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The diet of the New Zealand long-tailed bat, *Chalinolobus tuberculatus*

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“Our task must be to free ourselves from this prison by widening our circle of compassion to embrace all living creatures and the whole of nature in its beauty.” – Albert Einstein

Abstract

The long-tailed bat (*Chalinolobus tuberculatus* Forster, 1884) and the lesser short-tailed bat (*Mystacina tuberculata* Gray, 1883) are both endemic and the only extant bat species in New Zealand (Alexander, 2001). The long-tailed bat and the short-tailed bat are considered threatened; they are listed as vulnerable on the IUCN Red List of Threatened Animals and the Department of Conservation (DOC) lists long-tailed bats as 'nationally vulnerable', and lesser short-tailed bats as 'nationally endangered' (O'Donnell, Christie, Hitchmough, Lloyd, & Parsons, 2010). Research conducted on long-tailed bats has focused on roosting choice and behaviour with limited investigation of their diet. This leaves big gaps in our knowledge and due to both species inhabiting exotic plantation forests there is also the possibility for the bats to be important insect pest control agents.

Insect fragments were identified from New Zealand long-tailed bat faecal samples collected from under known roosts and harp traps in Kinleith Forest and Pureora Forest Park in the central North Island, New Zealand. In total 2247 fragments were mounted on slides (1335 from Pureora and 912 from Kinleith) and 15% of these were unidentifiable (346). Over both study sites, Diptera made up the largest percentage of the diet with 40%, Lepidoptera comprised 24%, Coleoptera 18%, Trichoptera 0.8%, and Hymenoptera 0.36%. Whole mites or mite remains comprised 0.8% of all fragments. Eleven fragments in total were found to be from Lepidoptera larvae which contradicts previous observations of long-tailed bats not eating terrestrial, non-winged insects. There were significant differences in the diet of the bats in native forest with the bats in exotic forest, showing long-tailed bats can be flexible in regards to the environment they live in whilst maintaining a normal diet.

The diets of the same two populations of New Zealand long-tailed bat were assessed by using stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis of faeces. This is the first instance where stable isotope analysis has been used to investigate New Zealand bat diet. Faecal samples from a population of New Zealand long-tailed bats in a Fiordland forest and a population of New Zealand short-tailed bats from Pureora Forest Park were also analysed to use as a comparison. The $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values of bat faeces were similar to those of Lepidoptera, Diptera, and Coleoptera implying these are the insects eaten most

often. Only minor similarities were found between the $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values of bat faeces and those of Trichoptera, Hymenoptera, and Hemiptera implying these insects are eaten less often. New Zealand long-tailed bats in Pureora Forest and Kinleith Forest have opportunistic, generalist diets. There were no significant differences in the diet of the bats in native forest with the bats in exotic forest showing bats inhabiting exotic plantation forests can maintain a good quality diet similar to bats inhabiting native forests. There were also no significant differences in the diet of Pureora Forest long-tailed bats and short-tailed bats which is strange considering the bats occupy different niches. In this study by combining physical search of faeces and stable isotope analysis, new information on the diet of the long-tailed bat was gained. After comparison, both techniques have their merits and that, if possible, it is best to utilise both when investigating diet.

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Author's Note

The following chapters have been structured as a general introduction followed by two interrelated but standalone papers. This leads to some repetition of information.

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Chapter One

1. General introduction

1.1. Bats

There are over 1100 species of bats divided into around 19 families, and of these approximately 25 % are globally threatened (Altringham, 2011; Wilson, 1997). Bats are present on every continent except Antarctica and are considered to be the most wide spread terrestrial mammal (Wilson, 1997). The fossil record of bats is very poor and because of this very little is known about their evolution and origin (Daniel, 1990). The first chiropterans may have evolved long before the earliest known fossils from the Eocene due to characteristics of these fossils being just as advanced as many of the modern species of bat (Daniel, 1990).

Traditionally bats were separated into two sub-orders, the Megachiroptera containing old world fruit bats and flying foxes and the Microchiroptera containing all remaining families of bats (Daniel, 1990; Jones, Purvis, MacLarnon, Bininda-Emonds, & Simmons, 2002). The Megachiroptera contained the single family *Pteropodidae* and are found in the old world tropics (Africa, Asia, Australia, and the Pacific Islands), mostly have large eyes and navigate by sight (Daniel, 1990; Wilson, 1997). The Microchiroptera, on the other hand, contained the remaining super-families (*Rhinolophoidea*, *Emballonuroidea*, *Vespertilionoidea*, and *Noctilionoidea*) and are found almost worldwide, have small eyes and generally navigate by echolocation (Daniel, 1990; Wilson, 1997). However two new suborders are now recognised, keeping the traditional characteristics for each group but slightly changing the families included. The Megachiroptera are now known as the Yinpterochiroptera and contains the super-family *Rhinolophoidea* as well as the original family *Pteropodidae* (Fenton, 2010; Teeling, Madsen, Murphy, Springer, & O'Brien, 2003). The Microchiroptera are now known as the Yangochiroptera and still contains the super-families *Emballonuroidea*, *Vespertilionoidea*, and *Noctilionoidea* but does not contain the super-family *Rhinolophoidea* (Fenton, 2010; Teeling et al., 2003). The Yangochiroptera is the suborder which contains New Zealand bat species.

Many species of bat, including both New Zealand species, only give birth to one offspring a year and because of this slow reproductive rate they are extremely vulnerable to

extinction (Gillingham, 1996). Bats are difficult to study due to their mostly cryptic and nocturnal behaviour, their distribution in frequently remote habitats with relatively small population sizes, and difficulties in their capture. This results in a limited knowledge of the ecology, diet and behaviour of many of the world's species of bats.

1.2. Bat ecology and diet

The diet of bats is extremely varied with around 70 % of bats being insectivorous and the remainder eating anything from fruit, nectar, pollen, and flowers to reptiles, birds, fish, and blood (Altringham, 2011). Insectivorous bats not only impact the structure of arthropod communities but can also influence whole terrestrial ecosystems (Moosman, Thomas, & Veilleux, 2012). Many bat species are predators of nocturnal, flying insects, several of which can be agricultural, horticultural, and forestry pests (Lee & McCracken, 2005; Long, Simpson, Ding, Heydon, & Reil, 1998; Moore, 2001). When large numbers of these pests are eaten, bats can potentially be successful biological control agents (Leelapaibul, Bumrungsri, & Pattanawiboon, 2005). It has been found that a colony of around 150 bats can consume over a million insects just in one season (Long et al., 1998), with lactating females consuming up to about two thirds of their body weight a night (Cleveland et al., 2006). Studies on the economic value of Brazilian free-tailed bats have found that these bats can increase the value of crops, such as cotton, by significantly reducing agricultural pest numbers and as a result reducing the frequency of pesticide spraying and delaying the need for new pesticides (Cleveland et al., 2006; Federico et al., 2008).

Bats can also have major roles in pollination, seed dispersal (Fleming & Sosa, 1994), and support their own unique, specialised, and often endemic ectoparasites (Dick & Patterson, 2006). There are only around eight mammalian families that are frugivores and even fewer, mostly bats, that are nectivores (Fleming & Sosa, 1994). Not only have bats been found to be successful in both pollination and seed dispersal but some plants have even evolved for bats to be their sole pollinator (Fleming & Sosa, 1994). Two species of bat are the sole pollinators of *Phenakospermum guyanense* and in the Solomon Islands, *Heliconia solomensis* is exclusively pollinated by one species of bat (Fleming & Sosa, 1994).

1.3. Methods of studying bat diet

The most well used and widely accepted method for studying bat diet is the physical search of faeces. Although the search of gut contents is much easier, as many of the contents have not been digested, this is not as commonly used because collection involves the death of often threatened or endangered bats (Whitaker, McCracken, & Siemers, 2009). Faeces collection, however, is cheap, fairly easy and is relatively non-invasive (Salvarina, Yohannes, Siemers, & Koselj, 2013). Faeces can be collected directly from bats caught in traps or held in cloth bags or they can be collected from below known roosts (Whitaker et al., 2009). Samples are often softened in ethanol and then teased apart and searched for identifiable fragments under a microscope (Shiel, McAney, Sullivan, & Fairley, 1997). Fragments are then identified down to the lowest possible taxonomic level (Shiel et al., 1997). Using the physical search of faecal pellets methodology, it was found that the diet of bats in Western Oregon were similar to the broad diets of the same species in other locations showing possible opportunistic feeding (Ober & Hayes, 2008). It has been found that these methods of physical search can provide an accurate picture of what bats have recently consumed in a non-destructive manner (Whitaker et al., 2009). In addition, many insectivorous bats can't digest the chitinous exoskeletons of insects and many large, identifiable pieces pass through the gut and are expelled in faecal pellets (Whitaker et al., 2009). However, many bats cull the easily identifiable fragments at their roost, eating only the soft, digestible parts of insects (Painter et al., 2009). This often results in the under-representation of soft bodied insects, such as moths and mayflies, in faecal pellets (Painter et al., 2009). Due to chewing by bats it is also often not possible to identify fragments in faecal pellets beyond order or family (Clare, Barber, Sweeney, Herbert, & Fenton, 2011).

Another commonly used method of studying bat diet is stable isotope analysis and this can prove very effective, especially when combined with physical search (York & Billings, 2009). Stable isotope analysis can be used to determine diet by comparing the isotopic differences of available food items with those incorporated into the tissues of the consumer (Herrera et al., 2001). Stable isotopes of animal tissues show dietary components over the time that those tissues were produced, so faeces are a good choice when recent diet is being investigated (Salvarina et al., 2013). (Painter et al., 2009) studied the diet of spotted bats, *Euderma maculatum*, in Arizona using stable carbon (^{13}C) and nitrogen (^{15}N) isotope

analysis. They found that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of faeces were similar to moths from the families Noctuidae, Lasiocampidae, and Geometridae so the bats were probably selecting these prey to eat (Painter et al., 2009). Stable isotope analysis can reveal ecological information other diet techniques can't, such as major dietary components, habitats used, trophic level, and individual foraging behaviours (Cryan, Stricker, & Wunder, 2012). However like physical faecal pellet search, it is usually impossible to identify dietary components down to species or even genus level.

Finally, DNA analysis is becoming a more regularly used method of studying bat diet. DNA from dietary fragments that have survived digestion can be recovered and used to make species level identifications (Whitaker et al., 2009). Polymerase Chain Reactions (PCR) are used to amplify the DNA of fragments left in a bats faeces and then the DNA sequences found are analysed to identify the foods actually eaten (Whitaker et al., 2009). (Clare et al., 2011) used molecular methods to study the diet of the little brown bat, *Myotis lucifugus*, and found that bats roosting in agricultural land had lower dietary richness than bats roosting in forests. It was also found that the bats had fluctuations in their diet over the maternity season, with fly species making up the majority of the diet early on and mayflies dominating later in the season (Clare et al., 2011). DNA analysis of arthropod fragments in bat faeces allows opportunities to not only identify prey to species level but also to characterise possible predator-prey relationships, such as opportunistic, specialised or generalised feeding (Clare, Fraser, Braid, Fenton, & Herbert, 2009). However disadvantages of DNA analysis, like the high cost and analytically challenging nature can be very off-putting to researchers (Clare et al., 2011).

Comparing native forest bat populations with those from exotic and/or altered forests and pasture can provide ground breaking information that is helpful to the conservation of bats. Studying bat diet can give information on how disturbances such as tree and habitat removal may affect some species (Fenton et al., 1998). Fenton et al. (1998) found that, after the loss of tree canopy in the African woodlands, prey availability did not differ significantly after canopy trees had been removed and bats present simply ate the most available prey. However, it was also found that bats were much more diverse, abundant and active in intact woodland than impacted and the bats would often roost in intact sites yet fly to adjacent impacted sites to forage (Fenton et al., 1998). Shiel, Duverge, Smiddy, and Fairley (1998)

studied the diet of the Leisler's bat by comparing pastoral and forest sites. They found that *Scathophaga stercoraria* and Scarabaeoidea were major components in pastoral bats diets but less significant in forest sites (Shiel et al., 1998). They also found that forest bat diet was more diverse than that of the pastoral bats (Shiel et al., 1998). Lacki, Johnson, Dodd, and Baker (2007) studied the diet of several species of bat in managed pine forests in Idaho and found that these bats consumed a very wide range of insect prey. They suggested that management of these forests should consider maintaining the diversity of insect communities so that bat populations residing there can obtain long-term health benefits (Lacki et al., 2007).

1.4. New Zealand bats

The only native terrestrial mammals present in New Zealand are bats (O'Donnell, 2000a). The long-tailed bat (*Chalinolobus tuberculatus* Forster, 1884), the lesser short-tailed bat (*Mystacina tuberculata* Gray, 1883), and the greater short-tailed bat (*Mystacina robusta* Dwyer, 1962) are all endemic and the only known species in New Zealand (Alexander, 2001). The greater short-tailed bat has not been seen since 1965 and is considered extinct even though its status has been revised to 'data deficient' (Daniel, 1990; O'Donnell et al., 2010). The long-tailed bat and the short-tailed bat are considered threatened; they are listed as vulnerable on the IUCN Red List of Threatened Animals and the Department of Conservation (DOC) lists long-tailed bats as 'nationally vulnerable', and lesser short-tailed bats as 'nationally endangered' (O'Donnell et al., 2010).

Both extant species of New Zealand bat were once widespread, but are now absent in many areas probably due to the reduction in forest area (Lloyd, 2001; O'Donnell, 2001). At present, the largest populations have been found in extensive areas of native forest, yet smaller numbers have been found in a variety of habitats, ranging from forest fragments and pine forest to scrubland and farmland (Lloyd, 2001; O'Donnell, 2001). The main reasons for the decline of bat populations are thought to be: loss of roosting and foraging habitat through forest clearance; competition for roost sites by introduced birds, mammals, and wasps; roost site disturbance by humans; and predation (O'Donnell, 2001). The New Zealand falcon, *Falco novaeseelandiae*, and Morepork, *Ninox novaeseelandiae*, are known avian predators of the long-tailed bat and short-tailed bat and in addition, the feral and domesticated cat is the introduced predator responsible for the majority of reported deaths

(Borkin & Ludlow, 2009; Lloyd, 2001; O'Donnell, 2001). Bat populations roosting in forests with limited forest clearing and habitat loss, for example beech forests, are still declining due to introduced mammalian predators such as rats and stoats, especially during beech masting years (Pryde, Lettink, & O'Donnell, 2006; Pryde, O'Donnell, & Barker, 2005).

The two species of short-tailed bats are the only species in the family Mystacinidae, which is a solely southern lineage endemic to New Zealand (Daniel, 1990). The closest relatives are thought to be the family Noctilionidae of South America and some fossil species have been identified in Australia implying Mystacinidae were present there in the early to middle Miocene (Lloyd, 2001; Teeling et al., 2003). The bats in New Zealand evolved separated from ground predators which is believed to be the reason for their remarkable adaptations to a partially terrestrial way of life (Altringham, 2011). The short-tailed bats have tough wing membranes which can be folded out of the way into skin pouches on the side of their bodies (Altringham, 2011; Lloyd, 2001). This, in addition to the short, stout legs and talons on the toes and thumbs, allows the bats to glean the forest floor and tree trunks for invertebrates as well as burrow into fallen trees to roost (Altringham, 2011; Lloyd, 2001). The majority of short-tailed bat diet consists of small invertebrates supplemented by fruit, nectar, and pollen (Jones, Webb, Sedgeley, & O'Donnell, 2003). Short-tailed bats consume the nectar of the native wood rose, *Dactylanthus taylorii*, and are the primary pollinator of this parasitic plant (Altringham, 2011; McCartney, Stringer, & Potter, 2007). Short-tailed bats are considered to be deep forest bats and are mainly associated with old growth indigenous forest, however small populations do exist in exotic forest and they have been detected at forest edges and will cross open areas to access food sources (Lloyd, 2005; Molloy, 1995).

In comparison, the long-tailed bat is a part of the very large and widespread family Vespertilionidae (Daniel, 1990). Its genus, *Chalinolobus*, contains five other species located in Australia, New Guinea, and New Caledonia (Hill & Smith, 1984). It is thought that the long-tailed bat evolved in isolation in New Zealand after an ancestral bat was windblown here from Australia (O'Donnell, 2005). Long-tailed bats are small, relatively fast flying, aerial insectivores (O'Donnell, 2001). They are widespread from the top of the North Island, through the west coast of the South Island, down to Stewart Island, and are even present on off shore Islands such as Kapiti Island, Great Barrier Island and Little Barrier Island

(O'Donnell, 2005). Historical anecdotes do, however, indicate that the long-tailed bat is now rare or absent from sites where it used to occur, such as Banks Peninsula (O'Donnell, 2000a). Long-tailed bats are most often associated with native forest, but are also found in plantation forest, and farmland (Alexander, 2001; Borkin & Parsons, 2011a). They frequently forage along forest edges, in clearings, above farmland, and above open water and streams (O'Donnell, Christie, & Simpson, 2006). Long-tailed bats mainly roost in the oldest trees present in the landscape (Borkin & Parsons, 2009; Sedgeley & O'Donnell, 1999b) as well as at least occasional use of caves, rock crevices, bridges, and buildings as roosts (O'Donnell, 2002; O'Donnell, 2005; Sedgeley & O'Donnell, 1999b). Knowledge of long-tail bat diet is based largely on observation and from one unpublished study (Gillingham, 1996). They apparently feed on flies (such as mosquitoes, crane flies and midges), beetles, small moths, and to a lesser degree caddisflies, mayflies, stoneflies and some true bugs (Molloy, 1995; O'Donnell, 2005).

Most research on New Zealand bats has focused on the rarer short-tailed bat because of its unique adaptations, broad diet, and pollinating role. Research on the short-tailed bats unique crawling behaviour has found that with increasing speed, the bats don't change from a walk to a run but simply stay with the same gait (Riskin, Parsons, Schutt, Carter, & Hermanson, 2006). O'Donnell et al. (2006) studied nocturnal activity in short-tailed bats and found that they were active through the whole night but more so at dawn and dusk. It was also found that most (82.6%) activity was measured further than 200 metres from the forest edge, indicating that short-tailed bats prefer foraging in forest interiors (O'Donnell et al., 2006). (Sedgeley, 2006) studied roosting ecology of short-tailed bats and found that trees with large stem diameters and large numbers of cavities were chosen most often for roosting. It was also found that bats in communal roosts were more selective of roosts than solitary bats (Sedgeley, 2006). (Borkin & Parsons, 2010b) found that short-tailed bats use plantation forests (*Pinus radiata*) for foraging, commuting, and roosting, and that these plantation forests were usually adjacent to native forests where these bats are known to inhabit.

