Leiopelma hochstetteri Fitzinger 1861 (Anura: Leiopelmatidae) Habitat Ecology in the Waitakere Ranges, New Zealand.

Eduardo Nájera Hillman

A thesis submitted to the Faculty of Health and Environmental Sciences,
Auckland University of Technology

in fulfilment of the requirements for the degree of

Doctor of Philosophy

Supervised by Dr. Andrea C. Alfaro

2009

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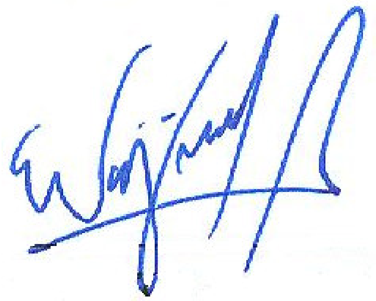
ATTESTATION OF AUTHORSHIP

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by other person (except where explicitly defined in the acknowledgements), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.



Eduardo Nájera Hillman

ACKNOWLEDGMENTS

This research was conducted with the financial support from the School of Applied Sciences, and the Earth and Oceanic Sciences Research Institute, Auckland University of Technology. My study fees and stay in New Zealand were sponsored by The National Council for Science and Technology (CONACyT), México (scholarship holder number: 205742).

I am thankful to my supervisors Andrea C. Alfaro, Barbara B. Breen and Steve O'Shea for scientific input and guidance. I am thankful to Brid Lorigan, Christine Silvester and Chris Whyburd for their technical support and to Severine Dewas, Emma Beatson, Tim Young, Jeremy Barker, Paul McBride**,** Ruben Wylie, Hernando Acosta, David Tung**,** Sue Dodd, Matthew Jones and Kathrin S. Bolstad for their field assistance and scientific input (all AUT). Peter King provided field access and invaluable field work support. I am grateful to the Auckland Regional Council for the permit granted to undertake research study at the Waitakere Ranges Regional Park (procured on 30/11/2006 by Su Sinclair, Acting Senior Ranger Conservation), to Department of Conservation for the permits to undertake dietary studies (national permit numbers AK-20230-RES and WK-20973-RES), and to the Waikato Stable Isotope Unit for processing the isotope samples. The New Zealand Native Frog Recovery Group provided valuable scientific inputs an open forum for constructive discussion. I am particularly grateful to Jennifer Germano for introducing me to the New Zealand frog-research group. I am grateful to the National Institute of Water & Atmospheric Research (NIWA) and the Ministry of the Environment (MfE) for providing data on New Zealand River Environment Classification.

I am deeply grateful to my family, specially my wife, Guadalupe, for all her support and love.

PREFACE

This thesis is structured as a sequence of five chapters which present primary data (Chapters 2–6), accompanied by chapters comprising general introduction and review of existing information on *L. hochstetteri* (Chapter 1), and synthesis and conclusions (Chapter 7).

Population survey data examined from three years (2007–2009) in Chapters 3, 4 and 5 were collected by me and some volunteer students and staff members of the Auckland University of Technology. I also was assisted in the field during population surveys (2007–2009) by Peter King (director of the community-based ecosystem restoration project: La Trobe Mainland Island) who assisted in collection and identification of botanical data for analysis in Chapter 4, and facilitated background information on pest-management operations.

Research from this thesis has contributed to the publication of three papers (Nájera-Hillman et al. 2009a, 2009b, 2009c), cited elsewhere in this thesis.

The need for ethical approval for this research was investigated with the University of Auckland's Animal Ethics Committee (AEC). The AEC Secretary (Janine Watene) informed me that if the animal is not manipulated in anyway then my research did not need an animal ethics approval. According to the definition of animal manipulation in section 3 of the *Animal Welfare Act 1999*, frogs weren't manipulated on this research.

Most of the research results contained in this thesis were presented on two conferences in New Zealand, one conference in Australia and two New Zealand Native Frog Recovery Group meetings:

- 12th Biennial Conference of the Society for Research on Amphibians and Reptiles in New Zealand. Otago University, February 9–11, 2007.
- Native Frog Recovery Group Meeting, October 24–25, 2007.
- Native Frog Recovery Group Meeting, October 20–21, 2008.
- 33rd Ecological Society of Australia Conference, University of Sydney, December 1–5, 2008.
- Second Meeting of the Australasian Societies for Herpetology, Massey University, February 20–22, 2009.

ABSTRACT

Declines and extinctions of amphibian populations are a global dilemma with complex local causes, which should be viewed in the context of a much larger biodiversity crisis. As other animal groups, amphibians with restricted distributions, such as island endemics, are thought to be more vulnerable to environmental change and susceptible to population declines. In the New Zealand archipelago, the only four native species of frogs (*Leiopelma hochstetteri, L. archeyi, L. hamiltoni* and *L. pakeka*) are classified as threatened. In particular *Leiopelma hochstetteri*, the most widespread and abundant endemic frog species in New Zealand, now survives only in spatially fragmented populations as a result of direct or indirect human activity. Hence, it is recognised as threatened and fully protected by legislation.

In the last fifty years, some *L. hochstetteri* populations have been studied, providing descriptive information, which may be used to assess the current status (increasing, stable or declining) of previously or never monitored populations. This thesis examines the diet and trophic level, the effects ship rats (*Rattus rattus*) as well as the distribution and abundance of *L. hochstetteri* on a habitat-use context, to provide a basis for evaluating conceivable decline-agents, and to establish a platform to design directed conservation strategies.

The Waitakere Ranges are considered a *Leiopelma hochstetteri* conservation management unit, on which *L. hochstetteri* has been previously studied. This area consists of a series of hills that run roughly north–south, which are mostly covered in regenerating indigenous vegetation. Today, 60% of the Waitakere Ranges fall within a Regional Park, which together with its surrounding residential areas is afforded protection to minimise the effects of development on the region. The accessibility and

conservation character of this area makes it an ideal area for the study of *L. hochstetteri* populations.

As a first step to characterise the diet and trophic level of *L. hochstetteri* within streams in the Waitakere Ranges, Auckland, stable carbon and nitrogen isotope analyses were undertaken on a variety of sympatric terrestrial and aquatic plant and animal species, including adult frogs. These results showed that: 1) aquatic and terrestrial food webs were linked by terrestrial inputs into the stream; 2) invertebrate and vertebrate predators separated well into distinct trophic groups; and 3) *L. hochstetteri* occupied an intermediate trophic position among predators, with a diet, at least as an adult, comprising terrestrial invertebrates. Shortfin eels and banded kokopu were identified as potential predators of *L. hochstetteri*, but data for rats were inconclusive.

The inconclusiveness of these trophic studies, with regard to the effects of ship rats on *L. hochstetteri* populations, lead me to evaluate the influence of a seven-year ship rat management operation on frog abundance. To achieve a reliable evaluation, the habitat characteristics that had significant influence on frog abundance were identified. Then, it was confirmed that the study areas represented similar habitats in terms of those variables, and finally the effect of the pest-management activities was evaluated. Presence/absence of pest-management operations did not have a significant effect on frog abundance. These results, together with the results of the diet and trophic level analyses, suggested that ship rats do not represent a significant threat for this frog species, at least in the Waitakere Ranges.

The results of distribution and abundance investigations indicated that in the Waitakere Ranges frogs are currently widely distributed, relatively abundant and that recruitment has occurred at least in the last ten years. Additionally, in order to identify associations between habitat characteristics and frog distribution and abundance, reliable and specifically designed monitoring methodologies were developed. Although this frog is known to occur in wet areas adjacent to shaded streams in forested catchments, quantitative ecological data previously did not exist to enable characterisation of its habitat. Here, novel data were reported on the current distribution and habitat requirements of this species in the Waitakere Ranges. Statistical modelling demonstrates frogs most likely occur in small, erosive streams with coarse substrates and cold waters, surrounded by mature or undisturbed riparian vegetation, where higher abundances of frogs may be found in steep areas with stable patches of cobbles and boulders lying against larger stream bed elements within the stream channel. Anthropogenic activities, such as clearing or logging, and upstream disturbances that potentially increase silt input into streams were identified as threats to these frog species.

Finally, the habitat-use information gathered during this investigation was utilised to develop a spatial decision support system (SDSS) as a tool to assess the quality and quantity of habitat available to *L. hochstetteri* populations associated with the Auckland Region. These results have important implications for the conservation of New Zealand native frog species and riparian stream habitat.

CHAPTER 1. General introduction

1.1 BIODIVERSITY CRISIS AND CONSERVATION

Biodiversity connotes the richness and variety of life on Earth. During the United Nations Conference on Environment and Development in Rio de Janeiro in 1992, this variety of life was distinguished at three different levels: genetic variation, the number of species and the variety of ecosystems (Selvik 2004). The concept of biodiversity is used widely, and its relatively rapid establishment within science and popular science is an indication that it is considered an important issue. Indeed, biodiversity is the very basis of human survival and economic well-being, and encompasses all life forms, ecosystems and ecological processes (Singh 2002).

Species extinctions are, of course, perfectly natural. All species begin in some restricted setting and then spread; most subsequently undergo differentiation, and eventually all species come to an end (Levin and Donald 2002). The diversity of species at any point in time is simply the result of these ongoing processes, which can wax and wane in intensity (Singh 2002). As long as the rate of speciation equals or exceeds the rate of extinction, biodiversity will remain constant or increase. In past geological periods the loss of existing species was eventually balanced or exceeded by the evolution of new species. However, the current losses are exceptional— 100 to 1000 times those of past rates (Primack 2004; Brooks et al. 2006). This recent episode of extinction is due almost exclusively to human activities (Leakey & Lewin 1996; Lövei 2001).

The major threats to biological diversity are habitat destruction, habitat fragmentation, habitat degradation (including pollution), global climate change, overexploitation of species, invasion of exotic species, increased spread of disease, and synergisms among these factors (Melchias 2001; Primack 2004). These seven threats to biodiversity are all caused by an expanding human population's ever-increasing use of the world's natural resources (Singh 2002; Primack 2004; Brooks et al. 2006; Chivian & Bernstein 2008).

Assuming no radical transformation in human behaviour, we can expect important changes in biodiversity and ecosystem services in the next 40 years (Jenkins 2003). Although, the impact of species deletions on ecosystem function and stability is still a subject of debate among ecologists (Singh 2002: Jenkins 2003), this does not mean, of course, that we can continue to manipulate or abuse the planet *ad infinitum*. In fact the processes driving extinction are eroding the environment services on which humanity depends (Millennium Ecosystem Assessment 2005). The later suggests that it is wise to take a precautionary approach and make serious attempts towards the conservation of biodiversity.

The leading response to the biodiversity crisis since the late 19^{th} century has been the creation of protected areas (Adams et al. 2004). However, other basic strategies for biodiversity conservation include *ex situ* strategies, such as the establishment of botanical and zoological gardens, reduction of anthropogenic pressure on natural populations by cultivating them elsewhere, and rehabilitation of threatened species through a variety of strategies (Singh 2002). Popular interest in protecting the world's biodiversity has intensified during the last few decades (Caughley & Gunn 1996). The desire of the scientific community to face this challenge has prompted the development of conservation biology as an integrated scientific discipline. Conservation biology represents a synthesis of many basic sciences, such as community ecology, biogeography, environmental law; that provide principles and new approaches for the applied fields of resource management, such as agriculture, management of natural areas and fisheries management (Wilson 1992; Primack 2004).

In New Zealand there is an ongoing biodiversity decline (Craig et al. 2000). New Zealand was one of the last places on earth to be settled by humans and since the settlement around 1000 years ago, humans and their accompanying pests have caused the extinction of several animal species (Ministry for the Environment 2002). For example, the flightless avifauna of at least 38 species has been reduced in a few centuries to nine, most of which are currently endangered (Jenkins 2003). Three of seven species of frogs have become extinct (Towns & Daugherty 1994; Bell 1994) and the remaining species have suffered drastic reductions in their distribution and population size (Bell et al. 2004a). Rain forest have been reduced from an original 78% of land area to approximately 23% (Ministry for the Environment 1997), and land use change analysis shows a continued loss of nearly 175 km^2 of indigenous habitat between 1996 and 2002 (OECD 2007). Despite sizable decreases in the numbers of certain pests (e.g. rats, possums, rabbits) in some areas, invasive species continue to pose serious risks to indigenous ecosystems and species (OECD 2007). The conservation legal framework is inadequate (Craig et al. 2000; Coombes 2003) and government funding allows less than 5% of the protected lands to be managed sustainably (Department of Conservation 1998). The 1997 report on *The State of the New Zealand's Environment* concluded that "biodiversity decline is New Zealand's most extensive and multi-faceted environmental issue".

On the positive side, greater than 30% of New Zealand's total land area and 7.5% of its territorial sea has been reserved, there is a single government agency responsible for most conservation activities, and the security of 200 threatened species has improved through effective species recovery programmes (Craig et al. 2000; OECD 2007). In February 2000 the *New Zealand Biodiversity Strategy* was launched as a 20-

year programme to halt the decline in indigenous biodiversity. This strategy is contributing to pest and weeds control and threatened species work on public conservation land, to take measures for protection of biodiversity in private land, and to improving understanding and protection of marine biodiversity (Ministry for the Environment 2002).

1.2 AMPHIBIAN DECLINES

1.2.1 Role of amphibians in the ecosystem

Amphibians are widely distributed throughout tropical and temperate regions, where they occupy many freshwater and moist terrestrial environments (Beebee 1996). Within these environments, amphibians are important predators (Malkmus 2000) and are themselves an important food source for many other organisms, including birds, snakes and fishes (Chivian & Bernstein 2008). As major predators of insects, amphibians fulfil an important role in the food chain. Without them, insects can multiply rapidly, causing large-scale damage to crops. Amphibians are regarded as particularly vulnerable to pollutants and other environmental stresses. Consequently amphibians have been used as environmental indicators for the quality of the environment and the potential threats to other animals, including humans (Bishop 2005). Moreover, amphibians possess an enormous variety of biologically active compounds, which are released from "granular glands" as a defence mechanism; some of these compounds (e.g. alkaloid toxins, antimicrobial peptides) could become important new medicines (Chivian & Bernstein 2008).

1.2.2 Amphibian susceptibility and causes of decline

Amphibian populations have declined dramatically in many areas of the world since the 1970s (Stuart et al. 2004). These declines appear to have worsened in the last 25 years, and amphibians are now considered to be more threatened than mammals or birds (Beebee & Griffiths 2005). A recent report for the IUCN's Global Amphibian Assessment indicates that as many as a third of amphibian species, now estimated at over 6350, have undergone severe declines or extinction (Stuart et al. 2004). Although biological research has led to great strides in our understanding of amphibian declines (Bebee & Griffiths 2005), it is still important to continue informing the issues with rigorous scientific data to improve our understanding of particular amphibian species and/or populations.

Amphibians as a group are especially susceptible to environmental degradation due to several basic characteristics: their relatively small size, their ectothermic physiology, their highly permeable skin and their dependence on aquatic or moist habitats (Murphy et al. 2000; Wells 2007). Especially, range-restricted populations of endemic amphibians are more vulnerable to environmental change and susceptible to population declines (Lecis & Norris 2003). However, amphibians as a group have been around for hundreds of millions of years and have experienced dramatic global changes in climate, habitat structure and even arrangement of continents (Wells 2007). Even over shorter time scales, such as the last 1000 years, there have been substantial and often quite rapid changes in temperature (Carey and Alexander 2003). Thus, the question is not whether amphibians can adapt to environmental change? But whether, the speed at which amphibians can adapt, either through evolution or phenotypic and behavioural responses to the environment.

There are several possible causes for recent amphibian declines, which include habitat change, over-exploitation, introduction of exotic species, global climate change, pollution and infectious diseases (Collins & Storfer 2003). Some suggested causes of amphibian declines, such as diseases and climate change, are still controversial. Other potential causes, such as habitat loss and the spread of exotic species, are now generally accepted (Chivian & Bernstein 2008). Nevertheless, there is evidence that many other animal groups with shared characteristics (e.g. freshwater fishes and molluscs) are threatened as well (Abell 2002). Hence, the decline of amphibian populations should be viewed in the context of a much larger biodiversity crisis (Halliday 2005; Wells 2007).

1.3 AMPHIBIANS IN NEW ZEALAND

In New Zealand the only amphibians are four endemic (*Leiopelma hochstetteri*, *L. archeyi*, *L. hamiltoni* and *L. pakeka*) and three introduced (*Litoria aurea*, *L. raniformis* and *L. ewingii*) frog species. However, it is worthy to mention that recent phylogenetic analyses suggest that classification of *L. pakeka* and *L. hamiltoni* as separate species appears to be unwarranted (Holyoake et al. 2001).

All New Zealand frogs live in relatively cool, moist habitats. Three species, *L. archeyi*, *L. hamiltoni* and *L. pakeka*, lay eggs in terrestrial nests. These hatch into advanced stage tadpoles that complete development without feeding. The third species, *L. hochstetteri*, lays aquatic eggs in water filled depressions on the ground. The eggs hatch into tadpoles at an earlier stage of development than the species that remain in the nest, but do not feed before metamorphosis (Wells 2007).

The family Leiopelmatidae, survives only in New Zealand. Two frog species (*Ascaphus truei* and *A. montanus*) of the North-American family Ascaphidae, represent the nearest living relatives (Gibbs 2006). These two frog families diverged from each other in the Jurassic (180 million years ago), when the megacontinent Pangaea was splitting apart (Roleants & Bossuyt 2005). Both families are structurally the most primitive of all frogs, because they posses certain skeletal features, such as fish like vertebrae (Ford & Cannatella 1993).

From the Holocene fossil record (11 700 years ago) we know that Leiopelmatid frogs were much more common prior to human arrival (Gibbs 2006). Before human colonisation, the archipelago's amphibian assemblage included seven known native frog species (Worthy, 1987). From these seven species, three became extinct mainly due to habitat alterations and the effects of introduced species (Towns & Daugherty 1994; Bell 1994). The remaining species have suffered drastic reductions in their distribution and population size (Bell et al. 2004a). *L. pakeka* and *L. hamiltoni* survive in two small islands in the Cook Strait between the North and South Islands of New Zealand, while *L. archeyi* and *L. hochstetteri* survive as fragmented remnant populations across the North Island. A number of biological features make them vulnerable to population decline or extinction. These native species have restricted distribution ranges, appear to be unusually long lived, have very low reproductive rates, and are vulnerable to introduced predators (Bell et al. 2004a).

All native frog species are classified as threatened both nationally and internationally. The New Zealand classification system lists *L. archeyi*, *L. hamiltoni* and *L. pakeka* as acutely threatened and *L. hochstetteri* as 'at risk' (Hitchmough et al. 2007). Actions towards the conservation of these frogs include translocations (Bell et al. 2004b); disease management (Bishop et al. 2009); and active predator control programmes (Fraser & Hauber 2008). Additionally, in 1996 the first *Frog Recovery Plan* was published (Newman 1996). Recovery plans are statements of the Department of Conservation (New Zealand) intentions for the conservation of a particular species, group of species or community for a defined period. This first plan had a span of 5 years and led to the formation of the native frog recovery group, an advisory panel of native frog conservation and research experts. In 2004, the recovery group recommended the preparation of a new recovery plan, which covers the period from 2009 to 2019. This plan spans a transitional phase to consolidate the security of the species, and sets the platform for their broader recovery (Bishop et al. 2009).

1.3.1 *Leiopelma hochstetteri*

For the effective management of an endangered species it is necessary to understand the life-history and ecology of the species. *Leiopelma hochstetteri* is the most widespread and abundant New Zealand native frog. However, subfossil remains (10 000–14 000 yr B.P.) found throughout the North Island and northern half of the South Island, indicate that its range was once greater (Worthy 1987). Currently, this frog species is ranked number 38 on the Zoological Society of London's amphibian EDGE list of the most evolutionarily distinct and globally endangered amphibians in the world. It is recognized as 'vulnerable' in the IUCN red list of threatened species, and is fully protected by the *New Zealand Wildlife Act 1953*. The New Zealand threat classification system lists *L. hochstetteri* "at risk" (Hitchmough et al. 2007), as it is a taxon with small widely scattered populations, due to direct or indirect human activities. Indeed, this species is only found in spatially fragmented populations across the northern half of the North Island, and on Great Barrier Island (Baber et al. 2006). Substantial genetic variation among frogs from different areas of its current distribution suggests that each population should be considered a distinct unit worthy of separate conservation (Green 1994; Fouquet et al. 2009). The last discovery of a new *L. hochstetteri* population was in 2004 at Maungatautari Scenic Reserve, South Waikato, suggesting that there is a possibility that further searches could locate additional new populations and emphasises the value of further efforts to actively protect New Zealand's amphibian biodiversity (Baber et al. 2006).

This small frog, up to 50 mm length, is semi-aquatic, highly cryptic and can be morphologically distinguished from other *Leiopelma* species by the presence of half webbed toes, which in other *Leiopelma* species are absent (Stephenson & Stephenson 1957). Over the past fifty years, several studies of *L. hochstetteri* populations (Stephenson & Stephenson 1957; McLennan 1985, Green & Tessier 1990; Tessier et al. 1991; Bradfield 2005) have provided information about the habitat requirements of the species. *Leiopelma hochstetteri* prefers cool, shady, rocky, forest creeks and seepages. During the daytime these frogs shelter beneath rocks, logs, vegetation and leaf litter (Bell 1982; McLennan 1985; Newman & Towns 1985).

Previous attempts to monitor some *L. hochstetteri* populations (e.g. Maungatautari, Waitakere Ranges, Golden Cross) have involved estimates of relative abundance counting individuals using area-constrained protocols (transects or quadrants; e.g. Green & Tessier 1990; Baber et al. 2006; Bradfield 2005). Usually surveys are conducted during daylight hours. These approaches are time consuming and subject to observer bias, but commonly used in amphibian population studies (Heyer et al. 1994). Although a new, statistically robust, technique (site occupancy) has been recently developed for effective monitoring of *L. hochstetteri* (Crossland et al. 2005), for continuity with earlier studies line transects searches for *L. hochstetteri* have been repeatedly undertaken in populations, such as, the Waitakere Ranges (Ziegler 1999; Bradfield 2005) providing data, which may be used to track changes in relative abundance, distribution or size-class population structure.

The areas recording the highest densities of *L. hochstetteri* are steep-sloped, minimally degraded, stream headwaters, with frogs found above the flood level of flood-prone streams, mostly within 25 cm of a watercourse but also up to 4 m away (McLennan 1985; Newman & Towns 1985; Green & Tessier 1990). This frog has been described as sedentary (Tessier et al. 1991), although it is known that this species can be found in the forest some distance away from streams (Robb 1986), and that individual frogs have been documented moving within and between streams in a catchment (Slaven 1992).

Breeding sites have been reported to be under rocks and logs in and around water seepages and smaller streams, where clutches of 10–22 eggs are laid and from which tailed swimming larvae hatch (Bell 1985). However, there are very few reports describing clusters of eggs or reproductive behaviour (e.g. McLennan 1985), which suggest that much more work is needed to understand the reproductive ecology of this species.

Little is known of the diet of *L. hochstetteri*, although some assumptions have been made. For example, it has been suggested that frogs emerge at night to forage on insects and spiders along the stream edge and within riparian vegetation (Chapman & Alexander 2006). Beetles, spiders, ants, millipedes, earthworms and slugs, found where frogs shelter, were thought to constitute an important food source for these frogs (Sharell 1966). Additionally, Stephenson & Stephenson (1957) reported a small, entire fresh-water crayfish in the stomach of one frog, suggesting an aquatic component in the diet of this species. In a study based on analysis of faecal samples, Kane (1980) found that *L. hochstetteri* prey consisted primarily of adult terrestrial arthropods, including beetles, flies, sawflies and amphipods. None of the above studies were specifically designed to characterise the diet of *L. hochstetteri*, or to determine its trophic position and relationships within forested stream food webs. Therefore, improving our understanding of their trophic position (their food sources and predators) will help elucidate their contribution to ecosystem functioning, and may assist conservation efforts of this threatened species (Hirai & Matsui 1999).

Quoting the current Native Frog (*Leiopelma* species) Recovery Plan (Bishop et al. 2009) — "agents of decline for this native frog species have not been conclusively demonstrated, particularly at the population level, and in some cases are speculative". However, habitat modifications (Stephenson & Stephenson 1957, McLennan 1985; Tessier et al. 1991) and predation by exotic species, especially *Rattus spp.* (Baber et al. 2006), are considered the major threats for this endemic frog species. Past and current management of this species consist primarily of habitat protection and statutory advocacy (legal protection of the species). In 2006, an outdoor captive breeding programme was established at Hamilton Zoo to develop captive husbandry techniques and secure one population from potential infection by amphibian diseases. The preferred recovery options for this species are to identify conservation management units (CMUs) and confirm agents of decline (Bishop et al. 2009).

This thesis examines the diet and trophic level, the effects of introduced predators as well as the distribution and abundance of *L. hochstetteri* on a habitat-use context, to provide a basis for evaluating conceivable decline-agents, and to establish a platform to design directed conservation strategies.

1.4 OBJECTIVES

General Objective: To examine the diet and trophic level of *L. hochstetteri* in the stream food web and to determine the effects of ship rats as potential predator (and incidentally the effects of ship rat pest management), as well as to examine the effect of habitat variability on the distribution and abundance of *L. hochstetteri* in the Waitakere Ranges, to provide a basis for evaluating frog habitat-use, conceivable decline-agents, and to establish scientific baseline data to assist in the design of directed conservation strategies.

Specific objectives:

1. To monitor *L. hochstetteri* populations to provide basic descriptive information to assess the current status (increase, stable or decline) of this frog populations.
2. To identify the diet and trophic position of *L. hochstetteri* in forested streams using stable isotopes ($\delta^{13}C$ and $\delta^{15}N$).
3. To establish a reliable estimate of frog distribution and to develop a statistical model to identify associations between frog distribution and habitat characteristics (e.g. riparian tree community structure, stream order, altitude).
4. To develop a method that accounts for the influence of habitat characteristics on *L. hochstetteri* abundance, to enable reliable evaluation of the effects that pest-management operations may have on frog abundance.

5. Develop a spatial decision support system (SDSS), which can be used to calculate frog-habitat suitability scores for all forested catchments within the Auckland Region.

CHAPTER 2. The current status of *Leiopelma hochstetteri* in the Waitakere Ranges, New Zealand.

2.1 INTRODUCTION

Amphibians are widely distributed throughout tropical and temperate regions of the planet, where they occupy many freshwater and moist terrestrial environments (Beebee 1996). However, amphibian populations have declined dramatically in many areas of the world since the 1970's. These declines appear to have worsened in the last 25 years, and amphibians are now considered to be more threatened than mammals or birds (Stuart et al., 2004). Although biological research has led to great strides in our understanding of amphibian declines (Bebee & Griffiths, 2005), it is still important to continue informing the issues with rigorous scientific data to improve our understanding of particular amphibian species and/or populations. Especially, range-restricted populations of endemic amphibians such as island endemics are more vulnerable to environmental change and susceptible to population declines (Lecis & Norris 2003).

In the New Zealand archipelago the only amphibians are four endemic (*Leiopelma hochstetteri*, *L. archeyi*, *L. hamiltoni* and *L. pakeka*) and three introduced (*Litoria aurea*, *L. raniformis* and *L. ewingii*) frog species. Roelants & Bossuyt (2005) proposed that the last common ancestor of living frogs may have had an appearance that was very similar to those of present-day *Ascaphus* and *Leiopelma*, suggesting that New Zealand native frogs (*Leiopelma* spp.) are among the most primitive living frogs in the world. Subfossil remains indicate that native frogs were once widely distributed all over New Zealand, and that since the arrival of humans, several species have become extinct (Worthy 1987).

Leiopelma hochstetteri (Fig. 2.1) is the most widespread and abundant New Zealand native frog. Nevertheless, this frog species is ranked number 38 on the Zoological Society of London's amphibian EDGE list of the most evolutionarily distinct and globally endangered amphibians in the world. It is recognized as 'vulnerable' in the IUCN red list of threatened species, and is fully protected by New Zealand legislation. This is the most aquatic and cryptic native frog in New Zealand.

Figure 2. 1 *Leiopelma hochstetteri* juvenile individual in the Waitakere Ranges, New Zealand. Photograph by Eduardo Nájera-Hillman.

Differences in the external morphology of extant *Leiopelma* spp. indicates a broad dichotomy between the semi-aquatic *L. hochstetteri* and the terrestrial remaining species (Bell 1994), suggesting that significant ecological and behavioural differences may exist among New Zealand native frogs. Although *L. hochstetteri* may be found in sympatry with *L. archeyi*, *L. hochstetteri* is more commonly found sheltered beneath rocks and logs, in wet habitats alongside shaded streams and where seepage occurs in forested catchments (McLennan 1985; Bell et al. 2004a), while *L. archeyi* habitat has been described as cool, secluded terrestrial sites under the cover of rocks, logs or vegetation consisting of rice grass, hook grass, tree fern and crown fern under forest or on open mist-prone ridges (Wakelin et al. 2003; Bell et al. 2004a). Currently *L. hochstetteri* survives in spatially fragmented populations across the northern half of North Island, and on Great Barrier Island, New Zealand (Fig. 2.2). Substantial genetic variation among frogs from different areas of its current distribution suggests that each population should be considered a distinct unit worthy of separate conservation (Green 1994; Gemmell et al. 2003; Fouquet et al. 2009).

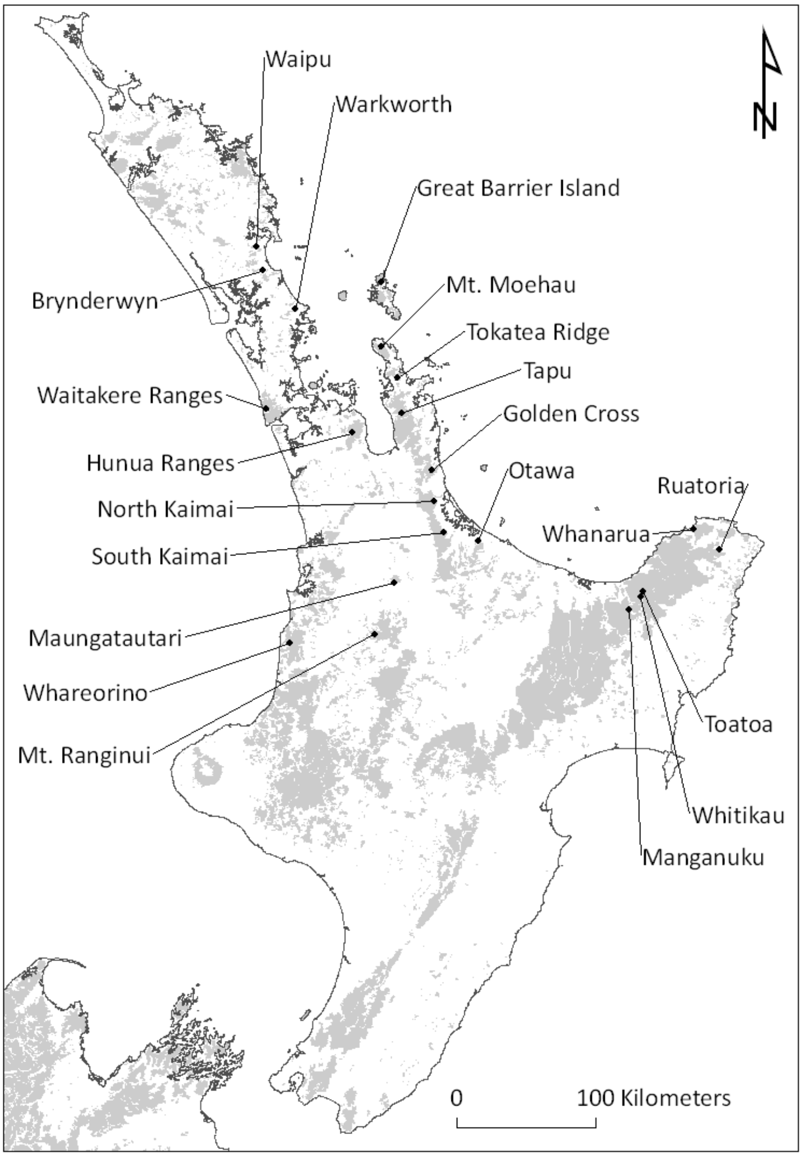


Figure 2. 2 Map with approximated locations of known *L. hochstetteri* populations in New Zealand's North Island and Great Barrier Island. Shaded areas = native forest cover. Map based on Baber et al. (2006).

