-	-	-	NS	-0.008
All	**Pres/Abs**	-	-	-	-	-	-	-	-	NS	-0.056

Table 4.9. Summary of invertebrate sample seasonal comparisons for male tomtits in the native habitat conducted for using ANOSIM. Conventions as for Table 4.2.

Season		Autumn		Winter		Spring		Summer		All	
		P	R	*P*	R	*P*	R	*P*	R	*P*	R
Autumn		-	-	NS	-0.040	NS	-0.113	NS	0.039	-	-
Winter		NS	0.012	-	-	NS	0.088	NS	-0.037	-	-
Spring		NS	-0.130	0.019	0.309	-	-	NS	-0.009	-	-
Summer		NS	0.035	NS	0.052	NS	0.040	-	-	-	-
All	**Count**	-	-	-	-	-	-	-	-	NS	-0.036
All	**Pres/Abs**	-	-	-	-	-	-	-	-	NS	-0.007

4.4 Discussion

Habitat differences in prey availability in this study were evident both in terms of invertebrate abundance and presence/absence of invertebrate orders. Proportions of the different invertebrate orders found in samples differed significantly between every habitat dyad pairing, and order differences were significant between pine and native, and pine and boundary habitats. It is generally accepted that the greater the habitat or vegetative heterogeneity the greater the biodiversity and biomass supported (Brockie, 1992; Stewart & Burrows, 1994). Therefore it would be anticipated that New Zealand native forest would contain more species than pine plantations, as has been found for other natural and agricultural habitat comparisons (Power *et al.*, 2004). Higher abundances of those species present might also be expected, as a plantation forest is essentially a monoculture although native and weedy ground cover and sub-canopy may develop.

The greatest habitat differences in prey availability were found between pine and native forests. Past researchers have noted that plantation forests are far less biologically diverse than natural forests (Saunders, 1983), with the biomass and diversity of invertebrates in leaf litter extracted from pine plantations less than that of native forest (Duncan *et al.*, 1999). A difference between pine and native habitats at the invertebrate order level was due to the lack of Archaeognatha, Dermaptera, and Neuroptera in the pine plantation. A similar pattern of variation was seen between pine and boundary habitats, with the boundary habitat supporting Archaeognatha, Blattodea, Neuroptera, and Onychophora, but lacking Nematoda which were found in the pine plantation. Nevertheless, past research has indicated that pine plantations contain good food resources for insectivorous birds (Clout & Gaze, 1984). When invertebrate availability was considered in terms of the proportion of individuals from each invertebrate order there were a smaller proportion of Amphipoda, and greater proportion of adult Coleoptera in the native versus pine forest. However, pine samples do not show an across the board lowering of invertebrates, and had a larger percentage of Collembola, but a smaller percentage of Diptera larvae than either of the other two habitats.

Invertebrate fluctuations between years are commonly reported (Holmes & Schultz, 1988; Taft & Haig, 2006; Kèrbiriou & Julliard, 2007). However, not all invertebrates, even within the same order, will contribute equally to prey availability due to interactions between predator and prey behaviour (Holmes & Schultz, 1988; Murakami, 1998). This concept can also be expanded to differences in food value within the same species due to differing individual size (Holmes & Schultz, 1988), and individual prey diet will also affect their nutritional value to predators. Significant differences were found between 2006 and 2007 for abundance and presence/absence data in pine and native forest samples. In both habitats adult Diptera constituted proportionally less of the invertebrates present in 2006 than 2007, although other orders and life stages showed diverse reactions. The variable responses are likely to be due to annual differences in local climate acting on prey availability differently in each habitat. The impacts of other predators can also have an effect on prey (Estany-Tigerström *et al.*, 2010), and these influences may be more accentuated during some years.

Differences in prey availability due to seasonal increases have been noted by past researchers for a variety of habitat types (McWilliam & Death, 1998), and may influence fledging success (Poulin & Lefebvre, 1997). In deciduous forests large seasonal changes in invertebrate availability are found due to bud break (Murakami, 1998). Although none of the forests investigated by this research are deciduous, seasonal differences were found and are most likely due to climatic and vegetative (e.g. leaf, flower, fruit, and seed production), influences. Indeed, season has been found to have a larger influence on arboreal invertebrate community assemblages in New Zealand native forest than either site or tree species (McWilliam & Death, 1998). However, the effect of season on invertebrates in my leaf litter samples does not appear to be as great as that of habitat; each habitat showed specific seasonal differences with no general trend observed. Within the pine habitat, significant seasonal differences were found between the proportion but not the presence of orders found in spring and summer. One marked difference was the smaller percentages of larval Diptera and larger percentages of adult Diptera in spring versus summer. Although the sample collection method and habitat were different, the same trend of high Dipteran abundance during spring and lower abundance in summer was observed by McWilliam and Death (1998). However, they note that the proportionally small number of Dipterans sampled in summer was largely due to the increase of other invertebrate groups.

As leaf litter samples were taken from specific foraging sites of observed birds, it was possible to allocate a sex category to the sample and compare the prey availability for male and female tomtits. Because I found that prey availability was different for tomtits between habitats, consideration of prey availability between and within sexes was restricted to samples from each habitat. No differences between male and female prey availability were found in any habitat regardless of data treatment or analyses. This was not a surprising result as often the sexes differentiate foraging niche by using different tree species, heights, substrates, and strategies (Jackson, 1970; Austin, 1976; Franzreb, 2010), and all my samples were from the same substrate. There were foraging substrate and height differences between tomtit sexes (see Chapter 3), however these results suggest this foraging niche partitioning does not extend to prey types within the leaf litter foraging substrate.

Annual and seasonal differences in prey availability were considered for each sex separately with no inter-annual or seasonal variation found for females. This may have been due to reduced sample sizes for females; females are less conspicuous than males both in terms of plumage and song and were therefore observed less often and had fewer foraging points sampled. Males showed significant differences in temporal prey availability in both native and pine forest samples. Their results reflect the general annual differences found in the pine with Nematoda and Platyhelminthes found in 2006 but not in 2007. Similarly, native samples for males showed a smaller proportion of adult Coleoptera, and a lack of Dermaptera and Nematoda but a presence of Archaeognatha, adult Lepidoptera, and Neuroptera in 2006. Seasonal count data for the males again reflected the trends seen for the general data set for the pine and native habitats. Significant dissimilarity between male foraging samples collected in the pine was found for winter versus summer, and presence/absence data for native habitat samples showed differences between winter versus spring.

It may have been useful to identify invertebrates to a lower taxonomic level. However, tomtits take a wide variety of invertebrates (Amphipoda, Araneida, Coleoptera, Diptera, Hemiptera, Hymenoptera, larval and adult Lepidoptera, and Orthoptera) (Moeed & Fitzgerald, 1982), so many of the orders recorded in the samples constitute known prey items. It is also likely that prey availability is more reliant on prey microhabitat use, clustering, diurnal activity levels, and nutritional value which do not necessarily relate to taxonomy (Poulin & Lefebvre, 1997). I targeted tomtit prey items by choosing a key foraging substrate and sampling from actual foraging points. Still, it should be noted that the differences causing variation between habitats, years, and seasons may not impact on all tomtit prey items. However, it seems likely that tomtit prey would be reacting to the same variables as the invertebrates collected.