Arkins, Winnington, Anderson, and Clout (1999) found that arthropod fragments recovered from short-tailed bat faeces could mostly be placed in the orders Coleoptera, Lepidoptera, Diptera, and Orthoptera. Pollen from *Knightia excelsa*, *Metrosideros* sp., and

Collospermum sp. have all been found in pellets and on the fur of short-tailed bats (Arkins et al., 1999). A variety of plant matter has also been found in pellets, such as wood and moss fragments and parts of flowers from *Knightia excelsa* and *Metrosideros* sp. (Arkins et al., 1999). In a study of captive short-tailed bats, (McCartney et al., 2007) found that the bats would take soft-bodied mealworms over heavily sclerotized beetles, weta, and crickets. In addition, nectar was visited at *Eucalyptus* sp., pohutukawa (*Metrosideros excelsa*), *Dactylanthus taylorii*, and *Clianthus puniceus* and sugar and water mixtures were readily taken (McCartney et al., 2007). However fruit, meat, eggs, cheese, snails, and some types of nectar were not visited at all (McCartney et al., 2007).

Research conducted on long-tailed bats has focused on roosting choice and behaviour with limited investigation of their diet. Long-tailed bats are highly selective of their roosts choosing large and old trees and cavities high above the ground (Sedgeley & O'Donnell, 1999a). In native forest they use many roosts in a small area often moving to new roosts each night and infrequently reusing roosts (O'Donnell & Sedgeley, 1999; Sedgeley & O'Donnell, 1999a, 1999b). These roost requirements may mean that these bats require large areas of mature forest and populations may be restricted by low availability of appropriate roost trees (Sedgeley & O'Donnell, 1999b). Long-tailed bats have been found to roost in exotic pine plantations and these forests are considered to be important in the preservation of bat populations because they provide a larger forest area than the likely alternative land use of pasture-based farming (Borkin, O'Donnell, & Parsons, 2011; Borkin & Parsons, 2009, 2010a; Moore, 2001). In exotic plantation forests, male long-tailed bats tend to choose roosts close to forest edges for optimal foraging, whereas females tend to choose roosts near to water sources (Borkin & Parsons, 2011a, 2011b). Long-tail bats are more active in summer, on warm nights, over rivers and riparian strips, and when invertebrate availability is high (Griffiths, 2007). Other studies have found that long-tailed bats forage along linear landscape features such as rivers, riparian strips, forest edges, and road habitats, often returning to the same sites on several occasions (O'Donnell, 2000b; O'Donnell et al., 2006).

Studies that have looked into the diet of long-tail bats have only involved physical searching of faecal material (Gillingham, 1996). In this study Gillingham (1996) found that Diptera made up the majority of the bats diet (29%) followed by Coleoptera (25%) and Lepidoptera (17%), with a large proportion of faecal fragments remaining unidentified.

These bats are present in plantation forests in New Zealand so there is potential for them to be of great value for forestry if they are eating insect pests. Like studies done elsewhere (see methods of studying bats), comparing diet in native forest to diet in exotic forest may give valuable information on the feeding habits of New Zealand bats.

1.5. Objectives

The aim of my thesis was to combine stable isotope analysis and traditional microscope analysis of faecal samples to identify the broad dietary components of long-tailed bats.

The specific objectives of this study were to:

1. Describe the diet of the New Zealand long-tailed bat using faecal and stable isotope analysis;
2. Describe any spatial differences in diet within and between plantation and native forest long-tailed bat populations;
3. Describe the diet of the New Zealand short-tailed bat and compare to the long-tailed bat;
4. Examine the proportions of the diet comprising aquatic versus terrestrial insects in the diet of long-tailed bats and short-tailed bats;
5. Analyse the ability of long-tailed bats to be pest control agents in plantation forests;
6. Compare the two dietary analysis techniques to find the most effective.

I hypothesise that stable isotope analysis will reveal that Lepidoptera are more important in the long-tailed bats diet than previously discovered due to the soft bodied insects being difficult to identify in faeces. The bats often discard the hard and easy to identify body parts such as the head and wings and simply eat the soft bodies so insects such as moths can often be under-represented when simply physically searching the bat pellets (Leelapaibul et al., 2005). I also hypothesise that long-tailed bats are opportunistic, generalist feeders and there will be marked differences in the diet of bats that roost in native forest compared to bats that roost in exotic forest.

1.6. References

- Alexander, J. (2001). *Ecology of long-tailed bats *Chalinolobus tuberculatus* (Forster, 1844) in the Waitakere Ranges: implications for monitoring*. (Master of Applied Science unpublished thesis), Lincoln University, Christchurch.
- Altringham, J. D. (2011). *Bats: from evolution to conservation* (Second ed.). New York: Oxford University Press.
- Arkins, A. M., Winnington, A. P., Anderson, S., & Clout, M. N. (1999). Diet and nectarivorous foraging behaviour of the short-tailed bat (*Mystacina tuberculata*). *Journal of Zoology, London*, 247, 183-187.
- Borkin, K. M., & Ludlow, E. (2009). Notes on New Zealand mammals 9: long-tailed bat (*Chalinolobus tuberculatus*) chased by morepork (*Ninox novaeseelandiae*). *New Zealand Journal of Zoology*, 36, 11-12.
- Borkin, K. M., O'Donnell, C., & Parsons, S. (2011). Bat colony size reduction coincides with clear-fell harvest operations and high rates of roost loss in plantation forest. *Biodiversity and Conservation*, 20(14), 3537-3548.
- Borkin, K. M., & Parsons, S. (2009). Long-tailed bats' use of a *Pinus radiata* stand in Kinleith Forest: Recommendations for monitoring. *New Zealand Journal of Forestry*, 53(4), 38-43.
- Borkin, K. M., & Parsons, S. (2010a). The importance of exotic plantation forest for the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). *New Zealand Journal of Zoology*, 37(1), 35-51.
- Borkin, K. M., & Parsons, S. (2010b). Plantation forests are used by the lesser short-tailed bat, *Mystacina tuberculata rhyacobia*. *New Zealand Journal of Zoology*, 37(1), 13-17.
- Borkin, K. M., & Parsons, S. (2011a). Home range and habitat selection by a threatened bat in exotic plantation forest. *Forest Ecology and management* 262, 845-852.
- Borkin, K. M., & Parsons, S. (2011b). Sex-specific roost selection by bats in clearfell harvested plantation forest: improved knowledge advises management. *Acta Chiropterologica*, 13(2), 373-383.
- Clare, E. L., Barber, E. R., Sweeney, B. W., Herbert, P. D. N., & Fenton, M. B. (2011). Eating local: influences of habitat on the diet of little brown bats (*Myotis lucifugus*). *Molecular Ecology*, 20, 1772-1780.

- Clare, E. L., Fraser, E. E., Braid, H. E., Fenton, M. B., & Herbert, P. D. N. (2009). Species on the menu of a generalist predator, the eastern red bat (*Lasiurus borealis*): using a molecular approach to detect arthropod prey. *Molecular Ecology*, *18*, 2532-2542.
- Cleveland, C. J., Betke, M., Federico, P., Frank, J. D., Hallam, T. G., Jason, H., . . . Kunz, T. H. (2006). Economic Value of the Pest Control Service Provided by Brazilian Free-Tailed Bats in South-Central Texas. *Frontiers in Ecology and the Environment*, *4*(5), 238-243.
- Cryan, P. M., Stricker, C. A., & Wunder, M. B. (2012). Evidence of cryptic individual specialisation in an opportunistic insectivorous bat. *Journal of Mammalogy*, *93*(2), 381-389.
- Daniel, M. J. (1990). Order Chiroptera. In M. C. King (Ed.), *The handbook of New Zealand mammals* (pp. 114-137). New Zealand: Oxford University Press
- Dick, C. W., & Patterson, B. D. (2006). Bat flies: Obligate ectoparasites of bats. In S. Morand, B. Krasnov, & R. Poulin (Eds.), *Micromammals and Macroparasites* (pp. 179-194). Japan: Springer
- Federico, P., Hallam, T. G., McCracken, G. F., Purucker, S. T., Grant, W. E., Correa-Sandoval, A. N., . . . Kunz, T. H. (2008). Brazilian Free-Tailed Bats as Insect Pest Regulators in Transgenic and Conventional Cotton Crops. *Ecological Applications*, *18*(4), 826-837.
- Fenton, M. B. (2010). Convergences in the diversification of bats. *Current Zoology*, *56*(4), 454-468.
- Fenton, M. B., Cumming, D. H. M., Rautenbach, I. L., Cumming, G. S., Cumming, M. S., Ford, G., . . . Mahlanga, Z. (1998). Bats and the Loss of Tree Canopy in African Woodlands. *Conservation Biology*, *12*(2), 399-407.
- Fleming, T. H., & Sosa, V. J. (1994). Effects of Nectarivorous and Frugivorous Mammals on Reproductive Success of Plants. *Journal of Mammalogy*, *75*(4), 845-851.
- Gillingham, N. J. (1996). *The behaviour and ecology of long-tailed bats (Chalinolobus tuberculatus Gray) in the central North Island*. (Master of Science Unpublished thesis), Massey University, Palmerston North.
- Griffiths, R. W. (2007). Activity patterns of long-tailed bats (*Chalinolobus tuberculatus*) in a rural landscape, South Canterbury, New Zealand. *New Zealand Journal of Zoology*, *34*(3), 247-258.

- Herrera, L. G., Hobson, K. A., Manzo, A., Estrada, D., Sanchez-Cordero, V., & Mendez, G. (2001). The role of fruits and insects in the nutrition of frugivorous bats: evaluating the use of stable isotope models. *Biotropica*, 33(3), 520-528.
- Jones, G., Webb, P. I., Sedgely, J. A., & O'Donnell, C. F. J. (2003). Mysterious Mystacina: how the New Zealand short-tailed bat (*Mystacina tuberculata*) locates insect prey. *The Journal of Experimental Biology*, 206(23), 4209-4216.
- Jones, K. E., Purvis, A., MacLarnon, A., Bininda-Emonds, O. R. P., & Simmons, N. B. (2002). A phylogenetic supertree of the bats (Mammalia : Chiroptera). *Biological Reviews*, 77(2), 223-259.
- Lacki, M. J., Johnson, J. S., Dodd, L. E., & Baker, M. D. (2007). Prey consumption of insectivorous bats in coniferous forests of north-central Idaho. *Northwest Science*, 81(3), 199-205.
- Lee, Y., & McCracken, G. F. (2005). Dietary variation of Brazilian free-tailed bats links to migratory populations of pest insects. *Journal of Mammalogy*, 86(1), 67-76.
- Leelapaibul, W., Bumrungsri, S., & Pattanawiboon, A. (2005). Diet of wrinkle-lipped free-tailed bat (*Tadarida plicata* Buchannan, 1800) in central Thailand: insectivorous bats potentially act as biological pest control agents. *Acta Chiropterologica*, 7(1), 111-119.
- Lloyd, B. (2005). Lesser short-tailed bat. In M. C. King (Ed.), *The Handbook Of New Zealand Mammals (2nd ed.)* (pp. 110-127). Melbourne: Oxford University Press.
- Lloyd, B. D. (2001). Advances in New Zealand mammalogy 1990-2000: Short-tailed bats. *Journal of the Royal Society of New Zealand*, 31(1), 59-81.
- Long, R. F., Simpson, T., Ding, T., Heydon, S., & Reil, W. (1998). Bats feed on crop pests in Sacramento Valley. *California Agriculture*, 52(1), 8-10.
- McCartney, J., Stringer, I., & Potter, M. A. (2007). Feeding activity in captive New Zealand lesser short-tailed bats (*Mystacina tuberculata*). *New Zealand Journal of Zoology*, 34, 227-238.
- Molloy, J. (1995). *Bat (Peka peka) recovery plan (Mystacina, Chalinolobus)*. Wellington: Department of Conservation.
- Moore, G. E. (2001). *Use of Kinleith forest by native New Zealand bats and effects of forestry* (Master of Science Unpublished thesis), Massey University, Palmerston North, New Zealand.

- Moosman, P. R., Thomas, H. H., & Veilleux, J. P. (2012). Diet of the widespread insectivorous bats *Eptesicus fuscus* and *Myotis lucifugus* relative to climate and richness of bat communities *Journal of Mammalogy*, *93*(2), 491-496.
- O'Donnell, C. F. J. (2000a). Conservation status and causes of decline of the threatened New Zealand Long-tailed Bat *Chalinolobus tuberculatus* (Chiroptera : Vespertilionidae). *Mammal Review*, *30*(2), 89-106.
- O'Donnell, C. F. J. (2000b). Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). *New Zealand Journal of Zoology*, *27*(3), 207-221.
- O'Donnell, C. F. J. (2001). Advances in New Zealand mammalogy 1990-2000: Long-tailed bat. *Journal of the Royal Society of New Zealand* *31*(1), 43-57.
- O'Donnell, C. F. J. (2002). Variability in numbers of long-tailed bats (*Chalinolobus tuberculatus*) roosting in Grand Canyon Cave, New Zealand: implications for monitoring population trends. *New Zealand Journal of Zoology*, *29*(4), 273-284.
- O'Donnell, C. F. J. (2005). NZ Long-tailed bat. In M. C. King (Ed.), *The handbook of New Zealand Mammals (2nd ed.)* (pp. 98-110). Melbourne: Oxford University Press.
- O'Donnell, C. F. J., Christie, J. E., Hitchmough, R. A., Lloyd, B., & Parsons, S. (2010). The conservation status of New Zealand bats, 2009. *New Zealand Journal of Zoology*, *37*(4), 297-311.
- O'Donnell, C. F. J., Christie, J. E., & Simpson, W. (2006). Habitat use and nocturnal activity of lesser short-tailed bats (*Mystacina tuberculata*) in comparison with long-tailed bats (*Chalinolobus tuberculatus*) in temperate rainforest. *New Zealand Journal of Zoology*, *33*, 113-124.
- O'Donnell, C. F. J., & Sedgely, J. A. (1999). Use of roosts by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate rainforest in New Zealand. *Journal of Mammalogy*, *80*(3), 913-923.
- Ober, H. K., & Hayes, J. P. (2008). Prey selection by bats in forests of western Oregon. *Journal of Mammalogy*, *89*(5), 1191-1200.
- Painter, M. L., Chambers, C. L., Siders, M., Doucett, R. R., Whitaker, J. O., Jr., & Phillips, D. L. (2009). Diet of spotted bats (*Euderma Maculatum*) in Arizona as indicated by fecal analysis and stable isotopes. *Canadian Journal of Zoology*, *87*, 865-875.

- Pryde, M. A., Lettink, M., & O'Donnell, C. F. J. (2006). Survivorship in two populations of long-tailed bats (*Chalinolobus tuberculatus*) in New Zealand. *New Zealand Journal of Zoology*, 33(2), 85-95.
- Pryde, M. A., O'Donnell, C. F. J., & Barker, R. J. (2005). Factors influencing survival and long-term population viability of New Zealand long-tailed bats (*Chalinolobus tuberculatus*): Implications for conservation. *Biological Conservation*, 126(2), 175-185.
- Riskin, D. K., Parsons, S., Schutt, W. A., Carter, G. G., & Hermanson, J. W. (2006). Terrestrial locomotion of the New Zealand short-tailed bat *Mystacina tuberculata* and the common vampire bat *Desmodus rotundus*. *Journal of Experimental Biology*, 209(9), 1725-1736.
- Salvarina, I., Yohannes, E., Siemers, B. M., & Koselj, K. (2013). Advantages of using fecal samples for stable isotope analysis in bats: evidence from a triple isotopic experiment. *Rapid Communications in Mass Spectrometry*, 27(17), 1945-1953.
- Sedgeley, J. A. (2006). Roost site selection by lesser short - tailed bats (*Mystacina tuberculata*) in mixed podocarp - hardwood forest, Whenua Hou/Codfish Island, New Zealand. *New Zealand Journal of Zoology*, 33(2), 97-111.
- Sedgeley, J. A., & O'Donnell, C. F. J. (1999a). Factors influencing the selection of roost cavities by a temperate rainforest bat (*Vespertilionidae* : *Chalinolobus tuberculatus*) in New Zealand. *Journal of Zoology*, 249, 437-446.
- Sedgeley, J. A., & O'Donnell, C. F. J. (1999b). Roost selection by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate New Zealand rainforest and its implications for the conservation of bats in managed forests. *Biological Conservation*, 88(2), 261-276.
- Shiel, C. B., Duverge, P. L., Smiddy, P., & Fairley, J. S. (1998). Analysis of the diet of Leiser's bat (*Nyctalus leisleri*) in Ireland with some comparative analyses from England and Germany. *Journal of Zoology, London*, 246, 417-425.
- Shiel, C. B., McAney, C., Sullivan, C., & Fairley, J. S. (1997). *Identification of arthropod fragments in bat droppings* (Vol. 7). London: The Mammal Society.
- Teeling, E. C., Madsen, O., Murphy, W. J., Springer, M. S., & O'Brien, J. (2003). Nuclear gene sequences confirm an ancient link between New Zealand's short-tailed bat and

South American noctilionoid bats. *Molecular Phylogenetics and Evolution*, 28(2), 308-319.

Whitaker, J. O., McCracken, G. F., & Siemers, B. M. (2009). Food habits analysis of insectivorous bats. In T. H. Kunz, & S. Parsons (Eds.), *Ecological and behavioural methods for the study of bats* (Second ed.). Baltimore: The Johns Hopkins University Press.

Wilson, D. E. (1997). *Bats in question*. Melbourne: CSIRO publishing.

York, H. A., & Billings, S. A. (2009). Stable-isotope analysis of diets of short-tailed fruit bats (Chiroptera: Phyllostomidae: *Carollia*). *Journal of Mammalogy*, 90(6), 1469-1477.

Chapter Two

2. The use of physical search methods to identify the diet of the New Zealand long-tailed bat, *Chalinolobus tuberculatus*.

2.1. Abstract

Insect fragments were identified from New Zealand long-tailed bat (*Chalinolobus tuberculatus*) faecal samples collected from under known roosts and harp traps in exotic Kinleith Forest and native Pureora Forest Park in the central North Island, New Zealand. In total 2247 fragments were mounted on slides (1335 from Pureora and 912 from Kinleith) and 15% of these were unidentifiable (346). Over both study sites, Diptera made up the largest percentage of the diet with 40%, Lepidoptera comprised 24%, Coleoptera 18%, Trichoptera 0.8%, and Hymenoptera 0.36%. Whole mites or mite remains comprised 0.8% of all fragments. Eleven fragments in total (one from Pureora and ten from Kinleith) were found to be from Lepidoptera larvae, which contradicts previous observations of long-tailed bats not eating terrestrial, non-winged insects. New Zealand long-tailed bats in Pureora Forest and Kinleith Forest were found to have opportunistic, generalist diets. There were significant differences in the diet of the bats in native forest with the bats in exotic forest, showing long-tailed bats can be flexible in regards to the environment they live in whilst maintaining a normal diet.

2.2. Introduction

In New Zealand there are only two extant species of bat, the long-tailed bat (*Chalinolobus tuberculatus*) and the lesser short-tailed bat (*Mystacina tuberculata*), both of which are endemic (Daniel, 1990). Each of these species are considered threatened; they are listed as vulnerable on the IUCN Red List of Threatened Animals and the Department of Conservation (DOC) lists long-tailed bats as 'nationally vulnerable', and short-tailed bats as 'nationally endangered' (O'Donnell et al., 2010). As the only extant representative, the short-tailed bat belongs to the distinctively southern family Mystacinidae, with fossil species also located in Australia (Lloyd, 2005). The long-tailed bat, on the other hand, belongs to the

largest family in the suborder Yangochiroptera and one of the most widely dispersed mammal families in the world, Vespertilionidae (O'Donnell, 2005).