Previous attempts to monitor some *L. hochstetteri* populations (e.g. Maungatautari, Waitakere Ranges, Golden Cross) have involved estimates of relative abundance counting individuals using area-constrained protocols (transects or quadrants; e.g. Green & Tessier 1990; Bradfield 2005; Baber et al. 2006). Usually surveys are conducted during daylight hours. These approaches are time consuming and subject to observer bias, but commonly used in amphibian population studies (Heyer et al. 1994). Nevertheless, for continuity with earlier studies line transects searches for *L. hochstetteri* have been repeatedly undertaken in populations, such as, the Waitakere Ranges (Ziegler 1999; Bradfield 2005) providing data, which may be used to track changes in relative abundance, distribution or size-class population structure.

Thus, the aims of this study are (1) to survey *L. hochstetteri* in the Waitakere Ranges to provide basic descriptive information to make comparisons with previous surveys to determine the current status (increasing, stable or declining) of this frog population, (2) to identify morphometric characteristics related to the ecology and behaviour of the species and (3) to recognise research issues necessary for a better understanding of *L. hochstetteri* relationships with their environment.

2.2 METHODS

2.2.1 Frog surveys

Day time searches for frogs were conducted at 30 stream sections in the Waitakere Ranges in the summer of 2007–08 and 2008–09 (Fig. 2.3). Frog searches were conducted in accordance with established New Zealand survey protocols (Crossland et al. 2005; Bradfield 2005; Baber et al. 2006). Streams sections were searched by slowly moving upstream from a start point (usually where streams intersected tracks), carefully examining all available refugia for frogs (underneath rocks, logs and leaves, and inside crevices and tunnels). All objects that had to be moved were carefully replaced in their original position to minimise habitat disturbance. Both stream banks and exposed areas of the stream bed were searched for frogs. However, the length of searches varied from 20-m transects to the total length of a specific stream section (up to 2000 m). On 10 stream sections the length of search was standardised to two 20-m transects, to obtain abundance estimates. In the remaining 20 stream sections, the searches were conducted along the whole section, to observe distribution patterns. Stream section altitude was recorded using a Skywatch GEOS N°11 handheld weather system. Of the 30 streams searched, 30% were located under 100 m of altitude, 33.3% between 100 and 200 m, and 36.7% above 200 m. Additionally, the numbers of frogs per shelter object (refugia) was recorded.

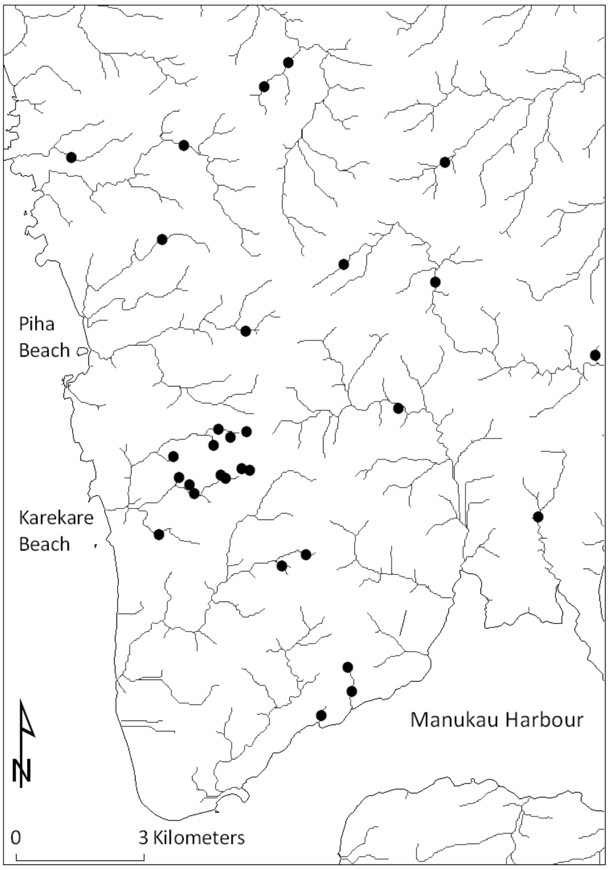


Figure 2. 3 Streams surveyed for *L. hochstetteri* in the Waitakere Ranges, New Zealand. Black dots = stream sections surveyed.

For each frog found, I recorded snout-vent length by holding callipers parallel to the frog. Some frogs (45) were captured and held individually in re-sealable plastic bags for weight measurements using a GS-500 pocket electronic balance. Time of containment was less than 5 minutes and new plastic bags were used for handling each frog to minimise stress and the potential spread of amphibian disease. There is very little sexual dimorphism in *L. hochstetteri* and the assignment of sex in field studies is ineffective (Green & Tessier 1990; Whitaker & Alspach 1999; Slaven 1992). Therefore, sex determination was not attempted in this project.

2.2.2 Frog morphometrics

Some features of the ecology and behaviour of amphibians may be related to some morphological characteristics (Choi et al. 2003), therefore a morphometric study was conducted on specimens of *L. hochstetteri*. In order to avoid unnecessary handling of live frogs, 41 individuals of *L. hochstetteri* from the Auckland Museum collection were measured for morphometric description. These specimens were collected from several locations throughout New Zealand. Measurements of the snout-vent length, inter-ilial width, head width and length, upper and forearm width and length, femur and lower leg width and length, were taken from forty one individuals with a Vernier calliper, precision of 0.01 mm.

2.3 RESULTS

2.3.1 Frog population description

During frog surveys approximately 600 person-hours were spent searching for a total of 241 frogs. The dimensions of frog-inhabited streams varied considerably from small seepages to large streams, several meters wide and a couple of meters deep. Frogs were detected at elevations from 40 to 320 m, although most frogs were found at altitudes over 160 m (Fig. 2.4). It is worthy to mention that the smaller frogs (< 18 mm) were only found at altitudes > 200 m, although there is not a significant relationship between frog size and altitude ($r^2 = 0.027$).

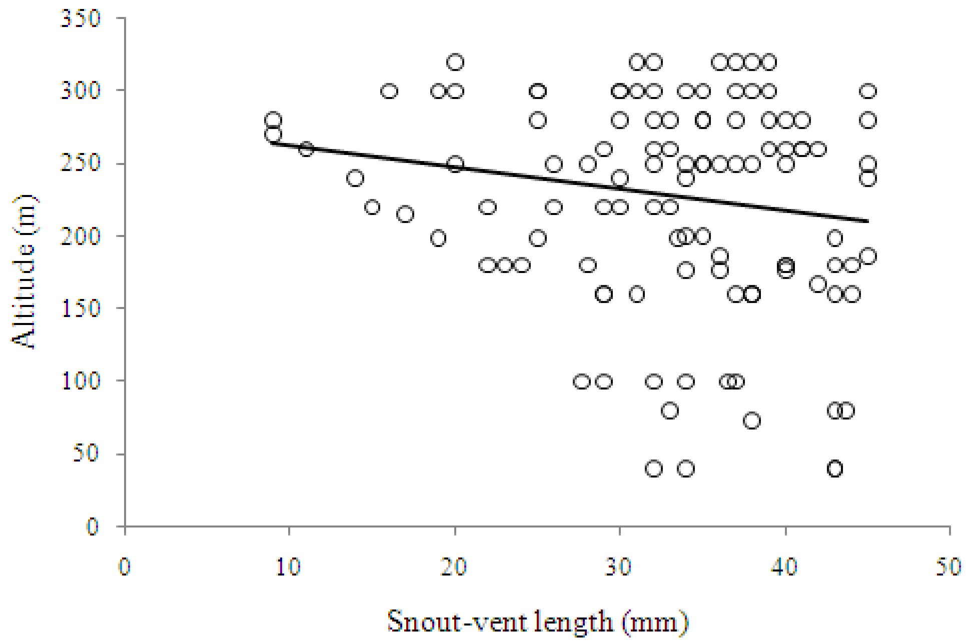


Figure 2. 4 Snout-vent lengths of *L. hochstetteri* individuals found at different altitudes in the Waitakere Ranges, New Zealand. $n = 132$. $r^2 = 0.027$

Almost all frogs were found sheltering under rocks 10–45 cm in diameter at a maximum distance of 0.5 m from the water's edge, with the exception of one frog found under a log at a distance of approximately 1.5 m from the water's edge. The habitat under rocks usually included smaller rocks and wet sand or gravel substrates. Dorsal colouration of *L. hochstetteri* individuals was predominantly brown resembling substrate colour, making it difficult to detect them as the rocks were removed. The first reaction of a frog to the removal of its sheltering rock was to stay still unless they were unintentionally touched— when they leaped away to the nearest sheltering rock or dived into the stream channel. A single rock sheltered up to 4 frogs; however most frogs were found alone (Fig. 2.5). Most frog groups were composed of large individuals with similar sizes (between 30 and 40 mm), although on one occasion a small frog (< 18 mm) was found in company of two larger frogs (> 30 mm).

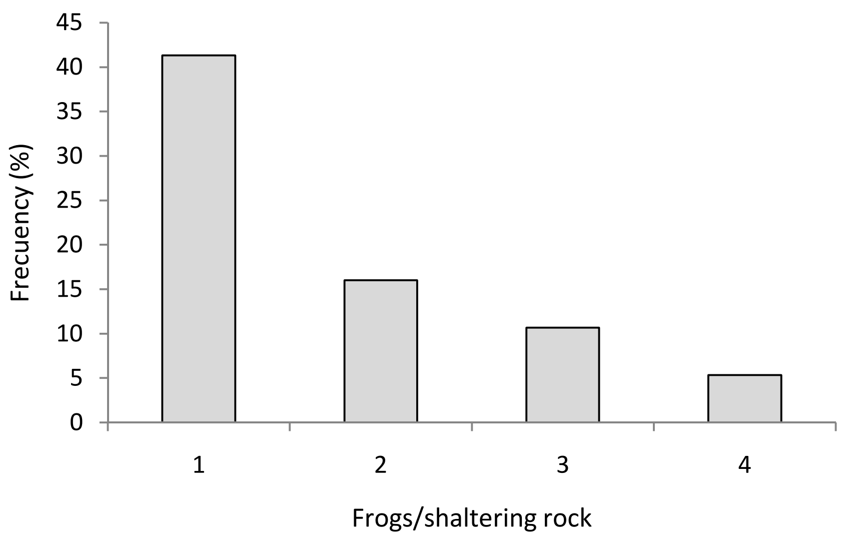


Figure 2. 5 Frequency distribution of ocassions in which *L. hochstetteri* individuals were found clustering or alone. n = 75.

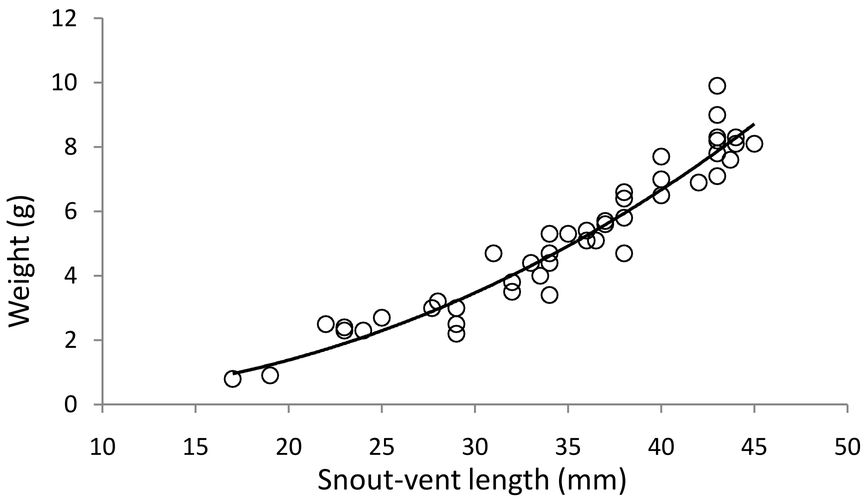


Figure 2. 6 Allometric growth of *L. hochstetteri* calculated from individuals found in the Waitakere Ranges, New Zealand. $n = 45$; $r^2 = 0.92$.

On the area-constrained trials (20-m transects), a total of 192 *L. hochstetteri* individuals were found. In the summer of 2007–08, relative frog abundance ranged from 0–21 frogs/20 m, with an average of 6.7 ± 1.2 SE frogs/20 m. In the summer of 2008–09 frogs were less abundant. Relative frog abundance ranged from 0–12 frogs/20 m, with an average of 4.8 ± 0.7 SE frogs/20 m.

Frog snout-vent length ranged from 9–45 mm. The smallest frog weighed < 0.8 g, while the largest (probably a gravid female) weighed 8.1 g. The allometric relationship between weight and snout-vent length was represented by a power curve. The equation $W = 0.001SVL^{2.276}$ (W = weight in g, SVL = snout-vent length in mm) gives the best fit for the data ($r^2 = 0.93$; Fig. 2.6). The size-frequency distribution for frogs detected in the summer of 2007–08, indicated that 33.9% of the individuals found had snout-vent lengths > 36 mm, 58.7% had snout-vent lengths > 20 mm ≤ 35 mm, and 7.3% were < 20 mm. In the summer of 2008–09, of the frogs found 34.9% had snout-vent lengths > 36 mm, 55.4% had snout-vent lengths > 20 mm ≤ 35 mm, and 9.6% were < 18 mm (Fig. 2.7 and Appendix C).

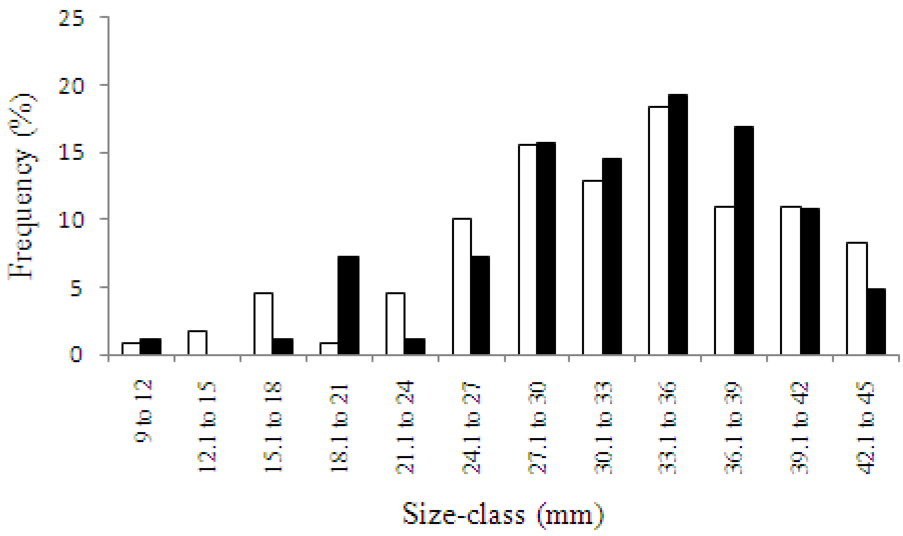


Figure 2. 7 Frequency distribution of body sizes (snout-vent lengths) of *L. hochstetteri* individuals found in the Waitakere Ranges, New Zealand. White bars = 2008, black bars = 2009. n = 241.

2.3.2 Frog morphometrics

Descriptive statistics of morphological measurements for *L. hochstetteri* specimens from the Auckland Museum are summarized in Table 2.1. These specimens were collected in several locations throughout New Zealand North and Great Barrier Islands. The total length for the fore and hind limbs was calculated by adding the lengths of the upper and lower sections of each limb. Both limbs (forelimb and hindlimb) were shorter that the snout-vent length, as illustrated by ratios < 1 between each limb length/snout–vent length (0.85 and 0.45, respectively). As a measurement of frog complexion (robust or slim), I calculated the ratio of the inter-ilial width to the snout-vent length, which was 0.38. The ratio head width/length (1.14) indicated that *L. hochstetteri* has wide-short jaws.

Table 2. 1 Descriptive statistics of morphological variables obtained from *L. hochstetteri* specimens from the Auckland Museum, New Zealand, $n = 41$.

Body part	Mean (mm)	± SE	Minimum	Maximum
Snout-vent length	29.83	1.53	8.7	50.5
Inter-ilial width	11.45	0.54	3.7	17.3
Head width	11.16	0.51	3.7	15.8
Head length	9.73	0.53	1.5	16.0
Upper arm length	7.14	0.38	2.3	12.9
Upper arm width	2.67	0.14	0.7	4.0
Forearm length	6.56	0.34	2.0	10.2
Forearm width	2.33	0.11	0.8	3.6
Total forelimb length	13.71	0.69	4.3	22.5
Femur length	11.74	0.58	3.7	17.6
Femur width	4.75	0.25	1.1	7.1
Lower leg length	13.81	0.68	3.7	20.1
Lower leg width	3.23	0.17	0.8	5.2
Total hindlimb length	22.55	1.24	7.7	36.6

2.4 DISCUSSION

2.4.1 Frog population status

Similar to the observations of previous researches in the Waitakere Ranges (Ziegler 1999; Bradfield 2005) and throughout New Zealand's North Island (McLennan 1985; Green & Tessier, 1990) *L. hochstetteri* was distributed on a variety of stream types; from seepages to large streams. Nevertheless, frogs were more commonly found at altitudes > 160 m, as noted in other locations (Stephenson & Stephenson 1957; Baber et al. 2006), suggesting that *L. hochstetteri* distribution may be influenced by altitude and other environmental variables, such as riparian vegetation and water quality. In the Waitakere Ranges the vegetation and water quality progressively degrade downstream with increasing agricultural and urban land uses (Barnes 2005).

As expected, most frogs were found under boulders over the stream banks and exposed areas of the stream bed. The interstitial spaces where these frogs seek shelter may represent a wet moist environment ideal to accommodate the high moisture requirements of *L. hochstetteri* (Cree 1988; Wakelin et al. 2003). Boulders and cobbles can be found in continuous aggregations, which can cover relatively large areas (≤ 20 m^2) within streams in the Waitakere Ranges. The extent of this habitat may affect the abundance at which this frog species may be found on particular streams.

In this study, the average abundances of *L. hochstetteri* found in the summers of 2007–08 and 2008–09 (6.7 and 4.8 frogs/20 m, respectively) were higher than average frog abundance (3.1 frogs/20 m), calculated from reports of several population studies, throughout the North Island of New Zealand (Green & Tessier, 1990; Tessier et al. 1991; Thurley & Bell 1994; Whitaker & Alspach 1999; Ziegler 1999; Bradfield 2005; Baber et al. 2006) and higher than the average frog abundance (2.5 frogs/20 m) reported by Bradfield (2005) in the Waitakere Ranges. This result suggests that *L. hochstetteri* individuals were effectively detected during this study, and that frogs were abundant within the Waitakere Ranges.

As might be expected, the allometric relationship between snout-vent length and weight found in this study was similar to that previously described by Green & Tessier (1990; Fig. 2.8). Additionally, the snout–vent length intervals and size–class population structures in the summers of 2007–08 and 2008–09 (Fig. 2.7) were similar, and similar to the snout–vent length intervals (10.3–47 mm) and size–class population structures found in many populations of this frog species in the northern half of New Zealand's North Island (Green & Tessier 1990; Tessier et al. 1991; Thurley & Bell 1994; Whitaker & Alspach 1999; Baber et al. 2006).

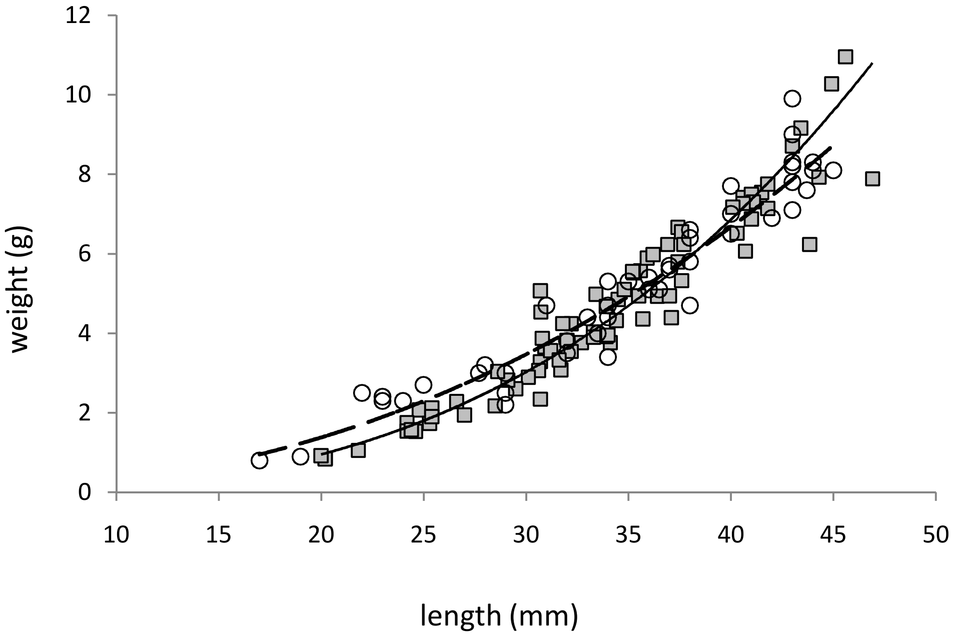


Figure 2. 8 Comparison of allometric growth of *L. hochstetteri* calculated from individuals found in this study (white circles and hyphenated line; $n = 45$; $r^2 = 0.92$) and by Green and Tessier (1990) (grey squares and solid line; n = 79; $r^2 = 0.94$).

According to the size–class intervals suggested by Slaven (1992), juvenile (< 20 mm) and sub-adult frogs (>20 < 35 mm) were detected in this investigation and in previous studies in the Waitakere Ranges (Ziegler 1999; Bradfield 2005), suggesting that there has been recruitment into the Waitakere Ranges population in the last 10 years. Although in general the proportion of juvenile, sub-adult and adult frogs was similar in this study and in previous researches (Ziegler 1999; Bradfield 2005) (Fig. 2.9), it is almost universally agreed that most local populations of amphibians are likely to fluctuate considerably in size-frequency distribution because recruitment is highly variable and survival rates of adult and juvenile stages often vary over several orders of magnitude (Alford & Richards 1999).

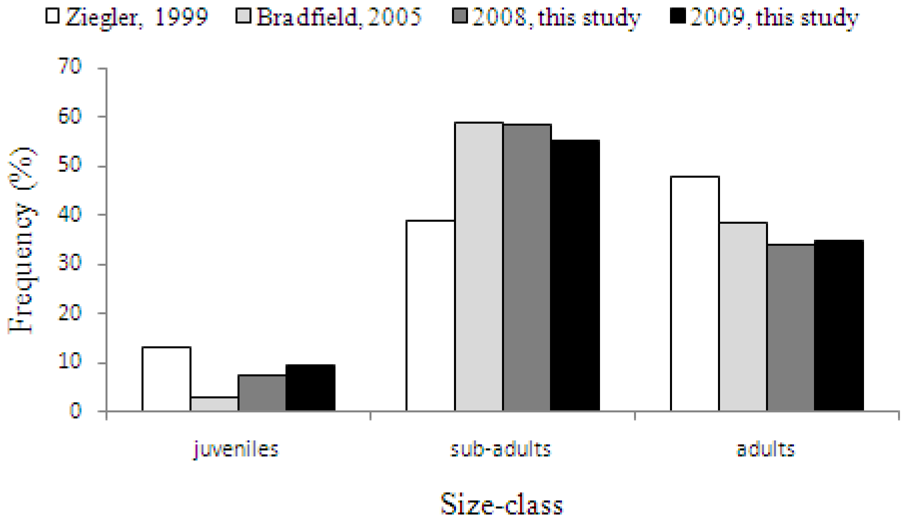


Figure 2. 9 Proportion of adult, sub-adult and juvenile frogs found in the Waitakere Ranges, New Zealand in the last 10 years.

The snout-vent length range was broader at altitudes > 200 m (9–45 mm), whereas at altitudes < 160 m we only found larger frogs (> 27 mm; Fig. 2.4). This observation may suggest that breeding areas may be located at higher altitudes. Other species of riparian amphibians (e.g. *Ascaphus truei* and *Rhycotriton variegatus*) are more likely to occur in higher elevations (Stoddard & Hayes 2005), and to move upstream to smaller, higher elevation streams to congregate during the breeding season (Kelsey 1995). Previously, the habitat where *L. hochstetteri* lays its eggs was described as rocky seepages on the banks of streams (McLennan 1985; Robb 1980). During this investigation, I surveyed areas matching this description. However, I did not find any eggs or indications of reproductive activity. Although frogs were observed to share daytime shelters (Fig. 2.5), as previously noted by McLennan (1985), I cannot be certain that this may be an indication of reproductive behaviour or other social behaviour. This frog species is thought to lay their eggs during spring or early summer (Robb 1980). However neither this investigation nor previous researches in the

Waitakere Ranges (Ziegler 1999; Bradfield 2005) have found frog eggs or evidence of reproductive behaviour.

The descriptive population data presented herein suggests that currently *L. hochstetteri* populations are stable in the Waitakere Ranges. The Waitakere Ranges contains one of the largest remnants of indigenous forest in the Auckland Region with numerous high quality rocky bottom waterways (Barnes 2005) which may provide high quality habitat for *L. hochstetteri*. The Waitakere Ranges Regional Park (60% of the Waitakere Ranges area) has been protected from clearing or logging of vegetation since the 1940s, and since April 2008 the Waitakere Ranges Heritage Area Act promotes the protection and enhancement of the terrestrial and aquatic ecosystems within the Park, in addition to residential areas. Therefore, if the current conservation management continues, the future is looking good for this threatened species in this area.

2.4.2 Frog morphometrics

The morphological measurements indicated that *L. hochstetteri* is a short-legged, robust frog with relatively short jaws. Among frogs, some morphological features are related to their locomotion mode and dietary habits. For example, Choi et al. (2003) demonstrated that in several frog species (e.g. *Rana nigromaculata*, *Bombina orientalis*, *Eleuthrodactylus fitzingeri*, *Bufo typhonius*, *Colostethus flotator*) the ratio between hindlimb and snout-vent length was positively associated with jumping speed and jumping distance. According to the hindlimb/snout-vent length ratio found in this study (0.85), *L. hochstetteri* is placed among frogs with poor-jumping capacity (cf. Choi et al. 2003). Furthermore, short-legged species of frog that move in a series of short leaps (hoppers) are frequently wide-ranging predators that cover relatively large areas as they search for food (Santos et al. 2004; Harvey et al. 2005). This behaviour makes frogs conspicuous to their own predators. Thus, most hopping frogs rely on crypsis or on distasteful skin secretions as defence mechanisms (Wells 2007; Santos et al. 2004). In accordance with this notion, *L. hochstetteri* is highly cryptic and possesses granular glands, which secrete toxic substances (Green 1988; Green & Tessier 1990).

Additionally, some aspects of the feeding behaviour of frogs are correlated with specific morphological features of the skull (Scott & Aquino 2005). The head width/length ratio (1.14) indicated that *L. hochstetteri* has relatively short jaws. According to the predictive biomechanical model developed by Emerson (1985), it is expected that frogs with relatively short jaws will feed on small, slow-moving prey. In accordance with this prediction, it has been suggested that *L. hochstetteri* prey consists primarily of small invertebrates (Stephenson & Stephenson 1957; Sharell 1966; Kane 1980; Chapman & Alexander 2006).

2.4.3 Implications for further research

The results presented herein have multiple implications which may help delineate the direction of further research efforts toward a better understanding of *L. hochstetteri* relationships with their environment. Here, I observed that the distribution of *L. hochstetteri* in the Waitakere Ranges may be influenced by factors, such as altitude, in part because the vegetation and water quality progressively degrade downstream with increasing agricultural and urban land uses (Barnes 2005) and because *L. hochstetteri* breeding sites may be located at higher altitudes. Thus, it is important to establish a reliable estimate of frog distribution and to identify associations between frog distribution and habitat characteristics, which in turn may facilitate identification of conservation areas and potential threats to the species.

Additionally, a technique which gives accurate measures of the abundance of *L. hochstetteri* is needed to accurately assess population trends. According to these results, *L. hochstetteri* abundance is highly variable (0–21 frogs/20 m) and it seems to be influenced by the amount of specific micro-habitat characteristics (i.e. high moisture interstitial spaces between boulders). Therefore, identifying associations between frog abundance and habitat characteristics may enable the development of a reliable monitoring technique, which may lead to appropriate evaluations of the effects that conservation and land management activities may have on *L. hochstetteri* populations.

It is known that the diet of *L. hochstetteri* consists primarily of small invertebrates (Stephenson & Stephenson 1957; Sharell 1966; Kane 1980; Chapman & Alexander 2006) and that this frog occupies an intermediate trophic position among stream predators, with a diet, at least as an adult, comprising terrestrial invertebrates (Chapter 3). However, some morphological characteristics appear to be related to frog dietary habits (Emerson 1985; Choi et al. 2003), suggesting that *L. hochstetteri* may have some dietary specialisations. These observations open some questions about the origin of the frog's food sources and role of the species in the stream ecosystem. This dietary information may be crucial for the understanding of frog life history, population fluctuations, and the impact of habitat modification on their populations (Anderson et al. 1999).

CHAPTER 3. Diet and trophic level characterisation ($\delta^{13}C$ and $\delta^{15}N$ isotopes) of *Leiopelma hochstetteri* in streams of the Waitakere Ranges, New Zealand.

Modified version of Nájera-Hillman et al. (2009a)

3.1 INTRODUCTION

Amphibians are widely distributed throughout tropical and temperate regions, where they occupy many freshwater and moist terrestrial environments (Beebee 1996). Within these environments, amphibians are important predators, and contribute to both aquatic and terrestrial food webs (Malkmus 2000). Therefore, improving our understanding of their trophic position (their food sources and predators) will help elucidate their contribution to ecosystem functioning, and may assist conservation efforts of threatened species (Hirai & Matsui 1999).

The Anura (frogs and toads) is the most diverse and species-rich order of amphibians. However, a global decline in richness and abundance of anuran species has followed localised population crashes and mass extinctions. What is more, at present, amphibians are more threatened, and are declining in numbers and richness more rapidly, than are either birds or mammals (Stuart et al. 2004).

Anuran conservation requires an improved understanding of their biology, diet and habitat requirements. Dietary information is crucial for the understanding of anuran life history, population fluctuations, and the impact of habitat modification on those populations (Anderson et al. 1999). For example, changes in canopy cover can decrease the abundance of food sources for amphibians, thereby depressing population fitness (Skelly et al. 2002; Thurgate & Pechmann 2007).

Frogs are described as generalist predators, with opportunistic foraging behaviour (Santos et al. 2004). Adults are predators of invertebrates, including molluscs, annelids and arthropods (Toft 1980; Duellman & Trueb 1986; Piñero & La Marca 1996; Lima and Magnusson 1998; Anderson et al. 1999), and juveniles are classed as herbivores or detritivores, although there is surprisingly little evidence to support these trophic assignments (Altig et al. 2007). In temperate regions, most species of frogs are thought to have an unspecialised diet, taking prey roughly in proportion to the food abundance in a given habitat (Jenssen & Klimstra 1966; Houston 1973; Blackith & Speight 1974; Labanick 1976; Cogălniceaunu et al. 1998; Anderson et al. 1999; Hirai & Matsui 1999; Kuzmin 1999; Meyer et al. 1999).

Techniques available to study frog diet and foraging behavior include direct observation of feeding activities, functional morphology, gut content and faecal analyses, fatty acid profiles, and stable isotopic analyses (Kane 1980; Toft 1981; Cogălniceaunu et al. 2000; Altig et al. 2007; Araújo et al. 2007; Wells 2007). Direct observations and morphological measurements may provide general feeding and diet information, but data may be difficult to obtain, especially when individuals are rare. More quantitative measurements can be attained with gut and faecal analyses, but these studies provide only a relative indication of what is assimilated (Alfaro et al. 2006), and may require lethal sampling and large sample sizes. Fatty acid profiles record the assimilated food types, and may afford useful dietary information for groups with known and unequivocal lipid biomarkers, but these are not available for many taxa (Alfaro 2008).