Summary

As predicted, this study showed highly significant dissimilarities in prey availability between habitats even at the level of order, with the biggest differences occurring between pine and native forests. Annual differences within pine and native forests habitats between years were also seen, but not observed for the boundary habitat. Although some seasonal variation was found, this occurred in ways particular to each

habitat and did not show a general trend across habitats. No differences between male and female prey availability were found. However, male foraging samples showed annual separation in both pine and native habitats, and between certain seasons within the pine and native forests. These results begin to tease apart the complexities of habitat and temporal differences in the prey availability between native and silviculture ecosystems for insectivorous native birds.

General discussion

Understanding the trophic structure of a habitat is vital to understanding the patterns and interactions of species and individuals within that habitat (Pimm, 2002; Winemiller, 2007). Trophic structure fluctuates annually and seasonally as a reflection of the nutrient and energy fluxes within an ecosystem (Winemiller, 2007). However, those fluxes are driven by interactions between individual organisms, so it is therefore pertinent to address trophic structure at the broad level of nutrient flux within a habitat, in addition to considering individual foraging decisions. To better understand habitat and temporal differences it can be insightful to focus on model species. This study investigated tomtit foraging and ground prey availability in this capacity as they occupy all habitats of interest and are territorial throughout the year (Skinner, 1978; Heather & Robertson, 2005; Kelly, 2005), therefore reflecting the influence of one habitat regardless of when they are observed. Tomtits are relatively easy to locate and follow within their habitat, hence highly suitable for behavioural observations. Also, foraging occurs on substrates (such as the ground and vegetation (Skinner, 1978; Moeed & Fitzgerald, 1982; Kelly, 2005)) that can easily be sampled to ascertain prey availability. In addition, rodents were used to compare the results of stable isotope versus stomach content analyses and add detail regarding omnivorous species with highly plastic dietary requirements in the selected habitats.

Foraging is fundamental to the continued survival and successful reproduction at an individual and species level. Individual foraging strategies are principally determined by the efficiency with which food may be exploited. This consequently depends for the most part on environmental conditions such as habitat type (Badan, 1986; Brotons *et al.*, 1998; Hartung & Brawn, 2005), habitat structure (Antos *et al.*, 2008; Martinez *et al.*, 2010; Petry & Krüger, 2010), and time of year (Glendinning & Brower, 1990; Adamík *et al.*, 2003; Cassaing *et al.*, 2007). When reintroduced to an island (Ulva Island, New Zealand) within their former range, Stewart Island robins (*Petroica australis rakiura*) preferentially settled in habitat which afforded more favourable foraging opportunities due to its structure (Michel *et al.*, 2010). Seasonal variation in tree preference was observed by Böhm and Kalko (2009) for foraging blue tit

(*Cyanistes caeruleus*), great tit (*Parus major*), chaffinch (*Fringilla coelebs*), blackcap (*Sylvia atricapilla*), and European starling (*Sturnus vulgaris*) inhabiting an alluvial forest in Burgaue, Germany. These species were found to switch tree preference due to seasonal leaf growth patterns and the associated changes in prey availability.

Throughout the world, all habitat types have been modified to some degree by human influence. A key impact of human modified landscapes on bird populations has been changes (often reductions) in the availability of food within the modified habitat, e.g. farmland or pine plantations (Carlson, 1986; Duncan *et al.*, 1999; Power *et al.*, 2004). Indeed, declining food resources have been implicated in the population declines of many species (Robinson & Sutherland, 2002). However, it can be difficult to measure trophic structure between and within habitats. Habitats can be separated in space and therefore show differences due to geographic location as opposed to habitat. They may also be limited in the number of common species whose behaviour can be monitored and compared between habitats. Within habitats trophic structure can be difficult to measure due to the inherent challenges in ascertaining diet using standard methods, although relatively recent advances utilising stable isotopes have been able to overcome a number of past problems. If food items are easily digested there may be little evidence of them in the stomach or faeces, however isotope analysis can show their dietary importance and origin if they are isotopically distinct (Harding & Stevens, 2001; Stapp & Polis, 2003; Caut *et al.*, 2008a; Hawke & Holdaway, 2009). Stable isotope analysis also eliminates the problem of looking at a snapshot of an animal's last meal, which may not be generally representative of diet, or parts of the diet that are assimilated (Romanek *et al.*, 2000; Stapp, 2002; Bennett & Hobson, 2009). Even direct foraging observations may be biased due to ease of observation of certain dietary items and foraging behaviours (Caut *et al.*, 2008a; b). In terms of understanding trophic structure carbon and nitrogen stable isotopes are particularly important. Carbon isotopes primarily indicate carbon source (Harding & Stevens, 2001; Caut *et al.*, 2008a), and nitrogen isotopes indicate the TL of species (Gannes *et al.*, 1998; Harding & Stevens, 2001; Caut *et al.*, 2008b), both of which are important when considering trophic structure within and between habitats.

In addition to the influence of habitat type and structure on foraging strategies, sex related foraging differences within species are commonly observed (Jackson, 1970; Austin, 1976; Peters Wm & Grubb Jr, 1983; VanderWerf, 1994; Olsson *et al.*, 2000; Forero *et al.*, 2005; Temeles *et al.*, 2005; Burns & Steer, 2006; Morrissey *et al.*, 2010). These differences often stem from similar resource requirements in concert with differences in competitive ability, with the less aggressive sex, commonly the female, often displaced from favoured prey or foraging habitats (Recher & Holmes, 2000; Steer & Burns, 2008). However, intersexual foraging variation may also be seasonal and due to a shift in foraging by the female during the egg production period (Morrissey *et al.*, 2010). This foraging separation of the sexes reduces niche overlap and therefore competition for paired birds (Recher & Holmes, 2000), and it has been suggested that niche overlap is most reduced during seasons when prey are substantially decreased (Jackson, 1970; Ligon, 1973).

In order to overcome the challenges outlined above, this research used a combination of techniques to compare the trophic structure of three distinct habitats (pine plantation, native forest, and the contiguous boundary of these habitats) in the Hunua Ranges, New Zealand. The habitats compared were in the same location and taxa studied (vegetation, caterpillars, predacious adult Coleoptera, mice, rats, and tomtits) were chosen because they occurred in all habitats. Samples were analysed for ^{13}C and ^{15}N isotopes to allow comparison of $\delta\ ^{13}C$ and $\delta\ ^{15}N$ values. Additionally, seasonal and sexual differences in diet were investigated when possible. Stomach content analyses were carried out for rodents collected from each habitat, with comparisons between habitats, species, seasons, and sexes carried out. These analyses were undertaken to understand how habitat, species, seasonal, and intersexual differences impact on prey choice and trophic structure.