Long-tailed bats are small but fast flying aerial insectivores (O'Donnell, 2001). They are mostly associated with native forest, yet have also been found to roost in caves, buildings, pine forest, and other exotic trees (Borkin & Parsons, 2011a; O'Donnell, 2002; O'Donnell, 2005; Sedgeley & O'Donnell, 1999b). They are known to frequently forage along forest edges, in clearings, above farmland, and above open water and streams (Alexander, 2001; Arkins et al., 1999; O'Donnell et al., 2006). Long-tailed bats are widely distributed throughout the North Island, through the Western South Island, to Stewart Island, and also present on many offshore islands such as Little Barrier, Great Barrier, and Kapiti Islands (O'Donnell, 2005). Although these bats are quite wide spread, there is some information and many historical anecdotes indicating that these bats are now present in lower numbers than before and are even absent in some areas where they used to be, such as Banks Peninsula (Molloy, 1995; O'Donnell, 2000a). Roosting choice and behaviour have been the main focus for long-tailed bat research, with limited investigation of their diet. Studies that have looked into the diet as part of a larger study have only involved physical searching of faecal material (Gillingham, 1996). Most of the information to date about diet of long-tailed bats has come from a single, unpublished study by Gillingham (1996). In that study it was found that Diptera made up the majority of the bats diet (29%) followed by Coleoptera (25%) and Lepidoptera (17%), with a large proportion (25.9%) of faecal fragments unidentified (Gillingham, 1996).

Information on ecology and behaviour can be obtained from knowledge of a species diet, and can be essential for their management (Painter et al., 2009; Whitaker & Karatas, 2009). When an endangered species is involved it is even more important as their diet may provide clues to potential drivers of their decline (Kurta & Whitaker, 1998). Learning more about diet may also assist with possible husbandry efforts if abandoned young or injured adult bats are found as well as with potential future translocation projects. As invertebrate ecosystem and community structure will obviously influence insectivorous bats; determinates of their distribution will also be an important part of bat management (Moosman et al., 2012). The physical search of faeces to determine diet is one of the most popular techniques and has been found to be highly reliable (Long et al., 1998; Whitaker et

al., 2009). Faeces collection is cheap, fairly easy and is relatively non-invasive for the bats, in stark contrast to using stomach contents for physical search methods (Salvarina et al., 2013; Whitaker et al., 2009). In this chapter I use traditional physical faecal sample search to identify the broad dietary components of two populations of long-tailed bat.

2.3. Methods

2.3.1. Study area

Insects and long tailed bat faecal samples were collected from two study sites, Pureora and Kinleith Forests. Pureora Forest Park is located between Lake Taupo and Te Kuiti (Fig. 1) on the North Island of New Zealand (latitude -38.56, longitude 175.68). In 1946 Pureora Forest Park was one of the last native forests to be opened for logging and it holds the last remnants of extensive native podocarp forests that once covered most of the central North Island. The Forest Park is managed by the Department of Conservation (DOC) in order to protect and monitor its natural and historic features. This protected area is 78,000 ha of rich lowland podocarp forest, comprising rimu (*Dacrydium cupressinum*), mataī (*Prumnopitys taxifolia*), miro (*Prumnopitys ferruginea*) and tawa (*Beilschmiedia tawa*) among others, and high altitude montaine forest with tōtara (*Podocarpus totara*), tāwheowheo (*Quintinia serrata*) and kamahi (*Weinmannia racemosa*) (Conservation, 2012). Nationally important wetlands and shrublands are also present within the park. These forests grow on pumice and ash derived soils and house many endangered native species including both species of New Zealand bat (Conservation, 2012).

Kinleith Forest is centred around Tokoroa on the North Island of New Zealand (latitude -37.47, longitude 175.53). The forest is about 96,652 ha of pine plantation (including production and non-production areas, unstocked areas, and reserves) first planted in 1924 (K. Borkin, personal communication). It comprises predominantly *Pinus radiata*, however, smaller plantings of *Pseudotsuga menziesii* and *Eucalyptus* are present (Borkin & Parsons, 2011a). Native shrubs, ground, and tree ferns are present in the understorey of many, especially older, stands (Moore, 2001). At least 10% of Kinleith Forest is protected native forest, such as broadleaf podocarp forests occupying gorges and riparian scrubland, fernland and wetlands (Moore, 2001). The native and exotic stands are home to many native birds and both species of New Zealand bat (Borkin & Parsons, 2011b). The highest

points of Kinleith Forest reach around 750 meters in altitude and the climate is cool and humid, with a mean rainfall of 1600 mm per year (Ogden, Braggins, Stretton, & Anderson, 1997). The soils are coarse and free draining because of deep pumice deposits (Ogden et al., 1997).

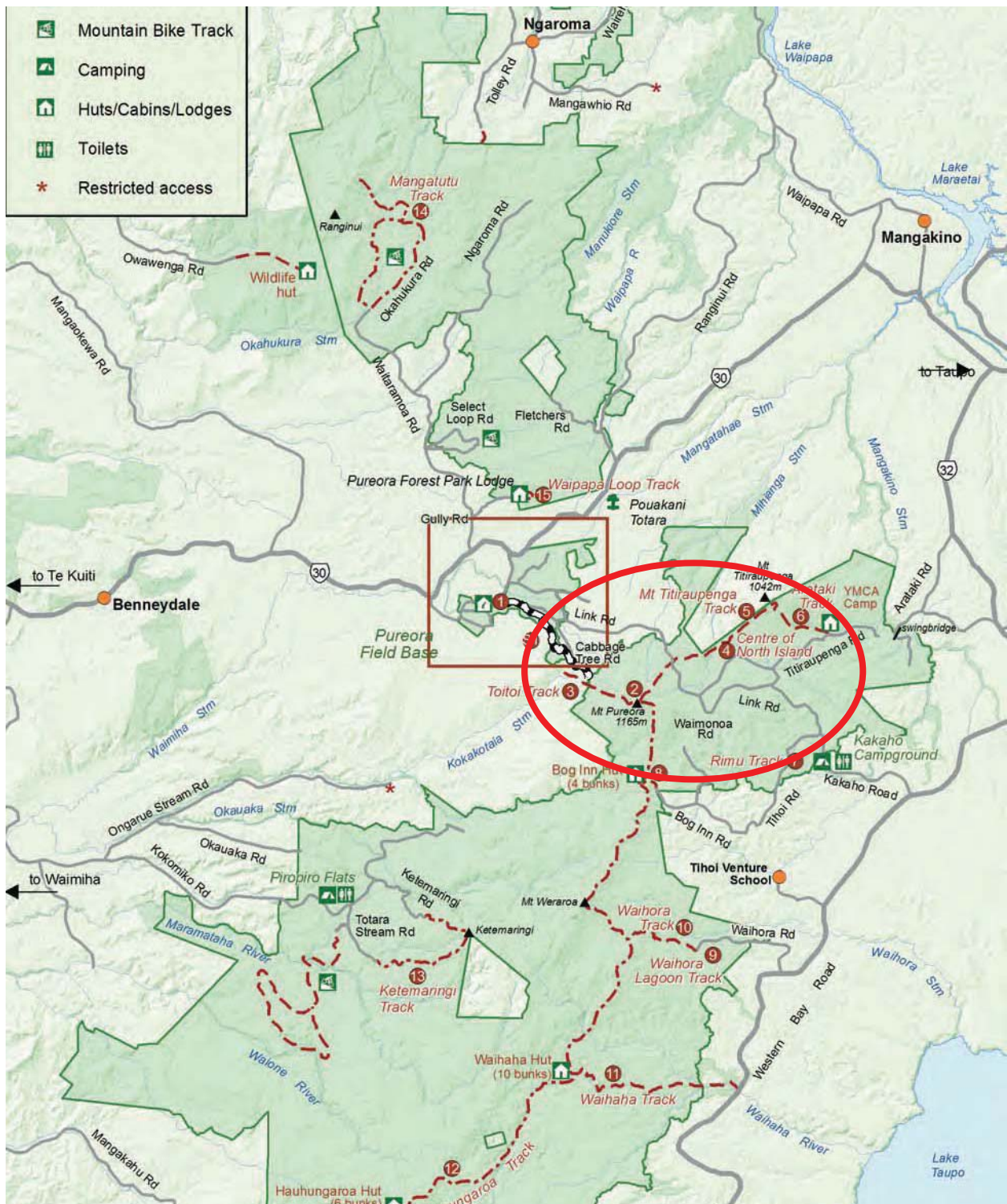


Figure 1 Map of Pureora Forest Park, in the central North Island of New Zealand, where all native forest sampling took place. Circled area is where all insect light trapping and long-tailed bat faecal sampling occurred. Image from Pureora Forest Park brochure (Conservation, 2012)

2.3.2. Faeces collection

Long-tailed bat faecal pellets were collected from Pureora Forest Park in January during the Austral summer of 2013. The bats were caught in harp traps placed in front of roost entrances and over streams known to be used for foraging at sunset. Captured bats were transferred into cloth bags where they were held for around twenty minutes while they were weighed, measured, and banded (if not already). Any faeces left behind in the cloth bags and in the harp traps themselves were collected for diet analysis. Ninety individual pellets were collected.

Faecal samples from long-tailed bats that were resident in Kinleith Forest were collected from under nine known roosts, in November and February of 2007 and in February and March of 2008, during a larger study into the ecology of bats within plantation forest (Borkin, 2010). These day roosts were found by radio-tracking bats during the day (radio transmitters Model BD-2, Holohil Systems Ltd, Canada) that were captured either using mistnets placed across forestry roads or at roost sites using nets. Bats in Kinleith Forest were captured, handled, and radiotracked under permits from the Department of Conservation (Low Impact, Research and Collection Permit BP-18899-RES under Section 53, Wildlife Act 1953) and the University of Auckland Animal Ethics Committee (AEC 08/2004/R282). Roosts were generally under peeling bark of long dead spars (Borkin, 2010).

2.3.3. Invertebrate sampling

Invertebrate light traps were set up in each study site in January 2013 to characterise potential food sources available to long-tailed bats present in each forest. The traps comprised a fluorescent light set over a white tray, which was filled with water and dish washing detergent. Insects were attracted to the light, fell in the water and were trapped. Six light traps were set up overnight (approximately eight hours) in Pureora Forest around the area where bat faecal samples were collected; three at locations along roads and three along streams (Fig. 1). Six light traps were also set up overnight (approximately eight hours) in Kinleith Forest around the Wawa Road area (long-tailed bat faecal samples were collected from a slightly larger area in this forest); one trap by a road in each of the three age groups of pine (0-5, 6-10, and 11-25 years), and one trap by a stream in each of the pine age groups (Fig. 2). The contents of each trap were frozen until analysis and insects identified to family level or lower where possible. Some Lepidoptera, however, were assigned to morphotypes.

Identification was aided with the use of insect keys, mostly from (Triplehorn & Johnson, 2005).

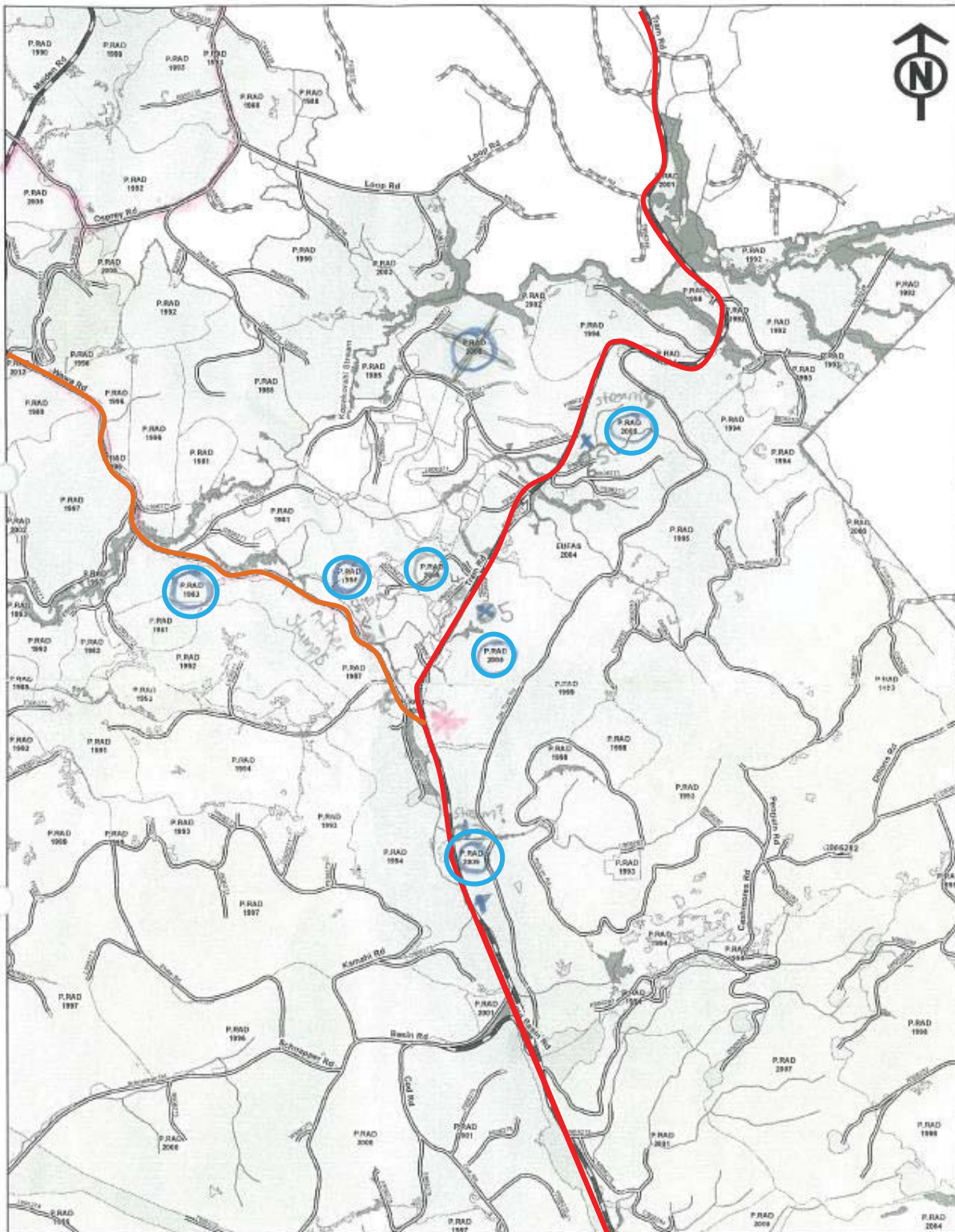


Figure 2 Map of Kinleith Forest, in the central North Island of New Zealand, where all exotic forest sampling took place. Circled areas are the stands of pine plantation where light traps were set, the red line is Tram Rd and the orange line is Wawa Rd.

2.3.4. Physical search of faeces

Methods for the physical search of long-tailed bat faeces were adapted from Whitaker et al. (2009) and Shiel et al. (1997). Twenty randomly chosen faecal pellets from Pureora Forest and twenty from Kinleith Forest were put in individual vials filled with 90% ethanol. These were left a minimum of 24 hours to soften and partially break up. Each vial was then tipped into a small petri dish filled with more ethanol. The faecal pellets were teased apart gently using fine entomological pins attached to metal rods and the contents searched under a dissection microscope for identifiable insect parts, such as parts of legs, claws, eyes, antennae, tarsi, segments of wing, eggs and halteres. Once found, these fragments were transferred onto labelled microscope slides in order to be identified once all pellets had been searched. Fragments were identified down to either order or family where possible using reference insects caught in light traps in Pureora and Kinleith Forest and pictures and keys in Whitaker et al. (2009) and Shiel et al. (1997). Percent frequency of prey items was calculated once identification was completed.

2.3.5. Data analysis

Insect fragments identified in Kinleith Forest and Pureora Forest long-tailed bat faeces were compared to each other and to the insects identified in light traps using a chi-squared analysis in Statistix (Version 9.0).

2.4. Results

2.4.1. Invertebrate sampling analyses

Over all sites, Lepidoptera (moths) accounted for 71% of insects collected in light traps (Fig. 3), with geometrid-like moths and noctuid-like moths comprising 31% and 20%, respectively (Table 1). Diptera (flies) accounted for 15% of the insects collected (with more caught in Pureora than Kinleith, Fig. 3), with the most common being Tipulidae (6%) and Mycetophilidae (3%) (Table 1). Other prevalent insect orders collected were Coleoptera (beetles) (Fig. 3, 4%), with the most common being Cerambycidae (1%) and Scarabeidae (1%) with more caught in Kinleith than Pureora, and Trichoptera (caddisflies) (7%) (Table 1). A few insects were collected from other orders but were rare and thus not considered further as potential prey.

2.4.2. Bat faeces diet analyses

Altogether, 2247 fragments were mounted on slides (1335 from Pureora and 912 from Kinleith) with 15% unidentifiable (346). Over both study sites, Diptera comprised 40% of all fragments (Table 2). This was followed by Lepidoptera comprising 24%, Coleoptera 18%, Trichoptera 0.8%, and Hymenoptera 0.36% of all fragments. Whole mites or mite remains comprised 0.8% of all fragments. In Pureora Forest, Diptera comprised 39% of fragments followed by Lepidoptera comprising 24% and Coleoptera 22% (Fig. 4). In Kinleith Forest, Diptera comprised 43% of fragments followed by Lepidoptera comprising 24% and Coleoptera 13% (Fig. 4). In addition, Hymenoptera comprised 0.88% and Trichoptera 0.2% of fragments in Kinleith Forest (Fig. 4). Whereas, in Pureora Forest, no Hymenoptera fragments were identified and Trichoptera made up 1.2% (Fig. 4). The diet of long-tailed bats in Pureora Forest was significantly different to that of long-tailed bats in Kinleith Forest ($\chi^2=51.17$, $df=6$, $P<0.001$). Trichoptera and Coleoptera were proportionally more abundant in Pureora Forest and Hymenoptera and Diptera were proportionally more abundant in Kinleith Forest. In both Kinleith Forest ($\chi^2=762.75$, $df=9$, $P<0.001$) and Pureora Forest ($\chi^2=878.94$, $df=9$, $P<0.001$) the faecal pellet invertebrate composition differed significantly from that in the light traps with Coleoptera and Diptera proportionally more abundant and Lepidoptera, Trichoptera, and Hemiptera less abundant in faecal pellets compared to the light trap collections.

Of the fragments that were identified to family, most were Tipulidae (6%, Table 2) followed by individual fragments from Culicidae, Chironomidae, Curculionidae, Carabidae, Scarabaeidae, and Elateridae. Double the number of Tipulidae fragments were identified in Kinleith samples compared to the Pureora samples (Table 2). Eleven (0.5%) fragments were identified to be from Lepidoptera larvae and 10 of these were found in Kinleith samples and only one in Pureora samples (Table 2). Larval Lepidoptera were identified from distinctive features such as true legs, mandibles, and anal combs.