Stable isotopes can be used to reliably identify assimilated food and trophic pathways within complex food webs (Romanuk & Levings 2005; Alfaro et al. 2006; Yi et al. 2006; Gustafson et al. 2007; Alfaro 2008); in particular, the ratios of ^{13}C:^{12}C and ^{15}N:^{14}N are useful for the identification of trophic relationships (Peterson & Fry 1987; Kling 1994). This technique relies on knowledge of the incorporation of stable isotopes into the metabolic process. In nature, isotopes of the same element can take part in the same chemical reactions, but because the atoms of different isotopes are of different sizes and weights, they react at different rates. Metabolic processes can produce reaction products that are isotopically heavier (enriched) or lighter (depleted) than their precursor materials. This fractionation process can be used to identify trophic interactions among dominant producers and consumers, and to describe food web dynamics. Specifically, $\delta^{13}C$ signatures indicate carbon assimilation and fluxes through food webs, while $\delta^{15}N$ can be used to identify the relative trophic position of various organisms within the food web.

Isotope studies on frogs are rare. However, a few studies on aquatic and terrestrial food webs have included amphibians as food-web components (Kupfer et al. 2006; Araújo et al. 2007; Verburg et al. 2007) facilitating the identification of trophic positions and food origins for several amphibian species. For example, a study using both carbon and nitrogen stable isotopes placed the Chinese forest frog (*Rana temporaria*) and Chinese big toad (*Bufo bufo*) at an intermediate trophic level on an alpine meadow ecosystem in the Tibetan Plateau (Yi et al. 2006). Kupfer et al. (2006) found that riparian frogs (*Hoplobatrachus chinensis*, *Phynoglossus martenssi* and *Occidozyga lima*) were part of the terrestrial food web surrounding a tropical river in Thailand, and placed them as second-level predators within the food web. Verburg et al. (2007) used carbon and nitrogen stable isotopic compositions to examine the trophic relationships in an ecosystem in which amphibians were dominant vertebrate taxa, and identified, tadpoles and adult amphibians as intermediate links in the aquatic and terrestrial food webs, respectively.

In New Zealand, the class Amphibia is represented by only four native (*Leiopelma hochstetteri*, *L. archeyi*, *L. hamiltoni* and *L. pakeka*) and three introduced (*Litoria aurea*, *L. raniformis* and *L. ewingii*) frog species. Frogs in the genus *Leiopelma* are unusual, with unique morphological characteristics which place them among the most primitive anurans in the world (Ford and Cannatella, 1993). *Leiopelma hochstetteri* is ranked number 38 on the Zoological Society of London's amphibian EDGE list of the most evolutionarily distinct and globally endangered amphibians in the world; in New Zealand this species is listed as threatened, and therefore is fully protected under the New Zealand *Wildlife Act 1953*.

Little is known of the diet of *L. hochstetteri*, although some assumptions have been made. For example, it has been suggested that frogs emerge at night to forage on insects and spiders along the stream edge and within riparian vegetation (Chapman & Alexander 2006). Beetles, spiders, ants, millipedes, earthworms and slugs, found where frogs shelter, were thought to constitute an important food source for these frogs Sharell (1966). Additionally, Stephenson & Stephenson (1957) reported a small, entire fresh-water crayfish in the stomach of one frog, suggesting an aquatic component in the diet of this species. In a study based on analysis of faecal samples, Kane (1980) found that *L. hochstetteri* prey consisted primarily of adult terrestrial arthropods, including beetles, flies, sawflies and amphipods.

None of the above studies was specifically designed to characterise the diet of *L. hochstetteri*, or to determine its trophic position and relationships within forested stream food webs. Thus, the aim of this Chapter was to provide these baseline data, for the first time clearly identifying the diet and trophic position of *L. hochstetteri* using stable isotopes $\delta^{13}C$ and $\delta^{15}N$. This research was conducted in forested streams in the Waitakere Ranges, Auckland, New Zealand. The hypothesis that *L. hochstetteri* occupies an intermediate trophic level in stream ecosystems, with its diet consisting of terrestrial rather than aquatic invertebrates was evaluated. I provided data significant to the conservation of remaining frog populations and their habitats in Waitakere Ranges that is equally likely to be relevant throughout the recognised distribution of this species in New Zealand.

3.2 METHODS

3.2.1 Study site

The study site, Company Stream, is located in Waitakere Ranges (36°53′–37°03′ S, 174°27′–34′ E), west of Auckland, New Zealand (Fig. 3.1). This area encompasses 277 km^2 of public and private land surrounded by urban areas to the east, farmland to the north, Tasman Sea to the west, and Manukau Harbour to the south, at elevations of 0–474 metres above sea level (Jongkind & Buurman 2006). Climate conditions range from warm humid summers to mild winters, 1400–2000 mm rainfall, and a prevailing southwest wind, although occasional strong gales do strike from the east and northeast. The Waitakere Ranges are composed of strongly leached and acid clay soils from weathered andesitic rocks, with a low natural fertility and good drainage structure (McEwen 1987). Vegetation throughout these ranges is dominated by regenerating secondary forest species. The nature of the original forest is unknown, but probably included kauri (*Agathis australis*), northern rata (*Metrosideros robusta*) and rimu (*Dacrydium cupressinum*) (Esler 2006). Milling and burning removed the primary native forest before the 1930s (Cranwell-Smith 2006). Subsequently, patchy logging and farming (Esler 2006) have permitted various states of forest regeneration and high habitat diversity. *L. hochstetteri* frogs are considered to be common in the Waitakere Ranges (Green & Tessier 1990), where they have been found at higher densities than in any other location throughout New Zealand (Bradfield 2005).

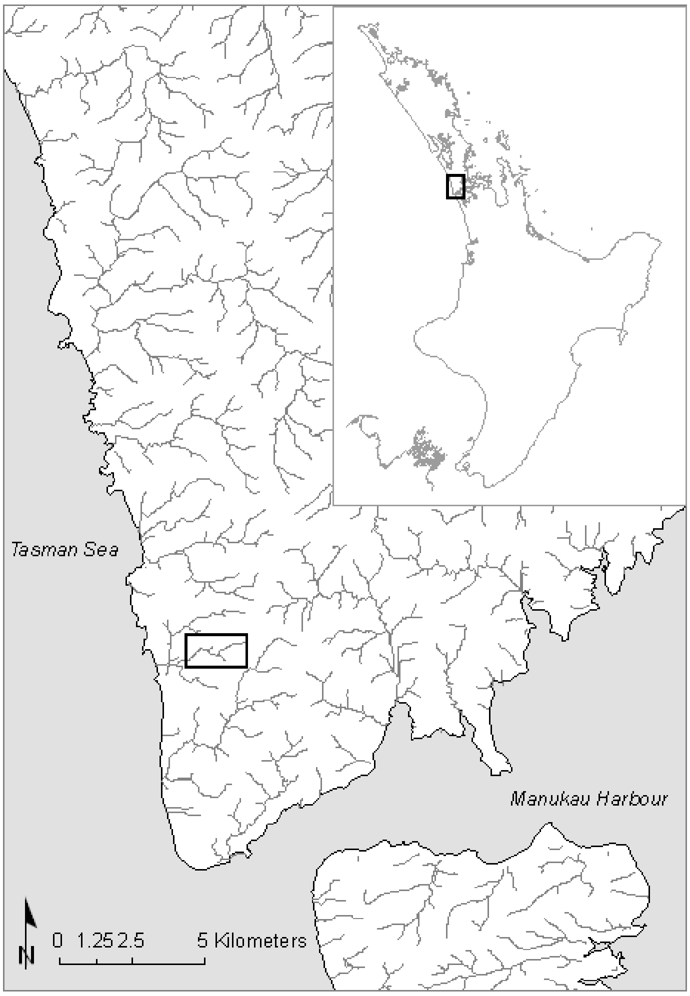


Figure 3. 1 Map of study location. *Inset*: North Island of New Zealand; rectangle on Waitakere Ranges depicts specific study site, Company Stream.

Throughout the survey site, Company Stream, and survey duration (early December 2006 to early January 2007), stream width and depth averaged about 3 m and 0.3 m respectively, and water temperature and pH averaged 12.9°C and 7.2 respectively.

The survey location, at an elevation of 180–230 meters above sea level, had a dense canopy cover of about 90%.

3.2.2 Sample collections

Initially, we conducted a prospective survey in early December 2006 to confirm the presence of *L. hochstetteri* at Company Stream. Then we collected samples of primary producers, invertebrates and vertebrate predators separately. All animal and plant samples were stored in plastic bags or containers to retain moisture, transported to the laboratory within 3 h, then stored at -20°C until processing.

Samples of primary producers (leaves of riparian trees, ferns, mosses and liverworts), leaf litter, and invertebrates (aquatic and terrestrial) were collected twice, in late December 2006 and early January 2007, for stable isotopic analyses. We used latex gloves to prevent contamination of samples collected by hand. Fresh leaves of the most abundant trees (i.e., *Beilschmiedia tarairi* and *Aristotelia serrata*) and ferns (i.e., *Cyathea medullaris* and *Blechnum chambersii*) were placed in sealed plastic bags. Samples of submerged liverworts, (*Monoclea forsteri*) the only evident aquatic primary producers in the stream at the study area also were collected. We searched widely for other potential aquatic primary producers, but the stream water and rocks were visually clear of phytoplankton and epilithon.

Aquatic invertebrates were captured from the stream channel by kick and hand-net methods, and stored in plastic containers; none were predatory. Terrestrial invertebrates were extracted from three leaf litter samples collected randomly at a maximum distance of 2 m from the stream channel. Litter samples consisted of all litter and loose topsoil within a 25 cm^2 quadrant. Samples were placed in a modified Tullgren funnel to separate the live invertebrates from the leaf litter matrix; extracted invertebrates then were stored at -20°C.Frog muscle samples were taken from three adult specimens that died accidentally in pit fall traps within the Company Stream catchment during the research of King (2007). Muscle tissue samples were taken from three rats captured in the vicinity of the study area and from banded kokopu (*Galaxias fasciatus*) and shortfin eels (*Anguilla australis*) collected in Company Stream.

3.2.3 Sample analyses

Thirty-five plant and animal samples were analysed for stable isotopes ($\delta^{13}C$ and $\delta^{15}N$). Vegetation samples consisted of 5 leaves of each plant species. Moss and leaf litter samples consisted of about 10 grams of material. The number of aquatic and terrestrial invertebrates per sample depended on animal size; thus, one or more specimens were required to obtain at least 2 mg of dried sample for isotopic analysis. Enough muscle tissue was removed from vertebrates to obtain a 2 mg sample. All vegetation and animal samples were oven-dried for 24 h at 80°C. After drying, samples were ground in an Agatha stone mortar to a fine, homogeneous powder.

Isotopic analyses were carried out at the Waikato Stable Isotope Unit on a fully automated Europa Scientific 20/20 isotope analyser, on which samples are combusted, and the resulting gases are separated by gas chromatography and analysed by continuous-flow mass spectrometry. The ratios of ^{13}C:^{12}C and ^{15}N:^{14}N were expressed as relative difference per mil (‰) using the equation:

$$\delta X = [(R_{sample} / R_{standard}) - 1] \times 10^3$$

where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $\delta^{13}C$ was measured to a precision of ±0.1‰, and the samples were referenced to pre-calibrated C_4 sucrose, which is cross-referenced to the Pee Dee belemnite standard (Craig 1957). The $\delta^{15}N$ was measured to a precision of ±0.3‰, and the samples were referenced to a urea standard, which is traceable to atmospheric nitrogen (Mariotti 1983).

3.3 RESULTS

The $\delta^{13}C$ and $\delta^{15}N$ isotopic composition provided a clear separation between primary producers and consumers, and evidence of a general enrichment with increasing trophic level. The range of $\delta^{13}C$ was from -41.7‰ for aquatic primary producers to -23.6‰ for rats (Fig. 3.2, Table 3.1). The range of $\delta^{15}N$ was from -6.7‰ for terrestrial primary producers to 8.8‰ for eels (Fig. 3.2, Table 3.1).

In terrestrial primary producers (riparian trees and ferns), the isotopic values of both carbon and nitrogen range widely (-33.8 to -29.4‰ and -6.7 to -2.9‰, respectively). These values generally overlapped with those of mosses and leaf litter. However, mosses were slightly more enriched in $\delta^{15}N$ (-2.6 to -2.4‰), and leaf litter was slightly more enriched in $\delta^{13}C$ (-29.8 to -29.4‰) (Fig. 3.2, Table 3.1).

Table 3. 1 Carbon and nitrogen isotopic values and sample numbers (*n*) of plant and animal samples collected for the reconstruction of the forested stream food web at Company Stream, Waitakere Ranges, New Zealand.

Trophic group Family (*Spp.*)	**Common Name**	***n***	**δ^{13}C (‰)**	**δ^{15}N (‰)**
Terrestrial Primary producers				
Cyatheaceae (*Cyathea medullaris*)	Mamaku	5	-32.94	-6.72
Elaeocarpaceae (*Aristotelia serrata*)	Wineberry	5	-29.39	-4.48
Blechnaceae (*Blechnum chambersii*)	Soil Fern	5	-33.76	-2.97
Lauraceae (*Beilschmiedia tarairi*)	Taraire	5	-32.75	-2.86
Mosses				
Hypopterygiaceae	Moss	1	-34.55	-2.65
Fissidentaceae	Moss	1	-30.84	-2.37
Leaf litter				
Leaf litter	-	-	-29.39	-3.80
Leaf litter	-	-	-29.83	-2.58
Aquatic Primary producer				
Monocleaceae (*Monoclea forsteri*)	Liverwort	2	-41.71	-1.74
Non-predatory terrestrial invertebrates				
Sphaerotheriidae	Millipede	6	-24.76	-1.69
Lumbricidae	Earthworm	2	-27.15	-1.37
Porcellionidae	Slater	5	-25.57	-0.60
Oniscidae	Isopod	7	-24.94	-.055
Talitridae < 5 mm	Amphipod	23	-25.50	0.21
Talitridae 5–10 mm	Amphipod	12	-26.48	-0.03
Talitridae > 10 mm	Amphipod	28	-26.66	0.81
Raphidophoridae	Weta	3	-27.47	1.80
Scarabidae	Beetle	1	-27.63	2.68
Predatory terrestrial invertebrates				
Soerensenella sp.	Harvestmen	3	-26.66	3.97
Araneae	Spider	6	-25.83	4.76
Non-predatory aquatic invertebrates				
Hydropsychidae	Caddisfly	3	-28.58	2.79
Leptophlebiidae	Mayfly	13	-26.62	3.44
Nesameletidae	Mayfly	4	-28.74	3.65
Coloburiscidae	Mayfly	5	-27.08	4.00
Vertebrate predators				
Leiopelma hochstetteri	Hochstetter's frog	1	-25.29	4.40
Leiopelma hochstetteri	Hochstetter's frog	1	-25.06	4.36
Leiopelma hochstetteri	Hochstetter's frog	1	-25.80	4.68
Rattus rattus	Ship rat	1	-23.58	4.63
Rattus rattus	Ship rat	1	-24.34	6.13
Rattus rattus	Ship rat	1	-24.42	6.66
Anguilla australis	Shortfin eel	1	-26.33	8.57
Anguilla australis	Shortfin eel	1	-26.19	8.78
Anguilla australlis	Shortfin eel	1	-26.31	8.80
Galaxias fasciatus	Banded kokopu	1	-25.10	5.31
Galaxias fasciatus	Banded kokopu	1	-25.01	5.32

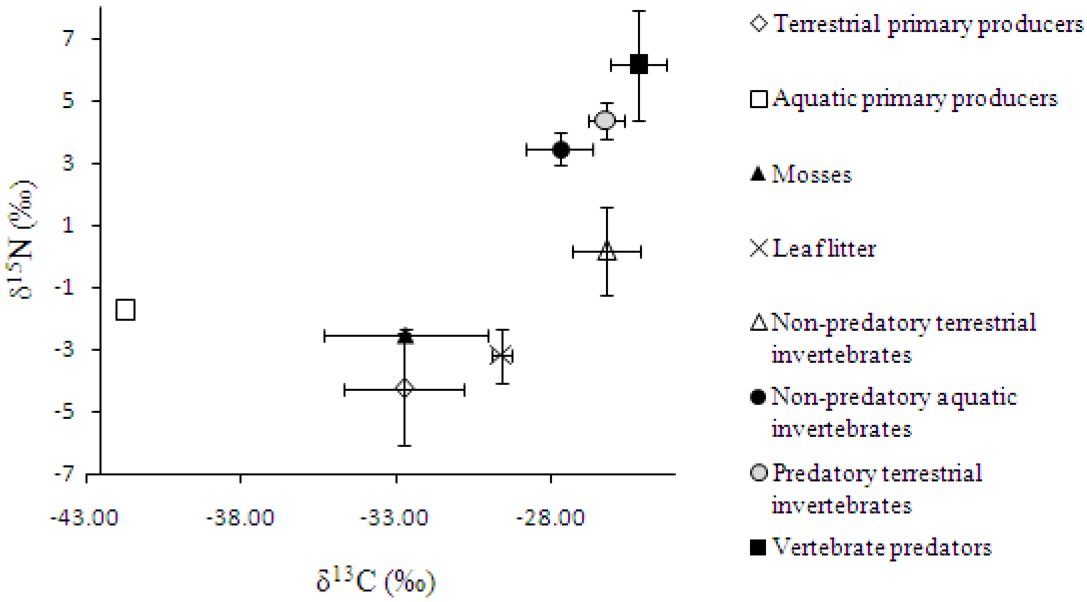


Figure 3. 2 Mean (±SD) carbon and nitrogen stable isotopic composition for major plant and animal groups found at Company Stream, Waitakere Ranges, New Zealand. (For species contributions to each trophic category see Table 3.1.)

Although only one aquatic primary producer (the liverwort, *Monoclea forsteri*) was collected, it was distinctly different from terrestrial primary producers. Terrestrial primary producers, leaf litter and mosses are apparently the primary food sources for both aquatic and terrestrial non-predatory invertebrates, rather than aquatic producers (Fig. 3.2). Non-predatory aquatic and terrestrial invertebrates separated well on the values of the $\delta^{15}N$ (about a 3.2‰ separation), and of the $\delta^{13}C$ signatures (about a 1.5‰ separation) (Fig. 3.2), because the aquatic representatives had such a narrow range in $\delta^{15}N$ values. Most of the non-predatory aquatic invertebrates were detritivores, although they may consume some fresh algae. Non-predatory terrestrial invertebrates had a higher diversity of feeding habits, including omnivores and soil/litter feeders. Predatory terrestrial invertebrates had slightly more enriched $\delta^{15}N$ values than non-predatory aquatic invertebrates, and significantly more enriched $\delta^{15}N$ values than non-predatory terrestrial invertebrates (Fig. 3.2).

In general, native predators had similar values of $\delta^{13}C$, but a wide range of $\delta^{15}N$ (Fig. 3.3). The invasive ship rat had more enriched $\delta^{13}C$ (-24.1±0.5‰) values than the native predators (-25.7±0.6‰). *L. hochstetteri* had intermediate $\delta^{13}C$ values (-25.4±0.2‰), similar to those of the native fish, *G. fasciatus* (-25.1±0.007).

In terms of $\delta^{15}N$, eels had the highest values (8.7±0.1‰), followed by the ship rat (5.8±1.05‰). Great overlap was observed in $\delta^{15}N$ values among predatory terrestrial invertebrates (4.7±0.5‰) and *L. hochstetteri* (4.5±0.2‰), while *G. fasciatus* had slightly higher $\delta^{15}N$ values (5.32±0.006‰) (Fig. 3.3).

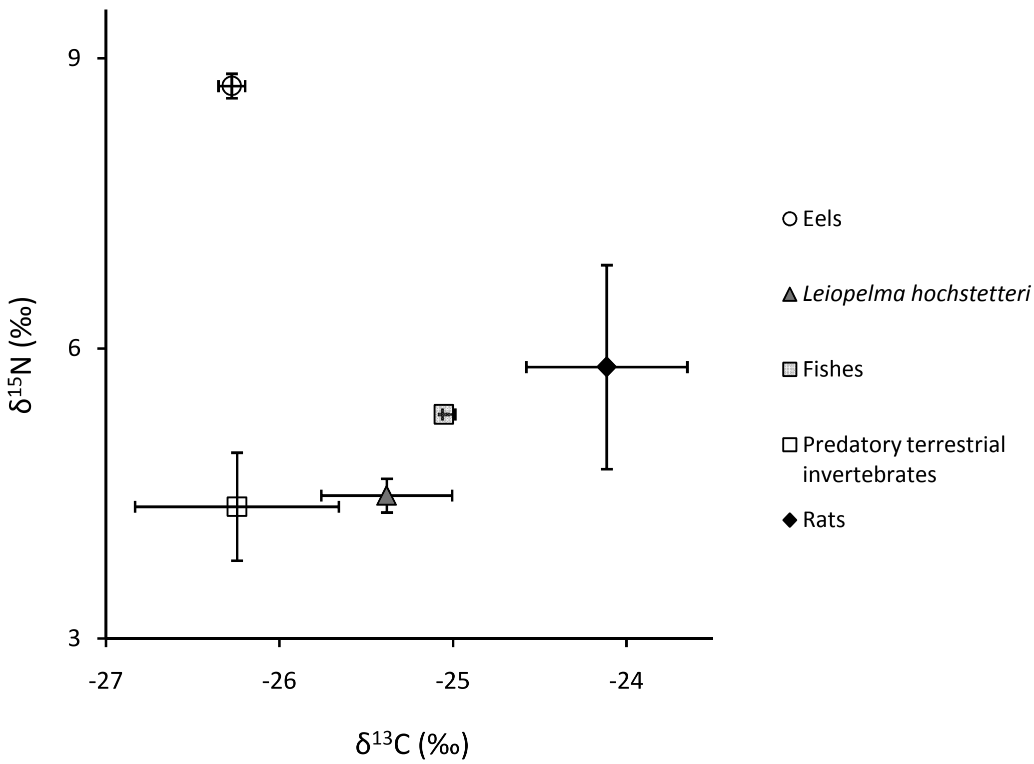


Figure 3. 3 Mean (±SD) carbon and nitrogen stable isotopic composition for invertebrate and vertebrate predators at Company Stream, Waitakere Ranges, New Zealand.

3.4 DISCUSSION

3.4.1 Trophic levels

Minawaga & Wada (1984) and Post et al. (2000) proposed a separation of 3.4 units of $\delta^{15}N$ to distinguish adjacent trophic levels. On that basis, I estimated three trophic levels for the aquatic food web and four levels for the terrestrial food web at Company Stream. These results are similar to those found in other temperate forest streams (Ponsard & Arditi 2000; Scheu & Falca 2000). Within the aquatic environment, there was a range of 10‰ in $\delta^{15}N$ between the liverwort (*M. forsteri*) and the top predator (the shortfin eel, *A. australis*); the terrestrial environment had a 13‰ range, from riparian trees and ferns to the ship rat, *R. rattus*.

3.4.1.1 Primary producers

The stable isotopic signatures for primary producers in aquatic (liverwort) and terrestrial (riparian trees and ferns) environments differed markedly. These results suggest a dependency of both aquatic and terrestrial non-predatory invertebrates on terrestrial rather than aquatic food sources. However, only one aquatic primary producer (liverwort) was visibly abundant at the study site, and it had highly depleted isotopic signatures. More enriched $\delta^{13}C$ values have been reported for other aquatic primary producers, such as filamentous green algae (-28.1‰) (Hicks 1997) and epilithic microorganisms (-35 to -23‰) (Parkyn et al. 2001). Regardless, it is likely that a significant terrestrial input, in the form of detritus and dead organic matter, sustains the aquatic food web at the study site. Indeed, detritus inputs from surrounding forests to headwater streams have been shown to exceed within-stream primary production (Wallace et al. 2008). In New Zealand, Hicks (1997) compared mean $\delta^{13}C$ and $\delta^{15}N$

values for aquatic primary producers, submerged leaf litter and aquatic invertebrates in shaded forest streams and found that food webs were clearly based on allochthonous material (leaf litter). Our results agree with the notion that leaf litter may be the link between aquatic and terrestrial food webs in forested streams.

3.4.1.2 Primary consumers

Aquatic non-predatory invertebrates had a slightly less enriched range of values for $\delta^{13}C$ compared with their terrestrial equivalents (1.5‰ difference). McDowall et al. (1996) observed the same pattern, and similar $\delta^{13}C$ values for aquatic and terrestrial non-predatory invertebrates in several streams throughout North and South Islands of New Zealand. On the other hand, for $\delta^{15}N$ the average step difference between leaf-litter and non-predatory aquatic invertebrates in this study was 6‰, twice as much as between leaf-litter and terrestrial non-predatory invertebrates (3‰). These differences between $\delta^{13}C$ and $\delta^{15}N$ suggest involvement contribution from a ‘nutrient microbial loop’, derived from heterotrophs growing in submerged leaf-litter. Dissolved substances leach from submerged leaf litter, and some of them are rapidly taken up by microorganisms (bacteria and fungi) elsewhere in the stream (Winterbourn 2004). This food source can contribute substantially to the nutrition of aquatic invertebrates, as observed by Collier et al. (2004) in other New Zealand forest streams. The aquatic non-predatory invertebrates in this study (caddis flies and mayflies) had similar trophic levels, as reflected in the narrow range of $\delta^{15}N$ values. Specifically, caddis flies are regarded as omnivores and mayflies as either herbivores (grazing on diatoms and algae) or detritivores (scraping detritus off submerged stones and leaves) (Hadlington & Johnston 1998).

Terrestrial non-predatory invertebrates were more variable in $\delta^{15}N$, suggesting a high diversity of feeding habits. Millipedes, earthworms and amphipods feed on wood and plant debris, while isopods, wetas and beetles are omnivorous (Brusca & Brusca 2003). Schmidt et al. (2004) found two main isotopic groups in a soil invertebrate community: including herbivorous and litter-feeding species, and the other, soil feeders. Unfortunately, we had insufficient samples to detect such trophic differentiation at Company Stream.

3.4.1.3 Predators

As expected, predators had the most enriched $\delta^{15}N$ values among the groups analysed, but significant differences were observed among them. Spiders and harvestmen (predatory invertebrates) and eels had the lowest $\delta^{13}C$ values, but these two groups differed greatly in $\delta^{15}N$ values. A stable isotope study by Collier et al. (2002) indicated a primarily aquatic insect pathway of carbon transfer to spiders alongside two streams in North Island, New Zealand, and estimated that spiders obtain between 61 and 55% of their body carbon from aquatic production. Similarly, the diet of shortfin eels has been reported to be dominated by aquatic taxa (Kelly & Jellyman 2007); Hicks (1997) identified up to 70% of the food items in shortfin eel stomachs as aquatic invertebrates. A high $\delta^{15}N$ (5.3‰) places eels at the top of the aquatic food chain; Kelly & Jellyman (2007) also showed shortfin eels to be top predators in a lake ecosystem in South Island, New Zealand, so it is possible that the banded kokopu, *G. fasciatus*, accounts for part of the diet of eels (Jellyman 1989).

Kokopu (*G. fasciatus*) and frogs (*L. hochstetteri*) had $\delta^{13}C$ and $\delta^{15}N$ values intermediate between arachnids and rats, which indicate similar diets including major contributions from terrestrial prey. Both galaxiids and frogs have been reported to eat mostly terrestrial invertebrates (Stephenson & Stephenson 1957; Sharell 1966; Kane 1980; Main & Lyon 1988; Halstead 1994; Hicks 1997; Chapman & Alexander 2006), although *G. fasciatus* also feeds on aquatic invertebrates (Hicks 1997), and one report suggests that *L. hochstetteri* does too (Stephenson & Stephenson 1957).

3.4.2 Predation on *L. hochstetteri*

Our results are consistent with the possibility that both shortfin eels and the kokopu are potential predators of *L. hochstetteri*. West et al. (2005) specifically stated that the banded kokopu consumes native frogs.

By contrast, although rats are generally considered to be a major threat to herpetofauna in New Zealand (Towns & Daugherty 1994), perhaps including native frogs (Thurley & Bell 1994), our results do not strongly support that hypothesis for *L. hochstetteri* in the study area. Further studies are needed to confirm the extent of ship-rat damage to *L. hochstetteri* populations.

In our data, ship rats had the highest $\delta^{13}C$ values of all animals analysed, which suggests consumption of additional or alternative food sources not available to the native predators we analysed. Ship rats are omnivorous, and in New Zealand they eat seeds, fruit and other plant parts, invertebrates, eggs, birds and mice both by scavenging and predation (McQueen & Lawrence 2008).

Predation of native frogs by the introduced frog *Litoria aurea* was reported by Thurley & Bell (1994). While we did not encounter introduced frogs during the course of this investigation, the slightly higher trophic position of *G. fasciatus* in relation to *L. hochstetteri* supports the notion that this fish may prey on this frog.

In summary, aquatic and terrestrial food webs at Company Stream appear to be linked through inputs of leaf litter into the stream channel. Leaf litter may be directly consumed by terrestrial invertebrates, while a microbial loop may assist carbon and nitrogen transfer from submerged leaf litter to aquatic invertebrates. Different trophic groups were distinguished among vertebrate predators, with the native frogs placed at an intermediate trophic level among them. The data suggest that *L. hochstetteri* consumes terrestrial invertebrates along the banks of the stream channel, and that eels and kokopu could be more significant potential predators than are rats. Our study of the trophic position and diet of *L. hochstetteri* could help design diets for captive populations of this native frog species.

3.4.3 Conservation of native frogs

Global declines in native frog populations are attributed, in part, to anthropogenic habitat alteration (Baber et al. 2006; Newman 1996). Recognising the terrestrial origin of *L. hochstetteri*'s food sources and its intermediate trophic position has important implications for future development of frog conservation strategies. For example, riparian vegetation should be protected, because it provides significant input of organic matter to sustain stream food webs.

Poison operations to control exotic mammals in New Zealand may affect non-target species (Davidson & Armstrong 2002). For example brodifacoum, an anti-coagulant poison, is used extensively in New Zealand for rodent control (including within Waitakere Ranges). Residues of this poison have been detected in insects found near poison baits (Ogilvie et al. 1997), and birds of several species have died after eating invertebrates that had consumed brodifacoum baits (Godfrey 1985). Therefore, poison operations may represent a threat to *L. hochstetteri* populations.

One limitation of this study is that no aerial invertebrates were collected for carbon and nitrogen isotopic analyses, so their potential contribution to the diet of *L. hochstetteri* is unknown. However, this is not a significant error, for three reasons.

(1) The aquatic invertebrate fauna analyzed in this study included the larval forms of flying insects (e.g., caddisflies and mayflies), which eventually metamorphose and emerge from the water to become part of the aerial invertebrate fauna, so this group has been represented, at least in part, in our study.

(2) Mayflies do not feed during their brief adult life (Winterbourn 2000) so the isotopic composition of these flying individuals should be the same as that of the larvae in the water.

(3) Frog tongues all have the same basic morphological structure, although they vary in their anatomical detail and the degree to which they can be protruded. The ancestral condition found in frogs such as *Leiopelma* is a short, disc-like structure that is broadly attached to the floor of the mouth, with little capacity for projection (Wells 2007). Stephenson and Stephenson (1957) noted that individuals of *L. hochstetteri* kept in captivity were not very adept at catching quick-flying insects, and had to be more or less hand-fed with immobile fly individuals. We consider that, at least *L. hochstetteri* living in the Company Stream food web, aerial invertebrates were not a major constituent of the potential prey.

CHAPTER 4. Habitat-use model for the New Zealand endemic frog *Leiopelma hochstetteri*.

Modified version of Nájera-Hillman et al. (2009b)

4.1 INTRODUCTION

Understanding the links between amphibian distribution and habitat structure are important first steps to address the current global decline in amphibian populations (Cushman 2006, Hamer & McDonnell 2008), in part, because the identification of ideal habitat characteristics may facilitate the identification of important areas for conservation of endangered on vulnerable species. In particular populations of island endemic amphibians are vulnerable to environmental change and are susceptible to population declines (Lecis & Norris 2003, Moore et al. 2004), because of their range-restricted distributions.