To determine whether the habitats differed in $\delta\ ^{13}C$ and $\delta\ ^{15}N$ values, samples were collected for each of the six selected taxa inhabiting the different habitats. These samples were predicted to differ in isotopic signature between habitats due to the different vegetation present and varied nitrogen inputs, (e.g. fertilisation of pine plantation). Habitats were found to differ significantly in terms of $\delta\ ^{13}C$ and $\delta\ ^{15}N$

values for certain taxa (δ ^{13}C: rat, tomtit; δ ^{15}N: vegetation, rat, tomtit) indicating different carbon sources and nitrogen availability within each habitat. Within each taxon those sampled from native habitat had the lowest δ ^{15}N levels, boundary samples usually had intermediate values, and pine plantation samples had the highest δ ^{15}N values. Significant separation between habitats despite limited sample sizes was observed for tomtits, and past researchers have also noted that trophic discrimination was found with relatively low sample sizes using stable isotopes (DeNiro & Epstein, 1978; Fry *et al.*, 1978b; Caut *et al.*, 2008b).

Vegetation δ ^{13}C values found for the three habitats investigated by this research were relatively consistent (mean range: -29.56 - -28.31‰) suggesting that the producers were utilising relatively similar carbon sources and experiencing consistent environmental conditions. This was unsurprising as all samples were collected within an 8 km range and therefore the plants would have experienced highly similar environmental regimes. The values were also similar to other New Zealand stable isotope studies investigating δ ^{13}C values for pine cellulose and native leaf litter (Barbour *et al.*, 2002; Najera-Hillman *et al.*, 2009) (Table 2.6). They were higher than values for both New Zealand native riparian vegetation (Najera-Hillman *et al.*, 2009), and plant material collected in other countries (Fry *et al.*, 1978a; Duarte *et al.*, 2005; Wooller *et al.*, 2005; Kohzu *et al.*, 2009), but lower than values for Australian leaf litter (Cook & Dawes-Gromadzki, 2005) (Table 2.6). These differences are due to the producers sampled having widely different growth conditions and carbon sources (Cook & Dawes-Gromadzki, 2005; Duarte *et al.*, 2005; Najera-Hillman *et al.*, 2009). In contrast δ ^{15}N values for vegetation were significantly different between the habitats investigated, with vegetation from the native habitat having the lowest value, followed by boundary, and pine habitat vegetation (Table 2.6). These values were consistent with those from other locations and plant species in New Zealand (Table 2.6), though higher than those found by Tozer *et al*. (2005) for epiphytic plants and lichen sampled from locations with geothermal activity. Australian plant material has been found to have greater δ ^{15}N values than those found by this study (Blüthgen *et al.*, 2003) (Table 2.6), which may be associated with higher nutrient availability (Cassaing *et al.*, 2007; Oleksyn *et al.*, 2007; Göthe *et al.*, 2009).

It was predicted that, within each habitat, vegetation, herbivores, and predators would vary in their $\delta^{15}N$ values due to their differing positions in the food chain, and the associated increase in $\delta^{15}N$ values from producer to predator with TL (Gannes *et al.*, 1998; Harding & Stevens, 2001; Caut *et al.*, 2008b). This was the pattern expected and has been found by past researchers investigating terrestrial food webs in a variety of habitat types and countries (Kohzu *et al.*, 2009; Najera-Hillman *et al.*, 2009; Hyodo *et al.*, 2010). To determine whether my predictions regarding trophic placement of taxa (vegetation<caterpillars<beetles<mice<rats<tomtits) were correct, $\delta^{15}N$ values were compared within each habitat. Taxa separated for both isotopes, with the degree of separation indicating two to four TLs. However, the predicted order was not always observed, with mice in the pine and boundary habitats having higher mean $\delta^{15}N$ than rats, and beetles in the boundary habitat also having a higher mean $\delta^{15}N$ than rats.

Even though the beetles examined are carnivorous it was not anticipated that they would have a mean $\delta^{15}N$ signature greater than that of rats due to the nature of the prey for each species. Beetles within the leaf litter will prey on invertebrates such as Acarina, Collembola, and Nematoda some of which are primarily, or potentially, detritivores (Moeed & Meads, 1985; Klimaszewski & Watt, 1997). When inhabiting forested ecosystems detritivores have lower $\delta^{15}N$ values than other consumers (Hyodo *et al.*, 2010), so the beetle $\delta^{15}N$ value was expected to reflect that of its likely prey. In contrast, rats are able to prey on a wider range of invertebrates, and also include vertebrates, in addition to plant material, in their diet. Additionally, when invertebrates and vertebrates within the same TL are compared, vertebrates have higher isotopic values than invertebrates due to their diet being more enriched in general, or because of prey selection (Kohzu *et al.*, 2009; Hyodo *et al.*, 2010). An increase in sample size would help resolve whether the deviations from expected are due to smaller sample sizes increasing variation of the isotopic values or whether they are indeed representative of rats having more vegetation (e.g. fruit) in their diet than anticipated.

Tomtits are almost solely insectivorous but they did not appear to constitute a top predator within the habitats examined. Future studies of this system should sample top predators, such as moreporks (*Ninox novaeseelandiae*), Australasian harriers (*Circus*

approximans), cats (*Felis catus*), or mustelids (weasels (*Mustela nivalis*), stoats (*M. erminea*), ferrets (*M. furo*)), from pine, native, and boundary habitats in order to determine the range of carbon and nitrogen signatures within each ecosystem. Although, as these top predators range across larger areas than the taxa currently investigated, they may be foraging across multiple habitats, which in itself would be interesting to examine. It was also notable that $\delta^{13}C$ values differed significantly between taxa within each habitat. Although ^{13}C can show trophic differentiation, it also indicates carbon source from producers (Harding & Stevens, 2001; Caut *et al.*, 2008a). Given the significant differences found between taxa within each habitat it may be that they are feeding on resources with different carbon signatures; for instance, vegetative material with a different carbon signature, or consumers that have fed on this material.

Seasonal comparisons were carried out for caterpillars, mice, and rats to test the hypothesis that these taxa showed seasonal variation in isotopic signature and evaluate the level of seasonal fluctuations in $\delta^{13}C$ and $\delta^{15}N$ values corresponding to changes in the location or TL of food resources. It was expected that seasonal fluctuations would be apparent due to varying climatic conditions causing shifts in the availability of vegetative material and invertebrate prey, and therefore shifts in $\delta^{15}N$ values. Season might also impact on the carbon source depending on whether prey items were sourced from different locations. Stable isotope fluctuations between seasons were only seen for rat $\delta^{13}C$ values, and may indicate seasonal foraging movements. The ability to undertake such movements of course depends on the ranging ability of the animal. For example, a caterpillar facing unfavourable conditions cannot undertake the level of movement necessary to significantly change the carbon signature of its resource. Additionally mice occupy a smaller home range (mean ±SE: 0.6 ±0.123 ha (Fitzgerald *et al.*, 1981)) than rats (mean ±SE: 0.79 ±0.1 ha (Dowding & Murphy, 1994)), and therefore carbon signatures of mice might be limited by scale of movement. Rats are able to undertake substantial movements (400 - 900 m within home ranges (Hooker & Innes, 1995)), and would certainly be able to exhibit shifts in $\delta^{13}C$ values if they travelled this distance linearly. Harding & Stevens (2001) found that they could assign habitat (marsh versus grassland) to voles (*Microtus californicus*) preyed on by raptors across a 500 m gradient.