Table 1 Insects identified in light traps from Pureora Forest (six traps set overnight) and Kinleith Forest (six traps set overnight) in January 2013.

Insects in traps	Total number	Pureora number	Kinleith number	Percent total	Percent Pureora	Percent Kinleith
<i>Lepidoptera</i>	1812	908	904	70.67	71.72	69.65
Geometrid-like moths	800	400	400	31.20	31.60	30.82
Noctuid-like moths	500	250	250	19.50	19.75	19.26
Tortricidae like moths	100	50	50	3.90	3.95	3.85
Tineidae like moths	50	25	25	1.95	1.97	1.93
Small black stripe moths	200	100	100	7.80	7.90	7.70
Medium fat body moths	150	75	75	5.85	5.92	5.78
Pterophoridae	12	8	4	0.47	0.63	0.31
<i>Trichoptera</i>	183	89	94	7.14	7.03	7.24
Helicopsychidae	69	59	10	2.69	4.66	0.77
Leptoceridae	31	2	29	1.21	0.16	2.23
Hydrobiosidae	24	3	21	0.94	0.24	1.62
Other	59	25	34	2.30	1.97	2.62
<i>Coleoptera</i>	98	24	74	3.82	1.90	5.70
Cerambycidae (Prionoplusreticularis)	30	10	20	1.17	0.79	1.54
Scarabaeidae (Odontriaxanthosticta)	29	1	28	1.13	0.08	2.16
Elateridae	17	1	16	0.66	0.08	1.23
Other	22	12	10	0.86	0.95	0.77
<i>Diptera</i>	389	221	168	15.17	17.46	12.94
Tipulidae	161	95	66	6.28	7.50	5.08
Mycetophilidae	73	59	14	2.85	4.66	1.08
Chironomidae	44	9	35	1.72	0.71	2.70
Culicidae	35	19	16	1.37	1.50	1.23
Other	76	39	37	2.95	3.09	2.85
<i>Hymenoptera</i>	20	11	9	0.78	0.87	0.69
<i>Hemiptera</i>	35	3	32	1.37	0.24	2.47
Cicadellidae	19	0	19	0.74	0.00	1.46
Other	7	3	4	0.63	0.24	1.01
<i>Orthoptera</i>	9	4	5	0.35	0.32	0.39
<i>Neuroptera</i>	3	1	2	0.12	0.08	0.15
<i>Ephemeroptera</i>	1	1	0	0.04	0.08	0.00
<i>Other</i>	14	4	10	0.55	0.32	0.77
Total	2564	1266	1298	100.00	100.00	100.00

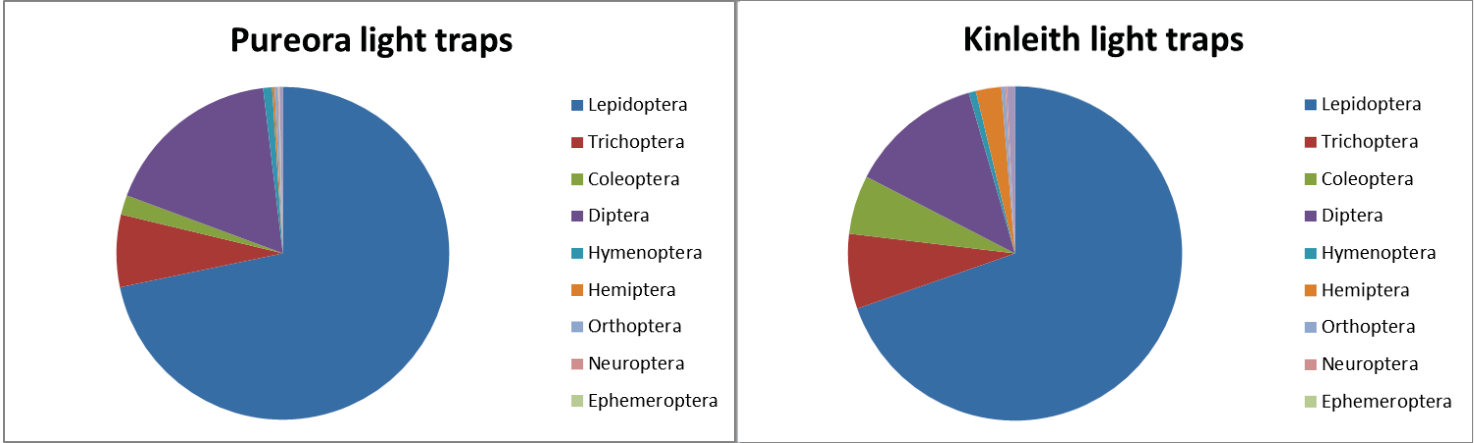


Figure 3 Percent frequency of insects identified in Pureora Forest and Kinleith Forest light traps

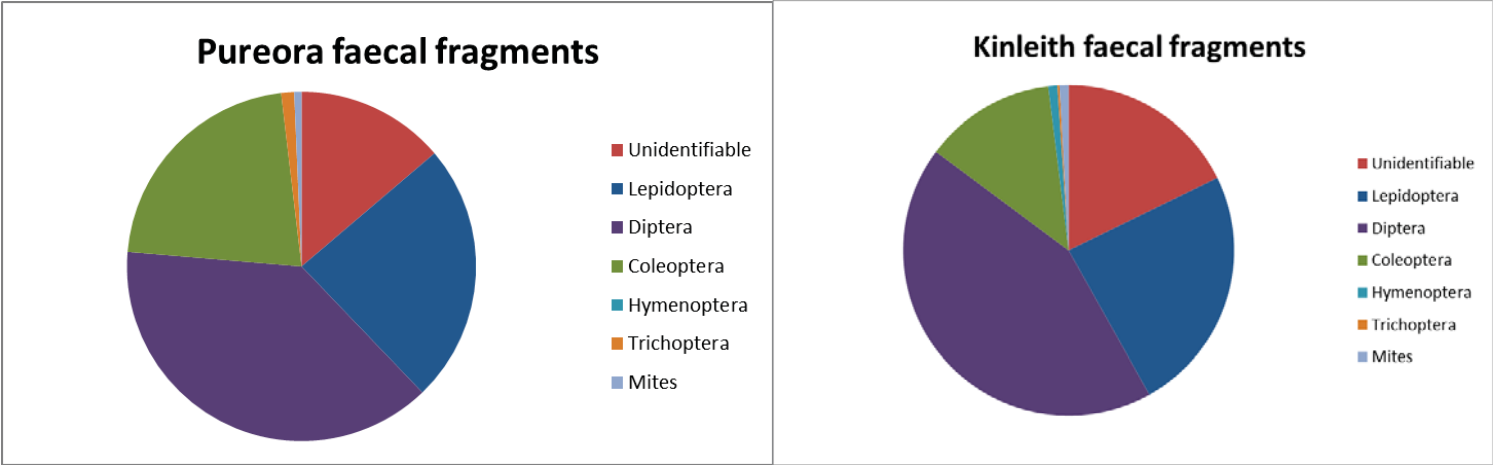


Figure 4 Percent frequency of insect fragments identified in Pureora Forest and Kinleith Forest long-tailed bat faeces.

Table 2 Fragments identified from Pureora Forest and Kinleith Forest long-tailed bat faeces.

Lepidoptera	541	321	220	24.08	24.04	24.12
<i>Larvae</i>	11	1	10	0.49	0.07	1.10
Diptera	909	514	395	40.45	38.50	43.31
<i>Tipulidae</i>	126	41	85	5.61	3.07	9.32
<i>Culicidae</i>	2	2	0	-	-	0.00
<i>Chironomidae</i>	2	0	2	-	0.00	-
Coleoptera	408	291	117	18.16	21.80	12.83
<i>Curculionidae</i>	1	0	1	-	0.00	-
<i>Carabidae</i>	2	2	0	-	-	0.00
<i>Scarabaeidae</i>	3	3	0	-	-	0.00
<i>Elateridae</i>	2	1	1	-	-	-
Hymenoptera	8	0	8	0.36	0.00	0.88
Trichoptera	18	16	2	0.80	1.20	0.22
Mites	17	9	8	0.76	0.67	0.88
Total	2247	1335	912	100.00	100.00	100.00

2.5. Discussion

Some of the most abundant insects caught in light traps, i.e. Lepidoptera and Diptera, were also the most abundant insect fragments identified from faecal pellets. When it was possible to identify Diptera fragments in faeces to the family level, it was most often Tipulidae, Culicidae, and Chironomidae which were also the most common families caught in traps. Tipulidae fragments were quite characteristic and could be easily identified from their antennae, eggs, legs, and halteres whereas, most other Diptera fragments were much harder to identify even to order. The heavy sclerotisation and larger size of Coleoptera fragments also made identification to order easier. However, identification to family was still difficult. Lepidoptera fragments were easily identified from the presence of scales and thin, transparent walls, yet it was not possible to distinguish any to family level. The few Hymenoptera fragments were identified because of the presence of a stinger or hamuli on the wing. Most invertebrate fragments eaten were small, however a few faecal pellets contained the remains of a sole large insect (Tipulidae and Curculionidae).

The bats appear to be eating what is most commonly available in the habitat suggesting they are opportunistic, generalist feeders. Selectivity between prey items in flight would be difficult due to the flying speed of the bats and the relatively short detection range of echolocation (Kurta & Whitaker, 1998). Therefore, long-tailed bats are probably selecting particular habitats to forage in and then feeding on the most abundant and appropriately-sized prey in those habitats, rather than selecting the insects themselves (Kurta & Whitaker, 1998). This would explain why more Trichoptera were caught in light traps than were found in faecal pellets; fewer bats would have been foraging in habitats where Trichoptera were more abundant (i.e. stream habitats) than those such as roads where other insects are much more abundant. Many more Coleoptera fragments were found in Pureora samples than in Kinleith despite many more Coleoptera being caught in the Kinleith light traps. This is because the Coleoptera present in Kinleith Forest were probably too large for long-tailed bats to consume (e.g. longhorn beetles) compared to those present in Pureora Forest. The opposite occurred for Diptera; more fragments were found in Kinleith samples than in Pureora despite more Diptera being caught in Pureora light traps than Kinleith. Again this was likely because the Diptera at Pureora were the larger sized Tipulidae whereas smaller Diptera dominated in Kinleith traps, such as a large number of Chironomidae (Table 1). A large number of Lepidoptera were caught in light traps at both study sites (71%), yet this was not reflected in Lepidoptera fragments identified in faecal samples (24%). This is discussed later in this chapter but is likely a result of many soft bodied insects, such as Lepidoptera, being under-represented in faecal pellets due to thorough chewing and digestion and large wings being discarded at roosts (O'Donnell, 2005).

Closely related Australian *Chalinolobus* are solely insectivorous and from observations of long-tailed bats feeding and the results from this study it seems that their diet is most likely composed exclusively of nocturnal, flying insects (Gillingham, 1996). However, this study also found several fragments that appear to be larval Lepidoptera; identified from distinctive features such as true legs, mandibles, and anal combs (Fig. 5). It is possible that larvae were ballooning (wind dispersing) from silk strands when the long-tailed bats were foraging, allowing the bats to feed on them whilst flying. For example, two invasive species in New Zealand, the gypsy moth (*Lymantria dispar*) and the light brown apple moth (*Epiphyas postvittana*), are known to balloon in order to disperse (Brockerhoff et al., 2011;

Ross, 2004). Alternatively long-tailed bats could be capable of facultative gleaning depending on changes in prey availability, as has been found for other bat species such as *Myotis lucifugus* and *M. septentrionalis* (Feldhamer, Carter, & Whitaker, 2009). A large number of whole and fragmented mites were also identified in long-tailed bat faecal pellets in this study. These mites were probably ingested while grooming or were present on other invertebrates, such as Scarabaeidae, and then ingested by the bats (Shiel et al., 1998).



Figure 5 Fragments identified in long-tailed bat Faecal pellets thought to belong to Lepidoptera larvae; (a) a true leg (b) a mandible and (c) an anal comb.

Gillingham (1996) found that the long-tailed bats in Grand Canyon Cave ate predominately Diptera (29%), Lepidoptera (25%), and Coleoptera (17%) with a large proportion of the fragments that were identifiable to family being Tipulidae. This is very similar to the results of this study, although a much larger percentage of fragments were Diptera (40%). However, some differences between the two studies were evident. Lepidoptera larval fragments were found in this study yet nothing of the sort was identified by Gillingham. In addition, it appears that the long-tailed bats from Grand Canyon Cave have a slightly more diverse diet than the bats from this study as fragments were found from Hemiptera, Ephemeroptera, Muscoidea, Psychodidae, and Calliphoridae (Gillingham, 1996). It is possible that the diet of bats from Pureora and Kinleith Forests may be equally as diverse, as some of these insects were caught in light traps, but fragments may have been too chewed and digested to be identified. However, Gillingham's study site was native bush bordered with farmland so it is more likely that these differences were due to different environments.

The diets of native Pureora Forest long-tailed bats are significantly different to those of exotic Kinleith Forest long-tailed bats. This means that when inhabiting different kinds of environment containing altered species diversity, long-tailed bats are likely to be able to adjust their diet to simply eat what insects are most abundant. Thus as the bats are clearly opportunistic, generalist feeders the absence of extensive tracts of native forest are obviously not detrimental to the bats as long as alternative stands of forest are available. If invertebrates are the right size and are abundant as pest species are likely to be then bats may be an effective biocontrol agent. However, as with other generalist opportunistic predators, they will never be as effective as more specialised species (McKracken et al., 2012). The abundance of adults of aquatic larvae in the diet in proportion to their abundance in the environment also suggests that bats are not reliant on nearby water ways for food supply.

The physical search of faeces to determine diet has always been the standard technique in Chiropterology (Long et al., 1998; Whitaker et al., 2009), however, bats have been found to cull and discard many of the hard and identifiable insect parts before ingestion and thorough chewing and digestion means many soft bodied insects may go unnoticed (Clare et al., 2011; Leelapaibul et al., 2005; Painter et al., 2009). Some insect

groups may be missed entirely and the majority of the remainder can only be identified to order or family (Clare et al., 2011; Whitaker et al., 2009). The proportion of Lepidoptera and Trichoptera in the diet of the long-tailed bat is thus probably underestimated in this study. Furthermore, the sampling of prey available was limited; accurate assessments of insect abundance are quite difficult to achieve and even then it may not be representative of the prey actually available to the bats (Andreas, Reiter, & Benda, 2012).

In summary, New Zealand long-tailed bats in Pureora Forest and Kinleith Forest have opportunistic, generalist diets. There were significant differences in the diet of the bats in native forest with the bats in exotic forest, showing long-tailed bats can be flexible in regards to the environment they live in whilst maintaining a normal diet. This study also showed that long-tailed bats in Pureora and Kinleith Forests are not significantly feeding on aquatic insects such as Trichoptera. Thus ongoing management probably needs to focus more on roosting and predation. It is hard to draw solid conclusions, especially in regards to potential pest control services of long-tailed bats, as it is nearly impossible to identify fragments to species level with physical faecal search methods in order to claim long-tailed bats are eating pine pests. For this reason, future research should be focused on DNA or stable isotope analysis of dietary items in order to get a more accurate identification. Although long-tailed bats are less active in winter, future research should also look into seasonal changes in diet over native and exotic habitat to identify any shifts in diet. Changes in diet over seasons could show flexible and opportunistic feeding or more selective feeding in certain seasons (Andreas et al., 2012). The techniques used here to characterise long-tailed bat diet will be used as a comparison in the next chapter.

2.6. References

- Alexander, J. (2001). *Ecology of long-tailed bats *Chalinolobus tuberculatus* (Forster, 1844) in the Waitakere Ranges: implications for monitoring*. Master of Applied Science unpublished thesis, Lincoln University, Christchurch.
- Andreas, M., Reiter, A., & Benda, P. (2012). Prey selection and seasonal diet changes in the western barbastelle bat (*Barbastella barbastellus*). *Acta Chiropterologica*, 14(1), 81-92.
- Arkins, A. M., Winnington, A. P., Anderson, S., & Clout, M. N. (1999). Diet and nectarivorous foraging behaviour of the short-tailed bat (*Mystacina tuberculata*). *Journal of Zoology, London*, 247, 183-187.
- Borkin, K. M. (2010). *Ecology of New Zealand's Long-tailed bat (*Chalinolobus tuberculatus*) in exotic plantation forest*. Doctor of Philosophy in Biological Science University of Auckland, Auckland.
- Borkin, K. M., & Parsons, S. (2011a). Home range and habitat selection by a threatened bat in exotic plantation forest. *Forest Ecology and management* 262, 845-852.
- Borkin, K. M., & Parsons, S. (2011b). Sex-specific roost selection by bats in clearfell harvested plantation forest: improved knowledge advises management. *Acta Chiropterologica*, 13(2), 373-383.
- Brockhoff, E. G., Suckling, D. M., Ecroyd, C. E., Wagstaff, S. J., Raabe, M. C., Dowell, R. V., & Wearing, C. H. (2011). Worldwide Host Plants of the Highly Polyphagous, Invasive Epiphyas postvittana (Lepidoptera: Tortricidae). *Journal of Economic Entomology*, 104(5), 1514-1524. doi: 10.1603/EC11160
- Clare, E. L., Barber, E. R., Sweeney, B. W., Herbert, P. D. N., & Fenton, M. B. (2011). Eating local: influences of habitat on the diet of little brown bats (*Myotis lucifugus*). *Molecular Ecology*, 20, 1772-1780.
- Conservation, D. O. (2012). Pureora Forest Park tracks. In D. O. Conservation (Ed.). Wellington, New Zealand: Publishing Team.
- Daniel, M. J. (1990). Order Chiroptera. In M. C. King (Ed.), *The handbook of New Zealand mammals* (pp. 114-137). New Zealand: Oxford University Press

- Feldhamer, G. A., Carter, T. C., & Whitaker, J. O., Jr. (2009). Prey consumed by eight species of insectivorous bats from southern Illinois. *The American Midland Naturalist*, 162(1), 43-51.
- Gillingham, N. J. (1996). *The behaviour and ecology of long-tailed bats (Chalinolobus tuberculatus Gray) in the central North Island*. Master of Science Unpublished thesis, Massey University, Palmerston North.
- Kurta, A., & Whitaker, J. O., Jr. (1998). Diet of the endangered Indiana bat (*Myotis sodalis*) on the Northern edge of its range. *The American Midland Naturalist*, 140(2), 280-286.
- Leelapaibul, W., Bumrungsri, S., & Pattanawiboon, A. (2005). Diet of wrinkle-lipped free-tailed bat (*Tadarida plicata* Buchannan, 1800) in central Thailand: insectivorous bats potentially act as biological pest control agents. *Acta Chiropterologica*, 7(1), 111-119.
- Lloyd, B. (2005). Lesser short-tailed bat. In M. C. King (Ed.), *The Handbook Of New Zealand Mammals (2nd ed.)* (pp. 110-127). Melbourne: Oxford University Press.
- Long, R. F., Simpson, T., Ding, T., Heydon, S., & Reil, W. (1998). Bats feed on crop pests in Sacramento Valley. *California Agriculture*, 52(1), 8-10.
- Molloy, J. (1995). *Bat (Peka peka) recovery plan (Mystacina, Chalinolobus)*. Wellington: Department of Conservation.
- Moore, G. E. (2001). *Use of Kinleith forest by native New Zealand bats and effects of forestry*. Master of Science Unpublished thesis, Massey University, Palmerston North, New Zealand.
- Moosman, P. R., Thomas, H. H., & Veilleux, J. P. (2012). Diet of the widespread insectivorous bats *Eptesicus fuscus* and *Myotis lucifugus* relative to climate and richness of bat communities *Journal of Mammalogy*, 93(2), 491-496.
- O'Donnell, C. F. J. (2001). Advances in New Zealand mammalogy 1990-2000: Long-tailed bat. *Journal of the Royal Society of New Zealand* 31(1), 43-57.
- O'Donnell, C. F. J. (2005). NZ Long-tailed bat. In M. C. King (Ed.), *The handbook of New Zealand Mammals (2nd ed.)* (pp. 98-110). Melbourne: Oxford University Press.
- O'Donnell, C. F. J., Christie, J. E., Hitchmough, R. A., Lloyd, B., & Parsons, S. (2010). The conservation status of New Zealand bats, 2009. *New Zealand Journal of Zoology*, 37(4), 297-311.