Endemic New Zealand frogs (*Leiopelma hochstetteri*, *L. archeyi*, *L. hamiltoni* and *L. pakeka*) are among the most primitive living frogs in the world (Ford & Cannatella 1993, Roelants & Bossuyt 2005). Subfossil remains indicate that this genus once was widely distributed throughout the New Zealand archipelago, but since human colonisation, several species became extinct (Worthy 1987). A number of biological features render these frogs vulnerable to population decline or extinction. These native species have restricted range distributions, appear to be long lived and have low reproductive rates (Wells 2007).

Leiopelma hochstetteri is currently the most widespread and abundant New Zealand native frog species. It is ranked number 38 on the Zoological Society of London's amphibian EDGE list of the most evolutionarily distinct and globally endangered amphibians in the world, is recognized as 'vulnerable' in the IUCN red list of threatened species, and is fully protected by New Zealand legislation. This is the most aquatic native frog species in New Zealand and now survives in spatially fragmented populations across the northern half of the North Island, and on Great Barrier Island (Baber et al. 2006). Substantial genetic variation among frogs from different areas of its current distribution suggests that each population should be considered a distinct unit worthy of separate conservation (Green 1994, Gemmell et al. 2003, Fouquet et al. 2009).

The Waitakere Ranges are considered a *Leiopelma hochstetteri* conservation management unit (CMU; Green 1994, Fouquet et al. 2009). This area consists of a series of hills that run roughly north–south, which contain several streams, a few lakes and some human-made water reservoirs. The vegetation cover in this area reflects the impact of timber milling, burning and farming (Esler 2006) — milling and burning of the native forest occurred prior to the 1930s. Today, 60% of the Waitakere Ranges falls within a Regional Park and is afforded protection to minimise the effects of development on the region, although much land surrounding the park is in private ownership, of which 78% is still covered in native forest (ARC 2003). Since April 2008 the *Waitakere Ranges Heritage Area Act* promotes the protection and enhancement of the terrestrial and aquatic ecosystems within the Park, in addition to residential areas.

Although, the abundance and distribution of *L. hochstetteri* have been surveyed in the Waitakere Ranges (Ziegler 1999, Bradfield 2005) and its habitat has been described as wet habitats, alongside shaded streams and seepages (McLennan 1985, Bell et al. 2004a), where frog abundance is positively associated with the amount of coarse substrates in the stream channel (Chapter 5), the links between *L. hochstetteri* distribution and habitat characteristics have not been quantitatively investigated.

Potential agents of decline for *L. hochstetteri* have been considered to be habitat loss and habitat modification, predation by introduced mammals and disease (Towns & Daugherty 1994, Baber et al. 2006, Bishop et al. 2009). However, according to Chapters 3 and 5 of this thesis there is not conclusive evidence that ship rats are a threat, and despite extensive surveys, the amphibian disease caused by the fungus *Batrachochytrium dendrobatidis,* has not been detected in *L. hochstetteri* (Bishop et al. 2009).

The distribution of amphibians as all other organisms is strongly determined by variability in habitat characteristics (Hutchinson 1957). Amphibian-habitat relationships can be described using statistical models that relate species distribution, richness, diversity and/or abundance to a range of factors, such as topography and vegetation (Cushman 2006), with binary logistic regression being a particularly useful technique for determining which habitat variables best explain species distribution over different spatial scales (Lecis & Norris 2003). However, it has long been acknowledged that a species may go undetected in a survey of a sampling unit, even when it is present (MacKenzie et al. 2002), particularly if a species is cryptic, leading to underestimation of the true distribution of a species (MacKenzie & Royle 2005). Unaccounted detection probability of a species could influence habitat-use models, causing biased estimates of habitat effects or misleading inferences about the 'conservation value' of different habitats (Tyre et al. 2003, Gu & Swihart 2004). However, if sampling units are repeatedly surveyed within a relatively short time frame, some methods, which incorporate estimates of detection probabilities, can be used to provide reliable distribution estimates (e.g. MacKenzie et al. 2002, Royle & Nichols 2003). Moreover, the models of MacKenzie et al. (2002) can be used to investigate the influence of environmental characteristics on *L. hochstetteri* detection probability and occurrence

(Crossland et al. 2005), and therefore are likely to provide reliable information about habitat-use of different populations and/or the species.

Herein results of *Leiopelma hochstetteri* monitoring in the Waitakere Ranges are presented that enable statistical modelling of its occupancy, detection probability and habitat-use. This information is likely to provide basic ecological data to facilitate appropriate conservation management of this endemic, range-restricted and threatened species. Therefore, the aims of this research are to (1) establish a reliable estimate of frog occupancy and to (2) to identify associations between frog occupancy and habitat characteristics.

4.2 METHODS

4.2.1 Study sites

Field work was conducted in the Waitakere Ranges, Auckland, New Zealand (36°53′–37°03′ S, 174°27–34′ E), between 16 and 300 m elevation. In order to assess the proportion of sites occupied (occupancy) and detection probability of *L. hochstetteri*, a total of twenty two sites were selected throughout the study area with aid of a 1:50,000 topographic map. Sites were always surrounded by native forest evenly distributed throughout the altitudinal gradient of the Waitakere Ranges (30% were located under 100 m of altitude, 33.3% between 100 and 200 m, and 36.7% above 200 m 30%). Sites were composed of stream sections, defined as the stream reach between two consecutive stream junctions. Selected sites resulted in stream sections of variable length and hierarchy (first, second and third order streams) (Fig. 4.1). No pre-existing knowledge regarding frog presence/absence was used for site selection.

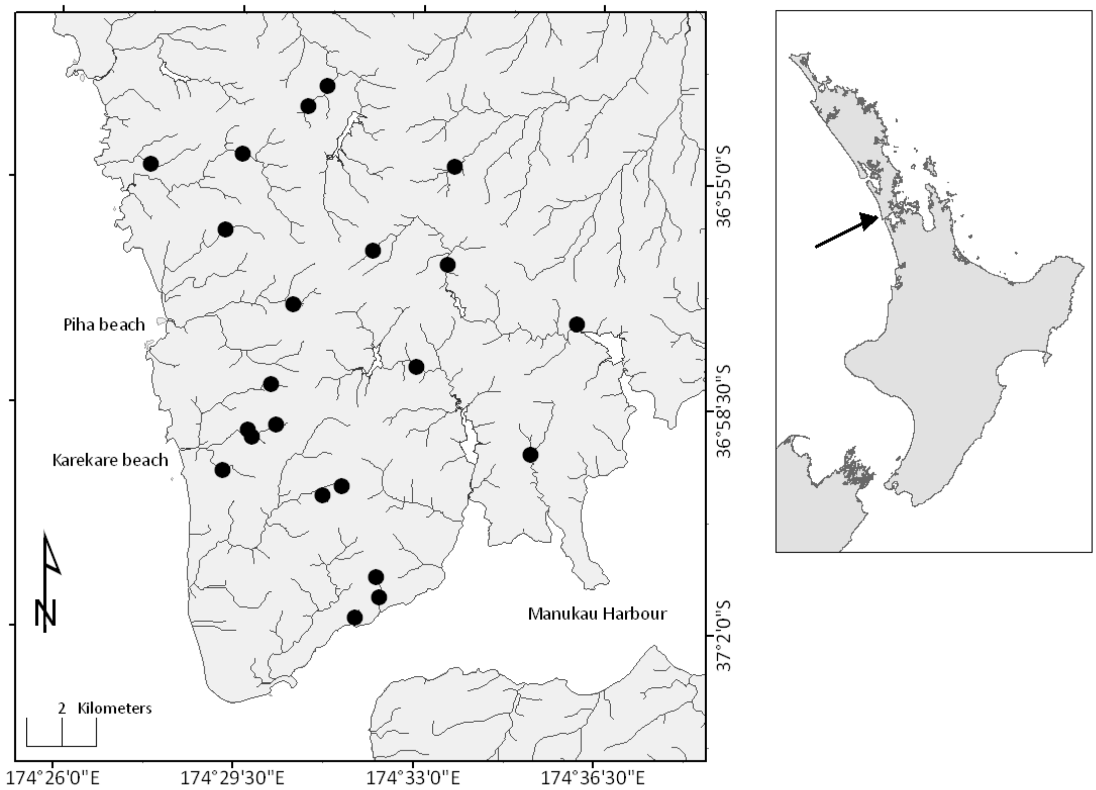


Figure 4. 1 Location map showing study sites (black dot). Small map: North Island, New Zealand; arrow, Waitakere Ranges.

4.2.2 Frog surveys

Frog searches were conducted within each selected stream section and were undertaken in accordance with established New Zealand survey protocols (Crossland et al. 2005, Bradfield 2005, Baber et al. 2006). Each stream section was searched entirely by moving upstream from a start point, carefully examining all available refugia for frogs (underneath rocks, logs and leaves, and inside crevices and tunnels). All objects that had to be moved were carefully replaced in their original position to minimise habitat disturbance. Both sides of the stream along each stream section were searched from the water's edge to the stream bank.

In order to establish frog occupancy and detection probability we followed recommendations of MacKenzie & Royle (2005). Five searches were conducted at each stream section during late spring 2007 and summer 2008. Repeated searches of stream sections were conducted as multiple discrete visits (i.e. on different days) using multiple observers. The observers searched within the stream section until one frog was found or until the section had been searched completely. In addition, survey biases were reduced by rotating sites among observers on any given day. All observers were previously trained for the surveys by experienced frog searchers.

4.2.3 Environmental characterisation

Detailed descriptions of the riparian tree community structure and stream section geomorphic characteristics were made; measurements of water chemistry and observations of weather conditions were undertaken at all sites. Stream section geomorphic characteristics were obtained from the New Zealand River Environment Classification (Ministry for the Eenvironment 2004) and confirmed by observations in situ. These included stream order, geology, hydraulic process (erosive or depositional) and upstream catchment area. Silt in stream water was visually assessed by recording presence of suspended fine sediments in stream water and/or by the incidence of accumulated fine sediments between coarse substrates (boulders and cobbles).

Species, density and diameter at breast height (DBH; approximately 1.4 m from the ground) of all riparian trees (≥3 cm DBH), were recorded in 6 belt transects at each stream section during the winter 2007. Transects were 10 metres long, 4 metres wide, oriented perpendicular to the stream channel, with the starting point located at the edge of the stream.

Water chemistry and weather conditions were recorded in situ on the day frog searches were conducted. Water temperature, pH, dissolved oxygen concentration, and conductivity were measured using a WTW MultiLine P4 water measurement pocket meter. Weather conditions, such as air temperature and relative atmospheric humidity, were recorded using a Skywatch GEOS N°11 Handheld Weather System.

4.2.4 Data analyses

The approach of MacKenzie et al. (2002) implemented in the program PRESENCE, was used to estimate the detection probability and occupancy of *Leiopelma hochstetteri*. This model assumes that the distribution of the frog is "closed" within a season (i.e. there are neither colonisations nor extinctions). Thus, I restricted frog surveys to a single season, and all five visits to a single site were completed within 15 days. To estimate occupancy I assumed detection probability to be constant across surveys and also to be survey specific.

Estimates of detection probabilities can be used to assess, with a specific degree of confidence, the number of visits necessary to determine if a species is truly absent from a site (Kéry 2002). We used the approach of Pellet & Schmidt (2005) to calculate the minimum number of visits necessary to be 95% certain that *Leiopelma hochstetteri* would be absent from a stream section in the Waitakere Ranges.

The association between the occupancy and detection probability of *Leiopelma hochstetteri* and habitat characteristics obtained from the environmental data, was modelled with an information-theoretic approach, which allows one to select a "best" model and to rank the remaining models (Burnham & Anderson 2002). Site specific variables (e.g. stream order and catchment area) were used to model frog occupancy and sampling occasion variables, such as water temperature and pH, were used to model frog detection probability. However, the average values per site of the sampling occasion variables, were used as site variables as well. Akaike's information criterion (AIC) was used to compare models with different environmental variables, the lowest values of this criterion are associated with models that more thoroughly explain the variation in the frog detection data without introducing the imprecision generated by the inclusion of additional parameters (Sherman & Runge 2002). However, due to the relatively low number of surveyed sites we adjusted the AIC for small sample size (AIC_c) in the model selection process (Burnham & Anderson 2002). Using the program PRESENCE, we compared the AIC_c values of each of the measured environmental variables alone, and we then combined the variables with the highest values to see if the combination produced a "post hoc" model that better fit the data than the best single variable model alone. AIC_c differences ($\Delta AIC_c = AIC_c - \min AIC_c$) were used to define the level of empirical support for the models that satisfactorily explained the occupancy and detection probability of *L. hochstetteri*, where: 0–3 substantial, 3.1–9 considerably less, and > 10 none (Johnson & Omland 2004, Hasui et al. 2007, Crawford & Semlitsch 2008).

Additionally, we calculated Akaike weights (w_i) to determine the weight of evidence in favour o each "post hoc" models. Last, we also judge the strength of the best model by verifying that the error estimates (Beta's) of the untransformed coefficients for each of the environmental variables included in the models did not encompassed zero.

4.3 RESULTS

4.3.1 Frog occupancy and detection probability

Leiopelma hochstetteri was detected at 15 of 22 sites. Thus, the average occupancy (naive estimate) was 68.18%. After accounting for detection probability in the program PRESENCE, the estimated occupancy was 0.68 ± 0.09 SE, either when detection probability was considered to be constant or to be survey specific. Parity between the average and estimated occupancy was not surprising given the high average detection probability (0.88 ± 0.04) of *L. hochstetteri* in this study.

According to the average detection probability (0.88), the total number of sites surveyed (22) and the number of frog searches per site (5), the minimum number of searches necessary to be 95% certain that *L. hochstetteri* would be absent from a stream section was 1.4, indicating that in practice two searches would suffice for this purpose.

4.3.2 Relationship between frog distribution and environmental characteristics

Habitat characteristics of sites that were and were not occupied by *L. hochstetteri* are summarised in Table 4.1. Frogs were detected primarily within first order streams, within small catchment areas located in high-altitude areas; frogs were also more commonly found at non-silted streams. Sites where frogs were present tended to have colder water, as well as colder air temperatures and higher atmospheric humidity.

Table 4. 1 Habitat characteristics of sites surveyed for *L. hochstetteri* presence. DBH = diameter at breast height.

Number of sites	Unoccupied N=7		Occupied N=15	
	Mean	±SE	Mean	±SE
Riparian trees				
Mean diameter (cm)	12.98	0.75	12.41	0.52
Standard deviation of DBH	9.57	0.96	8.57	0.55
Density (trees/m^2)	2.85	0.27	2.78	0.23
Species richness	14.43	0.78	14.00	0.70
Water chemistry				
Dissolved oxygen (mg/l)	8.22	0.64	8.67	0.16
Temperature (°C)	16.05	0.41	14.27	0.17
pH	7.13	0.26	7.14	0.07
Conductivity (µS/cm)	190.03	33.9	189.49	4.51
Atmospheric				
Relative humidity %	61.44	4.65	64.83	0.79
Temperature (°C)	20.57	0.71	18.02	0.29
Geomorphic				
Catchment area (ha)	354.30	125.3	160.15	14.6
Altitude (m.a.s.l.)	137.14	23.6	195.53	4.89
Stream order (number of sites)				
First (9)	22.2%		77.8%	
Second (8)	37.5%		62.5%	
Third (5)	40.0%		60.0%	
Geology (number of sites)				
Volcanic acidic (18)	33.3%		66.7%	
Soft sedimentary (4)	25.0%		75.0%	
Hydraulic process (number of sites)				
Erosive (17)	29.4%		70.6%	
Depositional (5)	40.0%		60.0%	
Water clarity				
Silted (5)	80.0%		20.0%	
Clear (17)	17.6%		82.4%	

Riparian vegetation characteristics (e.g. mean tree diameter, tree density) were similar in occupied and unoccupied sites (Table 4.1). Although, the structure of the riparian tree community was similar between unoccupied and occupied sites, with the most abundant tree species being the tree ferns *Dicksonia squarrosa* and *Cyathea* *dealbata*; Kanuka trees (*Kunzea ericoides*) were more abundant at sites not occupied by frogs, and Nikau palms (*Rhopalostylis sapida*), Tawa trees (*Beilschmiedia tawa*) and Kahikatea trees (*Dacrycarpus dacrydioides*) more abundant at frog occupied sites (Fig. 4.2).

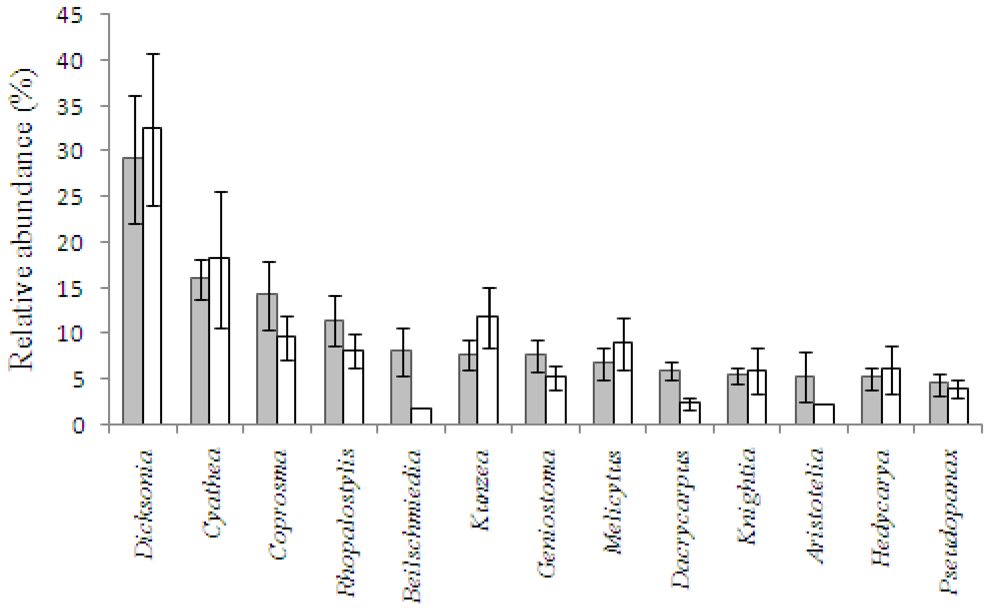


Figure 4. 2 Dominant riparian trees (genera) relative abundance (Mean ±SE) at study sites. Grey bars = frog-occupied sites, white bars = frog-unoccupied sites, N=132.

Of the 22 variables measured during this study, only 6 were substantially associated with *L. hochstetteri* occurrence ($\Delta AIC_c < 3$). Of these, water temperature best predicted the occurrence of *L. hochstetteri*, followed by air temperature and catchment area. The categorical variables erosive hydraulic process, first order streams and volcanic acidic geology were also substantially associated with frog occurrence, however, these models did not presented a better fit than the null model [Ψ(.), p(.); Table 4.2].

Table 4. 2 Summary of AIC_c model selection for single variable models for stream occupancy by *Leiopelma hochstetteri*, Waitakere Ranges, New Zealand. The symbol Ψ indicates the occupancy portion of the models, while the symbol *p* denotes de detection portion of the models. Values of Ψ and *p* are untransformed estimates.

Model	AIC_c	ΔAIC_c	Level of support for model	Ψ(SE)	*p*(SE)
Ψ(Water temperature), *p*(.)	85.17	0.00	+ + +	-1.12 (0.57)	1.99 (0.35)
Ψ(Air temperature), *p*(.)	85.86	0.69	+ + +	-1.05 (0.59)	1.99 (0.35)
Ψ(Catchment area), *p*(.)	87.09	1.92	+ + +	-0.96 (0.66)	1.99 (0.35)
Ψ(.), *p*(.)*	87.19	2.02	+ + +	0.68 (0.09)	0.88 (0.04)
Ψ(Erosive), *p*(.)	87.20	2.03	+ + +	0.87 (0.53)	1.99 (0.35)
Ψ(1st order), *p*(.)	87.22	2.05	+ + +	1.25 (0.80)	1.99 (0.35)
Ψ(Volcanic acidic), *p*(.)	88.13	2.96	+ + +	0.69 (0.50)	1.99 (0.35)
Ψ(Silted), *p*(.)	88.24	3.07	+ / -	-1.39 (1.12)	1.99 (0.35)
Ψ(Air relative humidity), *p*(.)	88.85	3.68	+ / -	0.51 (0.46)	1.99 (0.35)
Ψ(Soft sedimentary), *p*(.)	89.12	3.95	+ / -	1.10 (1.15)	1.99 (0.35)
Ψ(Standard deviation of DBH), *p*(.)	89.37	4.20	+ / -	-0.40 (0.47)	1.99 (0.35)
Ψ(2nd order), *p*(.)	89.66	4.49	+ / -	0.51 (0.73)	1.99 (0.35)
Ψ(Tree evenness), *p*(.)	89.79	4.62	+ / -	0.27 (0.45)	1.99 (0.35)
Ψ(Dissolved oxygen), *p*(.)	89.79	4.62	+ / -	0.27 (0.44)	1.99 (0.35)
Ψ(Mean tree diameter), *p*(.)	89.84	4.67	+ / -	-0.25 (0.44)	1.99 (0.35)
Ψ(3rd order), *p*(.)	89.97	4.80	+ / -	0.40 (0.91)	1.99 (0.35)
Ψ(depositional), *p*(.)	89.97	4.80	+ / -	0.40 (0.91)	1.99 (0.35)
Ψ(Tree species richness), *p*(.)	90.05	4.88	+ / -	-0.15 (0.44)	1.99 (0.35)
Ψ(Tree diversity), *p*(.)	90.11	4.94	+ / -	0.10 (0.43)	1.99 (0.35)
Ψ(Tree density), *p*(.)	90.14	4.97	+ / -	-0.07 (0.43)	1.99 (0.35)
Ψ(Altitude), *p*(.)	90.14	4.97	+ / -	-0.07 (0.44)	1.99 (0.35)
Ψ(pH), *p*(.)	90.17	5.00	+ / -	0.01 (0.43)	1.99 (0.35)
Ψ(Conductivity), *p*(.)	90.17	5.00	+ / -	0.02 (0.41)	1.99 (0.35)
Ψ(.), Survey-specific *p**	95.47	5.33	+ / -	0.68 (0.09)	*Srvy 1* 0.87 (0.09) *Srvy 2* 1.00 (0.00) *Srvy 3* 0.87 (0.09) *Srvy 4* 0.80 (0.10) *Srvy 5* 0.87 (0.09)
Ψ(.), *p*(Water temperature)	120.21	35.04	-	1.23 (0.64)	-1.01 (0.29)
Ψ(.), *p*(Air temperature)	125.33	40.16	-	1.08 (0.57)	-0.79 (0.27)
Ψ(.), *p*(pH)	132.87	47.70	-	0.88 (0.50)	-0.37 (0.25)
Ψ(.), *p*(Air relative humidity)	133.76	48.59	-	0.88 (0.50)	0.33 (0.28)
Ψ(.), *p*(Dissolved oxygen)	133.94	48.77	-	0.89 (0.50)	0.28 (0.25)
Ψ(.), *p*(Conductivity)	134.73	49.56	-	0.89 (0.50)	0.27 (0.39)

* These models show proportion values of Ψ and *p.*

All the models that considered the effect of survey specific variables (i.e. detection probability models) presented very low levels of support ($\Delta AIC_c > 10$) to explain frog detectability (Table 4.2). Therefore the multiple variable models ("post hoc" models) developed subsequently only included combinations of the 6 most important site specific variables (Table 4.3). Among the multiple variable models only one presented better fit to the data than the best single variable model. This model included water temperature and erosive hydraulic process as variables, and was 2.2 times more likely to be the best explanation for frog occurrence compared to the best single variable model, which included main water temperature only, as indicated by the Akaike weights values (0.31/0.14; Table 4.3). Water temperature was negatively associated with frog occurrence and erosive hydraulic process was positively associated with frog occurrence, both variables had a strong association with frog occurrence given that the error estimates for each of the variables did not encompassed zero (Tables 4.2 and 4.4).

Table 4. 3 Summary of AIC_c model selection for "post hoc" models for stream occupancy by *Leiopelma hochstetteri*, Waitakere Ranges, New Zealand. The global model includes all variables with substantial association with frog occurrence. The symbol Ψ indicates the occupancy portion of the models, while the symbol p denotes de detection portion of the models. K = number of parameters in the model.; w = Akaike weights.

Model	**AIC_c**	**ΔAIC_c**	**K**	***w***
Ψ (Water temperature, erosive), p(.)	84.30	0.00	3.00	0.31
Ψ (Water temperature), p(.)*	85.17	0.87	2.00	0.14
Ψ (Water temperature, volcanic acidic), p(.)	85.49	1.19	3.00	0.17
Ψ (Water temperature, 1^{st} order), p(.)	86.36	2.06	3.00	0.11
Ψ (Water temperature, catchment area, erosive), p(.)	87.25	2.95	4.00	0.12
Ψ (Water temperature, catchment area), p(.)	87.28	2.98	3.00	0.07
Ψ (Water temperature, catchment area, volcanic acidic), p(.)	88.22	3.92	4.00	0.07
Ψ (Water temperature, catchment area, 1^{st} order), p(.)	89.28	4.98	4.00	0.04
Ψ (Global), p(.)	94.44	10.14	6.00	0.02

Table 4. 4 Untransformed variable estimates and standard errors for explanatory variables from the best 'post hoc" occupancy model for *Leiopelma hochstetteri*, Waitakere Ranges, New Zealand.

variable	Estimate (Standard error)
Water temperature	-1.43 (0.76)
Erosive hydraulic process	1.16 (0.68)

4.4 DISCUSSION

4.4.1 Frog occupancy and detection probability

Leiopelma hochstetteri was found within most survey stream sections, and presence/absence data were adequately modelled to provide a reliable estimate of the occupancy of this species. The occupancy in the study area (0.68 ± 0.09 SE) was higher than that previously reported by Ziegler (1999) and Bradfield (2005) for the Waitakere Ranges (Table 4.5). However, these two latter studies did not take frog detection probability into consideration (i.e. sites were surveyed only once) while assessing frog distribution, and therefore could not compute standard error or confidence interval values of their occupancy measurements. Consequently, it cannot be determined whether differences in occupancy values in these three studies are significant. Although similar frog search protocols were used in all three studies (i.e day-time searches of potential refugia), the sampling units surveyed were different; specific length transects (5–50 m) were used in previous studies (Ziegler 1999, Bradfield 2005), in contrast to entire stream sections in this current study. Smaller sampling unit size, together with lack of detection probability incorporation, may have led to underestimation of occupancy in previous studies. Therefore, the current study provides, for the first time, a reliable estimate of occupancy for this *L. hochstetteri* population.

Table 4. 5 Proportion of sites occupied and survey features for *L. hochstetteri* distribution studies in the Waitakere Ranges.

Ψ (SE)	**Number of sites**	**Surveys per site**	**Sampling unit**	**Reference**
0.56	23	1	5-50 m transects	Ziegler (1999)
0.49	39	1	40 m transects	Bradfield (2005)
0.68 (0.09)	22	5	stream sections	This study

Our detection probability estimate ($p = 0.88 \pm 0.04$) indicates that during spring–summer, two frog searches on a particular stream section are enough to be 95% certain that *L. hochstetteri* is absent within that stream section, at least within the Waitakere Ranges. Nevertheless, it is worth mentioning that the detection probabilities of some amphibian species (e.g. *Ambystoma tigrinum*) may vary among years (MacKenzie et al. 2003), and consequently, the number of searches necessary to establish absence of a given species may need to be re-determined just prior to studies being conducted. Moreover, Crossland et al. (2005) demonstrated that the detection probability of *L. hochstetteri* may vary (p = 0.61–0.94) among different areas and/or according to the sampling unit utilized (i.e. specific length transects, rock patches within a stream). Therefore, should development of an area be proposed that could threaten sites where a protected species occurs, we suggest the developer should provide evidence that the protected species is absent from particular sites, and do so with statistical certainty, as suggested for other frog species (*Hyla arborea*, *Alytes obstetricans*, *Bufo calamita* and *Bombina variegata*) in other parts of the world (Pellet & Schmidt 2005).

4.4.2 Relationship between frog distribution and environmental characteristics

According to the modelling results, *Leiopelma hochstetteri* occurrence in the Waitakere Ranges is negatively associated with water temperature, air temperature and stream catchment area (Table 4.2). Also, it was positively associated with first order, erosive streams with volcanic acidic geology. According to the New Zealand River Environment Classification (Ministry for the Environment 2004), the channels of erosive streams with volcanic acidic geology tend to be steep and covered by coarse substrates (i.e boulders and cobbles); steep sloped stream channels covered by coarse substrates have been found to be positively associated with frog abundance (Chapter 5) and this study indicates that they are also positively associated with frog distribution. Furthermore, it has been noted that *L. hochstetteri* is vulnerable to any disturbance that affects substratum stability (Tessier et al. 1991), particularly, severe storms that cause sudden flooding (McLennan 1985); streams with small catchment areas are less susceptible to flooding than streams with large catchment areas (Gregory et al. 1991). This trend, may suggest, why frog occurrence was associated with small catchment streams in this study. However, this hypothesis should be tested in future investigations.

In terms of microclimatic conditions, *L. hochstetteri* has been repeatedly regarded as restricted to cool shaded streams (Robb 1980, Bell et al. 2004a). Thus, it is not surprising that our models showed water temperature to be negatively associated with frog occurrence. Streams must be cool and protected from direct sunlight by overhanging vegetation to accommodate this species' narrow temperature tolerance, as noted at the Hamilton Zoo captive population (Kara Goddard, per. comm.). In addition, this frog species has high moisture requirements (Cree 1988). Our results show that frog-occupied sites had slightly higher relative atmospheric humidity than unoccupied sites (64.8% and 61.4%, respectively). One of the primary effects of riparian forest on streams is shading, which induces both low water temperature and high atmospheric humidity (Sugimoto et al. 1997). Moreover, riparian vegetation provides significant input of organic matter to sustain the stream food webs on which *L. hochstetteri* occupies an intermediate trophic level (Chapter 3). Hence, it is likely that any activity that decreases riparian vegetation in catchments where this species occurs may have a detrimental effect on populations.

Frog-unoccupied sites showed higher abundance of Kanuka (*Kunzea ericoides*) than occupied sites; this tree species is characteristic of earlier successional stages in New Zealand forests (Payton et al. 1984, Platt 2002). In contrast, occupied sites had greater abundance of Nikau palms (*Rhopalostylis sapida*), Tawa trees (*Beilschmiedia tawa*) and Kahikatea trees (*Dacrycarpus dacrydioides*), species characteristic of climax forests (Platt 2002; Fig. 4.2). For this reason, we suggest that *L. hochstetteri* has greater affinity for streams with mature or undisturbed surrounding forest cover. However it has been suggested that the riparian tree community associated with frog occurrence in this study may be an indication of wet environments rather than different successional stages (Len Gillman per. comm.). Further research is needed to clarify this issue.

4.4.3 Implications for conservation

Today, *Leiopelma hochstetteri* is the most widespread endemic New Zealand frog species. However subfossil remains (10 000–14 000 yr B.P.) found throughout the North Island and northern half of the South Island, indicate that its range was once greater (Worthy 1987). Moreover, it has been suggested that *L. hochstetteri* populations may be susceptible to potential agents of decline, such as water pollution, damage to streams and riparian areas by cattle or feral pigs, population fragmentation and direct habitat destruction (Bell 1994, Green 1994, Whitaker & Alspach 1999, Baber et al. 2006). Since geographic and genetic subdivisions in *L. hochstetteri* populations indicate that conservation management practice should focus on populations rather than the species as a whole (Green 1994, Fouquet et al. 2009), the methods utilized in this study could be implemented to identify regional agents of decline for specific *L. hochstetteri* populations, and for other range-restricted populations of amphibians.

Field data collected during this study and the resulting model of frog distribution and habitat use provide a reliable description of the habitat requirements of *L. hochstetteri* in the Waitakere Ranges, against which future changes can be assessed. Although the best parsimonious occupancy model only included water temperature and erosive hydraulic process as predictive variables for frog occurrence, the other variables with substantial influence over frog occurrence may be also used to identify adequate areas for *L. hochstetteri* conservation. Thus, ideal stream habitat characteristics for *L. hochstetteri* in the Waitakere Ranges are identified as first order, erosive streams covered with coarse substrates with small catchment areas and mature or undisturbed riparian vegetation. This habitat is well represented in the Waitakere Ranges, as reflected by the high occupancy by *L. hochstetteri* (0.68).