Intersexual comparisons were made for rats, mice, and tomtits to test whether samples for males and females differed. No intersexual differences in $\delta^{15}N$ or $\delta^{13}C$ values were found for rats, mice, or tomtits, and no intersexual differences in stomach contents were observed for rodents. Although differences in male and female diet are a common phenomenon for a variety of bird and mammal species (Perkins & Speakman, 2001; Nassar *et al.*, 2003; Ben-David *et al.*, 2004; Forero *et al.*, 2005; Bearhop *et al.*, 2006; Lewis *et al.*, 2006; Morrissey *et al.*, 2010), they are not universal (Hobson & Wassenaar, 1999; Bearhop *et al.*, 2006; Hedd & Montevecchi, 2006; Kurle, 2009; Morrissey *et al.*, 2010). If intersexual differences were apparent it may have been due to competition for food resources between the sexes. In this instance the larger or more overtly aggressive sex would be expected to dominate food resources, or feed on a more preferred source.

The results suggested that for the tissues sampled the stable isotope signatures were acting as a broad indicator of habitat and species differences. When tomtits were considered, the stable isotope signatures for each sex did not reflect the intersexual foraging differences observed. The tomtit feather samples reflect diet during the period of feather growth (late summer), and during this season significant differences between the sexes were found in terms of foraging substrate and height for 2006 - 07 but not for 2007 - 08. However, no differences in ground prey availability were found for male and female tomtits. So it is likely that the lack of isotopic variation was due to a lack of foraging differences between male and female tomtits during late summer 2009. Morrissey *et al*. (2010) found isotopic differences in $\delta^{13}C$ between male and female Eurasian dippers, but only during the pre-breeding and laying period. Therefore if intersexual differences in stable isotopes occur in tomtits it may only be detectable during certain years and seasons.

Stable isotope and stomach content analyses were used to understand the diet of mice and rats in terms of nutrient components and prey taxonomy. The hypothesis that these two techniques would vary in their separation of the diet of these species was tested. In contrast to stable isotope results, the stomach content analyses undertaken for rodents did not show habitat separation for mice or rats, but revealed significant differences

between mouse and rat diet in the boundary habitat. Therefore the results indicate that rodents were feeding on similar types of prey in each habitat, even though their $\delta^{15}N$ and $\delta^{13}C$ values were distinct. If only one technique had been applied very different conclusions would have been drawn. Stomach content analysis alone would have led to the conclusion that prey items, and therefore presumably nutrient availability to the rodents, were the same in each habitat. Whereas stable isotope analysis alone would have led me to conclude that the rodents were accessing widely differing nitrogen and carbon sources, and therefore presumably prey items, in each habitat. The need to couple different methodologies in order to gain a better understanding of diet at a temporal level was also highlighted. Stomach content analysis alone would not have detected seasonal shifts in diet for rats that suggested movement to source food. When stable isotope results were coupled with the information from stomach content analyses it was found that, although the $\delta^{15}N$ values do not vary between seasons for the rodents investigated, the overall composition and $\delta^{13}C$ value of the diet does.

Observations of foraging tomtits were coupled with collection of leaf litter samples, where tomtits foraged, to assess foraging and prey availability differences between habitats, seasons, and sexes. The hypothesis that foraging differences exist between sexes was tested to investigate whether each tomtit sex targets the same prey items as characterised by the substrate, height, and strategy used. Striking differences in male and female tomtit foraging were found in terms of substrate and height use. However, these differences did not extend to stable isotope signatures or ground prey availability. It was anticipated that the males would be foraging on the most preferred resource due to their more overtly territorial behaviour. Recher & Holmes (2000) also found intersexual differences in the foraging substrate for rufous whistlers (*Pachycephala rufiventris*), and foraging height utilised by males and females of rufous whistlers, satin flycatchers (*Myiagra cyanoleuca*), crested shrike-tits (*Falcunculus frontatus*), white-throated treecreepers (*Cormobates lecuophaeus*), and red-browed treecreepers (*Climacteris erythrops*) observed in forest at Bondi, Australia. The intersexual differences they found were ascribed to competition or aggression reduction, expansion of breeding resources, or due to other behaviours influencing foraging parameters. Recher & Holmes (2000) also suggested overt male dominance for two of the species examined.

The result that male, but not female, tomtits changed their foraging significantly between years is intriguing, and suggests either male dominance of a preferred resource or female constraint due to a nutritional requirement. Burns and Steer (2006), Burns and van Horik (2007), and Steer and Burns (2008) fed New Zealand robin (*Petroica australis*) pairs and solo robins mealworms, then recorded aggressive interactions and prey caching. Although no changes in foraging behaviour were seen between paired versus solo tomtits in this study, it must be noted that the birds classed as paired did not necessarily have the adult of the opposite sex in attendance when the foraging event occurred; there was simply an observation of them being paired with another bird within one month of the event. Future research into tomtit foraging could include similar observations to those of undertaken by Burns and Steer (2006), Burns and van Horik (2007), and Steer and Burns (2006) to quantify aggressive encounters between male and female tomtits while foraging; it would be valuable to know what happens when both members of the pair are in attendance at the same time and presented with a food source.

Tomtit foraging was also evaluated for seasonal shifts, which may reflect either changing availability of prey or changing prey requirements between breeding and non-breeding seasons. It was anticipated that tomtits would exhibit seasonal changes in foraging, and this was found for both sexes in 2006 - 07, with relatively more ground use occurring in the non-breeding season, and more vegetation use (males: 3 - 6 m; females: 0 - 3 m) in the breeding season. The seasonal foraging shift may have been due to seasonal variation in prey availability, and some seasonal variation was found in the type of ground prey available, however prey variation did not show a general trend across habitats. Seasonal changes in foraging have also been observed by Jedlicka *et al.* (2006) for rufous-capped warblers (*Basileuterus rufifrons*) (Soconusco, Mexico). This insectivorous species showed a seasonal shift in foraging substrate and height despite unchanged invertebrate abundance between seasons. Although the occurrence of large invertebrates did decrease in the microhabitats they shifted from, and this change in prey, or competition with arriving migrant species, were suggested as reasons for the foraging microhabitat change by rufous-capped warblers.

Foraging behaviour was compared between years to test the hypothesis that tomtits show interannual variation in their foraging, which might reflect changing prey availability between years (presuming that tomtit nutritional requirements do not change annually). Male tomtits showed annual differences in foraging, using the ground significantly more in 2006 - 07 than 2007 - 08, but no annual differences were found for females. Craig & Beal (2001) found shifts in microhabitat use between years for forest dwelling bridled (*Zosterops conspicillatus*) and golden white-eyes (*Cleptornis marchei*) (Saipan, Micronesia), and speculated that this shift was to make use of differing food availability. Variables that potentially impact on prey availability include soil water reductions which can limit invertebrate availability (Peach *et al.*, 2004; Devereux *et al.*, 2006). Prey availability within pine and native forests habitats differed between years and it was anticipated that if prey availability fluctuated, tomtits would shift their foraging to accommodate this variation. Therefore the shift by male tomtits was possibly due to changing prey availability between years.