- Ogden, J., Braggins, J., Stretton, K., & Anderson, S. (1997). Plant species richness under *Pinus radiata* stands on the Central North Island Volcanic Plateau, New Zealand *New Zealand Journal of Ecology*, 21(1), 17-29.
- Painter, M. L., Chambers, C. L., Siders, M., Doucett, R. R., Whitaker, J. O., Jr., & Phillips, D. L. (2009). Diet of spotted bats (*Euderma Maculatum*) in Arizona as indicated by fecal analysis and stable isotopes. *Canadian Journal of Zoology*, 87, 865-875.
- Pryde, M. A., O'Donnell, C. F. J., & Barker, R. J. (2005). Factors influencing survival and long-term population viability of New Zealand long-tailed bats (*Chalinolobus tuberculatus*): Implications for conservation. *Biological Conservation*, 126(2), 175-185.
- Ross, M. G. (2004). *Response to a gypsy moth incursion within New Zealand*. Paper presented at the IUFRO, Hanmer.
- Salvarina, I., Yohannes, E., Siemers, B. M., & Koselj, K. (2013). Advantages of using fecal samples for stable isotope analysis in bats: evidence from a triple isotopic experiment. *Rapid Communications in Mass Spectrometry*, 27(17), 1945-1953.
- Shiel, C. B., Duverge, P. L., Smiddy, P., & Fairley, J. S. (1998). Analysis of the diet of Leisler's bat (*Nyctalus leisleri*) in Ireland with some comparative analyses from England and Germany. *Journal of Zoology, London*, 246, 417-425.
- Shiel, C. B., McAney, C., Sullivan, C., & Fairley, J. S. (1997). *Identification of arthropod fragments in bat droppings* (Vol. 7). London: The Mammal Society.
- Triplehorn, C. A., & Johnson, J. S. (2005). *Borror and DeLong's introduction to the study of insects* (Seventh ed.). USA: Thomson Brooks/Cole.
- Whitaker, J. O., Jr., & Karatas, A. (2009). Food and feeding habits of some bats from Turkey. *Acta Chiropterologica*, 11(1), 393-403.
- Whitaker, J. O., McCracken, G. F., & Siemers, B. M. (2009). Food habits analysis of insectivorous bats. In T. H. Kunz & S. Parsons (Eds.), *Ecological and behavioural methods for the study of bats* (Second ed.). Baltimore: The Johns Hopkins University Press.

Chapter Three

3. The use of stable isotope analysis to identify the diet of the New Zealand long-tailed bat, *Chalinolobus tuberculatus*.

3.1. Abstract

The diet of two populations of New Zealand long-tailed bat (*Chalinolobus tuberculatus*), Pureora Forest Park and Kinleith Forest, was assessed by using stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis of faeces. This is the first instance where stable isotope analysis has been used to investigate New Zealand bat diet. Faecal samples from a population of New Zealand long-tailed bats in a Fiordland forest and a population of New Zealand short-tailed bats (*Mystacina tuberculata*) from Pureora Forest Park were also analysed to use as a comparison. The $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values of bat faeces were similar to those of Lepidoptera, Diptera, and Coleoptera implying these are the insects eaten most often. Only minor similarities were found between the $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values of bat faeces and those of Trichoptera, Hymenoptera, and Hemiptera implying these insects are eaten less often. New Zealand long-tailed bats in Pureora Forest and Kinleith Forest appear to have opportunistic, generalist diets. There were no significant differences in the diet of the bats in native forest with the bats in exotic forest showing bats inhabiting exotic plantation forests can maintain a good quality diet similar to bats inhabiting native forests. In this study by combining physical search of faeces and stable isotope analysis, consistent results were achieved and new information, i.e. soft bodied insects such as Lepidoptera are more important in the diet of long-tailed bats than previously thought, was gained. After comparison, both techniques have their merits and that, if possible, it is best to utilise both when investigating diet.

3.2. Introduction

The long-tailed bat, *Chalinolobus tuberculatus*, is one of two extant species in New Zealand; the other is the lesser short-tailed bat, *Mystacina tuberculata* (Lloyd, 2005; O'Donnell, 2005). Both of these species are endemic to New Zealand and are considered threatened; they are listed as vulnerable on the IUCN Red List of Threatened Animals and

the Department of Conservation (DOC) lists the long-tailed bat as 'nationally vulnerable', and short-tailed bat as 'nationally endangered' (O'Donnell et al., 2010). The Department of Conservation has a bat recovery program to assist in the survival of all extant bat species throughout their current ranges, with the possibility of founding new populations within their historical range (Molloy, 1995).

Long-tailed bats are small but fast flying aerial insectivores (O'Donnell, 2001). They are mostly associated with native forest, yet have also been found to roost in caves, buildings, pine forest, and other exotic trees (Borkin & Parsons, 2011a; O'Donnell, 2002; O'Donnell, 2005; Sedgeley & O'Donnell, 1999b). They frequently forage along forest edges, in clearings, above farmland, and above open water and streams (Alexander, 2001; Arkins et al., 1999; O'Donnell et al., 2006). They are widely distributed throughout the North Island, through the Western South Island, to Stewart Island, and also present on many offshore islands such as Little Barrier, Great Barrier, and Kapiti Islands (Daniel, 1990; O'Donnell, 2005). Historical anecdotes suggest that long-tailed bats are now present in lower numbers than previously and are even absent in some areas where they used to be, such as Banks Peninsula (Molloy, 1995; O'Donnell, 2000a). Research conducted on long-tailed bats has focused on roosting choice and behaviour with limited investigation of their diet. Studies that have investigated diet have to date only involved physical searches through faeces (Gillingham, 1996). Although this can be useful as a method of determining diet (Long et al., 1998; Whitaker et al., 2009), the technique may underestimate the importance of soft-bodied invertebrates as bats can cull many of the hard and identifiable insect parts before ingestion (Clare et al., 2011; Leelapaibul et al., 2005; Painter et al., 2009). This not only means that some insects are missed entirely, but many may also be identified only to order or family (Clare et al., 2011; Whitaker et al., 2009). Most of the information to date about diet of long-tailed bats has come from a single, unpublished, study covering only one site by Gillingham (1996). Gillingham found that Diptera made up the majority of the long-tailed bat diet (29%) followed by Coleoptera (25%) and Lepidoptera (17%), however a large proportion of faecal fragments remained unidentified (Gillingham, 1996).

Knowledge of a particular animals diet can provide information on their ecology and behaviour and can be essential for their management (Painter et al., 2009; Whitaker & Karatas, 2009). When an endangered species is involved it is even more important as their

diet may provide clues to potential drivers of their decline (Kurta & Whitaker, 1998). Learning more about diet may also assist with possible husbandry efforts if abandoned young or injured adult bats are found as well as with potential future translocation projects. As invertebrate ecosystem and community structure will obviously influence insectivorous bats; determinates of their distribution will also be an important part of bat management (Moosman et al., 2012).

Stable isotope analysis is a technique which enables comparison of isotope ratios in potential food items (soft and hard) to identify dietary composition (Cryan et al., 2012; Painter et al., 2009). Each possible prey item has a distinct stable isotope ratio which, when consumed, is incorporated into the tissue of the consumer (Herrera et al., 2001; Painter et al., 2009). When prey and consumer stable isotope ratios are compared it is possible to determine what prey are incorporated into the diet (York & Billings, 2009). Faeces are ideal to use for this as they are easily collected, less invasive for the animal than taking tissue or blood samples, and give a good idea of the prey that were recently consumed (Painter et al., 2009; Salvarina et al., 2013). In this study I use stable isotope analysis of faecal and insect samples to identify the broad dietary components of two populations of North Island long-tailed bats and compare their diet to a population of North Island short-tailed bats and a population of Fiordland long-tailed bats. This is the first instance where stable isotope analysis has been used to investigate New Zealand bat diet. I also briefly compare the two dietary analysis techniques used (physical search and stable isotope analysis) to see which is more effective.

3.3. Methods

3.3.1. Study area

Insects and long tailed bat faecal samples were collected from two study sites, Pureora and Kinleith Forests. Pureora Forest Park is located between Lake Taupo and Te Kuiti (Fig. 1) on the North Island of New Zealand (Latitude 38.56, Longitude 175.68). In 1946, Pureora Forest was one of the last native forests to be opened up for logging and it holds the last remnants of extensive native podocarp forests that once covered most of the central North Island. The park is managed by the Department of Conservation (DOC) in order to protect and monitor its natural and historic features. This protected area is 78,000 ha of rich

lowland podocarp forest, comprising rimu (*Dacrydium cupressinum*), mataī (*Prumnopitys taxifolia*), miro (*Prumnopitys ferruginea*) and tawa (*Beilschmiedia tawa*) among others, and high altitude montaine forest with tōtara (*Podocarpus totara*), tāwheowheo (*Quintinia serrata*) and kamahi (*Weinmannia racemosa*) (Conservation, 2012). Nationally important wetlands and shrublands are also present within the park. These forests grow on pumice and ash derived soils and house many endangered native species including both species of bats (Conservation, 2012).

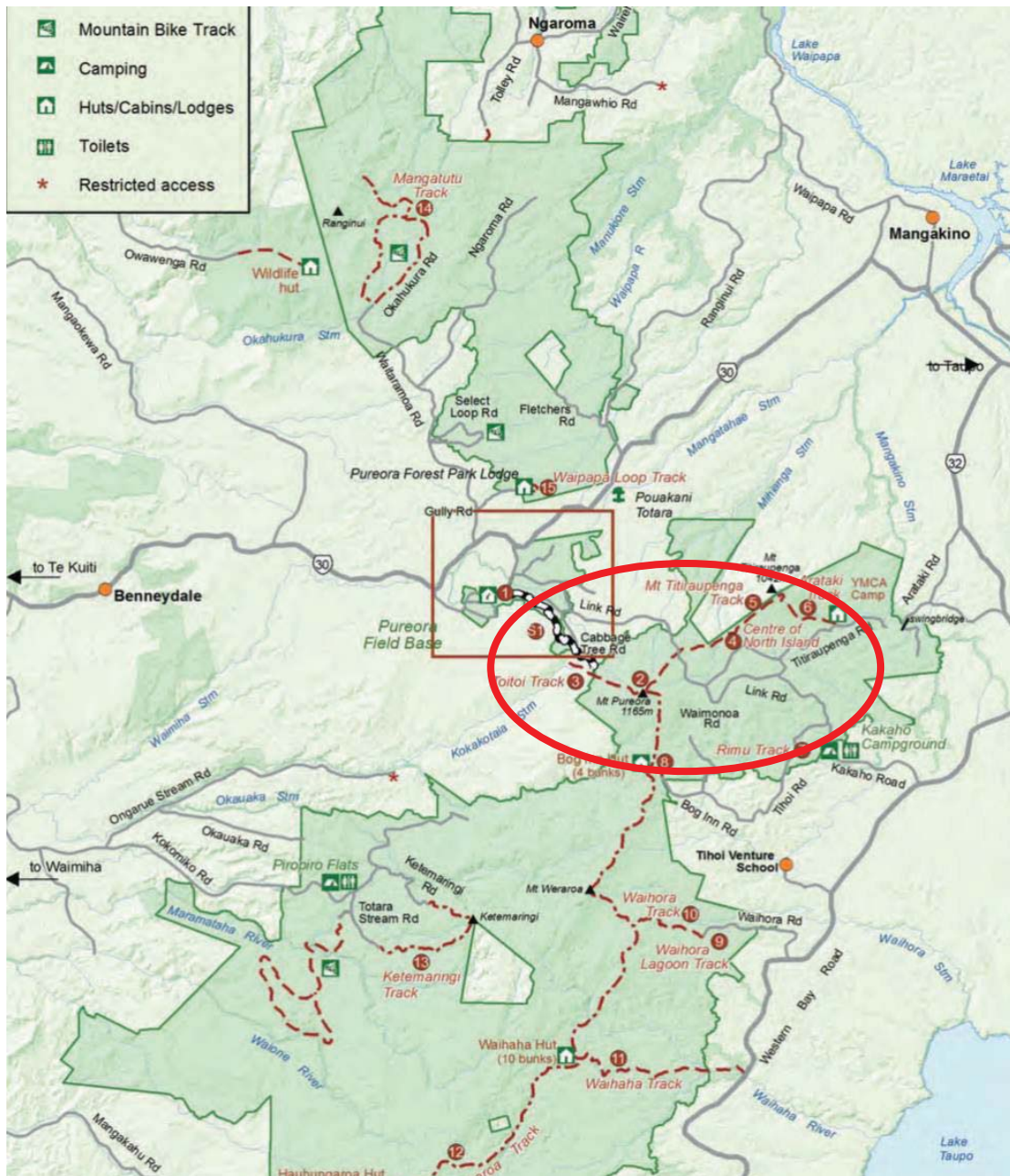


Figure 1 Map of Pureora Forest Park, in the central North Island of New Zealand, where all native forest sampling took place. Circled area is where all insect light trapping and long-tailed bat faecal sampling occurred. Image from Pureora Forest Park brochure (Conservation, 2012).

Kinleith Forest is centred around Tokoroa on the North Island of New Zealand (latitude - 37.47, longitude 175.53). The forest is about 96,652 ha of pine plantation (including production and non-production areas, unstocked areas, and reserves) first planted in 1924 (K. Borkin, personal communication). It comprises predominantly *Pinus radiata*, however, smaller plantings of *Pseudotsuga menziesii* and *Eucalyptus* are also present (Borkin & Parsons, 2011a). Native shrubs, ground, and tree ferns are present in the understory of many, especially older, stands (Moore, 2001). At least 10% of Kinleith Forest is protected native forest, such as broadleaf podocarp forests occupying gorges and riparian scrubland, fernland and wetlands (Moore, 2001). The highest points of Kinleith Forest reach around 750 metres in altitude and the climate is cool and humid, with a mean rainfall of 1600 mm per year (Ogden et al., 1997). The soils are coarse and free draining because of deep pumice deposits (Ogden et al., 1997). The native and exotic stands are home to many native birds and both species of New Zealand bat (Borkin & Parsons, 2011b).

3.3.2. Faeces collection

Long-tailed bat faecal pellets were collected from Pureora Forest Park in January during the Austral summer of 2013. The bats were caught in harp traps placed in front of roost entrances and over streams known to be used for foraging at sunset. Captured bats were transferred into cloth bags where they were held for around twenty minutes while they were weighed, measured, and banded (if not already). Any faeces left behind in the cloth bags and in the harp traps themselves were collected for diet analysis. Ninety individual pellets were collected.

Faecal samples from long-tailed bats that were resident in Kinleith Forest were collected from under nine known roosts, in November and February of 2007 and in February and March of 2008, during a larger study into the ecology of bats within plantation forest (Borkin, 2010). These day roosts were found by radio-tracking bats during the day (radio transmitters Model BD-2, Holohil Systems Ltd, Canada) that were captured either using mistnets placed across forestry roads or at roost sites using nets. Bats in Kinleith Forest were captured, handled, and radiotracked under permits from the Department of Conservation (Low Impact, Research and Collection Permit BP-18899-RES under Section 53, Wildlife Act 1953) and the University of Auckland Animal Ethics Committee (AEC 08/2004/R282). Roosts were generally under peeling bark of long dead spars (Borkin, 2010).

Twenty short-tailed bat faecal samples from Pureora Forest and twenty long-tailed bat faecal samples from a Fiordland native beech forest were also available and included in the stable isotope analysis. The short-tailed bat faecal samples were collected under known communal roost six (CR6) in Pureora Forest between January and March 2013. The long-tailed bat faecal samples were collected from the Eglinton valley, Fiordland between January and February 2013 by Gillian Dennis for her PhD. These samples were collected from harp traps that were placed outside known long-tailed bat roosts in order to catch the bats at emergence.

3.3.3. Invertebrate sampling

Invertebrate light traps were set up in Pureora and Kinleith Forest study sites in January 2013 to characterise potential food sources available to long-tailed bats present in each forest. The traps comprised a fluorescent light set over a white tray, which was filled with water and dish washing detergent. Insects were attracted to the light, fell in the water and were trapped. Six light traps were set up overnight (approximately eight hours) in Pureora Forest around the area where bat faecal samples were collected; three at locations along roads and three along streams (Fig. 1). Six light traps were also set up overnight (approximately eight hours) in Kinleith Forest around the Wawa Road area (long-tailed bat faecal samples were collected from a slightly larger area in this forest); one trap by a road in each of the three age groups of pine (0-5, 6-10, and 11-25 years), and one trap by a stream in each of the pine age groups (Fig. 2). The contents of each trap were frozen until analysis and insects identified to family level or lower where possible. Some Lepidoptera, however, were assigned to morphotypes. Identification was aided with the use of insect keys, mostly from (Triplehorn & Johnson, 2005).