Clearing or logging activities are identified as major threats for *Leiopelma hochstetteri*. Fortunately, the Waitakere Ranges Regional Park (60% of the Waitakere Ranges area) has been protected from clearing or logging of vegetation since the 1940s, and since April 2008 the *Waitakere Ranges Heritage Area Act* promotes the protection and enhancement of the terrestrial and aquatic ecosystems within the Park, in addition to residential areas.

In agreement with the notion that stream amphibians demonstrate strong potential as “sensitive species” (cf. Odum 1992), we conclude that measuring and monitoring *Leiopelma hochstetteri* populations can provide a highly suitable and extremely sensitive barometer for ecological stress derived from vegetation clearing and increased water temperature.

CHAPTER 5. Effect of pest-management operations on the abundance and size-frequency distribution of the New Zealand endemic frog *Leiopelma hochstetteri*.

Modified version of Nájera-Hillman et al. (2009c)

5.1 INTRODUCTION

Amphibian populations have declined dramatically in many areas of the world since the 1970's (Stuart et al. 2004). These declines appear to have worsened in the last 25 years, and amphibians are now considered to be generally more threatened than mammals or birds (Beebee & Griffiths 2005). Among the possible causes for amphibian declines are habitat change, over-exploitation, introduction of exotic species, global climate change, pollution and infectious diseases (Collins & Storfer 2003). Some of these, such as climate change, are still controversial. Others, such as habitat loss and the spread of exotic species, are now generally accepted (Wells 2007).

When exotic species are introduced to areas occupied by native amphibians, the population responses may include local extinctions, isolation of smaller populations or co-existence with the exotic species. Exotic species may affect amphibians by directly preying on them, excluding them from resources, infecting them with new diseases and/or altering their genetic composition through hybridization (Kats & Ferrer 2003). Among exotic predators, fishes, snakes, crayfish and other amphibians have been considered the most dangerous intruders, and the cause of several population declines and local extinctions (Alford & Richards 1999; Beebee & Griffiths 2005; Knapp et al. 2007). In contrast, there is little direct evidence that introduced mammals have had a widespread effect on amphibian populations (Wells 2007), except that declines of some amphibian island population have been attributed to introduced mammals (Towns & Daugherty 1994; Ahola et al. 2006).

In modern New Zealand, the Class Amphibia is represented by only four native (*Leiopelma hochstetteri*, *L. archeyi*, *L. hamiltoni* and *L. pakeka*) and three introduced (*Litoria aurea*, *L. raniformis*, and *L. ewingii*) frog species. However, before human colonisation, the archipelago's known amphibian assemblage included seven native frog species (Worthy, 1987). Three of these seven species could have been extinguished by habitat alterations and introduced mammals, especially rats (Towns & Daugherty 1994; Bell 1994).

The remaining species have suffered drastic reductions in their distribution and population size (Bell et al. 2004a). *L. pakeka* and *L. hamiltoni* survive in two small, rat-free islands in the Cook Strait between the North and South Islands of New Zealand, while *L. archeyi* and *L. hochstetteri* survive as fragmented remnant populations across the North Island. The latter two have coexisted with three species of rats (*Rattus exulans*, *R. norvegicus* and *R. rattus*), of which *R. exulans* was the first to arrive to New Zealand (about 800 years ago) followed by *R. norvegicus* and *R. rattus* (about 350 and 150 years ago, respectively) (Tennyson & Martinson 2006). At present, *R. rattus* is the most common rat species in New Zealand (Towns et al. 2006).

Leiopelma hochstetteri is the most widespread and abundant New Zealand native frog, found in wet habitats alongside shaded streams and seepages in forested catchments. The frogs are often found in daylight, sheltering beneath stable rocks and logs (McLennan 1985; Bell et al. 2004a). Substantial cytogenetic (chromosomal structure) variation among populations suggests that each population should be considered a distinct conservation unit (Green, 1994).

This frog species is ranked number 38 on the Zoological Society of London's amphibian EDGE list of the most evolutionary distinct and globally endangered amphibians in the world. It is recognized as ‘vulnerable’ in the IUCN red list of threatened species, and is fully protected by New Zealand legislation. According to the Native Frog Recovery Plan (Newman 1996), the effect of introduced mammalian predators on *L. hochstetteri* populations is uncertain, because frogs still co-exist with them throughout their range. Quoting the current Consultative Draft Native Frog (*Leiopelma* species) Recovery Plan (Bishop et al. 2009) — “agents of decline for this native frog species have not been conclusively demonstrated, particularly at the population level, and in some cases are speculative”. Suggested conservation management options for *L. hochstetteri* include research on the impacts of introduced mammals, especially ship rats (*R. rattus*), and the consequences of human attempts to control them.

The effects of predation on amphibian populations can be evaluated through correlating the distribution of exotic predators with local variation in relative amphibian abundance (Kats & Ferrer 2003; Beebee & Griffiths 2005). Measuring relative abundance of amphibians requires counting individuals using area-constrained protocols (e.g transects or quadrats). However, the probability of detection of an amphibian varies between observers, habitat characteristics and sampling time (i.e. seasons, years). In particular, the abundance of riparian amphibians can be influenced by variability of the stream substrate composition (Stoddard & Hayes 2005; Kluber et al. 2008). Therefore, amphibian monitoring methods should be standardised in order to account for the influence of habitat variability on measurements of frog abundance (Schmidt 2004). In New Zealand, pest-management operations to protect native species and ecosystems are conducted mainly through the use of poison (e.g. Brodifacoum or sodium fluoroacetate [1080]) for possum and rodent control (Fraser & Hauber 2008), including areas where frogs are found.

The aim of this study was to develop a statistical model to identify associations between frog abundance and stream substrate composition in the Waitakere Ranges. The model is designed to enable identification of equivalent habitats within streams inside and outside a pest-management operation area on which the effect of the pest-management operation on *L. hochstetteri* populations could be reliably assessed.

5.2 METHODS

5.2.1 Study sites

The two field study areas are on the western side of the Waitakere Ranges, New Zealand. La Trobe Mainland Island is a pest-managed area (treatment area) located within the Company Stream catchment, and the Karekare Stream catchment constituted a non-treatment control area (Fig. 5.1). Both streams drain the same catchment, in which vegetation is dominated by regenerating secondary forest species (Esler 2006). Milling and burning removed the primary native forest before the 1930s (Cranwell-Smith 2006).

The treatment area is part of an ongoing community-based ecosystem restoration project, established in 2002, covering c. 200 ha. The aim of this restoration project is to suppress numbers of ship rats (*R. rattus*), mice (*Mus musculus*) and possums (*Trichosurus vulpecula*), in order to minimize their negative influence on ecosystem regeneration. A network of poison bait lines 100 m apart is spread over the entire treatment area. On each line, poison bait stations (plastic boxes protecting the poison baits from weathering but accessible to rats and other introduced mammals) are established every 50 m in the lines. Bait stations are restocked with approximately 125 g of brodifacoum twice annually, in spring and in autumn. Brodifacoum is a second generation anti-coagulant, which may remain available from 1 to 6 months depending on weather conditions and on introduced mammal consumption (poison pellets may last longer under dry conditions). Until present there have been no reports of New Zealand native frogs poisoned with brodifacoum within the treatment area or elsewhere in New Zealand.

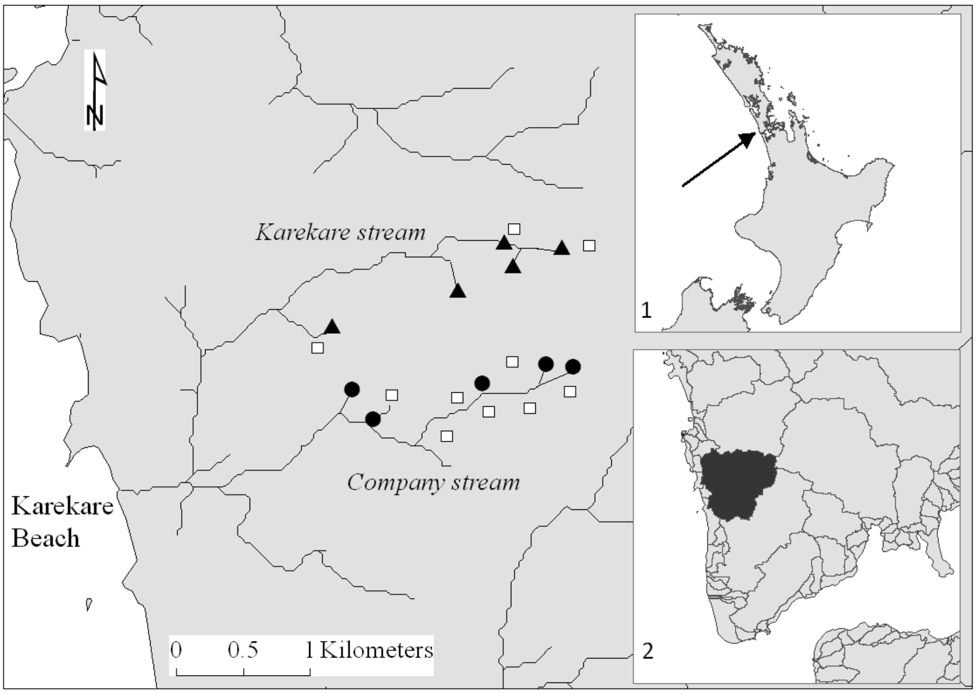


Figure 5. 1 Location of study sites; triangles = non-treatment sites; circles = treatment sites. White squares = rat monitoring locations. *Inset 1*: map of New Zealand's North Island pointing to location of Waitakere Ranges. *Inset 2*: map of Waitakere Ranges depicts catchment where study sites were located.

Ship rat monitoring was conducted in the treatment area from 2002 and in both areas since 2005. The monitoring used Black Trakka^{TM} plastic tracking tunnels to provide an index of ship rat abundance (King 2007). Within the treatment area rats were monitored on seven locations using a total of 60 tacking tunnels, within the non-treatment area rat monitoring was conducted at three locations using a total of 20 tracking tunnels (Fig. 5.1). This method has been reported to detect the presence of rodents even at low abundances (Gillies & Williams 2003). From January 2002 to December 2005, the average index of ship rat abundance was 7.8 ± 3.4% SE for the treatment area (King 2007). From January 2006 to February 2009, the average index of ship rat abundance was 2.8 ± 2.2% SE within the treatment area, and 72.9 ± 8.8% SE within the non-treatment control area (King, unpublished data 2009).

Within each area, five small headwater streams with similar elevations (> 200 m) and canopy covers (> 90%) were selected as survey sites (Fig. 5.1). Presence of *L. hochstetteri* was confirmed at all sites before this study began. In each study site two 20 meters transects were used as sampling units for frog monitoring in 2008 and 2009. Stream substrate characterisation was conducted over the same transects in 2009.

5.2.2 Stream substrate characterisation

The abundance of riparian amphibians can be influenced by variability of the stream substrate characteristics (Stoddard & Hayes 2005; Kluber et al. 2008). Moreover, some recent studies have found that variation in abundance of some species (e.g. *Dicamptodon spp*, *Ascaphus truei*, *Plethodon vehiculum*, *P. dunni* and *P. vandykei*) is more predictable at stream substrate composition scale (Welsh et al. 1997; Wilkings & Peterson 2000; Welsh & Lind 2002). Therefore, during the summer of 2009, I characterised the stream substrate composition (percent cover) for each site within both study areas. At each study site, ten two by two m grid were placed along each of the two 20 m transects used for frog monitoring (Fig. 5.2). Not all of the possible 200 grids were accessible, but 169 grids were measured, 79 on non-treatment and 90 on treatment sites. Each grid was divided into 16 squares of 50 cm^2. Presence/absence of each substrate type was recorded for every square within the grid, because a particular substrate type could be resting over another substrate type, a single square could have had many different substrate types within it (Fig. 5.3). The percent cover for each substrate type was calculated by dividing the number of squares in which a particular substrate was present over the total number of squares (16 squares per grid). Substrate type was classified as boulders (>25 cm), cobbles (<25 ≥ 6 cm), gravels (<6 cm ≥ 0.2 cm), mud (fine and smooth sediment), bedrock, leaf litter (including woody debris), and plants. The percent area covered by water was also considered as a variable for the stream substrate characterisation, and was obtained using the same grid. Frog numbers and positions in each grid were recorded in order to assess associations between substrate type and frog abundance.

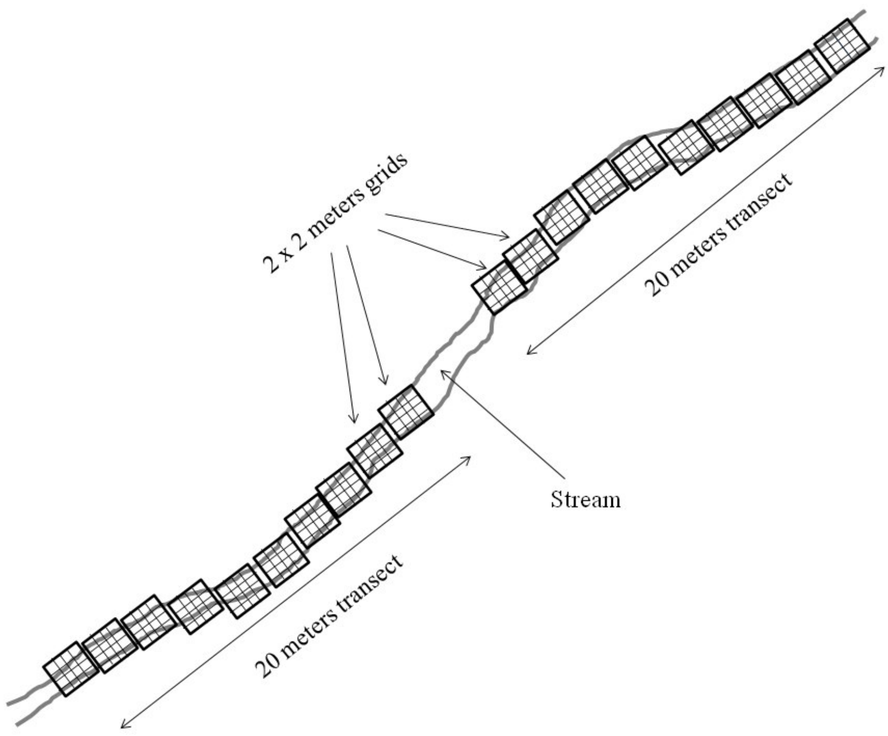


Figure 5. 2 Simplified example of a study site.

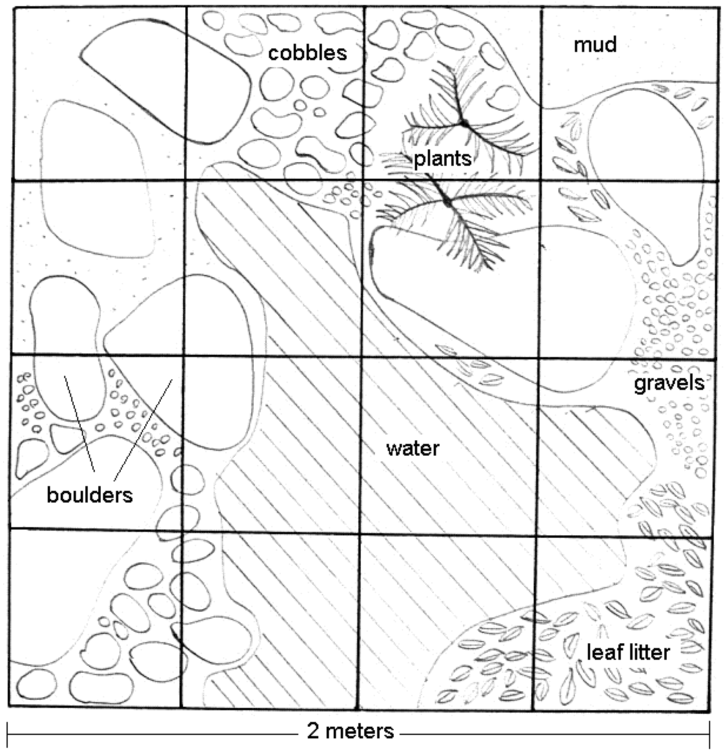


Figure 5. 3 Simplified example of a grid used for stream substrate characterisation.

5.2.3 Frog surveys

Frog counts were conducted during the day (between 9:00 am and 2:00 pm) in two 20 m transects within each site (for a total of 10 transects per study area) in the summer of 2008 and 2009 (Figs. 5.1 and 5.2). Rain effects on frog abundance (Whitaker & Alspach 1999) were avoided since the frog counts were always conducted after 5 days of dry weather and it never rained during the surveys. Surveys on the pest-managed area were always followed by surveys on the non-poisoned control area or *vice versa*.

Frog searches were undertaken at the same sites surveyed for the stream substrate characterisation and in accordance with established frog search protocols in New Zealand (Bradfield 2005; Crossland et al. 2005; Baber et al. 2006). Along each transect, searchers moved slowly upstream from the starting point, carefully examining all available refugia for frogs (i.e., underneath rocks, logs and leaves, and inside crevices and tunnels) on exposed areas of the stream bed and on both stream banks. All objects that had to be moved were carefully replaced in their original position to minimise habitat disturbance. The positions of frogs found along transects was recorded. To minimise observer bias, only one observer with previous experience in searching for *L. hochstetteri* searched all transects. In order to account for any potential difference in the size-frequency distribution of *L. hochstetteri* between the pest-managed and non-poisoned control areas, the snout–vent length of each frog found was measured by holding callipers parallel to the frog's body.

5.2.4 Statistical analyses

We used Generalized Linear Models (GLMs; McCulagh & Nelder 1989) to determine which environmental variable (area covered by boulders, cobbles, gravels, mud, bedrock, leaf litter and plants) had the greatest influence on *L. hochstetteri* abundance. A major advantage of the Generalized Linear Model (GLM) is that it can integrate data from different statistical distributions (i.e. normal in multiple regression, binomial for presence/absence data, poisson or negative binomial for species individual counts; McCulagh & Nelder 1989) with the appropriate modelling of statistical error. The counts of *L. hochstetteri*, recorded for each grid used for the stream substrate characterisation, approximated a Poisson distribution. The relationships between *L. hochstetteri* counts and stream substrate characteristics were therefore characterised using generalised linear models (GLMs), assuming a Poisson distribution (McCullagh & Nelder 1989) with a log link function.

Exploratory univariate GLMs were first run to assess the importance of all variables individually. Those variables which were significant at $\alpha \leq 0.2$ were included in the multivariate analysis (final model). Correlated explanatory variables may affect the reliability of the regression parameters (e.g estimate and *P* values) and make it difficult to accurately interpret the results (Berry & Feldman 1985; Hutcheson & Sofroniou 1999), so variables that were correlated ($p < 0.05$) with other variables but were less significant on their own were removed from the final model. The remaining variables were analysed through multivariate GLM to account for interactions between variables. We also checked whether different processes of model selection (i.e. back and forth stepwise) produced different results. The variables identified as significant and selected for the multivariate analysis were always the same, independently of the method used.

As a criterion for assessing goodness of fit for our final multivariate GLM, we used the ratio of the deviance to the degrees of freedom of the model. If our model fitted the data well, this ratio would be about one (UCLA, 2007). All statistical analyses were performed using SAS 9.1.

After identifying the stream substrate characteristics with significant influence on frog abundance, we performed ANOVAs on those variables to test whether the study areas (pest-managed and non-poisoned) represented similar habitats on which the effects of the pest-management operation could be reliably assessed. The relative abundance of *L. hochstetteri* on the two study areas also was compared by an ANOVA, and the frog size-frequency distribution was analysed graphically.

5.3 RESULTS

5.3.1 Relationship between stream substrate characteristics and frog abundance

Results from the univariate GLMs show that *L. hochstetteri* abundance was positively associated with area covered by boulders (χ^2 = 57.6, p = <.001) and cobbles (χ^2 = 4.4, p = 0.036), and negatively associated with the area covered by plants (χ^2 = 7.4, p = 0.006) and bedrock (χ^2 = 6.68, p = 0.010). Frog abundance was also negatively associated with the area covered by water (χ^2 = 10.1, p = 0.001). Nevertheless, the areas covered by cobbles, plants and bedrock were significantly correlated (correlation p < 0.05; Table 5.1) with the areas covered by boulders and/or by water. Therefore, those correlated variables (area covered by cobbles, plants and bedrock) were removed from the final multivariate analysis. Variables that showed no significant association with frog abundance were area covered by gravels, mud and leaf litter (Table 5.2) and were also excluded from the final multivariate analyses.

Table 5. 1 Correlation matrix (*p*-values) between stream substrate composition variables (percent area covered by each substrate type or water).

Variable	Boulders	Cobbles	Bedrock	Underwater	Gravels	Plants	Leaflitter
cobbles	<.001						
bedrock	<.001	<.001					
Area covered by water	0.484	<.001	0.746				
gravels	0.812	<.001	0.001	<.001			
plants	<.001	<.001	0.166	<.001	0.468		
leaflitter	0.005	<.001	0.02	<.001	0.107	0.029	
mud	0.002	0.283	0.008	0.183	0.084	0.202	0.075

Table 5. 2 Effects of stream substrate composition variables on the abundance of *L. hochstetteri* in the Waitakere Ranges, New Zealand (generalized linear models; GENMOD; Poisson regression).

Variable	Estimate	SE	Lower CI	Upper CI	χ^2	*P*
boulders	0.0402	0.0053	0.0298	0.0505	57.58	<.0001
water	-0.0241	0.0076	-0.0389	-0.0092	10.09	0.0015
plants	-0.0168	0.0062	-0.0290	-0.0047	7.40	0.0065
bedrock	-0.0192	0.0074	-0.0337	-0.0046	6.68	0.0097
cobbles	0.0128	0.0061	0.0008	0.0248	4.40	0.0359
gravels	-0.0089	0.0074	-0.0235	0.0057	1.44	0.2306
mud	-0.0127	0.0107	-0.0337	0.0083	1.41	0.2353
leaf litter	0.0007	0.0057	-0.0105	0.012	0.02	0.8981

Final multivariate GLM results are given in Table 5.3. *L. hochstetteri* abundance was positively associated with area covered by boulders, and negatively associated with area covered by water. Both variables were strongly associated with frog abundance ($p < .001$), and the model based on them presented a good fit for the data (deviance/degrees of freedom = 0.994).

Table 5. 3 GLM showing the most important variables influencing abundance of *L. hochstetteri* in the Waitakere Ranges, New Zealand. Ratio deviance:degrees of freedom = 0.994 (generalized linear models; GENMOD; Poisson regression).

Variable	Estimate	SE	Lower CI	Upper CI	χ^2	*P*
intercept	-2.0812	0.3673	-2.8011	-1.3613	32.11	<.0001
boulders	0.0399	0.0051	0.0298	0.0499	60.53	<.0001
water	-0.0278	0.0078	-0.043	-0.0126	12.79	0.0003

5.3.2 Comparisons of streams between pest-managed and non-poisoning areas

The ANOVA of percent area covered by boulders and water (F = 3.23, $p = 0.089$ and F = 3.34, $p = 0.084$, respectively) indicated that there were no significant differences in habitat composition between streams inside and outside the pest-management operation area. Taking into consideration that the percent areas covered by boulders and by water are reasonable indicators of the number of frogs that may be found in a particular area (Table 5.3), and that the frog monitoring method was standardised, we considered that comparisons of frog abundance between pest-management and non-poisoning areas could be reliable.

5.3.3 Effect of pest-management activities on frog abundance and size-frequency distribution

A total of 192 *L. hochstetteri* individuals was found during this study. A two-way ANOVA indicated that there was no difference in frog abundance either between the treatment and the non-treatment areas (F = 0.64, $p = 0.42$) or years surveyed (F = 1.84, $p = 0.18$). In 2008, frog abundance ranged from 1–15 frogs/20m (7.4 ± 1.52 SE) in the treatment area and from 0–21 frogs/20 m (6 ± 1.95 SE) in the non-treatment control area. In 2009, frog abundance ranged from 0–12 frogs/20 m (5.2 ± 1.1 SE) in the treatment area and from 1–9 frogs/20 m (4.3 ± 0.94 SE) in the non-treatment area (Fig. 5.4).

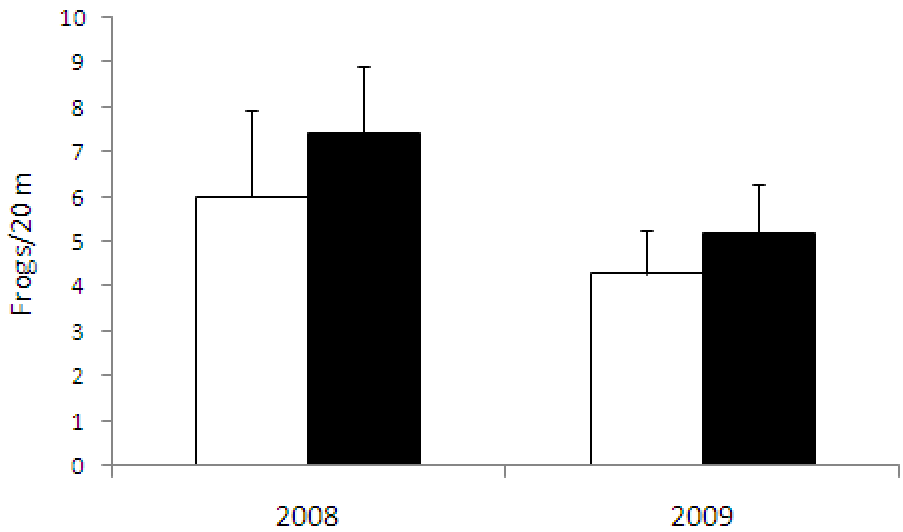


Figure 5. 4 Comparison of *L. hoshctetteri* abundance (Mean ±SE) found between the treatment area (black bars) and the non–treatment control area (white bars) in the summer of 2008 and 2009 in the western Waitakere Ranges, New Zealand. n = 192

Frog size-frequency distribution also was similar in the treatment and the non-treatment areas. Although the non-treatment area had more small frogs (< 30 mm) than the treatment area in 2008 and the opposite was observed in 2009. In 2008, the smallest individual was found within the non-treatment area, where snout–vent lengths ranged from 11–45 mm, while in the treatment area they ranged from 15–45 mm. Conversely, in 2009 the smallest individual was found within the treatment area, where snout–vent lengths ranged from 9–45 mm, while in the non-treatment area they ranged from 20–45 mm (Fig. 5.5). Nevertheless, additional statistical tests are suggested in order to have a more reliable comparison of the size frequency data between the non-treatment and the treatment area.

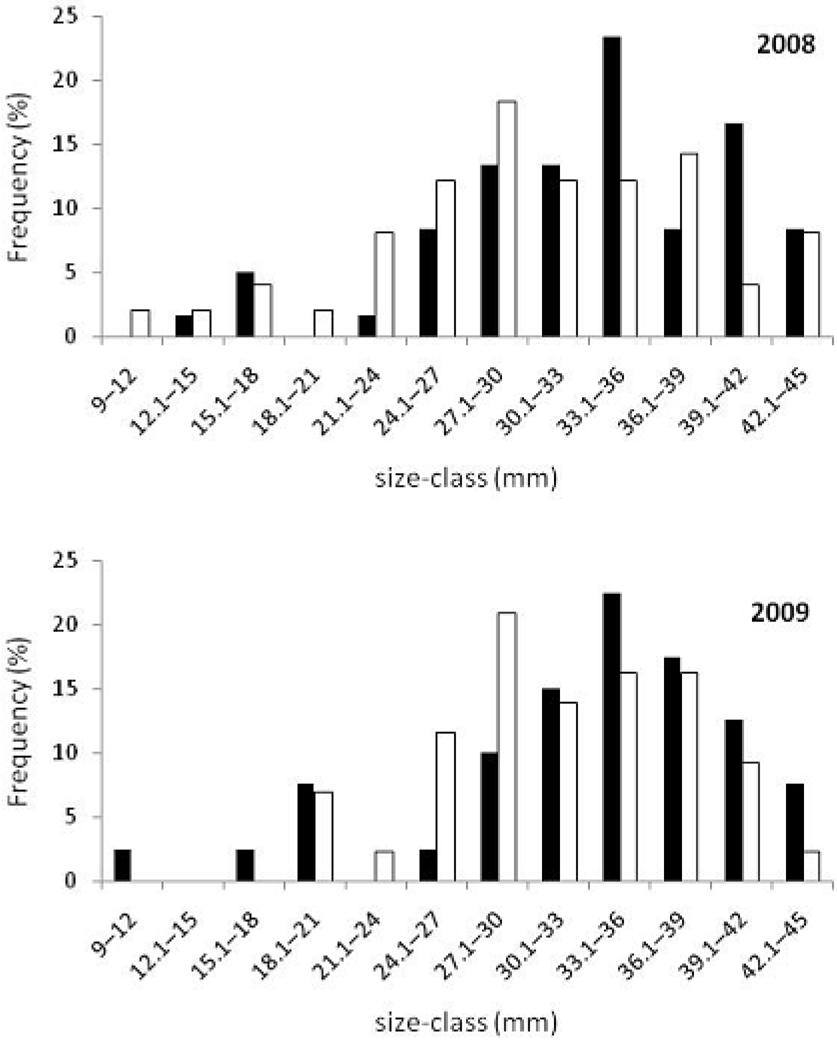


Figure 5. 5 Comparison of snout-vent lengths of *L. hochstetteri* sampled in the treatment area and the non–treatment control area in the summer of 2008 and 2009 in the western Waitakere Ranges, New Zealand. White bars = non-treatment control area; black bars = treatment area.

5.4 DISCUSSION

5.4.1 Relationship between frog abundance and stream parameters

We found that the percent area covered by boulders and water were the most important stream characteristics influencing *L. hochstetteri* abundance in the study areas (Table 5.4). It is well known that *L. hochstetteri* tends to shelter beneath boulders (Baber et al. 2006). However, previous studies (e.g. Thurley & Bell 1994) have focused their attention on whether boulders or logs are more commonly used as shelter rather than on analysing the association between frog abundance and stream substrate characteristics.

It has been shown that coarse substrates (e.g. boulders and cobbles) in forests can retain cool, moist conditions (Anderson et al. 2007), providing suitable micro-habitats for terrestrial or semi-aquatic amphibians (Kluber 2007). Likewise, the abundance of other riparian amphibian species elsewhere in the world, such as red-backed salamanders (*Plethodon vehiculum*) and tailed frogs (*Ascaphus truei*), also is positively associated with coarse substrate cover (Stoddard & Hayes 2005; Kluber et al. 2008).

Amphibians with specialized adaptations to specific micro-habitat requirements can be susceptible to environmental changes, which alter their ability to seek shelter and to forage for their prey. For example, it has been demonstrated that the infusion of fine sediments into streams prevents American amphibians (i.e. *Dicamptodon tenebrosus* and *Ascaphus truei*) from accessing interstices between coarse substrates, because the interstices can get filled with sediments (Welsh & Ollivier 1998). Accordingly, it is not surprising that *L. hochstetteri* has been reported to be absent from silted streams (Green & Tessier 1990; Tessier et al. 1991).

Abundance of *L. hochstetteri* also was negatively associated with the percent area covered by water in the stream (Table 5.3). Steep streams usually have narrower channels (less area covered by water), compared to the wider channels in streams with gentler slopes (Fukushima 2001). Moreover, steeper-sloped streams with a higher, more uniform velocity of water are less prone to trapping sediment (Montgomery & Buffington 1997), providing suitable habitat for *L. hochstetteri*.

Severe storms that cause sudden flooding seem to have negative effects on *L. hochstetteri* populations (McLennan 1985), because floods can significantly disturb stream periphyton and interstitial invertebrates (Scrimgeour & Winterbourn 1989). However, Biggs et al. (1997) showed that organised groupings of cobbles and boulders lying against larger stream bed elements can form stable substratum patches within the stream channel, providing abundant interstitial spaces and crevices for invertebrates to dwell in. It is therefore possible that patches of boulders and cobbles are serving as refugia for invertebrates, which in turn may represent food sources for *L. hochstetteri* (Sharell 1966).