The hypothesis that tomtits were foraging differently in different habitats (pine, native, and boundary) was tested to ascertain whether each habitat offered the same foraging potential to the birds. It was anticipated that tomtits would forage differently between habitats due to the differing structure and prey availability between habitats affecting their foraging. This was seen with vegetation utilised as a substrate and the 3 - 6 m height category used more frequently in the native forest than the pine or boundary habitat. Other studies have also noted insectivorous birds selectively foraging in particular vegetation types that have a preferred structure (Airola & Barrett, 1985; Virkkala, 1988). VanderWerf (1994) noted that *Chasiempis sandwichensis* foraged differently in undisturbed and disturbed forest habitats due to fewer perches and lower foliage density in disturbed habitats, a result echoed by this research. Foraging efforts are often focussed on substrates that harbour the most abundant or accessible prey (Holmes & Robinson, 1981; Murakami, 1998, 2002), and tomtits were probably concentrating their foraging effort to make use of microhabitats that afford the best foraging opportunities in each habitat.

It was predicted that the availability of ground-prey for tomtits would differ between habitats, and it was noteworthy that, even at the taxonomic level of order, differences in prey availability between the habitats were highly significant. The contrast between this result and that found for the rat stomach contents was particularly interesting; rats seemed able to access similar types and proportions of invertebrate prey, and a similar proportion of invertebrates to vertebrate remains and vegetation, regardless of the habitat they occupied. However, the ground invertebrate availability for tomtits differed significantly between habitats. The modification of ecosystems often results in changes that decrease biodiversity at some level (Duncan *et al.*, 1999; Robinson & Sutherland, 2002; Power *et al.*, 2004), and a similar result for tomtit ground prey availability was found. Foraging points sampled in the pine plantation lacked invertebrate orders represented in both the native and boundary habitats. The boundary habitat is an interesting environment as it reflects the influence of both the pine and native forest, sharing elements of each to differing degrees. The boundary habitat foraging point samples did not support the full complement of invertebrate orders detected in samples from pine and native forests, and some orders also differed in proportion. Both pine and native habitats showed annual variations in invertebrate availability, with a lack of annual variation found for the boundary habitat. However, if the boundary samples were split into their respective habitat types these fluctuations might become apparent. Tomtits and rodents alike make use of this habitat irrespective of the vegetation type, and leaf litter samples were collected from both the native and pine areas of the boundary habitat.

Tomtit ground prey availability was also compared between years to elucidate prey availability changes between years; if prey availability was constant and yet foraging behaviours change between years it might indicate fluctuating nutritional needs. Significant differences were found between 2006 and 2007 for both proportional and presence/absence data in the pine and native forest samples. Invertebrate fluctuations between years are commonly observed (Holmes & Schultz, 1988; Taft & Haig, 2006; Kèrbiriou & Julliard, 2007). It was assumed that if climatic conditions differed between years that prey availability would also change between years due to certain species being favoured or disadvantaged by the different conditions. However, the impacts of other predators may also affect prey (Estany-Tigerström *et al.*, 2010), additionally prey

food availability (Murakami, 1998, 2002) disease and parasitism prevalence influence prey availability dynamics (Van Dover *et al.*, 2007; Duffy & Hall, 2008).

Seasonal prey availability was also assessed, and it was anticipated that varying climatic conditions would change the occurrence, abundance, and accessibility of invertebrates. Fluctuations in prey availability according to season are commonly found (Frampton *et al.*, 2000; Tulp & Schekkerman, 2008; Vonshak *et al.*, 2009). However, the effect of season on invertebrates in leaf litter samples does not appear to be as great as that of habitat. Within each habitat certain pairwise seasonal differences were found to be significant, however no overall seasonal trends were observed.

Finally, the hypothesis that male and female tomtits have different ground prey availability was tested to determine whether male and female tomtits target different ground prey, which could potentially reduce competition between the sexes. No differences between male and female prey availability were found. However, past researchers have found forest inhabiting bird species to differentiate foraging niche between sexes by tree species, substrate, height, and strategy (Jackson, 1970; Austin, 1976; Franzreb, 2010). This study observed highly significant differences male and female tomtits in terms of foraging behaviour, when substrate and height were considered, therefore intersexual differences in prey availability may not occur within each substrate but between them.

In future studies using this system, stable isotope and stomach sample collection could be increased, in particular for taxa that do not currently show $\delta\ ^{15}N$ or $\delta\ ^{13}C$ differentiation, or were not captured in each habitat. The collection of more stable isotope samples from producers, e.g. leaf litter, leaves, bark, flowers, and fruit from a variety of tree species within each habitat could be coupled with additional invertebrate samples representing trophic groups (detritivores, e.g. Amphipoda, additional invertebrate herbivores, e.g. Orthoptera, and predators, e.g. Araneida). If collected along transects bisecting the rodent trapping grids they could be used to resolve the seasonal $\delta\ ^{13}C$ shift found, in addition to gauging whether the $\delta\ ^{15}N$ value progression (native<boundary<pine) holds true. The invertebrate orders suggested are confirmed

rodent prey within the habitats investigated, and recorded as potential tomtit prey items, so it would be possible to use mixing model analyses to further investigate the diet of these vertebrates. It would also be possible to analyse remains found in rodent stomachs directly and match their isotopic signatures with those of manually collected samples. Sampling multiple tissue types from individual rodents and tomtits captured and identifying stomach contents to a finer taxonomic level would also allow a more complete picture of temporal foraging to be built up, as tissues types have different nutrient turnover rates and could therefore clarify dietary shifts (Strode, 2009).

To further the understanding of tomtit foraging more samples of female tomtit foraging are required. In addition, as bird species have been found to target specific tree species, intersexual tree preferences and associated prey availability could be examined. Finally, the breeding success of tomtits within the different habitat types could be quantified and correlated with foraging parameters.

This study utilised multiple techniques and collected two years of behavioural and prey availability data which allowed the habitats of interest to be compared on a variety of levels and annual differences to be determined. The use of both stable isotope and stomach content analyses to assess rodent diet was valuable as it clarified the diet of these species to a greater extent than either method could have alone. I recommend that whenever possible dietary studies incorporate both stable isotope, and an alternate method of dietary analysis, to answer questions about prey composition at taxonomic, nutritive, and prey habitat levels. Although two years does not constitute a long term data set, conducting the observations of tomtit behaviour and collecting samples of potential invertebrate prey over this time period allowed annual comparisons to be made. This enabled significant annual differences to be observed for male tomtit foraging and prey availability within pine and native forests, and gave a more complete picture than a single year could have done. Many questions have been raised by this study and there is much scope for future research into the trophic structure of pine versus native forest, in particular the comparative worth of pine plantations as a foraging habitat for native birds.

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Appendix I

Table I. New Zealand map grid co-ordinates of vegetation, caterpillar, beetle, mouse, rat, and tomtit sample collection locations. NB all leaf litter samples used for prey availability assessment, all rodents used for stomach content analyses, and all mouse hair and tomtit feather samples analysed for stable isotopes.