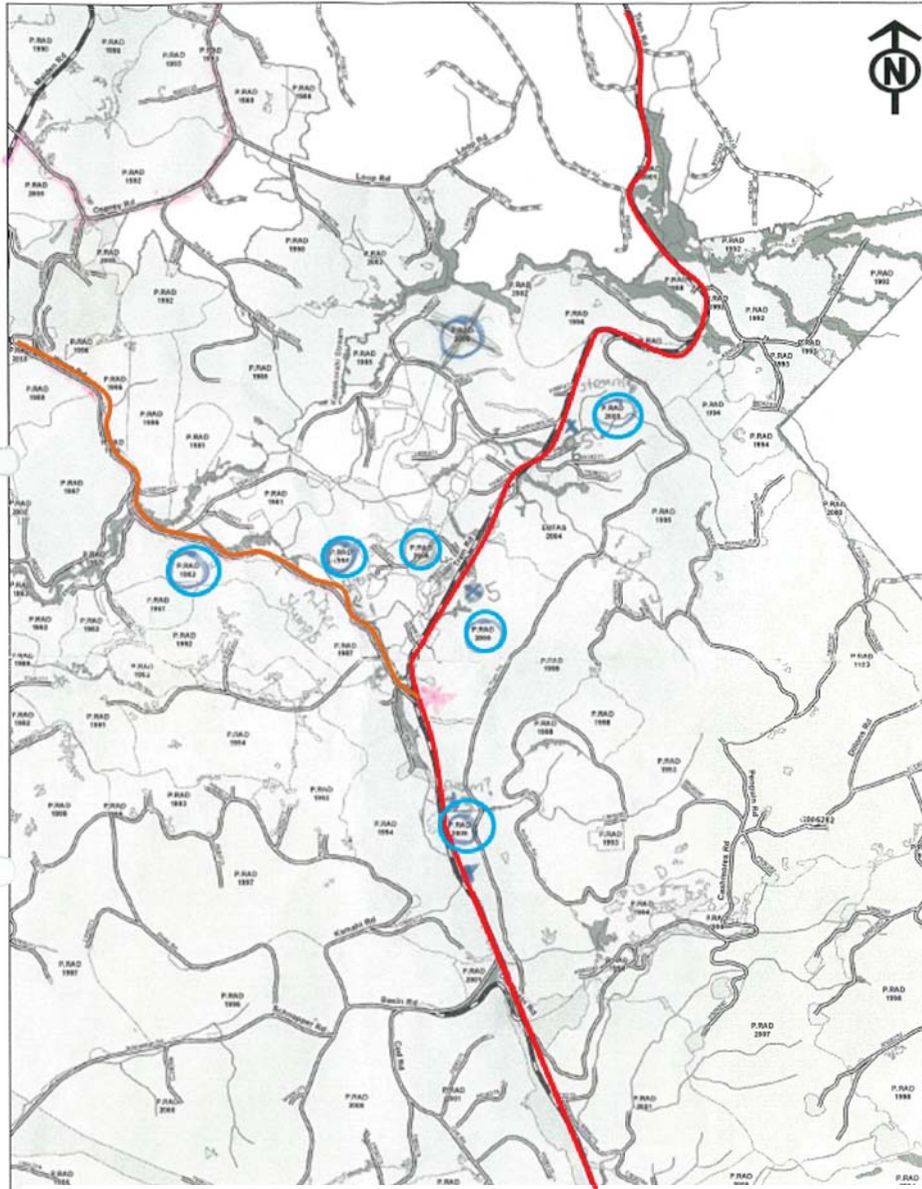


Figure 2 Map of Kinleith Forest, in the central North Island of New Zealand, where all exotic forest sampling took place. Circled areas are the stands of pine plantation where light traps were set, the red line is Tram Rd and the orange line is Wawa Rd.

3.3.4. Stable Isotope analysis

Fifty faecal samples from Pureora Forest and fifty from Kinleith Forest long-tailed bats were used for stable isotope analysis (of ^{13}C and ^{15}N). Individual pellets were put into a drying oven and dried at 60°C for around 24 hours. They were then ground in a mortar and pestle to homogenise them and approximately 1.25 mg was weighed out and put into tin capsules. The same process was carried out for the insect samples. Twenty faecal samples from short-tailed bats in Pureora Forest and twenty faecal samples from long-tailed bats in a Fiordland beech forest were also prepared for stable isotope analysis for comparison.

Samples were analysed by University of California, Davis Stable Isotope Facility (stableisotopefacility.ucdavis.edu/). They were analysed for ^{13}C and ^{15}N isotopes using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Carbon and Nitrogen stable isotope ratios ($\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰)) were analysed simultaneously from the same sample and final delta values were expressed relative to international standards V-PDB (Vienna PeeDee Belemnite) and Air for carbon and nitrogen, respectively after being standardized against NIST Standard Reference Materials (IAEA-N1, IAEA-N2, IAEA-N3, USGS-40, and USGS-41).

3.3.5. Data analysis

A one-way ANOVA was conducted in R (Version 3.0.2) to compare the $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values of bat diets and invertebrate samples. A Post-Hoc analysis was carried out using Tukey's HSD test in R (Version 3.0.2) in order to see where the differences lie in the ANOVA.

3.4. Results

3.4.1. Light trap collections

Over all sites Lepidoptera (moths) accounted for 71% of insects collected in light traps, with 31% being Geometrid-like moths and 20% being Noctuid-like moths (Table 1). Diptera (flies) accounted for 15% of insects collected (with more caught in Pureora than Kinleith), with the most common being Tipulidae (6%) and Mycetophilidae (3%) (Table 1). Other prevalent insect orders collected were Coleoptera (beetles) (4%), with the most common being Cerambycidae (1%) and Scarabeidae (1%) with more caught in Kinleith than Pureora, and Trichoptera (caddisflies) (7%) (Table 1). A few insects were collected from other orders but were rare and thus not considered further as potential prey.

Table 1 Insects collected in light traps from Pureora Forest (six traps) and Kinleith Forest (six traps) in January and February 2013.

Insects in traps	Total number	Pureora number	Kinleith number	Percent total	Percent Pureora	Percent Kinleith
<i>Lepidoptera</i>	1812	908	904	70.67	71.72	69.65
Geometrid-like moths	800	400	400	31.20	31.60	30.82
Noctuid-like moths	500	250	250	19.50	19.75	19.26
Tortricidae like moths	100	50	50	3.90	3.95	3.85
Tineidae like moths	50	25	25	1.95	1.97	1.93
Small black stripe moths	200	100	100	7.80	7.90	7.70
Medium fat body moths	150	75	75	5.85	5.92	5.78
Pterophoridae	12	8	4	0.47	0.63	0.31
<i>Trichoptera</i>	183	89	94	7.14	7.03	7.24
Helicopsychidae	69	59	10	2.69	4.66	0.77
Leptoceridae	31	2	29	1.21	0.16	2.23
Hydrobiosidae	24	3	21	0.94	0.24	1.62
Other	59	25	34	2.30	1.97	2.62
<i>Coleoptera</i>	98	24	74	3.82	1.90	5.70
Cerambycidae (Prionoplusreticularis)	30	10	20	1.17	0.79	1.54
Scarabaeidae (Odontriaxanthosticta)	29	1	28	1.13	0.08	2.16
Elateridae	17	1	16	0.66	0.08	1.23
Other	22	12	10	0.86	0.95	0.77
<i>Diptera</i>	389	221	168	15.17	17.46	12.94
Tipulidae	161	95	66	6.28	7.50	5.08
Mycetophilidae	73	59	14	2.85	4.66	1.08
Chironomidae	44	9	35	1.72	0.71	2.70
Culicidae	35	19	16	1.37	1.50	1.23
Other	76	39	37	2.95	3.09	2.85
<i>Hymenoptera</i>	20	11	9	0.78	0.87	0.69
<i>Hemiptera</i>	35	3	32	1.37	0.24	2.47
Cicadellidae	19	0	19	0.74	0.00	1.46
Other	7	3	4	0.63	0.24	1.01
<i>Orthoptera</i>	9	4	5	0.35	0.32	0.39
<i>Neuroptera</i>	3	1	2	0.12	0.08	0.15
<i>Ephemeroptera</i>	1	1	0	0.04	0.08	0.00
<i>Other</i>	14	4	10	0.55	0.32	0.77
Total	2564	1266	1298	100.00	100.00	100.00

3.4.2. Stable isotopes

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Pureora and Kinleith long-tailed bats have quite a broad range and overlap considerably (Fig.3). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Pureora short-tailed bats and Fiordland long-tailed bats, however, have a much smaller range (Fig.3). There is a small overlap in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Pureora and Kinleith long-tailed bat faeces and those of the Pureora short-tailed bat faeces, whereas there is little overlap with the Fiordland long-tailed bat faeces (Fig.3). Similar patterns occurred for $\delta^{13}\text{C}$ values (Fig.4a). When $\delta^{15}\text{N}$ values are examined separately, however, there is no difference between all four populations of bats apart from a larger spread of values in the Pureora and Kinleith long-tailed bat faeces (Fig.4b). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Pureora long-tailed bat faeces overlap considerably with the values of Lepidoptera, Diptera, and Coleoptera suggesting that these were most frequently consumed (Fig.5a). Slight overlap between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Pureora long-tailed bat faeces with Hymenoptera and Trichoptera can also be seen indicating they may be less frequently consumed (Fig.5a). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Kinleith long-tailed bat faeces also overlap considerably with Lepidoptera, Diptera, and Coleoptera suggesting these are most commonly consumed food items. There was no overlap between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Kinleith long-tailed bat faeces and Trichoptera and it seems they are not usually a food source (Fig.5b). A slight overlap can be seen between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Kinleith long-tailed bat faeces and Hemiptera suggesting that these insects could be less frequently consumed (Fig.5b).

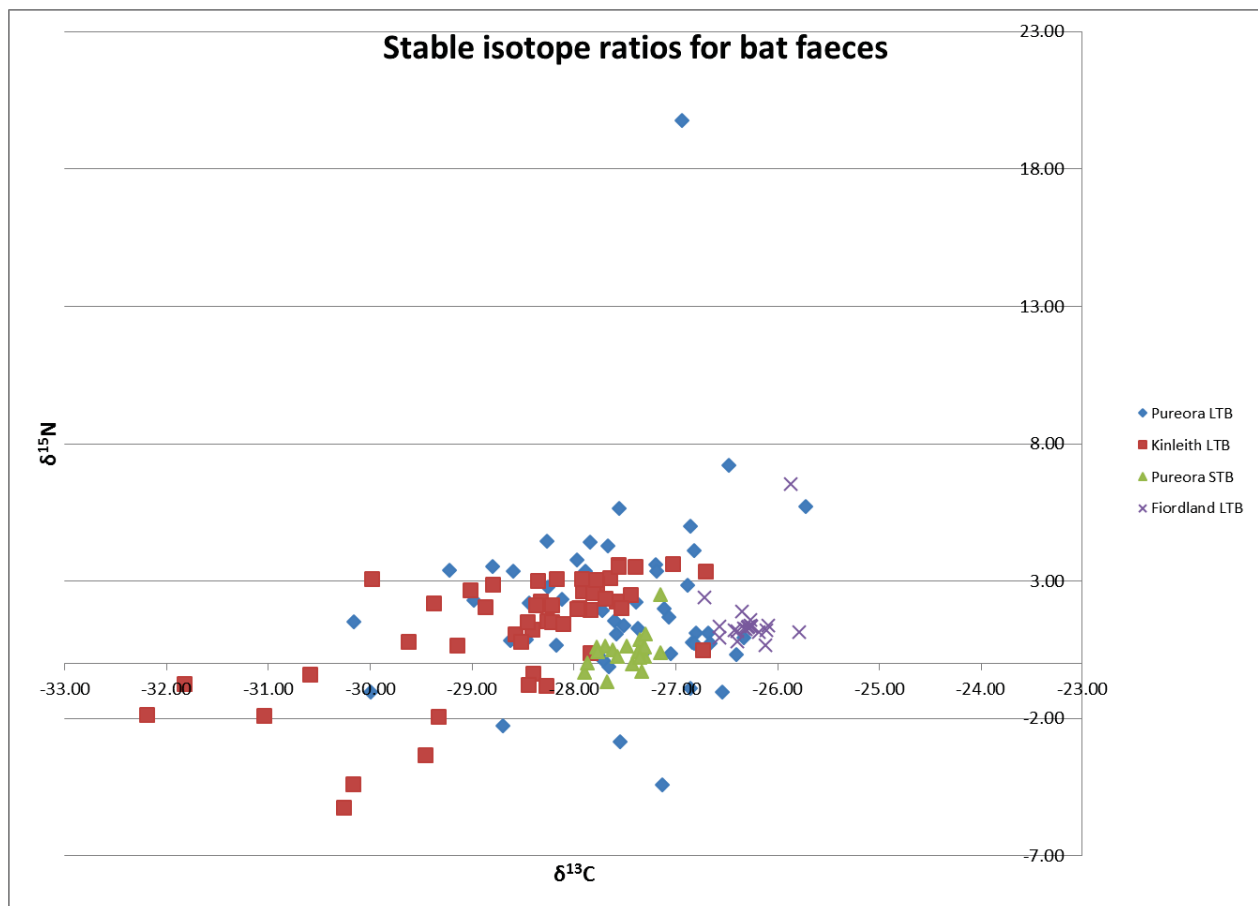


Figure 3 The $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values of faeces collected from long-tailed bats (LTB) and short-tailed bats (STB) from Pureora Forest, Kinleith Forest, and a Fiordland Beech forest.

There was a significant overall difference between the mean stable isotope results for both $\delta^{13}\text{C}$ ($F_{9,180}=6.26$, $P<0.001$) and $\delta^{15}\text{N}$ ($F_{9,180}=7.81$, $P<0.001$). Pureora long-tailed bat mean dietary isotope values were depleted in $\delta^{13}\text{C}$ (Fig. 4a) compared to Fiordland long-tailed bat values and depleted in $\delta^{15}\text{N}$ compared to Trichoptera values (Table 2). Pureora short-tailed bat mean dietary isotope values were significantly depleted in $\delta^{15}\text{N}$ compared to Diptera, Trichoptera, and Hymenoptera (Table 2). Kinleith long-tailed bat mean dietary isotope values were significantly depleted in $\delta^{13}\text{C}$ compared to Fiordland long-tailed bats (Fig. 4a) and Coleoptera and depleted in $\delta^{15}\text{N}$ compared to Diptera, Trichoptera, and Hymenoptera (Table 2). Fiordland long-tailed bat mean dietary isotope values were significantly enriched in $\delta^{13}\text{C}$ and depleted in $\delta^{15}\text{N}$ compared to Trichoptera (Table 2). There was no significant difference between Pureora and Kinleith long-tailed bats' diets ($P>0.05$).

Table 2 Summary table of results from the Post-Hoc analysis, Tukey's HSD test, showing where the significant differences lie among the d13C and d15N values of long-tailed (LTB) and short-tailed (STB) bat diets and invertebrate samples. Highlighted values show where the significant differences lie.

		d13C Diff	d13C Lower	d13C Upper	d13C P value	d15N Diff	d15N Lower	d15N Upper	d15N P value
Pureora LTB	Pureora STB	0.1024	-1.1579	1.3627	0.9999	-1.7367	-3.9237	0.4503	0.2526
	Kinleith LTB	0.9412	-0.01153	1.8939	0.05585	0.8544	-0.7988	2.5076	0.8184
	Fiordland LTB	-1.3084	-2.5687	-0.04805	0.03488	0.5987	-1.5883	2.7857	0.996
	Diptera	-0.2773	-1.7604	1.2057	0.9999	-2.02195	-4.5954	0.5515	0.2665
	Lepidoptera	0.07103	-1.8514	1.9934	1	-1.1415	-4.4773	2.1943	0.9845
	Coleoptera	-1.4283	-2.8687	0.01214	0.05401	1.2113	-1.2881	3.7108	0.8685
	Trichoptera	-1.2709	-3.0848	0.5431	0.4306	5.0183	1.8707	8.1659	3.58x10 ⁻⁵
	Hemiptera	0.7696	-2.062	3.6012	0.9971	2.6775	-2.236	7.5911	0.7676
	Hymenoptera	-0.5804	-2.8148	1.654	0.998	-3.4798	-7.3569	0.3973	0.1203
Pureora STB	Kinleith LTB	1.0436	-0.2167	2.3039	0.2015	-0.8823	-3.0693	1.3047	0.9542
	Fiordland LTB	-1.206	-2.7124	0.3004	0.2423	-1.138	-3.752	1.475	0.9275
	Diptera	-0.1749	-1.872	1.5222	0.9999	-3.7587	-6.7036	-0.8138	0.002574
	Lepidoptera	0.1734	-1.9286	2.2654	0.9999	-2.8782	-6.5083	0.7519	0.2546
	Coleoptera	-1.3259	-2.9858	0.3341	0.2452	-0.5254	-3.4058	2.3551	0.9999
	Trichoptera	-1.3733	-3.366	0.6195	0.4554	6.755	3.297	10.213	0.1x10 ⁻⁶
	Hemiptera	0.872	-2.0774	3.8214	0.9946	0.9408	-4.177	6.0587	0.9999
	Hymenoptera	-0.478	-2.8598	1.9038	0.9997	-5.2165	-9.3495	-1.0835	0.003054
Kinleith LTB	Fiordland LTB	-2.2496	-3.5099	-0.9893	1.9x10 ⁻⁶	-0.2557	-2.4427	1.9313	0.9999
	Diptera	-1.2185	-2.7016	0.2645	0.2105	-2.8764	-5.4498	-0.3029	0.01559
	Lepidoptera	0.8702	-1.0522	2.7926	0.9093	1.9959	-1.3399	5.3317	0.6576
	Coleoptera	-2.3695	-3.8099	-0.9291	1.69x10 ⁻⁵	0.3569	-2.1425	2.8564	0.9999
	Trichoptera	-0.3297	-2.1436	1.4843	0.9999	5.8727	2.7251	9.0203	0.5x10 ⁻⁶
	Hemiptera	-0.1716	-3.0032	2.66	1	1.823	-3.0904	6.7367	0.9733
		Hymenoptera	-1.5216	-3.756	0.7128	0.4731	-4.3342	-8.2113	-0.4571
Fiordland LTB	Diptera	1.0311	-0.666	2.7282	0.6374	-2.6207	-5.5656	0.3242	0.1277
	Lepidoptera	-1.3794	-3.4714	0.7126	0.5212	1.7402	-1.8899	5.3703	0.8758
	Coleoptera	-0.1199	-1.7798	1.5401	1	0.6126	-2.2678	3.4931	0.9996
	Trichoptera	-2.5793	-4.572	-0.5865	0.002067	5.617	2.159	9.075	2.3x10 ⁻⁵
	Hemiptera	-2.078	-5.0274	0.8714	0.4221	-2.0788	-7.1967	3.039	0.9522
	Hymenoptera	-0.728	-3.1098	1.6538	0.9931	4.0785	-0.05455	8.2115	0.05641