These results predict that within streams occupied by *L. hochstetteri*, areas with high abundance of coarse substrates (i.e. boulders) and narrower, steeper channels may support more frogs. The surveyed streams inside and outside the treatment area were significantly similar in terms of percent area covered by boulders and water, so we can be confident that these streams provided suitable comparative areas for the assessment of this pest-management operation (La Trobe Mainland Island). Additionally, these results emphasise the significance of quantifying habitat characteristics, if the effects of exotic predators are going to be assessed through correlative studies between presence/absence of pest-management operations and relative native frog abundance.

5.4.2 Effect of the pest-management operation on frog abundance

The relative abundance of *Leiopelma hochstetteri* was similar in the treatment area and the non-treatment control area (Fig. 5.4). In both years surveyed, frog abundance measurements were higher within the study areas (> 4.3 frogs/20 m) than the average abundance (3.1 frogs/20 m) calculated from reports of several population studies throughout New Zealand's North Island (Green & Tessier 1990; Tessier et al. 1991; Thurley & Bell 1994; Whitaker & Alspach 1999; Ziegler 1999; Bradfield 2005;

Musset 2005; Baber et al. 2006). This result suggests that *L. hochstetteri* individuals were effectively detected during this study, and that frogs were abundant within both study areas.

Snout–vent length intervals and size–class population structures also were similar between the treatment and the non-treatment areas (Fig. 5.5), and similar to the snout–vent length intervals (10.3–47 mm) and size–class population structures found in many populations of this frog species throughout New Zealand (Green & Tessier 1990; Tessier et al. 1991; Thurley & Bell 1994; Whitaker & Alspach 1999; Baber et al. 2006). According to the size–class intervals suggested by Whitaker & Alspach (1999), juvenile (< 18 mm) and sub-adult frogs (>18 < 24 mm) were detected in this investigation and in previous studies (Ziegler 1999; Bradfield 2005), suggesting that there has been some effective recruitment into the Waitakere Ranges population between 1999 and 2009. Although, I found juveniles in 2008 within the non-treatment control area, I was not able to detect them in 2009. Nevertheless, the proportion of sub-adult frogs in the population is a better measure of recruitment than the proportion of juveniles, mostly because juvenile *L. hochstetteri* individuals are much more difficult to detect than sub-adults, and are often overlooked (Whitaker & Alspach 1999; Bradfield 2005).

There are some observations supporting the idea that rats may have a negative influence on native frog populations. For example, the extinctions of two native frog species (*Leiopelma markhami* and *L. waitomoensis*) in the North Island, New Zealand, coincided with rat invasions (Worthy 1987). However, these extinctions also coincided with human colonization and the consequential habitat modification. Habitat modification is recognized as the primary cause of amphibian population decline worldwide (Gardner et al. 2007). In addition, Musset (2005) recorded higher abundance of *L. hochstetteri* in a treatment area compared with an adjacent area without pest control. However, I'm not aware if the difference was influenced by other habitat characteristics (e.g. variability of stream substrate composition).

There is little direct evidence that introduced mammals have had a widespread effect on amphibian populations, whereas other introduced species such as fishes, amphibians, snakes and crayfish, have been directly implicated in many declines of amphibian populations in other parts of the world (Wells 2007). Until now, there have been no published reports of direct predation of *L. hochstetteri* by ship rats (*R. rattus*), and although tooth marks have been found on dead *L. archeyi* individuals (Thurley & Bell 1994), the evidence is not conclusive in terms of predation of live frogs. Moreover, the results of Chapter 3 do not strongly support the hypothesis that rats are a threat to native frogs in New Zealand. Leiopelmatid frogs are known to have anti-predator mechanisms, such as eluding capture when disturbed and defensive granular glands that secrete deterrent chemicals. Both of these characteristics may represent advantages against predation (Green 1988; Green & Tessier 1990).

It is well known that poisoning operations to control rodents also result in some by-kill of non-target species (Davidson & Armstrong 2002). Therefore, is important to assess the impact of pest control on populations with high conservation value, such as *L. hochstetteri* in the Waitakere Ranges. Previous attempts to evaluate the effect of poisoning operation on *L. hochstetteri* have been inconclusive (Perfect & Bell 2005). Frogs are not likely to eat the poison baits directly, but *L. hochstetteri* is an invertebrate feeder (Chapter 3), which may be at risk of secondary poisoning if they eat invertebrates that have fed on brodifacoum baits (Eason & Spurr 1995). Forest invertebrate species that fed on toxic baits have been recorded to contain significant residues of brodifacoum. Invertebrates carrying brodifacoum were found to disperse up to 10 metres from the source of the toxin (loaded bait stations) and bird species that consume substantial numbers of invertebrates are at risk of secondary poisoning from their food supply during pest control operations using brodifacoum (Craddock 2003). The same could easily apply to *L. hochstetteri* in the treatment area, since some of the bait stations are located approximately 10 metres from streams were frogs occur. However, the abundance of *L. hochstetteri* does not appear to be influenced by the pest-management practices conducted in La Trobe Mainland Island.

The results of this study have a number of implications for the current native frog recovery plan (Bishop et al. 2009). For example, management of introduced mammals to protect native frogs is planned for priority mainland native frog populations by 2016. Therefore, the risk of pest control must be carefully balanced against the benefits. These benefits can be substantial if it is proven that introduced mammals (e.g. ship rats) threaten native frogs or other native species with extinction. Therefore, monitoring frog populations subject to pest-management programmes is necessary to evaluate the success of such activities. The results presented herein provide an initial evaluation for the Waitakere Ranges population, and indicate that this pest-management operation does not represent either a risk or a benefit for *L. hochstetteri*.

On the other hand, another aim of the native frog recovery plan is to identify the primary agent(s) of decline for all native frogs by 2013. The association between frog abundance and percent cover by coarse substrates (boulders) found in this research suggests that increased sediments inputs into streams have the potential to threaten *L. hochstetteri* populations. Sedimentation of stream ecosystems is a common outcome of some land management activities, such as road works and grazing (Welsh & Ollivier 1998; Patrick & Sheridan 2002). Therefore, we suggest exploring management options that can be recommended to road developers and farmland owners in order to minimize the impact of such activities on locally surviving native frogs.

CHAPTER 6. A spatial decision support system for evaluation of *Leiopelma hochstetteri* habitat.

6.1 INTRODUCTION

Leiopelma hochstetteri is the most widespread and abundant New Zealand native frog. However, subfossil remains (10 000–14 000 yr B.P.) found throughout the North Island and northern half of the South Island, indicate that its range was once greater than it is today (Worthy, 1987). Currently, this frog species is ranked number 38 on the Zoological Society of London's amphibian EDGE list of the most evolutionarily distinct and globally endangered amphibians in the world. It is recognized as 'vulnerable' in the IUCN red list of threatened species, and is fully protected by the *New Zealand Wildlife Act 1953*. The New Zealand threat classification system lists *L. hochstetteri* "at risk" (Hitchmough et al. 2007), as it is a taxa with small widely scattered populations, due to direct or indirect human activities. This species is only found in spatially fragmented populations across the northern half of the North Island, and on Great Barrier Island (Baber et al., 2006).

A species may become endangered as a result of negative environmental changes, which affect survivorship and/or fecundity. If a species decline is to be halted, then a management programme must overcome the detrimental factors and improve survivorship and fecundity (Crawley 1982). The main agents of decline for *L. hochstetteri* are considered to be habitat loss and habitat modification, predation by introduced mammals and diseases (Bishop et al. 2009; Towns & Daugherty 1994; Baber et al. 2006). However, Chapter 3 and 5 did not show conclusive evidence that predation by ship rats was a threat to *L. hochstetteri* populations in the Waitakere Ranges, northern New Zealand, and Daugherty et al. (1994) suggested that the more aquatic nature of this frog species makes it less vulnerable to the effects of introduced mammals. Moreover, the results presented in chapter 5 indicate that presence or absence of pest-management for introduced mammals (ship rats in particular) did not have an effect on *L. hochstetteri* abundance for the studied population. In the last ten years, an amphibian disease caused by the fungus *Batrachochytrium dendrobatidis* has emerged as a significant new threat to the congener native frog *L. archeyi* (Bell et al. 2004a). However, despite extensive surveys, this disease has not been detected in *L. hochstetteri* (Bishop et al. 2009).

Habitat modifications are thought to pose the major threat for *Leiopelma hochstetteri* (Stephenson & Stephenson 1957, McLennan 1985; Tessier et al. 1991). These native frogs are absent from silted and disturbed streams, especially where there is no forest cover (Green and Tessier 1991). The results obtained in chapters 4 and 5, indicate that clearing or logging activities and upstream disturbances, such as road works and grazing, may increase silt inputs into streams, and are likely to present a major threat for *L. hochstetteri* populations.

For the effective management of an endangered species, it is necessary to understand the life-history and ecology of the species. Over the past fifty years, several studies on *L. hochstetteri* populations (Stephenson & Stephenson 1957; McLennan 1985, Green & Tessier 1991; Tessier et al. 1991; Bradfield 2005) have provided information about the habitat requirements of the species. *Leiopelma hochstetteri* is the most aquatic native frog in New Zealand, inhabiting wet areas alongside shaded streams and seepages in forested catchments (Stephenson & Stephenson 1957; Bell et al. 2004a). These frogs tend to shelter beneath rocks and logs that are generally stable (McLennan 1985; Newman and Towns 1985; Wakelin et al. 2003). They are known to disperse across upland habitats and move considerable distances between streams

(Slaven 1992). Moreover, results presented in chapters 4 and 5 of this thesis indicate that ideal stream habitat characteristics for *L. hochstetteri* are small streams, located at altitudes above 160 m with cold and clear waters, and surrounded by mature or undisturbed riparian vegetation. In these habitats, frogs may be found in higher abundances, especially within steep areas with stable patches of cobbles and boulders lying against larger stream bed elements within the stream channel.

Under the *Wildlife Management Act 1953,* the *Reserves Act 1977* and the *Conservation Act 1987* protection of critical habitats and conservation of endangered species are required for the preservation of New Zealand's biodiversity. In order to select appropriate conservation areas for endangered species, it is important to know the environmental factors affecting their distribution, and also to have methods for determining the suitability of an area for certain species.

Habitat-use models are often used to identify areas suitable for species of interest (e.g. Gerrard et al. 2001; Store & Kangas 2001). Species-specific habitat-use models are typically made by statistically exploring the relationship between existing occurrences of the species and habitat characteristics (e.g. Chapters 4 and 5). Because these habitat-use models are often based on empirical information obtained from particular sites, it is difficult to extrapolate this information to other areas. This is particularly true when the habitat characteristics utilised are not available as geographic digital data. One possibility for dealing with this problem is to employ the available habitat-use knowledge to associate existing geographic digital data with a rating of values as species habitat requirements. Because all habitat requirements of a species are important, and the relationships between them could be complex, spatial decision support systems (SDSS) have been shown to be useful tools to assess the quality and quantity of habitat available to animal populations associated with specific land tracts (Garcia & Armbuster 1997; Matthies et al. 2007).

Originally developed to support business managers, decision support systems (DSS) have attracted much interest in the field of environmental quality management. A DSS has been defined in many different ways, but it can be regarded, in general, as an interactive, flexible, and adaptable computer-based information system especially developed for supporting the recognition and solution of a complex, poorly structured or unstructured, strategic management problem for improved decision-making (BfG 2000). When DSS are required in support of strategic planning for conservation of endangered species, the spatial dimension is very important, and for this reason DSSs often become SDSSs, by integrating functionalities or coupling with existing geographic information system (GIS) tools (Matthies et al. 2007).

In this Chapter I propose a method for translating *L. hochstetteri* habitat-use information into geographic digital data, which can be processed with a decision support system (DSS) to calculate frog habitat suitability scores for all forested catchments within the Auckland Region. This information then can be stored in a GIS and then integrated in a spatial decision support system (SDSS).

6.2 METHODS

Using the *L. hochstetteri* habitat requirement characteristics, a frog-habitat geographic database was developed for the Auckland Region (Fig. 6.1). In order to generate this frog-habitat geographic database, appropriate digital data of environmental variables were gathered (Table 6.1). Knowing that *L. hochstetteri* is associated with forested streams, the primary environmental database available was the River Environment Classification (REC) system (Ministry for the Environment 2004). The REC organises and maps information about the physical characteristics of New Zealand's streams and rivers, including catchment climate, topography, geology and land cover (e.g. indigenous forest, urban, pastoral). Other geographic data included the NZTopo (Land Information New Zealand 2000), which contains several topographic features, such as roads, tracks and elevation.

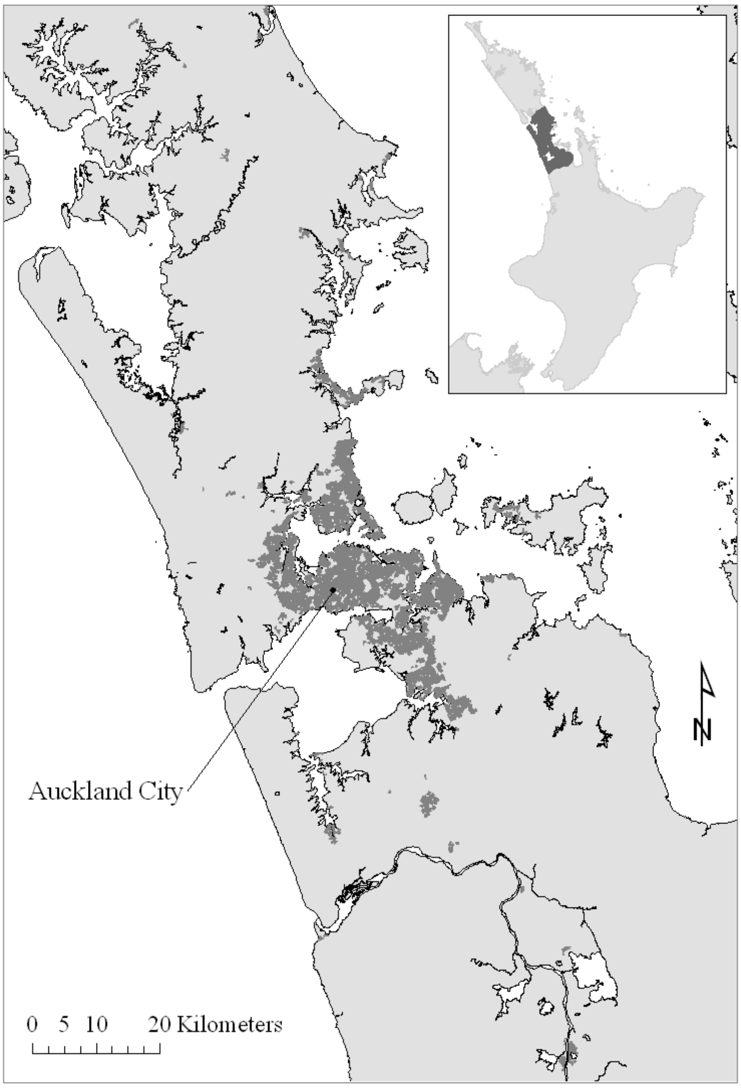


Figure 6. 1 Locator map. *Inset*: depicts Auckland Region in New Zealand's North Island.

A total of 124 catchments within mainland Auckland Region were selected for this study. Catchments represent common conservation management units for endangered species (Wissmar & Beschta 1998; Gerrard et al. 2001; Collares-Pereira & Cowx 2004). Catchment selection criteria consisted of the presence of at least one stream segment covered by indigenous forest. Because the REC information is mapped by individual stream segment, all data were converted to catchment format. In the REC, classification of each stream segment are defined by six criteria (climate, source of flow, geology, land cover, network position and valley landform) and subdivided into sub-criteria (e.g. criteria = land cover: sub-criteria = indigenous forest, exotic forest, urban, pastoral, scrub). Additionally, the average altitude for each catchment was calculated. Road and track density (e.g. roads/ha) for each catchment was calculated as a measurement of isolation from human disturbance.

In order to calculate frog habitat suitability, scores for all forested catchments within the Auckland Region, a simple multi-attribute rating technique (SMART; Edwards 1971) implemented in the program Criterium Decision Plus 3.03 (InfoHarvest 2000) was used as DSS. SMART is the simplest form of the multi-attribute decision making methods, where the frog-habitat score of a particular catchment was obtained simply as the weighed (by rating category) algebraic mean of the criteria and sub-criteria values associated with it (Edwards 1971).

The first step, before performing the SMART analysis, was to rate all criteria and sub-criteria according to their influence on *L. hochstetteri* distribution and abundance. The rating categories were, unimportant, important, very important and critical (Table 6.2). The variability within each criterion also was considered for the rating. For example, there are three sub-criteria within the criterion climate (warm-wet, warm-dry and cold-dry), and 95% of the total stream length in the Auckland region was classified under the sub-criterion warm-wet. Therefore, the criterion climate has little variability and it was rated as unimportant. However, frogs are known to most likely occur in wet habitats, alongside shaded streams with an average water temperature, at least during summer, of 14.3 ± 1.8 SD °C (Chapter 4). The sub-criterion warm-wet indicates high precipitation, high relative atmospheric humidity and similar temperatures to those required by *L. hochstetteri*. Therefore, this sub-criterion, warm-wet, was rated as very important.

Table 6.1 Habitat requirements of *L. hochstetteri* and associated environmental digital data. GIS = geographic information system; REC = river environment classification; NZTopo = New Zealand topographic digital database.

Source of information	**Frog habitat requirements**	**Related digital data (database)**
Chapter 4, this study. Robb 1980; McLennan 1985; Green & Tessier 1990; Tessier et al. 1991; Bell at al. 2004.	Mean summer water temperature (14.3 ± 1.8 SD °C).	Land cover (REC) Climate (REC)
	Clear water streams without suspended fine sediment and/or accumulated fine sediments between coarse substrates.	Land cover (REC) Source of flow (REC) Geology (REC) Roads and tracks (NZTopo)
Chapter 4, this study. Cree 1988.	Cool temperatures and high relative humidity.	Land cover (REC) Climate (REC)
Chapter 5, this study. Thruley and Bell 1994; Baber et al. 2006.	Coarse substrates (boulders and cobbles).	Geology (REC) Valley landform (REC)
Chapter 3 and 4, this study. Robb 1980; Bell et al. 2004a	Cool shaded streams with mature or undisturbed riparian forest.	Land cover (REC)
Chapters 2, 4 and 5, this study. Stephenson & Stephenson 1957; McLennan 1985; Tessier et al. 1991.	Small (low order) steep streams located at altitudes > 160 m.	Network position/Stream order (REC) Valley landform (REC) Altitude (NZTopo)
Chapters 4 and 5, this study. Stephenson & Stephenson 1957; McLennan 1985; Green and Tessier 1990.	Forested catchments without clearing or logging activities, and upstream disturbances that have the potential to increase silt input into streams.	Land cover (REC) Roads and tracks (NZTopo)

Once the rating of all criteria and sub-criteria was completed, the SMART analysis was performed and the decision scores (frog habitat suitability scores) were obtained. Additionally, in order to investigate how changing the rating category of various frog habitat criteria affected the determination of suitable catchments, I performed a sensitivity analysis. Low sensitivity values (≤ 5%) indicate that a slight change in the rating category of particular criteria can change the outcome of the model. Therefore, if all criteria presented sensitivity values > 5%, the model was considered stable (Wolters & Mareschal 1995). Finally, the frog habitat suitability scores were stored in a GIS database and displayed as a frog-habitat suitability map. The process used to estimate the suitability score of all forested catchments within the Auckland Region as potential frog habitat is summarised in figure 6.2.

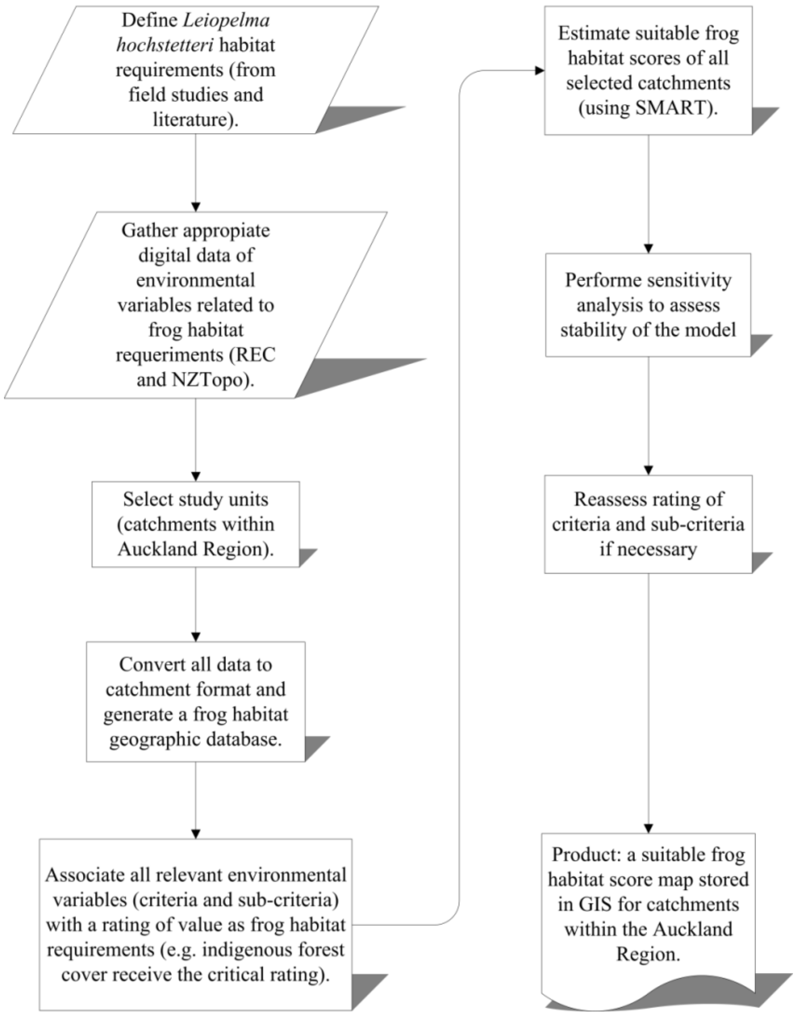


Figure 6. 2 Overview of process to develop frog habitat suitability SDSS for forested catchments in the Auckland Region.

Table 6.2 Rating of value as frog habitat requirements for all criteria and sub-criteria included in the frog habitat suitability model. U = unimportant; I = important; Vi = very important; C = critical.

Criteria	Criterion Rating	Sub-criteria	Sub-criterion Rating	Association with frog habitat	Environmental features considered for rating.
Climate	U	Warm Wet	Vi	+	Mean annual water temperature > 12°C, high relative humidity.
		Warm Dry	I	-	Low relative humidity.
		Cold Wet	I	-	Mean annual water temperature < 12°C.
Source of flow	Vi	Hill	I	-	High to medium sediment loads and unstable substrates.
		Low Elevation	Vi	+	Low sediment supply, stable substrates.
		Lake	U	+	Low sediment supply, stable substrates.
Geology	Vi	Hard Sedimentary	Vi	+	Low suspended sediment concentrations, coarse substrates (boulders).
		Soft Sedimentary	I	-	High suspended sediment concentrations, fine substrates (silt and mud).
		Alluvium	U	-	Variable suspended sediment concentrations, unstable substrates.
		Volcanic Acidic	I	+	Coarse substrates when stream channel is steep and eroding.
		Miscellaneous	Vi	-	Related to urban areas.
Land cover	C	Exotic Forest	I	+	Suspended sediment concentration, water temperature and relative humidity dependent on age of the forest. Mature forest similar to indigenous forests.
		Indigenous Forest	C	+	Low suspended sediment concentrations, cool high clarity waters, shaded streams with increased atmospheric humidity. Indirect food source.
		Pastoral	I	-	Low water clarity and increased suspended sediment.
		Urban	C	-	High concentration of many contaminants and suspended sediment.
		Scrub	I	-	Immature and/or disturbed forest cover.
Network position	Vi	Low Order	Vi	+	Small headwater streams, 1st and 2nd orders.
		Middle Order	I	-	3rd and 4th orders.
		High Order	Vi	-	Main streams, > 5th order.
Valley landform	C	High gradient	C	+	Steep erosive streams, coarse substrates.
		Medium gradient	I	+	Varied morphology, typically a pool-riffle-run sequence.
		Low gradient	C	-	Low water velocity, wide deep stream channels.
Isolation	I	Road density	C	-	Increased sediment input into streams, source of disturbance.
		Track density	U	-	Potential source of disturbance (trampers within stream channels).
Topography	I	Total stream length	Vi	+	Extent of potential frog habitat.
		Catchment area	Vi	+	Extent of potential frog habitat.
		Altitude	Vi	+	Frogs more likely found above > 160 m.

6.3 RESULTS

The score map resulting from the SMART analysis for *L. hochstetteri* habitat suitability is presented in figure 6.3. In this calculation, the maximum suitability score in the Auckland Region was 0.76 and the minimum was 0.48 (scale 0–1); the mean value was 0.64. Of all the catchments selected for this study, 86.3% were located within the Hunua, Waitakere or Rodney ecological districts. An ANOVA of frog habitat suitability scores between catchments located within these three ecological districts (Fig. 6.3) demonstrated that the Hunua and Waitakere ecological districts had significantly ($F = 0.97$; $p \leq 0.001$) higher frog habitat suitability scores than the catchments on the Rodney ecological district (Fig. 6.4). Catchments facing the coast revealed higher scores. The range of variation in the score value in the Auckland Region was moderate. However, catchements with high scores were clearly clustered. For example, the catchments within the Waitakere and Hunua Ranges represented large continuous high score areas.

Sensitivity of the criteria for the frog habitat suitability analysis are summarised in table 6.3. All of the criteria presented sensitivity values > 5%. Therefore, the model was considered stable. The most sensitive criterion was climate (7.9%), indicating that the outcome of the model was more sensitive to changes in the rating category of this criterion. The least sensitive criterion was network position (59.2%), indicating that a change on the rating category of this criterion would be unlikely to change the outcome of the SMART analysis.

Table 6.3 Sensitivity list for criteria considered for *L. hochstetteri* suitability analysis.

Sensitivity value (%)	Criteria
7.9	Climate
8.4	Topography
9.9	Geology
11.8	Valley landform
22.1	Land cover
33.3	Source of flow
59.2	Network position

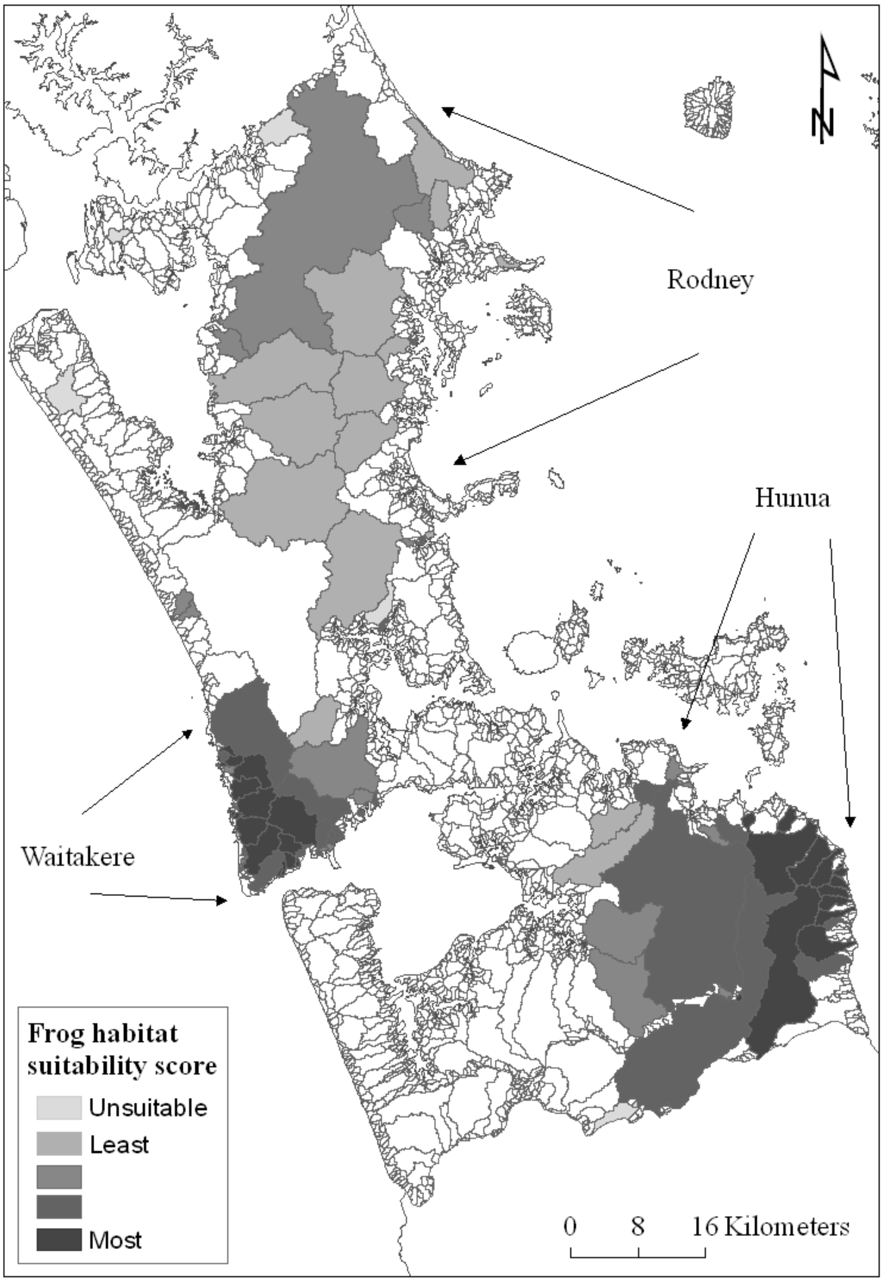


Figure 6. 3 *Leiopelma hochstetteri* habitat suitability scores for forested catchments in mainland Auckland Region.

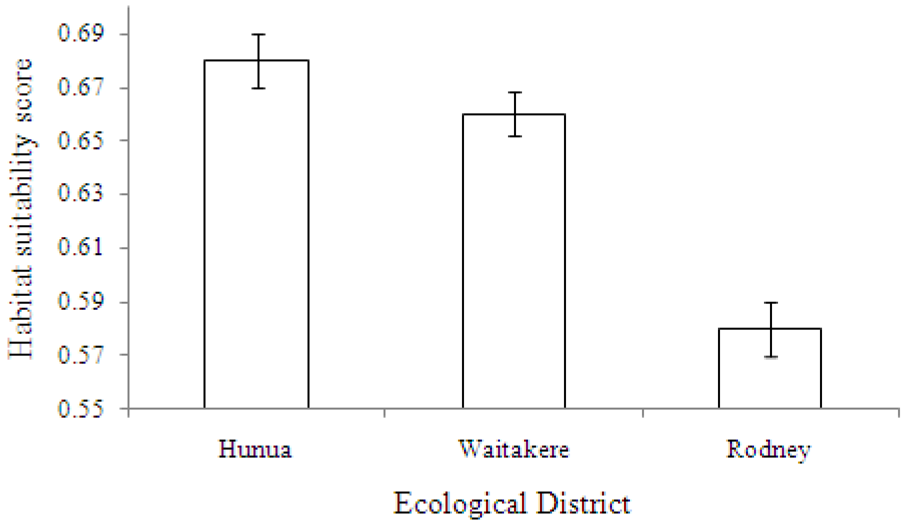


Figure 6. 4 Comparison of *L. hochstetteri* habitat suitability decision scores (Mean ±SE) between forested ecological districts in the Auckland Region, New Zealand.

6.4 DISCUSSION

The Auckland Region houses close to one-third of New Zealand's human population, but retains a rich natural heritage. Although the vast majority (63%) of mainland Auckland Region streams are in rural land uses and 16% are either on urban or forestry land uses, 21% is still covered by indigenous forest (Maxted 2005). Forest remnants on the Auckland Region are worthy of protection not only because they support relatively high proportion of New Zealand's plant diversity (Ogden 1995), but also because they support *L. hochstetteri* populations (Green 1994, Gemmell et al. 2003; Bradfield 2005). In particular, the most extensive remaining opportunities for forest conservation are to be found within the Hunua, Waitakere and Rodney ecological districts (Cutting & Cocklin 1992), and my results indicate that these three ecological districts represent opportunities for conservation of *L. hochstetteri* as well.