Sample type	Sample number	New Zealand map grid co-ordinates	
		Easting	Northing
Leaf litter	0107N1	2704391	6460533
Leaf litter	0107N2	2704396	6460527
Leaf litter[1, 4]	0107N3	2703882	6459720
Leaf litter[1, 3, 4]	0107P1	2703346	6461881
Leaf litter	0107P2	2702941	6462123
Leaf litter	0107P3	2702850	6461852
Leaf litter[2, 3]	0107P4	2702995	6462447
Leaf litter	0107P5	2703076	6462090
Leaf litter	0108P1	2703581	6461532
Leaf litter	0108P2	2703355	6461631
Leaf litter[2, 4]	0207B1	2699485	6458943
Leaf litter[2, 4]	0207B2	2698729	6457762
Leaf litter	0208B1	2701970	6462275
Leaf litter	0208B2	2699472	6458891
Leaf litter[3]	0208B3	2699471	6457688
Leaf litter	0208N1	2704545	6459803
Leaf litter	0208N2	2704428	6459534
Leaf litter	0208N3	2704493	6459708
Leaf litter[1]	0208N4	2704518	6459270
Leaf litter[3]	0208N5	2704260	6459423
Leaf litter[1]	0208P3	2699594	6458304
Leaf litter	0208P4	2703480	6461383
Leaf litter[1, 3, 4]	0208P5	2703633	6461412
Leaf litter	0306N1	2704844	6456775
Leaf litter	0306P1	2703606	6461411
Leaf litter	0306P2	2703013	6462097
Leaf litter	0307P1	2703593	6461490
Leaf litter	0307P2	2703185	6461701
Leaf litter	0307P3	2703169	6461370
Leaf litter	0307P4	2702981	6461846
Leaf litter	0307P5	2703691	6461459
Leaf litter	0406N2	2705587	6456872
Leaf litter	0406N3	2704575	6459802
Leaf litter	0406P3	2703541	6461557
Leaf litter	0406P4	2703541	6461557
Leaf litter	0406P5	2703070	6462172
Leaf litter	0407B1	2702436	6462589
Leaf litter	0407B1	2702436	6462589
Leaf litter[3]	0407B2	2702417	6462586
Leaf litter	0407N1	2704442	6460432
Leaf litter	0407N2	2704409	6460485

Leaf litter[3]	0407N3	2704150	6460666
Leaf litter	0407N3	2704150	6460666
Leaf litter	0506N1	2704206	6460019
Leaf litter	0506N2	2704333	6460219
Leaf litter[1, 3, 4]	0506N3	2703885	6459745
Leaf litter	0506N4	2704017	6459891
Leaf litter	0506N5	2703632	6459353
Leaf litter	0506P1	2703099	6461360
Leaf litter	0506P2	2702910	6462057
Leaf litter[1, 4]	0506P3	2702902	6462102
Leaf litter	0507N1	2704508	6460314
Leaf litter	0507N2	2704398	6460518
Leaf litter[1]	0507N3	2704128	6460963
Leaf litter	0507P1	2703329	6461424
Leaf litter	0507P2	2702910	6462115
Leaf litter	0507P3	2702920	6462112
Leaf litter	0507P4	2703497	6461627
Leaf litter	0507P5	2703485	6461632
Leaf litter	0606B1	2701923	6462246
Leaf litter	0606B2	2702345	6462541
Leaf litter	0606B3	2702558	6462695
Leaf litter	0606B4	2702583	6462722
Leaf litter[2, 3]	0606B5	2703138	6462561
Leaf litter	0606P3	2703519	6461421
Leaf litter[1]	0606P4	2703041	6461722
Leaf litter	0606P5	2703055	6461720
Leaf litter	0607B1	2701995	6462287
Leaf litter[1, 3]	0607N4	2699778	6459256
Leaf litter	0607N5	2704480	6460363
Leaf litter	0706B1	2702660	6462796
Leaf litter	0706B2	2702299	6462538
Leaf litter	0706B3	2702002	6462293
Leaf litter	0706B4	2702432	6462615
Leaf litter	0706N1	2704505	6460247
Leaf litter	0706N2	2704483	6460214
Leaf litter	0706P1	2703073	6462192
Leaf litter	0706P2	2703048	6462104
Leaf litter	0706P3	2703386	6461892
Leaf litter	0707N2	2704291	6460486
Leaf litter	0707P1	2703040	6462081
Leaf litter	0707P2	2703035	6462082
Leaf litter[3]	0707P3	2702985	6462519
Leaf litter	0707P4	2702982	6462431
Leaf litter[2, 3]	0707P5	2703081	6462193
Leaf litter[2, 3]	0807B1	2699536	6458843
Leaf litter	0807B2	2699596	6458618
Leaf litter[1, 3]	0807B3	2699605	6457655
Leaf litter[2, 3]	0807B4	2699560	6457682
Leaf litter[2]	0807B5	2699480	6458858
Leaf litter[1, 3]	0807N3	2699753	6457156

Leaf litter[1, 3]	0807N4	2699692	6459086
Leaf litter	0807N5	2704151	6461125
Leaf litter	0906B1	2702464	6462645
Leaf litter	0906B3	2702327	6462553
Leaf litter	0906B5	2702189	6462524
Leaf litter	0906N1	2704515	6460244
Leaf litter	0906N2	2703910	6459808
Leaf litter	0906N3	2703803	6459605
Leaf litter[4]	0906N4	2704554	6460123
Leaf litter	0906N5	2703688	6459361
Leaf litter	0906P1	2703354	6461424
Leaf litter	0906P2	2703458	6461410
Leaf litter	0906P3	2703560	6461534
Leaf litter	0906P4	2703545	6461498
Leaf litter[3]	0906P5	2703003	6462544
Leaf litter[1, 3]	0907B1	2699589	6458629
Leaf litter	0907B2	2699561	6458773
Leaf litter[1]	0907N1	2705124	6456773
Leaf litter[1]	0907N2	2704146	6461103
Leaf litter	0907N3	2704133	6461113
Leaf litter[2, 3]	0907P1	2703079	6461353
Leaf litter[2, 3]	0907P2	2703548	6461530
Leaf litter	0907P3	2703540	6461504
Leaf litter	0907P4	2703340	6461423
Leaf litter	0907P5	2703687	6461458
Leaf litter[1, 3, 4]	1007B3	2699581	6457675
Leaf litter[3]	1007B4	2699375	6457740
Leaf litter[3]	1007B5	2699466	6458924
Leaf litter	1106B1	2702031	6462301
Leaf litter[2]	1106N1	2704099	6461074
Leaf litter	1106P1	2703349	6461422
Leaf litter[3]	1106P2	2703453	6461397
Leaf litter	1107P1	2703464	6461361
Leaf litter	1107P2	2703622	6461415
Leaf litter	1107P3	2703473	6461560
Leaf litter	1206B2	2701853	6462150
Leaf litter	1206N2	2704506	6460181
Leaf litter	1206N3	2704118	6460980
Leaf litter	1206P3	2703577	6461543
Leaf litter	1206P4	2702906	6462126
Leaf litter[2, 3, 4]	1206P5	2702979	6461815
Leaf litter[1]	1207B1	2699583	6458632
Mouse	0407BM1	2702430	6462581
Mouse	0407BM2	2702410	6462593
Mouse	0407BM3	2702432	6462605
Mouse	0407BM4	2702486	6462696
Mouse	0407BM5	2702407	6462621
Mouse	0407BM6	2702470	6462635
Mouse	0707BM1	2702469	6462616
Mouse	0707BM2	2702407	6462569