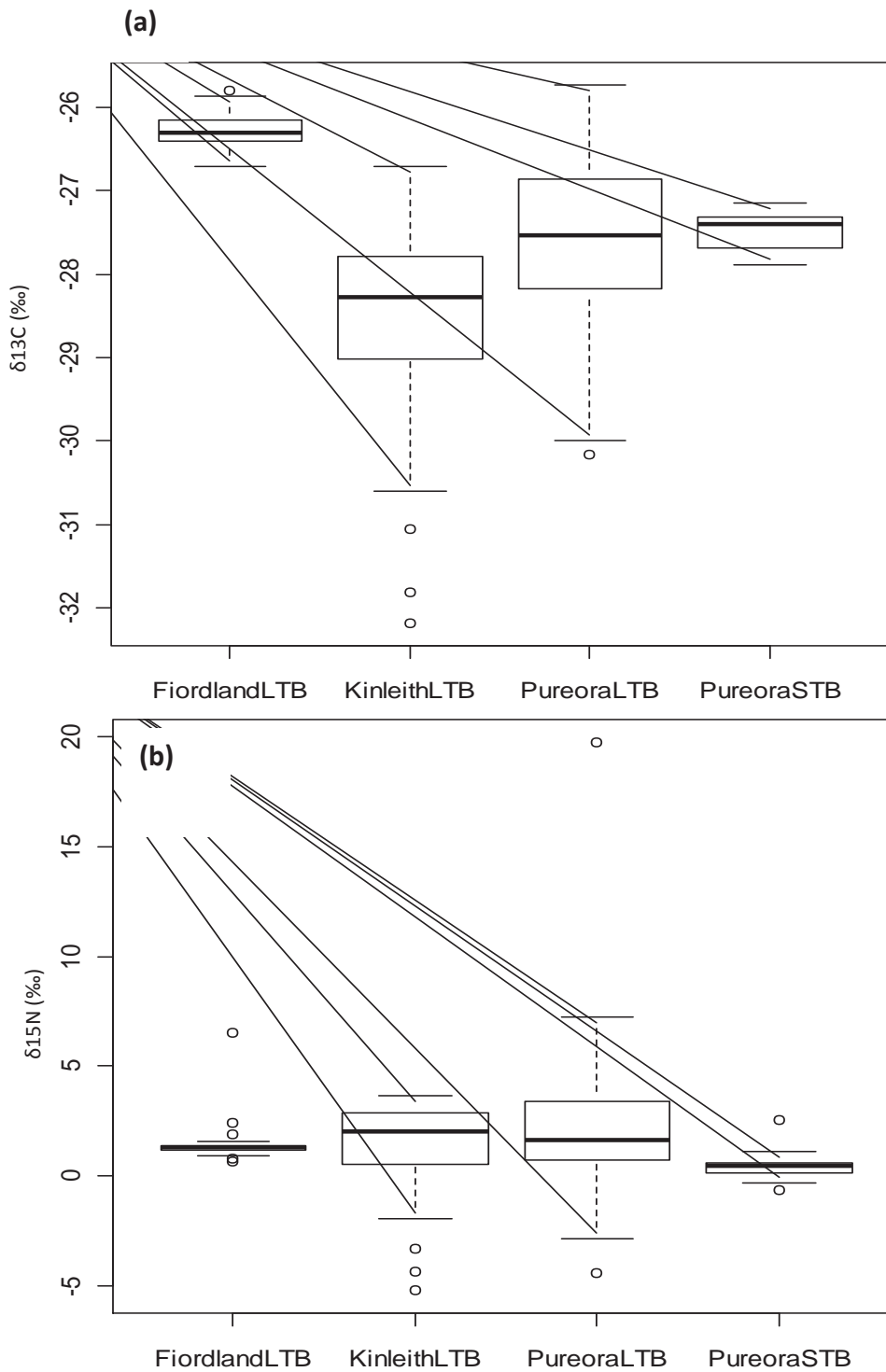


Figure 4 Box plots comparing (a) $\delta^{13}\text{C}$ (‰) values and (b) $\delta^{15}\text{N}$ (‰) values of Fiordland beech forest long-tailed bat (LTB), Kinleith Forest long-tailed bat (LTB), and Pureora Forest long-tailed (LTB) and short-tailed bat (STB) faeces.

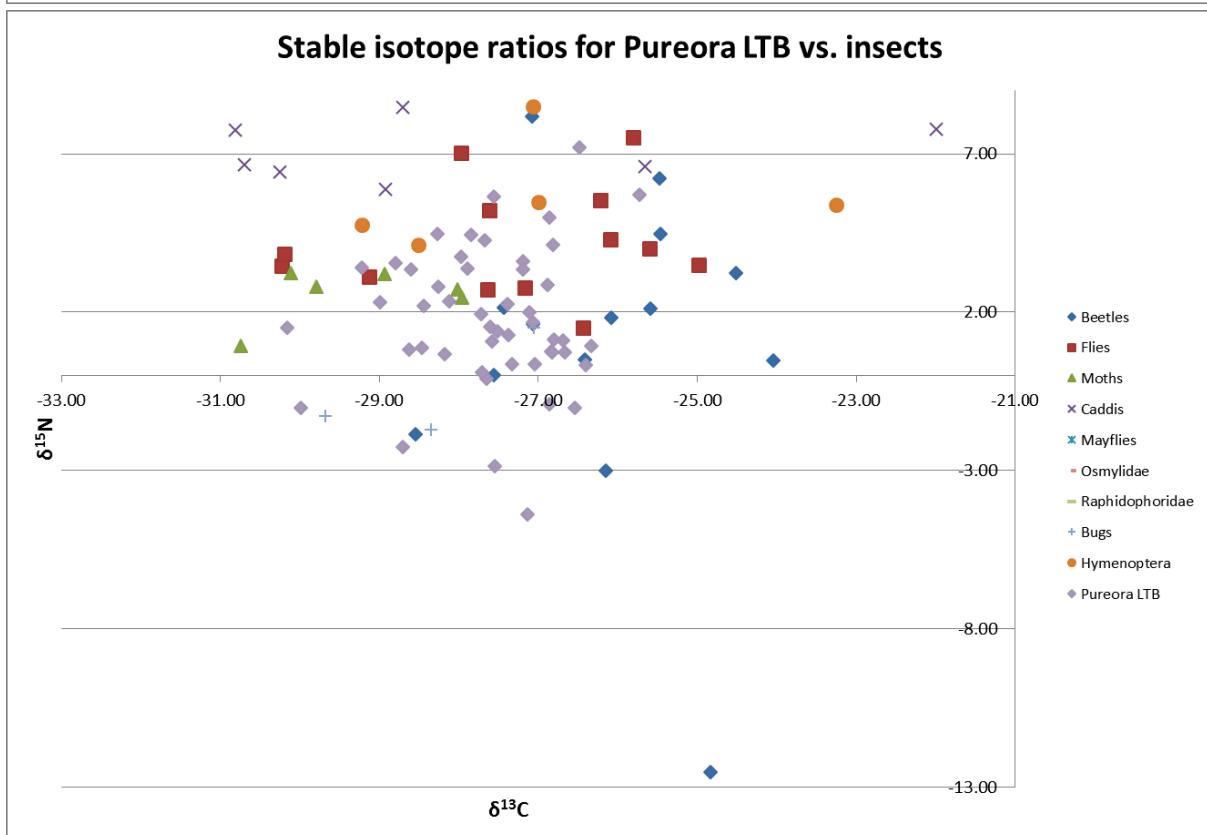
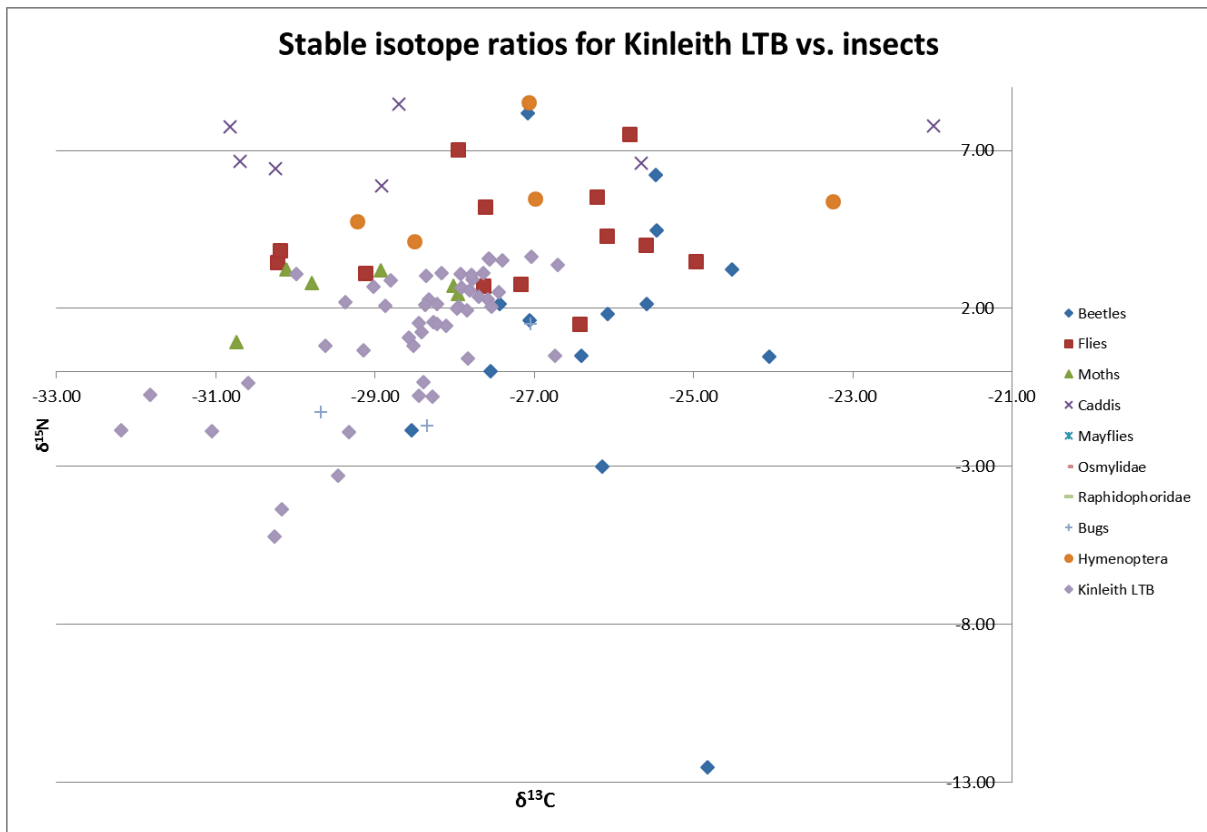


Figure 5 The $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values of (a) Kinleith Forest long-tailed bat faeces and (b) Pureora Forest long-tailed bat faeces compared with insect values.

3.5. Discussion

The stable isotope ratios in the long-tailed bat faeces and those of the Diptera, Lepidoptera, and Coleoptera supports the view that these insect orders are the primary food sources for both Pureora and Kinleith long-tailed bats (Fig.5). Diptera, Lepidoptera, and Coleoptera were also the most abundant insects caught in light traps (Table 1). The bats are clearly opportunistic, generalist feeders eating the insects that they encounter most often. There was also a small overlap of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between long-tailed bat faeces and Hymenoptera, Trichoptera, and Hemiptera suggesting these insect orders are also consumed but less often than other insect orders in Pureora and Kinleith Forests (Fig.5). Hymenoptera, Trichoptera, and Hemiptera were also less abundant in the light traps and are therefore likely to be less available as food sources for long-tailed bats at both the Pureora and Kinleith Forest study sites (Table 1).

Although the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Pureora and Kinleith long-tailed bats' faeces are very similar (Fig. 3), there were slight differences in diets of long-tailed bats in native (Pureora) and exotic forest (Kinleith). Both Pureora and Kinleith long-tailed bat $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of faeces overlap most with Lepidoptera, Coleoptera, and Diptera (Fig. 5). However, Kinleith long-tailed bat mean faecal isotope values differed significantly in $\delta^{13}\text{C}$ values from Coleoptera and in $\delta^{15}\text{N}$ values from Diptera whereas values obtained from long-tailed bats in Pureora were not different from Coleoptera and Diptera. Thus the Kinleith long-tailed bats are not eating as many Coleoptera and Diptera as the Pureora long-tailed bats. This also suggests that Kinleith long-tailed bats are eating more Lepidoptera than initially thought as their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were similar to those of Lepidoptera.

Another slight difference between Pureora and Kinleith Forest sites is the slightly higher mean $\delta^{15}\text{N}$ value in Kinleith long-tailed bats than Pureora long-tailed bats (Fig. 4b). This may indicate that Kinleith long-tail bats are eating more predatory/carnivorous insects than the Pureora bats as $\delta^{15}\text{N}$ is indicative of trophic positioning (McFadden, Sambrotto, Medellín, & Gompper, 2006; Schillaci et al., 2014). Higher $\delta^{15}\text{N}$ has also been found to correlate with Nitrogen content in faeces, which is an indicator of crude protein (Codron, Codron, Lee-Thorp, Sponheimer, & De Ruiter, 2005; Sare, Millar, & Longstaffe, 2005; Walter, Leslie, Hellgren, & Engle, 2010). Thus Kinleith long-tailed bats could be obtaining more protein from their diet than the long-tailed bats in Pureora Forest. To further support this, Kinleith

long-tailed bats have higher $\delta^{13}\text{C}$ values than Pureora bats (Fig. 4a) and $\delta^{13}\text{C}$ values in animals with high protein diets are expected to be higher as protein is enriched in ^{13}C (Sare et al., 2005). Nevertheless, the diets did not differentiate enough to suggest these differences are dramatic.

The diet of bats sampled from different locations in New Zealand not surprisingly also differed. The spread of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig. 3) showed greater dietary heterogeneity in Kinleith and Pureora long-tailed bats than Pureora short-tailed or Fiordland long-tailed bats. The $\delta^{13}\text{C}$ values vary over location (Fig. 4a), with Pureora long-tailed bats and short-tailed bats having very similar means, Kinleith long-tailed bats having a slightly larger mean, and Fiordland long-tailed bats having a significantly larger mean $\delta^{13}\text{C}$ value than the rest ($P=0.035$ and $P=1.9 \times 10^{-6}$, Pureora long-tailed bats and Kinleith long-tailed bats respectively). Stable isotope $\delta^{13}\text{C}$ values reflect whether prey items have consumed primarily C_4 plants, such as grasses, or C_3 plants, such as most other plants (Kelly, 2000). C_3 plants generally have a $\delta^{13}\text{C}$ value between -35‰ and -21‰ so Pureora long-tailed bats and short-tailed bats, Kinleith long-tailed bats and Fiordland long-tailed bats are all likely to be eating prey that have been relying on C_3 plants (Fig. 4a) (Codron et al., 2005; Kelly, 2000). The $\delta^{15}\text{N}$ values, however, do not vary significantly over location (Fig. 4b) apart from Kinleith and Pureora long-tailed bats having a larger range of $\delta^{15}\text{N}$ values and Kinleith long-tailed bats having a slightly higher mean $\delta^{15}\text{N}$ value. Stable isotope $\delta^{15}\text{N}$ values indicate crude protein levels and trophic positioning (Codron et al., 2005; Schillaci et al., 2014). This suggests that all of the bat populations sampled are at the same trophic level and are obtaining diets of similar crude protein levels whether they inhabit native or exotic forest. Protein is important as it is generally associated with a higher quality diet (Walter et al., 2010).

Pureora long-tailed bats and short-tailed bats did not have a significantly different diet in this study. Although mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Pureora long-tailed and short-tailed bat faeces are very similar, the spread of these values are quite different (Fig. 4a,b). Pureora long-tailed bat faeces have a much wider spread of data for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. This is quite unusual and the opposite of what would be expected considering short-tailed bats occupy a different niche with their crawling, gleaning, and nectivorous behaviours as well as catching insects in flight. This broad array of foraging techniques means short-tailed bats eat

a much wider diet and would therefore be expected to have a much wider spread of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than long-tailed bats.

The isotope analysis indicated similar diets to those determined from the physical search method in chapter two. Over both Pureora Forest and Kinleith Forest sites, Diptera comprised 40%, Lepidoptera 24%, Coleoptera 18%, Trichoptera 0.8%, and Hymenoptera 0.36% of all insect fragments found in long-tailed bat faeces. Diptera, Lepidoptera, and Coleoptera were also the three main food sources for Pureora and Kinleith long-tailed bats in the stable isotope analysis. In addition the stable isotope analysis indicated Trichoptera and Hymenoptera were also less common food sources. However, using physical search methods in chapter two, Pureora long-tailed bats were found to have significantly different diets to Kinleith long-tailed bats yet this was not the case with stable isotope analysis. This is most likely due to the differences in these two techniques, mainly stable isotope analysis looking at broader trophic patterns in diet and physical search picking up slightly more detail. These differences are discussed later in this chapter. (Gillingham, 1996) found the long-tailed bats in Grand Canyon Cave also ate mainly Diptera (29%), Lepidoptera (25%), and Coleoptera (17%) with a small number of Hemiptera, Trichoptera, and Ephemeroptera. This is very similar to the results from this study, where Diptera, Lepidoptera, and Coleoptera are the primary food sources of Pureora and Kinleith long-tailed bats and Trichoptera, Hemiptera, and Hymenoptera are eaten less often. This is the first instance where stable isotope analysis has been used to investigate New Zealand bat diet. The similarities in findings between the physical search of faeces and stable isotope analysis suggest this may be an easier and reliable method to investigate diet of New Zealand bat species.

Stable isotope analysis is especially useful when needing to make inferences on the diet of endangered and/or cryptic animals as it increases the amount of information that can be obtained from possibly rare instances of capture and when observations in the wild are particularly difficult or infrequent (McFadden et al., 2006). Stable isotope analysis is also useful for picking up the presence of soft or well digested dietary items that would otherwise be undetected or under-represented with visual inspection of gut contents or faeces. Furthermore, stable isotope analysis gives a good outline of an animal's diet by comparing overlaps of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios, however, it is almost impossible to distinguish specific species consumed which leaves you with limited data (York & Billings, 2009). For

stable isotope analysis, faeces are ideal to work with when investigating immediate diet because they are relatively non-invasive to collect, contain the remains of recent diet and, multiple stable isotope ratios can be measured from one sample (Salvarina et al., 2013). However, a possible disadvantage of stable isotope analysis with faeces is that it is simply showing what the bats have eaten and not the diet they are actually assimilating (Salvarina et al., 2013).

Both stable isotope analysis and physical searching techniques have their limitations. Dietary items cannot be identified down as low as species level in most cases with either of these techniques (Whitaker et al., 2009; York & Billings, 2009). The physical search of faeces can often leave soft bodied insects under-represented compared to insects with harder chitinous exteriors (Clare et al., 2011; Leelapaibul et al., 2005). Whereas, stable isotope analysis can pick up these overlooked insects but often can then miss the more unusual or unexpected dietary items found by physically searching. I believe that both techniques have their merits and that, if possible, it is best to utilise both when investigating diet. In this study by combining physical search of faeces and stable isotope analysis new information on the diet of the long-tailed bat was gained. Physical search discovered the inclusion of Lepidoptera larvae in the diet when previously it was thought only flying insects were eaten (Chapter 2). Physical searching also shed light on what insect families were being eaten, such as Tipulidae, whereas stable isotope analysis lacked that detail, but showed that soft bodied insects such as Lepidoptera are more important in the diet of the long-tailed bat than previously thought. Stable isotope analysis also indicated slight differences in bat diets between study sites that otherwise wouldn't be identified. Where more detailed sampling was not possible, such as with the Eglington long-tailed bat samples in this study, stable isotope analysis is good for rapid assessment and allowed these samples to be used as a comparison.