The Rodney ecological district is now a fragmented forest landscape, where only a few large indigenous forest remnants exist. In this district, habitat modification has occurred due to agriculture and other productive activities, such as forestry. According to Cutting & Coklin (1992), 18% of the total land area is covered in indigenous forest. However, only three percent of the district has been afforded some form of habitat protection. In addition, forest remnants on private land may be subject to modification by subdivision and development of valued commodities (Coombes 2003). The Rodney ecological district presented the lowest frog habitat suitability scores (Fig. 6.4), and although some *L. hochstetteri* populations have been reported from the Warkworth area (Green and Tessier 1991; Green et al. 1994; Newman 1996), monitoring is needed to asses the current status of this frog species in this area.

Catchments with the highest frog habitat suitability decision scores were located within the Waitakere and Hunua ecological districts. Most of the streams within these ecological districts are in “hard-rock” geology (e.g. boulders and cobbles) and mostly in protected native forest catchments (Maxted 2005). Both of these environmental features are positively related to *L. hochstetteri* habitat requirements (Tables 6.1 and 6.2). Moreover, the Waitakere ecological district retains its natural forest cover, although in most places there has been a high degree of modification in the past (Esler 2006). In the Waitakere Ranges, frogs have been reported to be common (Green & Tessier 1991; Chapter 4) and occur in high densities (Bradfield 2005; Chapters 2 and 5). In the Hunua ecological district, a range of vegetation patterns remain, including several large areas of indigenous forest, although outside these large forest blocks the environment is highly modified (Cutting and Cocklin 1992). Monitoring of *L. hochstetteri* in the Hunua Ranges (Crossland et al. 2005) has demonstrated a high average frog detection probability within this area.

The path taken to arrive at the final frog habitat suitability score map in Fig. 6.3 is not unique. There were many decision points along the way. For example, stream segments could have been used as study units instead of catchments, and the result would have been a more detailed frog habitat suitability score map. Nevertheless, it is worthy mentioning that instead of having 124 alternatives (catchments) I would have more than 1500 alternatives (stream segments) for the SMART analysis. The state-of-the-art of this decision-analysis method (SMART) as implemented in Criterium Decision Plus 3.03 only allows a maximum of 200 alternatives.

Other aspects of our approach, such as the rating categories for the criteria and sub-criteria utilised in this study may vary according to frog-ecology expert opinion or to changes in variables, such as climate. However, one of the major advantages of the method used in this study is the possibility it offers for producing frog habitat suitability scores for different scenarios (e.g. different rating of criteria). For instance, according to our sensitivity analysis, changes in the rating category of the criterion climate may produce changes on the outcome of our model (i.e. the catchments with the highest frog habitat suitability score). Interestingly, given the now ample evidence of the ecological impacts of recent climate change (Gian-Reto et al. 2002); the flexible habitat suitability analysis implemented in this study may have the potential to be used as a tool to assess the impact of climate change on *L. hochstetteri* distribution.

The effectiveness of the REC as a tool to differentiate biophysically meaningful stream classes from GIS-derived data has been questioned in previous investigations (Inglis et al. 2008), suggesting that field analyses of physical and biological habitat (e.g. microclimatic stream condition) are required as a supplementary tool to interpret ecological relationships for differing catchment or stream types. Some of the assumptions, about the relationship between frog habitat requirements and REC variables (Tables 6.1 and 6.2), were based on the frog habitat-use model described in Chapter 4, where the associations between detailed stream habitat characteristics and frog detection probability (FDP) were statistically analysed in the Waitakere Ranges. An overlap between the available FDP geographic data and the frog habitat suitability score map (Fig. 6.3) revealed a consistent relationship between high frog habitat suitability scores and high FDP in the Waitakere Ranges (Fig. 6.5), giving validation to the use of the REC for development of a SDSS as a tool for conservation of endangered species.

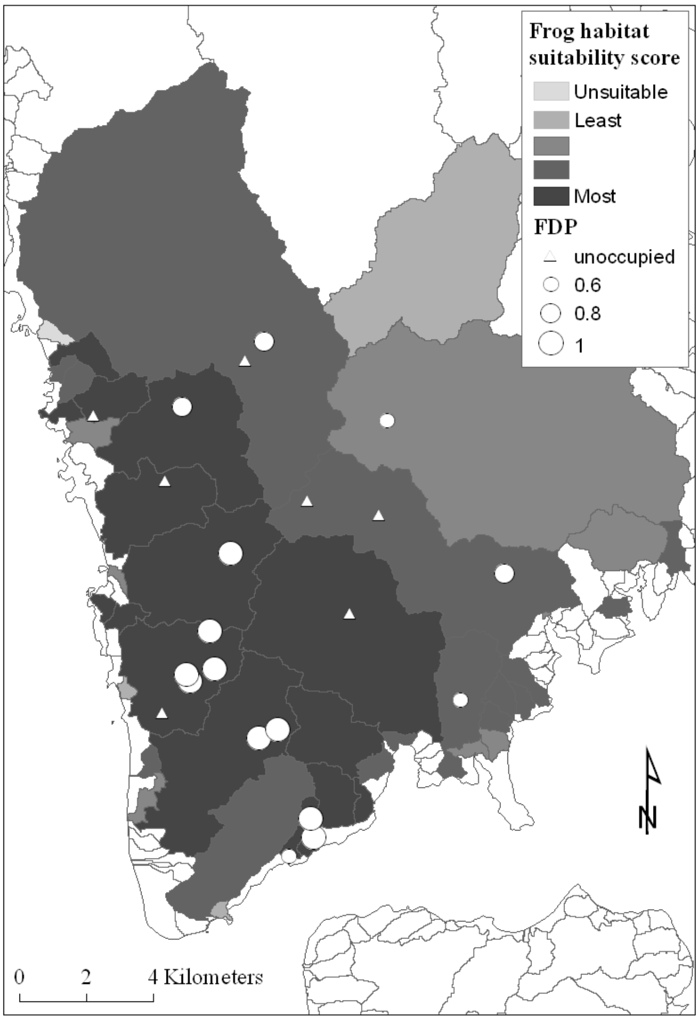


Figure 6. 5 Frog detection probability (FDP) and catchment frog habitat suitability scores in the Waitakere Ranges, New Zealand.

The strategy in this investigation was to incorporate as much biological information as possible to create a model of frog habitat suitability in a GIS format. The REC was the paramount environmental layer because of the known association of *L. hochstetteri* with streams. The NZTopo database was particularly useful to include information about potential threats, such as the presence of roads in the vicinity of forested streams. Other significant layers could be added later without altering the basic technique. Although mainland Auckland Region has been used to illustrate this procedure, the same or similar methods could be used in other New Zealand's regions where this frog species occurs (e.g. Waikato, Northland, Great Barrier Island). This would likely involve different assumptions regarding frog habitat requirements. However, the general type of process implemented here for developing a frog habitat suitability map has proven to be effective. Presenting a general method that may be tailored to particular circumstances will be of the most use to frog conservation practitioners, such as the Native Frog Recovery Group in New Zealand. For example, this procedure may be applicable for the identification of priority sites for native frog surveys in the North Island or to investigate the potential impacts of land use activities, such as roading, subdivisions or production forestry. Furthermore, many other species could have their potential habitat evaluated using the same basic approach.

CHAPTER 7. Synthesis and conclusions

7.1 WAITAKERE RANGES POPULATION STATUS

During this investigation, *Leiopelma hochstetteri* frogs were abundant and widely distributed on a variety of stream types— from seepages to relatively large streams in the Waitakere Ranges.

The proportion of sites occupied by frogs in this study was higher than those previously reported for the Waitakere Ranges (Table 4.4). This is the first study to incorporate detection probability for estimation of the proportion of area occupied (PAO) in the Waitakere Ranges, and constitutes a reliable estimate of distribution for this *L. hochstetteri* population (see Chapter 4).

The average abundance of *L. hochstetteri* reported in this thesis was higher than those found previously in the Waitakere Ranges and northern half of New Zealand's North Island. Other population parameters, such as allometric growth, snout-vent length intervals and size-class population structures were similar to many populations of this frog species in the northern half of New Zealand's North Island (see Chapters 2 and 5 for details).

One approach that has been used to examine trends within populations of amphibians is simple correlations of size-frequency distributions with time (Alford & Richards 1999). The proportion of juvenile, sub-adult and adult frogs appeared to be relatively constant in the last ten years, suggesting that there has been recruitment into the Waitakere Ranges population at least during that time, and that the population is stable (see Chapter 2). However, it is almost universally agreed that most local populations of amphibians are likely to fluctuate considerably in size-frequency distribution and relative abundance, because recruitment is highly variable and survival rates of adult and juvenile stages often vary (Alford & Richards 1999). Therefore, continued frog monitoring of the proportion of area occupied, size-frequency distribution and abundance is needed to keep track of potential changes in the population.

7.2 HABITAT-USE

Leiopelma hochstetteri habitat-use analyses were scale-dependent, described at broad and fine scales with adequate sampling rigor and statistical analyses (Chapters 4 and 5). Frog distribution and detection probability were related to broad scale factors, and frog abundance was related to fine scale factors. Additionally, the diet and trophic level of *L. hochstetteri* were characterised to examine its feeding relationships in the stream food web (Chapter 3).

The habitat-use information generated in this thesis indicated that ideal stream habitat characteristics for *L. hochstetteri* are small streams, located at altitudes above 160 m with cold and clear waters, and surrounded by mature or undisturbed riparian vegetation. In these areas, frogs may be found in higher abundances, especially within steep areas with stable patches of cobbles and boulders lying against larger stream bed elements within the stream channel. Small frogs were only found at relatively higher altitudes, suggesting that breeding areas may be located at higher altitudes. Other species of riparian amphibians (e.g. *Ascaphus truei* and *Rhycotriton variegatus*) are known to move upstream to smaller, higher elevation streams to congregate during the breeding season (Kelsey 1995). However, I did not find any eggs or indications of reproductive activity.

Diet and trophic level characterisation results demonstrated that frogs feed, at least as an adult, on terrestrial invertebrates, and that riparian vegetation provides significant input of organic matter to sustain the stream food webs on which *L. hochstetteri* occupies an intermediate trophic level (Chapter 3). Additionally, some morphological characteristics suggested that *L. hochstetteri* may have some dietary specialisations, such as preference for small, slow-moving prey.

In the Auckland Region the Waitakere and Hunua Ranges represent high quality areas in terms of *L. hochstetteri* habitat-use. Although frogs are known to occur in some streams within the Rodney ecological district, frog habitats in this district are degraded as a result of anthropogenic habitat modifications, such as roads, agricultural activities and land subdivisions.

In conclusion, frog distribution, detection probability and habitat-use were adequately estimated in this thesis. This investigation represents the most comprehensive and quantitative description of *L. hochstetteri* habitat-use to date (Appendix A). This frog has similar habitat-use to those of sensitive riparian amphibian species from North America, like the tailed frog (*Ascaphus truei*) and the red-backed salamander (*Plethodon vehiculum*), which are considered good indicators of ecosystem health (Welsh and Ollivier, 1998; Stoddard & Hayes 2005). Hence, if *L. hochstetteri* populations are diminished or disappear, it could be considered as a result of habitat change in their immediate, local environment.

7.3 THREATS

7.3.1 Habitat modification

Clearing or logging activities and upstream disturbances that have the potential to increase silt input into streams were identified as major threats for *Leiopelma hochstetteri*. Clearing or logging activities cause abrupt changes in the physical and biological characteristics of steam habitat and affect the trophic structure of the stream food web. Sedimentation represents a threat to *L. hochstetteri* populations, in part because it can reduce the interstitial spaces where these frogs seek shelter. Sedimentation is a common outcome of some land management activities, such as road works and grazing (Welsh & Ollivier 1998). In particular, roads that cross streams occupied by *L. hochstetteri* also may affect the movement patterns of the species, and increase concentrations of runoff pollutants, such as heavy metals (Forman & Alexander 1998). Habitat modification is recognized as the primary cause of amphibian population decline worldwide (Gardner et al. 2007). In this thesis, habitat modification also was recognised as the main threat for *L. hochstetteri* in the Waitakere Ranges.

7.3.2 Introduced ship rats

The trophic studies conducted as part of this thesis (Chapter 3) did not strongly support the hypothesis of ship rat predation on *L. hochstetteri*. Moreover, the results presented in Chapter 5 indicated that presence or absence of pest-management for introduced mammals (ship rats in particular) did not have an effect on frog abundance. Therefore, ship rats are not considered a significant threat to *L. hochstetteri*, at least in the Waitakere Ranges. On the other hand, *L. hochstetteri* is an invertebrate feeder (Chapter 3), which may be at risk of secondary poisoning if they eat invertebrates that have fed on poison baits (Eason & Spurr 1995). Nevertheless, according to the results presented in Chapter 5 there was no evidence that poisoning of frogs has occurred in the Waitakere Ranges.

7.3.3 Other threats

In New Zealand some ecological responses to recent climate change have been already observed (e.g. advancement of the tree line toward higher altitudes due to general climate warming; Gian-Reto et al. 2002). *L. hochstetteri* has high moisture requirements and is restricted to cool shaded streams (Chapter 4 and 5). Thus, it is expected that this species will be affected by increasing water and atmospheric temperatures. Moreover, the sensitivity analysis of the criteria used for *L. hochstetteri* habitat evaluation in Chapter 6 indicates that quantity and quality of frog habitat may be affected if climate becomes a more important environmental issue (e.g. increased drought) in the years to come.

L. hochstetteri is similar to other stream-dwelling amphibians adapted to cool climates (e.g. *Ascaphus truei*, *Rhyacotriton variegates, Dicamptodon tenebrosus*), which are also extremely sensitive to changes in water temperature (Welsh & Hodgson 2008). These kinds of amphibians are among the most vulnerable to increased environmental temperatures. In part because higher temperature can depress their metabolic rates and cause vertical contraction of their distribution ranges (Wells 2007).

In the last ten years, an amphibian disease caused by the fungus *Batrachochytrium dendrobatidis* has emerged as a significant new threat to amphibians in New Zealand and around the world (Bell et al. 2004a). However, despite extensive surveys, this disease has not been detected in *L. hochstetteri* (Bishop et al. 2009).

In conclusion, it was possible to identify potential threats to *Leiopelma hochstetteri* populations in the Waitakere Ranges. However, since geographic and genetic subdivisions in *L. hochstetteri* populations indicate that conservation management practice should focus on populations rather than the species as a whole (Green 1994; Fouquet et al. 2009); the methods utilized in this study could be implemented to identify regional agents of decline for specific *L. hochstetteri* populations, and for other range-restricted populations of amphibians.

7.4 IMPLICATIONS FOR CONSERVATION

7.4.1 Riparian forest

In this thesis, riparian forest was recognised as a mayor factor in maintaining the ecological stability of *L. hochstetteri* habitat. Riparian forests not only induces low water temperature and high atmospheric humidity, essential to accommodate this species' narrow temperature tolerance and high moisture requirements (Chapters 2, 4 and 5), but it also provides significant input of organic matter to sustain stream food webs (Chapter 3) and reduced sediment inputs into the stream channel. Moreover, the results presented herein suggest that *L. hochstetteri* has greater affinity for small streams with mature or undisturbed surrounding riparian forest cover (Chapter 4).

Today, small native-forested streams and seepages draining the lowlands or coastal hill-country are difficult to find in most parts of New Zealand, where 85% of lowland forest has been cleared (Storey & Cowley 1997). The value of riparian vegetation for protecting and restoring stream ecosystems in New Zealand has been recognised by resource managers (Smith 1993) and by the *Resource Management Act 1991*. However, there has been little research on the benefits of riparian forests to stream threatened fauna, such as galaxid fishes or *L. hochstetteri*. This study is a first quantitative attempt to understand the benefits of riparian forests in providing suitable habitat conditions for *L. hochstetteri*. Although it is known that protection of river and stream associated fauna from the effects of agriculture and other anthropogenic disturbances can be improved through the provision of riparian forest margins, either by retention or planting of native trees (Collier 1995; Storey & Cowley 1997), it would be appropriate to conduct studies about the biologically relevant size of riparian forest margins for *L. hochstetteri*. This thesis provides detailed data about the riparian tree community structure (Appendices E and H), which may be used as reference for restoration programmes on areas with suitable geomorphic characteristics in terms of *L. hochstetteri* habitat-use.

Fortunately, the Waitakere Ranges Regional Park (60% of the Waitakere Ranges area) has been protected from clearing or logging of vegetation since the 1940s, and since April 2008 the *Waitakere Ranges Heritage Area Act* promotes the protection and enhancement of the terrestrial and aquatic ecosystems within the Park, in addition to residential areas. However, other areas of potential *L. hochstetteri* distribution, such as the Rodney ecological district, are still at risk of habitat modification (Chapter 6).

7.4.2 Roads and livestock disturbances

In this thesis, road and live stock disturbances were identified as potential decline-agents to *L. hochstetteri* populations (Chapters 4 and 5). In the Waitakere Ranges some roads cross streams where *L. hochstetteri* populations exist (e.g. Whatipu road crosses over Baker stream) and road works are conducted almost every summer.

Thus, I suggest exploring management options that can be recommended to road developers in order to minimize the impact of their activities. For example, good management practices could include well-placed road drainage systems and diversion of eroded material into buffer systems, which can offset water quality degradation from erosion (Lane & Sheridan 2002). However, the potential for degraded water quality is high at stream crossings, where sediment sources often combine with sort pathways, lessening opportunities for infiltration, trapping or diversion of sediment-laden runoff (Forman & Alexander 1998).

Livestock trampling on stream banks leads similar adverse effects on *L. hochstetteri* populations. Streams become wider and shallower as trampling leads to channel widening, which could lead to increased suspended sediment concentrations either through direct introduction of particles, or by creating cleared areas on stream banks that are susceptible to erosion by subsequent high flows (Bengeyfield 2007). In the Waitakere Ranges some farms are located within catchments where some streams are occupied by frogs (e.g. Karekare and Anawhata catchments). Therefore, I suggest that in order to maintain acceptable sediment levels in streams, farmers could implement restriction of livestock access to stream channels either through fencing or effective herding when livestock are present.

7.4.3 Pest-management

Management of introduced mammals to protect native frogs is desired for priority mainland native frog populations by 2016 (Bishop et al. 2009). Therefore, the risk of pest control must be carefully balanced against the benefits. These benefits can be substantial if it is proven that introduced mammals (e.g. ship rats) threaten native frogs or other native species with extinction. Therefore, monitoring frog populations subject to pest-management programmes is necessary to evaluate the success of such activities. Thus, the results presented herein provide an initial evaluation, for the Waitakere Ranges population, and indicate that this pest-management operation does not represent either a risk or a benefit for *L. hochstetteri* (Chapter 5). However, continued monitoring is recommended in order to assess long-term effects of this pest-management practice.

7.4.4 Frog monitoring

The survey techniques utilised in this thesis provide two significant advances for the monitoring of this frog species in the Waitakere Ranges. First, the detection probability estimate of *L. hochstetteri* indicated that only two frog searches are enough to be 95% certain that *L. hochstetteri* is absent in a particular stream section (Chapter 4). Thus, since previously it was considered that at least four searches were necessary (Crossland et al. 2005), survey efforts and costs may be reduced in future distribution monitoring programmes. Nevertheless, it is worthy mentioning that the detection probabilities may vary among years and consequently, the number of searches necessary to establish absence may need to be re-determined just prior to studies being conducted. Second, the survey methods implemented in Chapter 5 represent a standardised technique, which incorporates the effects of environmental variables on frog abundance. Therefore, this technique could be used for reliable evaluation of the impacts that some management (e.g. pest-management) or development activities (e.g. roads works) may have on *L. hochstetteri* abundance.

Field data collected during this study (Appendices B, C, E, F, G and H) and the resulting models of frog distribution and habitat-use (Chapters 4 and 5) provide a reliable description of the habitat requirements of *L. hochstetteri* in the Waitakere

Ranges, against which future changes can be assessed. Moreover, the spatial decision support system developed in Chapter 6 is a good example of how the information contained in this thesis may be used for development of management tools for the conservation of *L. hochstetteri*.

Although only the Waitakere Ranges population was studied in this thesis, the same or similar methods could be used in other *L. hochstetteri* populations (e.g. Hunua Ranges, Great Barrier Island). Furthermore, many other species stream-associated species could be evaluated and monitored using the same basic approach. Finally, in agreement with the notion that stream amphibians demonstrate strong potential as "sensitive species" (cf. Odum 1992), I conclude that measuring and monitoring *Leiopelma hochstetteri* populations can provide a highly suitable and extremely sensitive barometer for ecological stress derived from fine sediment inputs, vegetation clearing, and increased water temperature.

7.5 PRIORITY RESEARCH DIRECTIONS

Based on the findings of this study, it is recommended that the research actions listed below be considered a priority for incorporation into new research projects for the species. I consider that these research actions are currently the most appropriate to further address the conservation of the species, and to assess the potential impact of proposed land use activities within the species habitat.

7.5.1 Reproduction

During the course of this investigation approximately 600 person-hours were spent searching for frogs, including areas matching the description of the habitat where *L. hochstetteri* lays its eggs. However, neither eggs nor indications of reproductive activity were observed. Although this frog species has been reported to lay their eggs in autumn (McLennan 1985), spring and early summer (Robb 1980), the available information about their reproduction is limited to descriptions of the breeding sites and the tailed swimming larvae (Bell 1985). In 2006, an outdoor captive breeding programme was established at the Hamilton Zoo to develop captive husbandry techniques. However, until today there have been no reproductive events (Kara Goddard per. comm.). Therefore, it is imperative that knowledge is increased about *L. hochstetteri* reproduction ecology and behaviour if we want to secure conservation of this endemic species.

7.5.2 Assessment of quality and quantity of habitat available to *L. hochstetteri*.

Chapter 6 illustrated a method for translating *L. hochstetteri* habitat-use information into geographic digital data, which then was processed with a decision support system (DSS) to calculate frog habitat suitability scores for all forested catchments within the Auckland Region. The information was integrated in a spatial decision support system (SDSS). However, the resulting frog habitat suitability score map was not very detailed. Nevertheless, it is possible to develop a fine detail habitat suitability map based on stream segments rather than on catchments, as long as the geographic information is processed on a computer programme which allows the analysis of unlimited study units.

The Auckland Region was used to illustrate our procedure. However, the same or similar methods could be used in other to identify priority sites for native frog surveys in the North Island, or to investigate the potential impacts of land use activities, such as road works, subdivisions and production forestry. Furthermore, many other species could have their potential habitat evaluated using the same basic approach.

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APPENDICES

Appendix A Research effort by stream in the Waitakere Ranges, New Zealand. FDP = frog detection probability.

Site no.	Stream name	Abundance surveys	Distribution and FDP surveys	Pest-management surveys	Trophic surveys
1	Anawhata		X		
2	Bald Spur		X		
3	Cowan		X		
4	Destruction Gully		X		
5	Farley	X		X	
6	Hidden Valley	X	X	X	
7	Huia		X		
8	Kakamatua		X		
9	Karekare	X	X	X	
10	Karekare waterfall	X		X	
11	Kuataika		X		
12	Kubi's	X	X	X	X
13	La Trobe night	X		X	
14	Lower Baker		X		
15	Lower Cascade		X		
16	Lower Company	X	X	X	X
17	Lower Nihotupu		X		
18	Marawhara		X		
19	Opal Pool		X		
20	Paratanifa	X		X	
21	Piha		X		
22	R6	X		X	
23	R9	X		X	
24	Stoney Creek		X		
25	Top of Karekare	X		X	
26	Tyree		X		
27	Upper Baker		X		
28	Upper Cascade		X		
29	Upper Company	X	X	X	X
30	Upper Nihotupu		X		

Appendix B *Leiopelma hochstetteri* detection probability data for streams in the Waitakere Ranges, New Zealand.

Stream Name	Site no.	Detection probability	Survey no.				
			1	**2**	**3**	**4**	**5**
Upper Baker	1	1	1	1	1	1	1
Lower Baker	2	1	1	1	1	1	1
Cowan	3	1	1	1	1	1	1
Tyree	4	1	1	1	1	1	1
Piha	5	1	1	1	1	1	1
Destruction Gully	6	0.6	1	1	1	0	0
Kakamatua	7	0.6	0	1	0	1	1
Bald Spur	8	0.8	1	1	1	0	1
Lower Nihotupu	9	0	0	0	0	0	0
Lower Cascade	10	0.8	1	1	1	0	1
Upper Cascade	11	0	0	0	0	0	0
Anawhata	12	0.8	1	1	0	1	1
Upper Nihotupu	13	0	0	0	0	0	0
Upper Company	14	1	1	1	1	1	1
Lower Company	15	1	1	1	1	1	1
Stoney Creek	16	0.6	0	1	1	1	0
Marawhara	17	0	0	0	0	0	0
Opal Pool	18	0	0	0	0	0	0
Hidden Valley	19	1	1	1	1	1	1
Kuataika	20	0	0	0	0	0	0
Kare kare	21	1	1	1	1	1	1
Huia	22	0	0	0	0	0	0

Appendix C *Leiopelma hochstetteri* size frequency distribution by year.

Size class (mm)	2008		2009	
	No. frogs	Relative abundance	No. frogs	Relative abundance
9 to 12	1	0.92	1	1.20
12.1 to 15	2	1.83	0	0
15.1 to 18	5	4.59	1	1.20
18.1 to 21	1	0.92	6	7.23
21.1 to 24	5	4.58	1	1.20
24.1 to 27	11	10.09	6	7.23
27.1 to 30	17	15.60	13	15.66
30.1 to 33	14	12.84	12	14.46
33.1 to 36	20	18.35	16	19.28
36.1 to 39	12	11.01	14	16.87
39.1 to 42	12	11.01	9	10.84
42.1 to 45	9	8.26	4	4.82

Appendix D Location of sites for evaluation of pest-management operations on *L. hochstetteri*.

Pest-management	Name	Latitude S	Longitude E
Non-poisoning	Top of Karekare	36°58.216'	174°30.587'
	Karekare track	36°58.197'	174°30.298'
	Paratanifa	36°58.397'	174°30.068'
	Farley	36°58.549'	174°29.437'
	Karekare waterfall	36°58'175'	174°30'205'
Pest-managed	Hidden valley	36°58.803'	174°29.541'
	Kubi's	36°58.772'	174°30.200'
	r6	36°58.413'	174°30'311'
	r9	36°58.698'	174°30.652'
	La Trobe night	36°58.923'	174°29.650'

Appendix E Relative abundance by genera of riparian trees found in streams occupied by *L. hochstetteri* in the Waitakere Ranges, New Zealand.

Genera	Relative abundance %
Dicksonia	21.8
Cyathea	14.9
Kunzea	2.4
Coprosma	11.5
Melicytus	6.5
Rhopalostylis	7.8
Pseudopanax	3
Knightia	4.7
Geniostoma	6.6
Hedycarya	3.4
Olearia	2.1
Others	15.3

Appendix F Frog abundance data for evaluation of pest-management operations on *L. hochstetteri*.

Predator control	Stream	Year	Transect	No. frogs
Non-poisoning	Top of Karekare	2008	1	2
			2	21
		2009	1	4
			2	8
	Karekare track	2008	1	9
			2	10
		2009	1	6
			2	2
	Karekare waterfall	2008	1	1
			2	0
		2009	1	1
			2	1
	Paratanifa	2008	1	5
			2	4
		2009	1	9
			2	1
	Farley	2008	1	5
			2	3
		2009	1	5
			2	6
Pest-managed	Kubi's	2008	1	3
			2	15
		2009	1	5
			2	3
	Hidden Valley	2008	1	12
			2	13
		2009	1	9
			2	8
	La Trobe night	2008	1	1
			2	5
		2009	1	0
			2	2
	R6	2008	1	10
			2	3
		2009	1	12
			2	5
	R9	2008	1	5
			2	7
		2009	1	4
			2	4

Appendix G Raw data of frog abundance and stream substrate percent cover collected in summer 2008–09 in the Waitakere Ranges, New Zealand.

0 = non-poisoning control area; 1 = pest-managed area..