Mouse	0707BM3	2702432	6462605
Mouse	0707BM4	2702407	6462569
Mouse	0707BM5	2702410	6462593
Mouse	0707BM6	2702407	6462569
Mouse	0707BM7	2702489	6462654
Mouse	0707PM1	2703043	6462046
Mouse	0707PM2	2703052	6462101
Rat[5]	0108BR1	2702413	6462672
Rat[5]	0108BR2	2702436	6462674
Rat[5]	0108N2M1	2703429	6459224
Rat[5]	0108N2R1	2703439	6459160
Rat[5]	0108N2R4	2703424	6459171
Rat[5]	0108N2R5	2703453	6459202
Rat[5]	0108PR1	2702998	6462050
Rat[5]	0407BR1	2702494	6462678
Rat[5]	0407BR2	2702407	6462635
Rat[5]	0407BR3	2702487	6462623
Rat[5]	0407BR4	2702494	6462678
Rat[5]	0407BR5	2702382	6462607
Rat[5]	0407BR6	2702494	6462678
Rat[5]	0407BR7	2702470	6462635
Rat	0407NR1	2704455	6460183
Rat[5]	0407NR10	2704431	6460171
Rat[5]	0407NR11	2704388	6460156
Rat	0407NR12	2704455	6460183
Rat	0407NR13	2704453	6460104
Rat[5]	0407NR14	2704398	6460060
Rat[5]	0407NR2	2704411	6460161
Rat[5]	0407NR3	2704388	6460156
Rat[5]	0407NR4	2704388	6460156
Rat	0407NR5	2704385	6460127
Rat[5]	0407NR6	2704372	6460086
Rat[5]	0407NR7	2704394	6460078
Rat[5]	0407NR8	2704398	6460060
Rat	0407NR9	2704431	6460171
Rat[5]	0407PR1	2703084	6462108
Rat[5]	0407PR2	2703085	6462075
Rat[5]	0407PR3	2703043	6462046
Rat[5]	0407PR4	2703026	6462046
Rat[5]	0407PR5	2703013	6462030
Rat[5]	0407PR6	2703085	6462075
Rat[5]	0407PR7	2703033	6461999
Rat[5]	0707BR1	2702486	6462696
Rat[5]	0707BR10	2702470	6462635
Rat[5]	0707BR2	2702436	6462674
Rat[5]	0707BR3	2702407	6462621
Rat[5]	0707BR4	2702382	6462607
Rat	0707BR5	2702413	6462672
Rat[5]	0707BR6	2702469	6462616
Rat	0707BR7	2702407	6462621

Rat	0707BR8	2702462	6462670
Rat[5]	0707BR9	2702432	6462605
Rat[5]	0707NR1	2704453	6460104
Rat[5]	0707NR2	2704388	6460156
Rat[5]	0707NR3	2704377	6460157
Rat[5]	0707NR4	2704385	6460127
Rat[5]	0707NR5	2704398	6460060
Rat[5]	0707NR6	2704388	6460156
Rat[5]	0707NR7	2704377	6460157
Rat[5]	0707NR8	2704398	6460060
Rat[5]	0707NR9	2704385	6460127
Rat[5]	0707PR1	2703091	6462071
Rat[5]	0707PR2	2703125	6462002
Rat[5]	0707PR3	2703043	6462028
Rat[5]	0707PR4	2703033	6461999
Rat[5]	0707PR5	2703026	6462046
Rat[5]	0707PR6	2703013	6462030
Rat[5]	0707PR7	2703013	6462019
Rat[5]	0707PR8	2703013	6462030
Rat[5]	1007BR1	2702486	6462696
Rat	1007BR10	2702494	6462678
Rat[5]	1007BR2	2702382	6462607
Rat[5]	1007BR3	2702425	6462636
Rat[5]	1007BR4	2702457	6462602
Rat[5]	1007BR5	2702470	6462635
Rat[5]	1007BR6	2702486	6462696
Rat[5]	1007BR7	2702457	6462602
Rat[5]	1007BR8	2702407	6462569
Rat[5]	1007BR9	2702451	6462650
Rat[5]	1007N2R1	2703385	6459204
Rat[5]	1007N2R2	2703453	6459202
Rat[5]	1007N2R3	2703439	6459160
Rat[5]	1007N2R4	2703385	6459204
Rat[5]	1007N2R5	2703439	6459160
Rat[5]	1007N2R6	2703424	6459171
Rat[5]	1007N2R7	2703453	6459202
Rat[5]	1007PR1	2703013	6462030
Rat[5]	1007PR2	2703125	6462002
Rat[5]	1007PR3	2703028	6461993
Rat[5]	1007PR4	2703026	6462046
Rat[5]	1208N2R2	2703385	6459204
Rat[5]	1208N2R3	2703429	6459224
Tomtit	0609NT1	2704570	6459813
Tomtit	0609NT2	2704570	6459813
Tomtit	0609NT3	2704464	6459644
Tomtit	0609NT4	2704330	6459435
Tomtit	0609NT5	2704431	6459548
Tomtit	0609PT2	2699702	6459089
Tomtit	0609PT3	2703306	6461938
Tomtit	0609PT4	2703306	6461938

Tomtit	0609PT5	2702906	6462126
Tomtit	0609PT6	2703185	6461375

[1]Vegetation from this leaf litter sample gave a reliable result for ^{13}C only.

[2]Vegetation from this leaf litter sample gave a reliable result for both ^{13}C and ^{15}N.

[3]Caterpillars from this leaf litter sample used for stable isotope analyses.

[4]Beetles from this leaf litter sample used for stable isotope analyses.

[5]Hair from this animal used for stable isotope analyses.

Table II. Summary of total nitrogen and carbon comparisons for taxa between habitats.

	Carbon			**Nitrogen**		
	n	Statistical value	*P*	n	Statistical value	*P*
Vegetation	30	H = 0.784	0.675	11	U = 9.000	0.329
Caterpillar	26	H = 5.378	0.067	26	$F_{2, 23} = 0.315$	0.732
Beetle	12	$F_{2, 9} = 2.259$	0.160	12	H = 0.529	0.767
Rat	76	$F_{2,73} = 0.276$	0.759	76	$F_{2,73} = 0.115$	0.891
Tomtit[1]	10	$t_8 = 1.954$	0.086	11	$t_9 = -0.590$	0.569

[1] Test between pine and native habitats.

Appendix II

Table I. Percentage of invertebrate orders comprising >5% of invertebrates from samples of one sex displayed for males and females in each habitat. Bracketed number denotes number of samples.