In summary, New Zealand long-tailed bats in Pureora Forest and Kinleith Forest have opportunistic, generalist diets. There were no significant differences in the diet of the bats in native forest with the bats in exotic forest showing bats inhabiting exotic plantation forests can maintain a good quality diet similar to bats inhabiting native forests. Stable $\delta^{15}\text{N}$ values were similar over Pureora Forest short-tailed and long-tailed bats, Kinleith long-tailed bats, and Fiordland long-tailed bats meaning that all of these bat populations are at the

same trophic level and are obtaining the same amount of crude protein in their diets whether they are in native or exotic forests. Both stable isotope analysis and physical search methods give valuable information but don't give insight into specific species consumed (York & Billings, 2009). Because pests are defined at the species level, this makes it difficult to assess whether long-tailed bats are eating insect pests (Federico et al., 2008). Future research should be focused on DNA analysis of dietary items in order to obtain species-level identification and to be able to draw conclusions on the potential pest control service these bats could be giving us and their potential economic value. Although bats are less active in winter, future research should also look into seasonal changes in long-tailed and short-tailed bats diet over native and exotic habitat to identify any shifts in diet. Changes in diet over seasons could show flexible and opportunistic feeding or more selective feeding in certain seasons (Andreas et al., 2012). This has been shown in a study on pallid bats where they use diet plasticity to benefit from ample nectar in spring but change to an insectivorous diet at other times (Frick, Shipley, Kelly, Heady, & Kay, 2014).

3.6. References

- Alexander, J. (2001). *Ecology of long-tailed bats *Chalinolobus tuberculatus* (Forster, 1844) in the Waitakere Ranges: implications for monitoring*. (Master of Applied Science unpublished thesis), Lincoln University, Christchurch.
- Altringham, J. D. (2011). *Bats: from evolution to conservation* (Second ed.). New York: Oxford University Press.
- Andreas, M., Reiter, A., & Benda, P. (2012). Prey selection and seasonal diet changes in the western barbastelle bat (*Barbastella barbastellus*). *Acta Chiropterologica*, 14(1), 81-92.
- Arkins, A. M., Winnington, A. P., Anderson, S., & Clout, M. N. (1999). Diet and nectarivorous foraging behaviour of the short-tailed bat (*Mystacina tuberculata*). *Journal of Zoology, London*, 247, 183-187.
- Borkin, K. M. (2010). *Ecology of New Zealand's Long-tailed bat (*Chalinolobus tuberculatus*) in exotic plantation forest*. (Doctor of Philosophy in Biological Science), University of Auckland, Auckland.
- Borkin, K. M., & Ludlow, E. (2009). Notes on New Zealand mammals 9: long-tailed bat (*Chalinolobus tuberculatus*) chased by morepork (*Ninox novaeseelandiae*). *New Zealand Journal of Zoology*, 36, 11-12.
- Borkin, K. M., O'Donnell, C., & Parsons, S. (2011). Bat colony size reduction coincides with clear-fell harvest operations and high rates of roost loss in plantation forest. *Biodiversity and Conservation*, 20(14), 3537-3548.
- Borkin, K. M., & Parsons, S. (2009). Long-tailed bats' use of a *Pinus radiata* stand in Kinleith Forest: Recommendations for monitoring. *New Zealand Journal of Forestry*, 53(4), 38-43.
- Borkin, K. M., & Parsons, S. (2010a). The importance of exotic plantation forest for the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). *New Zealand Journal of Zoology*, 37(1), 35-51.
- Borkin, K. M., & Parsons, S. (2010b). Plantation forests are used by the lesser short-tailed bat, *Mystacina tuberculata rhyacobia*. *New Zealand Journal of Zoology*, 37(1), 13-17.
- Borkin, K. M., & Parsons, S. (2011a). Home range and habitat selection by a threatened bat in exotic plantation forest. *Forest Ecology and management*, 262, 845-852.

- Borkin, K. M., & Parsons, S. (2011b). Sex-specific roost selection by bats in clearfell harvested plantation forest: improved knowledge advises management. *Acta Chiropterologica*, *13*(2), 373-383.
- Brockerhoff, E. G., Suckling, D. M., Ecroyd, C. E., Wagstaff, S. J., Raabe, M. C., Dowell, R. V., & Wearing, C. H. (2011). Worldwide Host Plants of the Highly Polyphagous, Invasive *Epiphyas postvittana* (Lepidoptera: Tortricidae). *Journal of Economic Entomology*, *104*(5), 1514-1524.
- Clare, E. L., Barber, E. R., Sweeney, B. W., Herbert, P. D. N., & Fenton, M. B. (2011). Eating local: influences of habitat on the diet of little brown bats (*Myotis lucifugus*). *Molecular Ecology*, *20*, 1772-1780.
- Clare, E. L., Fraser, E. E., Braid, H. E., Fenton, M. B., & Herbert, P. D. N. (2009). Species on the menu of a generalist predator, the eastern red bat (*Lasiurus borealis*): using a molecular approach to detect arthropod prey. *Molecular Ecology*, *18*, 2532-2542.
- Cleveland, C. J., Betke, M., Federico, P., Frank, J. D., Hallam, T. G., Jason, H., Jr, J. D. L., McCracken, G. F., Medellín, R. A., Moreno-Valdez, A., Sansone, C. G., Westbrook, J. K., & Kunz, T. H. (2006). Economic Value of the Pest Control Service Provided by Brazilian Free-Tailed Bats in South-Central Texas. *Frontiers in Ecology and the Environment*, *4*(5), 238-243.
- Codron, D., Codron, J., Lee-Thorp, J. A., Sponheimer, M., & De Ruiter, D. (2005). Animal diets in the Waterberg based on stable isotopic composition of faeces. *South African Journal of Wildlife Research*, *35*(1), 43-52.
- Conservation, D. O. (2012). Pureora Forest Park tracks. In D. O. Conservation (Ed.). Wellington, New Zealand: Publishing Team.
- Cryan, P. M., Stricker, C. A., & Wunder, M. B. (2012). Evidence of cryptic individual specialisation in an opportunistic insectivorous bat. *Journal of Mammalogy*, *93*(2), 381-389.
- Daniel, M. J. (1990). Order Chiroptera. In M. C. King (Ed.), *The handbook of New Zealand mammals* (pp. 114-137). New Zealand: Oxford University Press
- Dick, C. W., & Patterson, B. D. (2006). Bat flies: Obligate ectoparasites of bats. In S. Morand, B. Krasnov & R. Poulin (Eds.), *Micromammals and Macroparasites* (pp. 179-194). Japan: Springer

- Federico, P., Hallam, T. G., McCracken, G. F., Purucker, S. T., Grant, W. E., Correa-Sandoval, A. N., Westbrook, J. K., Medellín, R. A., Cleveland, C. J., Sansone, C. G., Jr, J. D. L., Betke, M., Moreno-Valdez, A., & Kunz, T. H. (2008). Brazilian Free-Tailed Bats as Insect Pest Regulators in Transgenic and Conventional Cotton Crops. *Ecological Applications*, *18*(4), 826-837.
- Feldhamer, G. A., Carter, T. C., & Whitaker, J. O., Jr. (2009). Prey consumed by eight species of insectivorous bats from southern Illinois. *The American Midland Naturalist*, *162*(1), 43-51.
- Fenton, M. B. (2010). Convergences in the diversification of bats. *Current Zoology*, *56*(4), 454-468.
- Fenton, M. B., Cumming, D. H. M., Rautenbach, I. L., Cumming, G. S., Cumming, M. S., Ford, G., Taylor, R. D., Dunlop, J., Hovorka, M. D., Johnston, D. S., Portfors, C. V., Kalcounis, M. C., & Mahlanga, Z. (1998). Bats and the Loss of Tree Canopy in African Woodlands. *Conservation Biology*, *12*(2), 399-407.
- Fleming, T. H., & Sosa, V. J. (1994). Effects of Nectarivorous and Frugivorous Mammals on Reproductive Success of Plants. *Journal of Mammalogy*, *75*(4), 845-851.
- Frick, W. F., Shipley, J. R., Kelly, J. F., Heady, P. A., III, & Kay, K. M. (2014). Seasonal reliance on nectar by an insectivorous bat revealed by stable isotopes. *Oecologia*, *174*(1), 55-65.
- Gillingham, N. J. (1996). *The behaviour and ecology of long-tailed bats (Chalinolobus tuberculatus Gray) in the central North Island*. (Master of Science Unpublished thesis), Massey University, Palmerston North.
- Griffiths, R. W. (2007). Activity patterns of long-tailed bats (*Chalinolobus tuberculatus*) in a rural landscape, South Canterbury, New Zealand. *New Zealand Journal of Zoology*, *34*(3), 247-258.
- Herrera, L. G., Hobson, K. A., Manzo, A., Estrada, D., Sanchez-Cordero, V., & Mendez, G. (2001). The role of fruits and insects in the nutrition of frugivorous bats: evaluating the use of stable isotope models. *Biotropica*, *33*(3), 520-528.
- Hill, J. E., & Smith, J. D. (1984). *Bats. A natural history*. London: Rigby.
- Jones, G., Webb, P. I., Sedgeley, J. A., & O'Donnell, C. F. J. (2003). Mysterious Mystacina: how the New Zealand short-tailed bat (*Mystacina tuberculata*) locates insect prey. *The Journal of Experimental Biology*, *206*(23), 4209-4216.

- Jones, K. E., Purvis, A., MacLarnon, A., Bininda-Emonds, O. R. P., & Simmons, N. B. (2002). A phylogenetic supertree of the bats (Mammalia : Chiroptera). *Biological Reviews*, 77(2), 223-259.
- Kelly, J. F. (2000). Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology*, 78(1), 1-27.
- Kurta, A., & Whitaker, J. O., Jr. (1998). Diet of the endangered Indiana bat (*Myotis sodalis*) on the Northern edge of its range. *The American Midland Naturalist*, 140(2), 280-286.
- Lacki, M. J., Johnson, J. S., Dodd, L. E., & Baker, M. D. (2007). Prey consumption of insectivorous bats in coniferous forests of north-central Idaho. *Northwest Science*, 81(3), 199-205.
- Lee, Y., & McCracken, G. F. (2005). Dietary variation of Brazilian free-tailed bats links to migratory populations of pest insects. *Journal of Mammalogy*, 86(1), 67-76.
- Leelapaibul, W., Bumrungsri, S., & Pattanawiboon, A. (2005). Diet of wrinkle-lipped free-tailed bat (*Tadarida plicata* Buchannan, 1800) in central Thailand: insectivorous bats potentially act as biological pest control agents. *Acta Chiropterologica*, 7(1), 111-119.
- Lloyd, B. (2005). Lesser short-tailed bat. In M. C. King (Ed.), *The Handbook Of New Zealand Mammals (2nd ed.)* (pp. 110-127). Melbourne: Oxford University Press.
- Lloyd, B. D. (2001). Advances in New Zealand mammalogy 1990-2000: Short-tailed bats. *Journal of the Royal Society of New Zealand*, 31(1), 59-81.
- Long, R. F., Simpson, T., Ding, T., Heydon, S., & Reil, W. (1998). Bats feed on crop pests in Sacramento Valley. *California Agriculture*, 52(1), 8-10.
- McCartney, J., Stringer, I., & Potter, M. A. (2007). Feeding activity in captive New Zealand lesser short-tailed bats (*Mystacina tuberculata*). *New Zealand Journal of Zoology*, 34, 227-238.
- McFadden, K. W., Sambrotto, R. N., Medellín, R. A., & Gompper, M. E. (2006). Feeding habits of endangered pygmy raccoons (*Procyon pygmaeus*) based on stable isotope and fecal analyses. *Journal of Mammalogy*, 87(3), 501-509.
- McCracken, G. F., Westbrook, J. K., Brown, V. A., Eldridge, M., Federico, P., & Kunz, T. H. (2012). Bats track and exploit changes in insect pest populations. *PLoS ONE*, 7(8), 1-10.

- Molloy, J. (1995). *Bat (Peka peka) recovery plan (Mystacina, Chalinolobus)*. Wellington: Department of Conservation.
- Moore, G. E. (2001). *Use of Kinleith forest by native New Zealand bats and effects of forestry* (Master of Science Unpublished thesis), Massey University, Palmerston North, New Zealand.
- Moosman, P. R., Thomas, H. H., & Veilleux, J. P. (2012). Diet of the widespread insectivorous bats *Eptesicus fuscus* and *Myotis lucifugus* relative to climate and richness of bat communities *Journal of Mammalogy*, *93*(2), 491-496.
- O'Donnell, C. F. J. (2000a). Conservation status and causes of decline of the threatened New Zealand Long-tailed Bat *Chalinolobus tuberculatus* (Chiroptera : Vespertilionidae). *Mammal Review*, *30*(2), 89-106.
- O'Donnell, C. F. J. (2000b). Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). *New Zealand Journal of Zoology*, *27*(3), 207-221.
- O'Donnell, C. F. J. (2001). Advances in New Zealand mammalogy 1990-2000: Long-tailed bat. *Journal of the Royal Society of New Zealand*, *31*(1), 43-57.
- O'Donnell, C. F. J. (2002). Variability in numbers of long-tailed bats (*Chalinolobus tuberculatus*) roosting in Grand Canyon Cave, New Zealand: implications for monitoring population trends. *New Zealand Journal of Zoology*, *29*(4), 273-284.
- O'Donnell, C. F. J. (2005). NZ Long-tailed bat. In M. C. King (Ed.), *The handbook of New Zealand Mammals (2nd ed.)* (pp. 98-110). Melbourne: Oxford University Press.
- O'Donnell, C. F. J., Christie, J. E., Hitchmough, R. A., Lloyd, B., & Parsons, S. (2010). The conservation status of New Zealand bats, 2009. *New Zealand Journal of Zoology*, *37*(4), 297-311.
- O'Donnell, C. F. J., Christie, J. E., & Simpson, W. (2006). Habitat use and nocturnal activity of lesser short-tailed bats (*Mystacina tuberculata*) in comparison with long-tailed bats (*Chalinolobus tuberculatus*) in temperate rainforest. *New Zealand Journal of Zoology*, *33*, 113-124.
- O'Donnell, C. F. J., & Sedgeley, J. A. (1999). Use of roosts by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate rainforest in New Zealand. *Journal of Mammalogy*, *80*(3), 913-923.

- Ober, H. K., & Hayes, J. P. (2008). Prey selection by bats in forests of western Oregon. *Journal of Mammalogy*, *89*(5), 1191-1200.
- Ogden, J., Braggins, J., Stretton, K., & Anderson, S. (1997). Plant species richness under *Pinus radiata* stands on the Central North Island Volcanic Plateau, New Zealand *New Zealand Journal of Ecology*, *21*(1), 17-29.
- Painter, M. L., Chambers, C. L., Siders, M., Doucett, R. R., Whitaker, J. O., Jr., & Phillips, D. L. (2009). Diet of spotted bats (*Euderma Maculatum*) in Arizona as indicated by fecal analysis and stable isotopes. *Canadian Journal of Zoology*, *87*, 865-875.
- Pryde, M. A., Lettink, M., & O'Donnell, C. F. J. (2006). Survivorship in two populations of long-tailed bats (*Chalinolobus tuberculatus*) in New Zealand. *New Zealand Journal of Zoology*, *33*(2), 85-95.
- Pryde, M. A., O'Donnell, C. F. J., & Barker, R. J. (2005). Factors influencing survival and long-term population viability of New Zealand long-tailed bats (*Chalinolobus tuberculatus*): Implications for conservation. *Biological Conservation*, *126*(2), 175-185.
- Riskin, D. K., Parsons, S., Schutt, W. A., Carter, G. G., & Hermanson, J. W. (2006). Terrestrial locomotion of the New Zealand short-tailed bat *Mystacina tuberculata* and the common vampire bat *Desmodus rotundus*. *Journal of Experimental Biology*, *209*(9), 1725-1736.
- Ross, M. G. (2004). *Response to a gypsy moth incursion within New Zealand*. Paper presented at the IUFRO, Hanmer.
- Salvarina, I., Yohannes, E., Siemers, B. M., & Koselj, K. (2013). Advantages of using fecal samples for stable isotope analysis in bats: evidence from a triple isotopic experiment. *Rapid Communications in Mass Spectrometry*, *27*(17), 1945-1953.
- Sare, D. T. J., Millar, J. S., & Longstaffe, F. J. (2005). Tracing dietary protein in red-backed voles (*Clethrionomys gapperi*) using stable isotopes of nitrogen and carbon. *Canadian Journal of Zoology*, *83*(5), 717-725.
- Schillaci, M. A., Castellini, J. M., Stricker, C. A., Jones-Engel, L., Lee, B. P. Y. H., & O'Hara, T. M. (2014). Variation in hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in long-tailed macaques (*Macaca fascicularis*) from Singapore. *Primates*, *55*(1), 25-34.

- Sedgeley, J. A. (2006). Roost site selection by lesser short-tailed bats (*Mystacina tuberculata*) in mixed podocarp-hardwood forest, Whenua Hou/Codfish Island, New Zealand. *New Zealand Journal of Zoology*, 33(2), 97-111.
- Sedgeley, J. A., & O'Donnell, C. F. J. (1999a). Factors influencing the selection of roost cavities by a temperate rainforest bat (Vespertilionidae : *Chalinolobus tuberculatus*) in New Zealand. *Journal of Zoology*, 249, 437-446.
- Sedgeley, J. A., & O'Donnell, C. F. J. (1999b). Roost selection by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate New Zealand rainforest and its implications for the conservation of bats in managed forests. *Biological Conservation*, 88(2), 261-276.
- Shiel, C. B., Duverge, P. L., Smiddy, P., & Fairley, J. S. (1998). Analysis of the diet of Leiser's bat (*Nyctalus leisleri*) in Ireland with some comparative analyses from England and Germany. *Journal of Zoology, London*, 246, 417-425.
- Shiel, C. B., McAney, C., Sullivan, C., & Fairley, J. S. (1997). *Identification of arthropod fragments in bat droppings* (Vol. 7). London: The Mammal Society.
- Teeling, E. C., Madsen, O., Murphy, W. J., Springer, M. S., & O'Brien, J. (2003). Nuclear gene sequences confirm an ancient link between New Zealand's short-tailed bat and South American noctilionoid bats. *Molecular Phylogenetics and Evolution*, 28(2), 308-319.
- Triplehorn, C. A., & Johnson, J. S. (2005). *Borror and DeLong's introduction to the study of insects* (Seventh ed.). USA: Thomson Brooks/Cole.
- Walter, W. D., Leslie, J. D. M. L., Hellgren, E. C., & Engle, D. M. (2010). Identification of subpopulations of North American elk (*Cervus elaphus* L.) using multiple lines of evidence: habitat use, dietary choice, and fecal stable isotopes. *Ecological Research*, 25(4), 789-800.
- Whitaker, J. O., Jr., & Karatas, A. (2009). Food and feeding habits of some bats from Turkey. *Acta Chiropterologica*, 11(1), 393-403.
- Whitaker, J. O., McCracken, G. F., & Siemers, B. M. (2009). Food habits analysis of insectivorous bats. In T. H. Kunz & S. Parsons (Eds.), *Ecological and behavioural methods for the study of bats* (Second ed.). Baltimore: The Johns Hopkins University Press.
- Wilson, D. E. (1997). *Bats in question*. Melbourne: CSIRO publishing.

York, H. A., & Billings, S. A. (2009). Stable-isotope analysis of diets of short-tailed fruit bats (Chiroptera: Phyllostomidae: *Carollia*). *Journal of Mammalogy*, 90(6), 1469-1477.