	Pine		Native		Boundary	
	Male (46)	**Female (11)**	**Male (31)**	**Female (11)**	**Male (26)**	**Female (8)**
Amphipoda	13	7	6	3	15	8
Annelida	4	8	1	3	1	7
Araneida	2	3	5	0	3	27
Coleoptera - larvae	13	0	8	3	9	1.
Coleoptera - adults	14	18	14	13	10	5
Collembola	20	15	8	15	14	9
Dermaptera	0	14	0	6	0	8
Diplopoda	11	0	8	0	2	0
Diptera - larvae	9	14	34	7	24	6
Diptera - adults	3	6	3	38	2	18
Hemiptera	5	0	6	0	12	0
Hymenoptera	0	8	2	6	2	6

Table II. Summary of selected invertebrate sample comparisons conducted using ANOSIM.

Comparison		**R**	***P***
Count data between males, females	pine	-0.117	0.906
	native	-0.113	0.917
	boundary	-0.019	0.531
Presence/absence data between males, females	pine	-0.020	0.548
	native	-0.103	0.836
	boundary	-0.121	0.845
Count data female samples between 2006, 2007	pine	0.003	0.385
	native	-0.045	0.641
	boundary	-0.010	0.514
Presence/absence data female samples between 2006, 2007	pine	-0.088	0.721
	native	-0.137	0.959
	boundary	0.031	0.343
Count data: boundary male samples between	all seasons	0.048	0.256
	autumn, winter	-0.107	0.500
	autumn, spring	-0.075	0.375
	autumn, summer	-0.238	0.625
	winter, spring	-0.018	0.497
	winter, summer	0.150	0.070
	spring, summer	0.043	0.248
Presence/absence data: boundary male samples between	all seasons	0.038	0.293
	autumn, winter	-0.334	0.917
	autumn, spring	-0.347	0.875
	autumn, summer	-0.463	1.000
	winter, spring	0.038	0.278
	winter, summer	0.147	0.071
	spring, summer	0.040	0.224

Count data: pine female samples between	all seasons	0.335	0.059
	autumn, winter	0.464	0.133
	autumn, spring	0.750	0.067
	autumn, summer	0.389	0.086
	winter, spring	-0.250	1.000
	winter, summer	-0.083	0.700
	spring, summer	-0.250	1.000
Presence/absence data: pine female samples between	all seasons	0.161	0.195
	autumn, winter	0.232	0.267
	autumn, spring	0.482	0.067
	autumn, summer	0.343	0.086
	winter, spring	-0.625	1.000
	winter, summer	-0.417	1.000
	spring, summer	0.000	0.500
Count data: native female samples between	all seasons	-0.231	0.955
	autumn, winter	-0.333	1.000
	autumn, spring	0.000	1.000
	autumn, summer	-0.250	0.867
	winter, spring	0.000	0.500
	winter, summer	-0.259	0.886
	spring, summer	-0.286	0.933
Presence/absence data: native female samples between	all seasons	-0.244	0.959
	autumn, winter	-0.250	0.700
	autumn, spring	0.000	1.000
	autumn, summer	-0.429	1.000
	winter, spring	0.083	0.400
	winter, summer	-0.185	0.886
	spring, summer	-0.393	1.000
Count data: boundary female samples between	all seasons[1]	-0.050	0.581
	autumn, winter	0.214	0.733
	autumn, spring	0.000	1.000
	winter, spring	0.071	0.400
Presence/absence data: boundary female samples between	all seasons[1]	-0.275	0.895
	autumn, winter	-0.714	1.000
	autumn, spring	0.000	1.000
	winter, spring	-0.071	0.600

[1]Comparison between autumn, winter, and spring as no samples collected during summer.

Table III. Percentage of invertebrate orders comprising >5% of invertebrates for male tomtit samples per year and habitat. Bracketed number denotes number of samples.

	Pine		Native		Boundary	
	2006 (24)	**2007 (22)**	**2006 (17)**	**2007 (14)**	**2006 (11)**	**2007 (15)**
Amphipoda	15	13	6	8	19	16
Coleoptera - larvae	14	16	10	8	13	8
Coleoptera - adults	17	14	13	27	10	12
Collembola	26	16	9	9	11	18
Diplopoda	14	11	10	9	3	2
Diptera - larvae	7	16	41	31	37	21
Hemiptera	4	11	7	6	5	18

Table IV. Percentage of invertebrate orders comprising >5% of invertebrates for female tomtit samples per year and habitat. Bracketed number denotes number of samples.

	Pine		Native		Boundary	
	2006 (5)	**2007 (6)**	**2006 (5)**	**2007 (6)**	**2006 (4)**	**2007 (3)**
Amphipoda	4	11	3	3	13	5
Annelida	8	9	6	1	11	4
Araneida	6	1	0	0	0	47
Coleoptera - adults	23	12	16	12	9	2
Collembola	19	12	19	12	12	6
Dermaptera	15	14	7	5	14	5
Diptera - larvae	12	17	8	6	6	6
Diptera - adults	7	5	30	49	21	16
Hymenoptera	2	15	6	6	10	3

Table V. Percentage of invertebrate orders comprising >5% of invertebrates for male tomtit samples per season and habitat. Bracketed number denotes number of samples. A = autumn, W = winter, Sp = spring, Su = summer.

	Pine				Native				Boundary			
	A (14)	**W (9)**	**Sp (13)**	**Su (10)**	**A (13)**	**W (5)**	**Sp (7)**	**Su (6)**	**A (1)**	**W (11)**	**Sp (7)**	**Su (7)**
Amphipoda	9	15	24	14	5	3	12	8	4	22	19	2
Coleoptera - larvae	15	12	16	15	9	9	11	10	15	10	6	16
Coleoptera - adults	15	26	9	14	14	29	13	21	9	9	13	14
Collembola	28	15	12	30	8	6	7	19	8	8	16	42
Diplopoda	13	13	8	15	12	6	9	7	1	3	3	2
Diptera - larvae	12	8	14	7	41	42	40	25	54	32	22	12
Hemiptera	5	7	15	1	9	2	5	6	6	13	17	9

Table VI. Percentage of invertebrate orders comprising >5% of invertebrates for female tomtit samples per season and habitat. Bracketed number denotes number of samples. Conventions as for Table V.

	Pine				Native				Boundary			
	A (4)	**W (2)**	**Sp (2)**	**Su (3)**	**A (2)**	**W (3)**	**Sp (2)**	**Su (4)**	**A (1)**	**W (4)**	**Sp (2)**	**Su (0)**
Amphipoda	4	18	0	8	1	2	3	8	16	8	8	-
Annelida	9	2	5	15	1	3	2	10	10	8	1	-
Araneida	1	2	1	12	0	0	1	1	0	32	1	-
Coleoptera - adults	24	7	25	6	1	24	6	22	6	5	7	-
Collembola	15	17	27	9	10	13	31	12	30	7	12	-
Dermaptera	12	21	2	21	10	2	3	14	3	9	4	-
Diptera - larvae	18	2	14	16	8	6	7	8	16	6	5	-
Diptera - adults	3	10	11	7	62	38	35	15	3	14	55	-
Hymenoptera	8	14	10	2	4	7	7	6	13	6	2	-