					Stream substrate percent cover								
Predator control area	**Stream**	**Transect**	**Grid**	**Frogs**	Boulders	Cobbles	Bedrock	Underwater	Gravels	Plants	Leaf litter	Mud	Stream width
0	Karekare waterfall	1	1	1	68.75	87.5	12.5	68.75	0	0	0	0	2.4
0	Karekare waterfall	1	2	0	100	50	0	62.5	6.25	0	0	0	2.4
0	Karekare waterfall	1	3	1	68.75	25	12.5	43.75	12.5	0	0	0	2.4
0	Karekare waterfall	1	4	0	87.5	62.5	0	43.75	0	6.25	0	0	2.4
0	Karekare waterfall	1	5	0	81.25	62.5	0	37.5	0	0	0	0	2.4
0	Karekare waterfall	2	1	1	100	31.25	0	25	0	0	0	0	3.22
0	Karekare waterfall	2	2	0	56.25	56.25	0	50	0	0	31.25	0	3.22
0	Karekare waterfall	2	3	0	18.75	0	81.25	43.75	0	0	31.25	0	3.22
0	Karekare waterfall	2	4	0	0	0	100	50	0	0	12.5	0	3.22
0	Karekare waterfall	2	5	0	25	37.5	68.75	93.75	0	0	0	0	3.22
0	Karekare top	1	1	0	62.5	18.75	0	56.25	50	43.75	12.5	25	0.8
0	Karekare top	1	2	0	87.5	62.5	0	37.5	25	6.25	12.5	6.25	0.8
0	Karekare top	1	3	0	87.5	75	0	37.5	6.25	0	31.25	0	0.8
0	Karekare top	1	4	3	93.75	31.25	0	25	18.75	0	6.25	0	0.8
0	Karekare top	1	5	0	37.5	75	0	43.75	37.5	0	18.75	6.25	0.8
0	Karekare top	1	6	1	75	25	0	25	0	12.5	6.25	6.25	0.8
0	Karekare top	1	7	0	50	25	0	25	25	0	43.75	25	0.8
0	Karekare top	1	8	0	25	12.5	0	43.75	6.25	56.25	0	87.5	0.8

0	Karekare top	1	9	0	31.25	31.25	0	18.75	12.5	25	37.5	56.25	0.8
0	Karekare top	1	10	0	50	56.25	0	18.75	6.25	12.5	37.5	31.25	0.8
0	Karekare top	2	1	0	25	31.25	0	37.5	12.5	68.75	0	0	0.8
0	Karekare top	2	2	0	43.75	18.75	0	37.5	6.25	56.25	0	0	0.8
0	Karekare top	2	3	0	31.25	50	0	31.25	12.5	43.75	37.5	25	0.8
0	Karekare top	2	4	2	75	37.5	0	12.5	0	6.25	37.5	0	0.8
0	Karekare top	2	5	4	100	43.75	6.25	12.5	25	6.25	0	0	0.8
0	Karekare top	2	6	1	93.75	37.5	0	6.25	6.25	0	37.5	0	0.8
0	Karekare top	2	7	0	25	6.25	0	18.75	12.5	75	6.25	0	0.8
0	Karekare top	2	8	0	37.5	56.25	0	18.75	18.75	6.25	43.75	18.75	0.8
0	Karekare top	2	9	0	43.75	25	12.5	18.75	12.5	6.25	37.5	0	0.8
0	Karekare top	2	10	1	75	12.5	0	18.75	0	18.75	25	0	0.8
0	Karekare Track	1	1	3	100	87.5	0	25	25	0	6.25	0	3.1
0	Karekare Track	1	2	0	93.75	68.75	0	81.25	31.25	0	0	0	3.1
0	Karekare Track	1	3	1	100	93.75	0	31.25	18.75	0	0	0	3.1
0	Karekare Track	1	4	1	93.75	62.5	0	56.25	18.75	0	0	0	3.1
0	Karekare Track	1	5	1	81.25	87.5	6.25	43.75	6.25	0	6.25	0	3.1
0	Karekare Track	2	1	0	31.25	75	0	43.75	43.75	31.25	6.25	0	2.9
0	Karekare Track	2	2	0	62.5	81.25	0	81.25	6.25	31.25	0	0	2.9
0	Karekare Track	2	3	0	68.75	75	12.5	56.25	31.25	0	6.25	0	2.9
0	Karekare Track	2	4	0	100	31.25	0	81.25	12.5	0	6.25	0	2.9
0	Karekare Track	2	5	2	87.5	43.75	0	25	12.5	0	6.25	0	2.9
0	Paratanifa	1	1	0	68.75	68.75	0	6.25	0	18.75	68.75	6.25	0.9
0	Paratanifa	1	2	3	68.75	62.5	0	6.25	12.5	25	37.5	6.25	0.9
0	Paratanifa	1	3	0	87.5	50	0	0	43.75	50	12.5	0	0.9
0	Paratanifa	1	4	0	62.5	68.75	6.25	12.5	18.75	31.25	31.25	0	0.9
0	Paratanifa	1	5	3	81.25	56.25	6.25	0	6.25	18.75	0	6.25	0.9

0	Paratanifa	1	6	1	100	0	0	0	0	31.25	75	0	0.9
0	Paratanifa	1	7	2	81.25	43.75	0	6.25	6.25	37.5	31.25	0	0.9
0	Paratanifa	1	8	0	68.75	43.75	0	12.5	31.25	31.25	12.5	0	0.9
0	Paratanifa	1	9	0	56.25	25	0	6.25	0	50	12.5	0	0.9
0	Paratanifa	1	10	0	37.5	31.25	0	6.25	12.5	43.75	25	12.5	0.9
0	Paratanifa	2	1	1	62.5	6.25	18.75	9.375	12.5	43.75	31.25	0	0.9
0	Paratanifa	2	2	0	31.25	12.5	25	3.125	12.5	43.75	6.25	0	0.9
0	Paratanifa	2	3	0	43.75	12.5	6.25	3.125	12.5	50	12.5	0	0.9
0	Paratanifa	2	4	0	43.75	6.25	18.75	3.125	0	31.25	12.5	0	0.9
0	Paratanifa	2	5	0	0	0	100	0	0	0	0	0	0.9
0	Paratanifa	2	6	0	0	0	50	43.75	0	31.25	25	0	0.9
0	Paratanifa	2	7	0	18.75	18.75	56.25	25	0	43.75	12.5	0	0.9
0	Paratanifa	2	8	0	0	25	87.5	12.5	0	25	18.75	0	0.9
0	Paratanifa	2	9	0	6.25	25	43.75	0	25	50	6.25	0	0.9
0	Farley	2	1	0	62.5	56.25	6.25	50	31.25	0	37.5	0	1.3
0	Farley	2	2	0	37.5	56.25	18.75	37.5	56.25	0	18.75	0	1.3
0	Farley	2	3	3	68.75	50	18.75	12.5	43.75	0	50	0	1.3
0	Farley	2	4	0	50	81.25	0	25	56.25	0	25	0	1.3
0	Farley	2	5	0	87.5	75	6.25	21.875	0	0	37.5	0	1.3
0	Farley	2	6	1	100	62.5	12.5	9.375	25	0	31.25	0	1.3
0	Farley	2	7	2	75	25	31.25	6.25	0	12.5	43.75	0	1.3
0	Farley	2	8	0	93.75	12.5	12.5	18.75	6.25	0	56.25	0	1.3
0	Farley	2	9	0	87.5	25	31.25	18.75	18.75	0	25	0	1.3
0	Farley	2	10	0	31.25	68.75	12.5	18.75	12.5	0	50	0	1.3
0	Farley	1	1	1	81.25	43.75	6.25	12.5	0	25	50	0	1.3
0	Farley	1	2	0	56.25	31.25	43.75	43.75	0	18.75	0	0	1.3
0	Farley	1	3	0	56.25	31.25	18.75	25	12.5	6.25	12.5	0	1.3

0	Farley	1	4	2	100	31.25	0	0	12.5	6.25	18.75	0	1.3
0	Farley	1	5	1	75	31.25	6.25	6.25	43.75	18.75	12.5	0	1.3
0	Farley	1	6	0	56.25	25	12.5	18.75	0	12.5	31.25	0	1.3
0	Farley	1	7	0	50	37.5	12.5	12.5	12.5	37.5	25	0	1.3
0	Farley	1	8	0	62.5	43.75	25	6.25	6.25	6.25	31.25	0	1.3
0	Farley	1	9	0	31.25	37.5	68.75	43.75	18.75	6.25	25	0	1.3
0	Farley	1	10	1	100	50	0	0	0	0	18.75	0	1.3
1	Kubi's	1	1	2	75	31.25	0	25	0	25	31.25	12.5	2.65
1	Kubi's	1	2	0	81.25	43.75	6.25	18.75	0	0	12.5	6.25	2.65
1	Kubi's	1	3	1	43.75	0	56.25	18.75	0	0	0	0	2.65
1	Kubi's	1	4	0	0	0	100	56.25	0	0	0	0	2.65
1	Kubi's	1	5	2	25	0	75	25	0	0	6.25	0	2.65
1	Kubi's	2	1	1	93.75	43.75	0	37.5	0	0	0	12.5	2.68
1	Kubi's	2	2	1	81.25	81.25	0	37.5	6.25	0	6.25	0	2.68
1	Kubi's	2	3	0	62.5	43.75	0	43.75	12.5	6.25	0	0	2.68
1	Kubi's	2	4	0	81.25	31.25	0	37.5	0	0	12.5	0	2.68
1	Kubi's	2	5	1	93.75	50	0	37.5	12.5	0	6.25	0	2.68
1	Hidden Valley	1	1	2	56.25	31.25	0	3.125	0	0	68.75	0	1.8
1	Hidden Valley	1	2	0	31.25	43.75	0	3.125	0	0	68.75	0	1.8
1	Hidden Valley	1	3	0	18.75	31.25	0	18.75	0	0	68.75	18.75	1.8
1	Hidden Valley	1	4	0	37.5	12.5	0	3.125	0	0	81.25	6.25	1.8
1	Hidden Valley	1	5	2	56.25	0	0	3.125	0	0	56.25	6.25	1.8
1	Hidden Valley	1	6	0	37.5	37.5	0	3.125	0	0	56.25	18.75	1.8
1	Hidden Valley	1	7	0	37.5	37.5	0	6.25	18.75	6.25	43.75	0	1.8
1	Hidden Valley	1	8	1	56.25	31.25	0	6.25	0	0	43.75	18.75	1.8
1	Hidden Valley	1	9	1	62.5	50	0	12.5	0	0	56.25	0	1.8
1	Hidden Valley	1	10	3	62.5	25	0	3.125	0	0	25	12.5	1.8

1	Hidden Valley	2	1	1	37.5	0	50	3.125	6.25	18.75	25	6.25	1.9
1	Hidden Valley	2	2	0	18.75	0	18.75	3.125	0	0	93.75	37.5	1.9
1	Hidden Valley	2	3	0	18.75	12.5	12.5	3.125	0	6.25	93.75	12.5	1.9
1	Hidden Valley	2	4	3	56.25	12.5	43.75	3.125	0	0	68.75	0	1.9
1	Hidden Valley	2	5	2	56.25	18.75	18.75	3.125	0	0	75	0	1.9
1	Hidden Valley	2	6	1	50	0	0	3.125	0	0	43.75	6.25	1.9
1	Hidden Valley	2	7	0	31.25	18.75	0	3.125	0	0	62.5	6.25	1.9
1	Hidden Valley	2	8	1	37.5	12.5	25	3.125	12.5	0	31.25	12.5	1.9
1	Hidden Valley	2	9	0	6.25	0	37.5	3.125	0	0	56.25	0	1.9
1	Hidden Valley	2	10	0	0	0	12.5	3.125	0	50	68.75	0	1.9
1	R6	1	1	0	75	37.5	0	25	37.5	68.75	31.25	0	0.8
1	R6	1	2	0	56.25	43.75	0	31.25	31.25	18.75	50	0	0.8
1	R6	1	3	4	81.25	31.25	0	25	0	37.5	31.25	0	0.8
1	R6	1	4	0	62.5	37.5	0	12.5	18.75	25	25	0	0.8
1	R6	1	5	0	62.5	37.5	0	37.5	25	12.5	62.5	0	0.8
1	R6	1	6	0	68.75	0	0	6.25	6.25	12.5	87.5	0	0.8
1	R6	1	7	2	56.25	18.75	0	9.375	31.25	31.25	43.75	0	0.8
1	R6	1	8	0	62.5	31.25	0	6.25	31.25	6.25	50	0	0.8
1	R6	1	9	2	75	31.25	0	25	25	12.5	43.75	0	0.8
1	R6	1	10	4	100	37.5	0	12.5	12.5	25	56.25	0	0.8
1	R6	2	1	0	12.5	31.25	0	12.5	18.75	56.25	50	0	0.8
1	R6	2	2	0	43.75	12.5	0	18.75	25	50	62.5	0	0.8
1	R6	2	3	1	6.25	31.25	0	6.25	18.75	50	56.25	0	0.8
1	R6	2	4	1	56.25	12.5	0	0	12.5	43.75	93.75	0	0.8
1	R6	2	5	0	62.5	25	0	6.25	18.75	12.5	68.75	0	0.8
1	R6	2	6	0	25	0	0	18.75	12.5	43.75	37.5	0	0.8
1	R6	2	7	3	68.75	12.5	0	12.5	25	18.75	31.25	0	0.8

1	R6	2	8	0	37.5	0	0	31.25	50	18.75	68.75	0	0.8
1	R6	2	9	0	12.5	12.5	0	25	31.25	25	50	0	0.8
1	R6	2	10	0	18.75	18.75	0	6.25	18.75	25	62.5	0	0.8
1	R9	1	1	1	43.75	62.5	0	18.75	25	25	62.5	0	0.8
1	R9	1	2	0	18.75	0	0	43.75	25	75	56.25	18.75	0.8
1	R9	1	3	0	0	25	0	6.25	25	75	68.75	25	0.8
1	R9	1	4	0	0	43.75	0	0	0	43.75	43.75	100	0.8
1	R9	1	5	0	6.25	0	0	0	0	43.75	31.25	81.25	0.8
1	R9	1	6	1	31.25	37.5	0	0	25	50	37.5	0	0.8
1	R9	1	7	1	56.25	56.25	0	18.75	12.5	31.25	18.75	0	0.8
1	R9	1	8	1	87.5	43.75	18.75	6.25	12.5	31.25	31.25	0	0.8
1	R9	1	9	0	50	0	25	0	0	68.75	43.75	0	0.8
1	R9	1	10	0	43.75	18.75	6.25	0	0	75	37.5	0	0.8
1	R9	2	1	0	56.25	25	18.75	18.75	25	50	6.25	0	0.8
1	R9	2	2	0	62.5	6.25	18.75	12.5	18.75	43.75	31.25	0	0.8
1	R9	2	3	0	18.75	0	18.75	0	0	93.75	25	0	0.8
1	R9	2	4	0	25	6.25	18.75	12.5	0	68.75	31.25	0	0.8
1	R9	2	5	0	50	12.5	18.75	0	12.5	37.5	31.25	0	0.8
1	R9	2	6	0	12.5	25	0	25	0	93.75	93.75	0	0.8
1	R9	2	7	0	25	12.5	37.5	6.25	6.25	37.5	43.75	0	0.8
1	R9	2	8	0	75	25	12.5	12.5	12.5	18.75	6.25	0	0.8
1	R9	2	9	4	62.5	62.5	0	6.25	6.25	25	31.25	6.25	0.8
1	R9	2	10	0	6.25	6.25	0	6.25	0	87.5	87.5	12.5	0.8
1	La Trobe night	1	1	0	0	0	25	0	0	12.5	62.5	0	1
1	La Trobe night	1	2	0	6.25	25	6.25	9.375	68.75	6.25	25	0	1
1	La Trobe night	1	3	0	50	18.75	18.75	34.375	37.5	18.75	12.5	0	1
1	La Trobe night	1	4	0	31.25	31.25	43.75	6.25	0	0	31.25	0	1

1	La Trobe night	1	5	0	56.25	37.5	37.5	9.375	0	6.25	25	0	1
1	La Trobe night	1	6	0	25	12.5	12.5	0	31.25	25	31.25	0	1
1	La Trobe night	1	7	0	0	18.75	0	18.75	50	25	37.5	0	1
1	La Trobe night	1	8	0	25	37.5	25	56.25	68.75	6.25	12.5	0	1
1	La Trobe night	1	9	0	25	56.25	0	100	93.75	0	6.25	0	1
1	La Trobe night	1	10	0	18.75	31.25	0	100	50	0	0	0	1
1	La Trobe night	2	1	0	25	6.25	56.25	0	0	50	18.75	0	1
1	La Trobe night	2	2	0	31.25	18.75	43.75	0	0	12.5	18.75	0	1
1	La Trobe night	2	3	1	25	31.25	18.75	9.375	0	12.5	50	0	1
1	La Trobe night	2	4	0	6.25	0	62.5	12.5	0	25	37.5	0	1
1	La Trobe night	2	5	0	31.25	37.5	25	12.5	6.25	43.75	6.25	0	1
1	La Trobe night	2	6	0	12.5	6.25	25	50	25	12.5	18.75	18.75	1
1	La Trobe night	2	7	1	43.75	25	12.5	25	0	6.25	12.5	18.75	1
1	La Trobe night	2	8	0	18.75	25	0	25	25	50	18.75	0	1
1	La Trobe night	2	9	0	18.75	25	56.25	31.25	25	25	18.75	0	1
1	La Trobe night	2	10	0	43.75	43.75	12.5	43.75	12.5	0	0	0	1

Appendix H Raw data of frog presence/absence and stream environmental characteristics collected in summer 2007–08 in the Waitakere Ranges, New Zealand.

		Environmental characteristics																			
Stream	**Frog presence/absence**	First order streams	Second order streams	Third order streams	Volcanic acidic Geology	Soft sedimentary Geology	Erosive stream	Depositional stream	Silt presence/absence	Catchment area (Ha)	Mean tree diameter (cm)	Standard deviat5ion of tree diameter	Tree density (trees/m^2)	Tree species richness	Altitude (m)	Water temperature (°C)	pH	Conductivity (µS/cm/100)	Dissolved oxygen	Relative atmospheric humidity (%)	Air temperature (°C)
Upper Baker	1	1	0	0	1	0	1	0	0	80	13.42	12.26	2.08	13.00	186	12.10	7.18	1.82	10.50	0.75	13.20
Lower Baker	1	1	0	0	1	0	1	0	0	80	14.01	10.48	2.21	14.00	176	12.10	7.18	1.82	10.50	0.75	13.20
Cowan	1	1	0	0	1	0	1	0	0	107	8.99	9.21	2.88	16.00	198	12.20	7.15	1.54	8.95	0.58	16.40
Tyree	1	0	1	0	1	0	1	0	0	64	12.78	12.35	3.54	16.00	198	12.20	7.15	1.54	8.95	0.58	16.40
Piha	1	0	1	0	1	0	1	0	0	182	9.87	6.91	3.67	18.00	73	11.70	7.05	1.59	9.96	0.70	11.90
Destruction Gully*	1	1	0	0	0	1	0	1	1	43	15.72	7.51	1.67	9.00	167	12.90	7.26	2.23	7.21	0.58	17.50
Kakamatua	0	0	0	1	1	0	0	1	0	314	12.55	6.45	2.54	13.00	16	14.40	7.80	1.75	8.93	0.72	17.80
Bald Spur	1	1	0	0	0	1	1	0	0	41	8.91	5.04	4.13	14.00	80	14.10	8.19	2.68	11.64	0.69	18.20
Lower Nihotupu	0	0	0	1	1	0	0	1	1	756	9.79	9.04	3.50	13.00	215	15.10	6.97	0.94	11.44	0.66	17.10
Lower Cascade	1	0	1	0	1	0	1	0	0	264	12.95	7.57	2.67	14.00	100	15.00	7.68	1.83	11.61	0.49	23.50
Upper Cascade	0	0	1	0	1	0	1	0	0	131	14.15	15.47	2.42	12.00	120	15.00	7.68	1.83	11.61	0.49	23.50
Anawhata	1	0	0	1	1	0	0	1	0	619	11.47	6.45	2.75	14.00	80	18.50	8.06	1.79	11.10	0.55	25.40
Upper Nihotupu	0	1	0	0	1	0	0	1	1	117	10.97	8.02	4.17	16.00	280	14.60	6.33	0.98	7.50	0.71	19.80

Upper Company	1	1	0	0	1	0	1	0	0	80	13.22	10.19	1.29	10.00	180	14.70	7.13	2.15	8.70	0.76	16.90
Lower Company	1	0	1	0	1	0	1	0	0	166	14.97	8.64	1.92	10.00	180	14.70	7.13	2.15	8.70	0.76	16.90
Stoney Creek	0	0	0	1	0	1	1	0	0	258	11.86	10.24	4.63	19.00	100	16.10	6.96	1.19	6.43	0.76	19.20
Marawhara	0	0	1	0	1	0	1	0	1	171	12.72	8.02	2.88	17.00	200	15.60	7.70	1.64	6.94	0.63	20.10
Opal Pool	0	0	1	0	1	0	1	0	1	202	14.13	10.12	2.38	17.00	80	18.60	6.68	3.21	8.67	0.63	20.00
Hidden Valley	1	1	0	0	1	0	1	0	0	35	14.71	8.64	2.25	16.00	215	15.00	4.93	3.11	4.92	0.67	18.60
Kuataika	0	1	0	0	1	0	1	0	0	122	16.30	7.45	2.75	12.00	45	16.50	7.50	3.36	6.57	0.63	20.10
Kare kare	1	0	1	0	1	0	1	0	0	69	10.68	6.57	3.46	14.00	200	14.10	6.37	1.45	7.30	0.73	16.20
Huia	0	0	0	1	0	1	1	0	0	980	12.79	8.85	1.83	14.00	100	16.60	7.77	1.32	7.66	0.55	22.50
Upper Baker	1	1	0	0	1	0	1	0	0	80	13.42	12.26	2.08	13.00	186	12.10	7.18	1.82	10.50	0.75	13.20
Lower Baker	1	1	0	0	1	0	1	0	0	80	14.01	10.48	2.21	14.00	176	12.10	7.18	1.82	10.50	0.75	13.20
Cowan	1	1	0	0	1	0	1	0	0	107	8.99	9.21	2.88	16.00	198	12.20	7.15	1.54	8.95	0.58	16.40
Tyree	1	0	1	0	1	0	1	0	0	64	12.78	12.35	3.54	16.00	198	12.20	7.15	1.54	8.95	0.58	16.40
Piha	1	0	1	0	1	0	1	0	0	182	9.87	6.91	3.67	18.00	73	11.70	7.05	1.59	9.96	0.70	11.90
Destruction Gully*	1	1	0	0	0	1	0	1	1	43	15.72	7.51	1.67	9.00	167	12.90	7.26	2.23	7.21	0.58	17.50
Kakamatua	1	0	0	1	1	0	0	1	0	314	12.55	6.45	2.54	13.00	16	14.40	7.80	1.75	8.93	0.72	17.80
Bald Spur	1	1	0	0	0	1	1	0	0	41	8.91	5.04	4.13	14.00	80	14.10	8.19	2.68	11.64	0.69	18.20
Lower Nihotupu	0	0	0	1	1	0	0	1	1	756	9.79	9.04	3.50	13.00	215	15.10	6.97	0.94	11.44	0.66	17.10
Lower Cascade	1	0	1	0	1	0	1	0	0	264	12.95	7.57	2.67	14.00	100	15.00	7.68	1.83	11.61	0.49	23.50
Upper Cascade	0	0	1	0	1	0	1	0	0	131	14.15	15.47	2.42	12.00	120	15.00	7.68	1.83	11.61	0.49	23.50
Anawhata	1	0	0	1	1	0	0	1	0	619	11.47	6.45	2.75	14.00	80	18.50	8.06	1.79	11.10	0.55	25.40
Upper Nihotupu	0	1	0	0	1	0	0	1	1	117	10.97	8.02	4.17	16.00	280	14.60	6.33	0.98	7.50	0.71	19.80
Upper Company	1	1	0	0	1	0	1	0	0	80	13.22	10.19	1.29	10.00	180	14.70	7.13	2.15	8.70	0.76	16.90
Lower Company	1	0	1	0	1	0	1	0	0	166	14.97	8.64	1.92	10.00	180	14.70	7.13	2.15	8.70	0.76	16.90
Stoney Creek	1	0	0	1	0	1	1	0	0	258	11.86	10.24	4.63	19.00	100	16.00	7.97	1.19	7.96	0.68	18.60
Marawhara	0	0	1	0	1	0	1	0	1	171	12.72	8.02	2.88	17.00	200	14.30	5.08	1.65	5.79	0.84	19.30
Opal Pool	0	0	1	0	1	0	1	0	1	202	14.13	10.12	2.38	17.00	80	16.50	7.29	3.23	8.04	0.66	17.20

Hidden Valley	1	1	0	0	1	0	1	0	0	35	14.71	8.64	2.25	16.00	215	15.00	4.93	3.11	4.92	0.67	18.60
Kuataika	0	1	0	0	1	0	1	0	0	122	16.30	7.45	2.75	12.00	45	16.50	7.50	3.36	6.57	0.63	20.10
Kare kare	1	0	1	0	1	0	1	0	0	69	10.68	6.57	3.46	14.00	200	14.10	6.37	1.45	7.30	0.73	16.20
Huia	0	0	0	1	0	1	1	0	0	980	12.79	8.85	1.83	14.00	100	16.60	7.77	1.32	7.66	0.55	22.50
Upper Baker	1	1	0	0	1	0	1	0	0	80	13.42	12.26	2.08	13.00	186	12.10	7.19	1.84	9.60	0.63	14.80
Lower Baker	1	1	0	0	1	0	1	0	0	80	14.01	10.48	2.21	14.00	176	12.10	7.19	1.84	9.60	0.63	14.80
Cowan	1	1	0	0	1	0	1	0	0	107	8.99	9.21	2.88	16.00	198	13.10	6.63	1.53	8.61	0.57	19.10
Tyree	1	0	1	0	1	0	1	0	0	64	12.78	12.35	3.54	16.00	198	13.10	6.63	1.53	8.61	0.57	19.10
Piha	1	0	1	0	1	0	1	0	0	182	9.87	6.91	3.67	18.00	73	12.80	7.21	1.67	9.25	0.67	16.20
Destruction Gully*	1	1	0	0	0	1	0	1	1	43	15.72	7.51	1.67	9.00	167	13.20	7.35	2.24	7.67	0.56	18.40
Kakamatua	0	0	0	1	1	0	0	1	0	314	12.55	6.45	2.54	13.00	16	15.30	7.91	1.79	9.11	0.58	19.00
Bald Spur	1	1	0	0	0	1	1	0	0	41	8.91	5.04	4.13	14.00	80	15.80	8.11	2.23	10.60	0.65	18.60
Lower Nihotupu	0	0	0	1	1	0	0	1	1	756	9.79	9.04	3.50	13.00	215	15.20	7.12	1.17	11.63	0.50	23.30
Lower Cascade	1	0	1	0	1	0	1	0	0	264	12.95	7.57	2.67	14.00	100	16.10	7.50	1.81	9.03	0.63	22.80
Upper Cascade	0	0	1	0	1	0	1	0	0	131	14.15	15.47	2.42	12.00	120	16.10	7.50	1.81	9.03	0.63	22.80
Anawhata	0	0	0	1	1	0	0	1	0	619	11.47	6.45	2.75	14.00	80	19.00	8.12	1.69	8.75	0.63	21.40
Upper Nihotupu	0	1	0	0	1	0	0	1	1	117	10.97	8.02	4.17	16.00	280	15.90	6.41	1.07	7.67	0.76	20.60
Upper Company	1	1	0	0	1	0	1	0	0	80	13.22	10.19	1.29	10.00	180	15.10	7.18	2.15	9.37	0.69	19.90
Lower Company	1	0	1	0	1	0	1	0	0	166	14.97	8.64	1.92	10.00	180	15.10	7.18	2.15	9.37	0.69	19.90
Stoney Creek	1	0	0	1	0	1	1	0	0	258	11.86	10.24	4.63	19.00	100	16.00	7.97	1.19	7.96	0.68	18.60
Marawhara	0	0	1	0	1	0	1	0	1	171	12.72	8.02	2.88	17.00	200	14.30	5.08	1.65	5.79	0.08	19.30
Opal Pool	0	0	1	0	1	0	1	0	1	202	14.13	10.12	2.38	17.00	80	16.50	7.29	3.23	8.04	0.66	17.20
Hidden Valley	1	1	0	0	1	0	1	0	0	35	14.71	8.64	2.25	16.00	215	15.00	4.93	3.11	4.92	0.67	18.60
Kuataika	0	1	0	0	1	0	1	0	0	122	16.30	7.45	2.75	12.00	45	16.50	7.50	3.36	6.57	0.63	20.10
Kare kare	1	0	1	0	1	0	1	0	0	69	10.68	6.57	3.46	14.00	200	14.10	6.37	1.45	7.30	0.73	16.20
Huia	0	0	0	1	0	1	1	0	0	980	12.79	8.85	1.83	14.00	100	16.60	7.77	1.32	7.66	0.55	22.50
Upper Baker	1	1	0	0	1	0	1	0	0	80	13.42	12.26	2.08	13.00	186	11.80	7.13	1.83	8.65	0.65	13.60

Lower Baker	1	1	0	0	1	0	1	0	0	80	14.01	10.48	2.21	14.00	176	11.80	7.13	1.83	8.65	0.65	13.60
Cowan	1	1	0	0	1	0	1	0	0	107	8.99	9.21	2.88	16.00	198	13.10	6.63	1.53	8.61	0.57	19.10
Tyree	1	0	1	0	1	0	1	0	0	64	12.78	12.35	3.54	16.00	198	13.10	6.63	1.53	8.61	0.57	19.10
Piha	1	0	1	0	1	0	1	0	0	182	9.87	6.91	3.67	18.00	73	12.80	7.14	1.69	9.32	0.61	17.80
Destruction Gully*	0	1	0	0	0	1	0	1	1	43	15.72	7.51	1.67	9.00	167	13.00	7.48	2.22	7.05	0.53	18.60
Kakamatua	1	0	0	1	1	0	0	1	0	3.14	12.55	6.45	2.54	13.00	0.16	15.30	7.91	1.79	9.11	0.58	19.00
Bald Spur	0	1	0	0	0	1	1	0	0	0.41	8.91	5.04	4.13	14.00	0.80	15.80	8.11	2.23	10.60	0.65	18.60
Lower Nihotupu	0	0	0	1	1	0	0	1	1	7.56	9.79	9.04	3.50	13.00	2.15	15.20	7.12	1.17	11.63	0.50	23.30
Lower Cascade	0	0	1	0	1	0	1	0	0	2.64	12.95	7.57	2.67	14.00	1.00	16.10	7.50	1.81	9.03	0.63	22.80
Upper Cascade	0	0	1	0	1	0	1	0	0	1.31	14.15	15.47	2.42	12.00	1.20	16.10	7.50	1.81	9.03	0.63	22.80
Anawhata	1	0	0	1	1	0	0	1	0	6.19	11.47	6.45	2.75	14.00	0.80	15.40	7.60	1.78	8.87	0.43	22.30
Upper Nihotupu	0	1	0	0	1	0	0	1	1	1.17	10.97	8.02	4.17	16.00	2.80	15.20	6.42	1.05	8.20	0.64	19.60
Upper Company	1	1	0	0	1	0	1	0	0	0.80	13.22	10.19	1.29	10.00	1.80	15.00	6.89	2.16	8.08	0.71	18.20
Lower Company	1	0	1	0	1	0	1	0	0	1.66	14.97	8.64	1.92	10.00	1.80	15.00	6.89	2.16	8.08	0.71	18.20
Stoney Creek	1	0	0	1	0	1	1	0	0	2.58	11.86	10.24	4.63	19.00	1.00	17.30	7.63	1.08	7.87	0.71	20.10
Marawhara	0	0	1	0	1	0	1	0	1	1.71	12.72	8.02	2.88	17.00	2.00	15.70	6.84	1.43	6.87	0.74	18.60
Opal Pool	0	0	1	0	1	0	1	0	1	2.02	14.13	10.12	2.38	17.00	0.80	18.50	7.52	3.13	8.16	0.68	20.60
Hidden Valley	1	1	0	0	1	0	1	0	0	0.35	14.71	8.64	2.25	16.00	2.15	15.20	5.06	3.18	5.04	0.67	18.40
Kuataika	0	1	0	0	1	0	1	0	0	1.22	16.30	7.45	2.75	12.00	0.45	16.30	7.84	3.28	7.29	0.57	20.30
Kare kare	1	0	1	0	1	0	1	0	0	0.69	10.68	6.57	3.46	14.00	2.00	15.00	6.40	1.48	5.52	0.72	16.70
Huia	0	0	0	1	0	1	1	0	0	9.80	12.79	8.85	1.83	14.00	1.00	16.60	7.77	1.32	7.66	0.55	22.50
Upper Baker	1	1	0	0	1	0	1	0	0	0.80	13.42	12.26	2.08	13.00	1.86	11.80	7.13	1.83	8.65	0.65	13.60
Lower Baker	1	1	0	0	1	0	1	0	0	0.80	14.01	10.48	2.21	14.00	1.76	11.80	7.13	1.83	8.65	0.65	13.60
Cowan	1	1	0	0	1	0	1	0	0	1.07	8.99	9.21	2.88	16.00	1.98	12.20	7.01	1.53	9.45	0.73	15.50
Tyree	1	0	1	0	1	0	1	0	0	0.64	12.78	12.35	3.54	16.00	1.98	12.20	7.01	1.53	9.45	0.73	15.50
Piha	1	0	1	0	1	0	1	0	0	1.82	9.87	6.91	3.67	18.00	0.73	12.80	7.14	1.69	9.32	0.61	17.80
Destruction Gully*	0	1	0	0	0	1	0	1	1	0.43	15.72	7.51	1.67	9.00	1.67	13.00	7.48	2.22	7.05	0.53	18.60

Kakamatua	1	0	0	1	1	0	0	1	0	3.14	12.55	6.45	2.54	13.00	0.16	17.70	7.86	1.81	11.49	0.68	22.90
Bald Spur	1	1	0	0	0	1	1	0	0	0.41	8.91	5.04	4.13	14.00	0.80	16.00	8.15	2.24	10.70	0.50	23.30
Lower Nihotupu	0	0	0	1	1	0	0	1	1	7.56	9.79	9.04	3.50	13.00	2.15	17.30	7.30	1.11	8.63	0.78	20.90
Lower Cascade	1	0	1	0	1	0	1	0	0	2.64	12.95	7.57	2.67	14.00	1.00	16.70	6.88	1.80	6.76	0.58	21.50
Upper Cascade	0	0	1	0	1	0	1	0	0	1.31	14.15	15.47	2.42	12.00	1.20	16.70	6.88	1.80	6.76	0.58	21.50
Anawhata	1	0	0	1	1	0	0	1	0	6.19	11.47	6.45	2.75	14.00	0.80	15.40	7.60	1.78	8.87	0.43	22.30
Upper Nihotupu	0	1	0	0	1	0	0	1	1	1.17	10.97	8.02	4.17	16.00	2.80	15.20	6.42	1.05	8.20	0.64	19.60
Upper Company	1	1	0	0	1	0	1	0	0	0.80	13.22	10.19	1.29	10.00	1.80	15.00	6.89	2.16	8.08	0.71	18.20
Lower Company	1	0	1	0	1	0	1	0	0	1.66	14.97	8.64	1.92	10.00	1.80	15.00	6.89	2.16	8.08	0.71	18.20
Stoney Creek	0	0	0	1	0	1	1	0	0	2.58	11.86	10.24	4.63	19.00	1.00	17.30	7.63	1.08	7.87	0.71	20.10
Marawhara	0	0	1	0	1	0	1	0	1	1.71	12.72	8.02	2.88	17.00	2.00	15.70	6.84	1.43	6.87	0.74	18.60
Opal Pool	0	0	1	0	1	0	1	0	1	2.02	14.13	10.12	2.38	17.00	0.80	18.50	7.52	3.13	8.16	0.68	20.60
Hidden Valley	1	1	0	0	1	0	1	0	0	0.35	14.71	8.64	2.25	16.00	2.15	15.20	5.06	3.18	5.04	0.67	18.40
Kuataika	0	1	0	0	1	0	1	0	0	1.22	16.30	7.45	2.75	12.00	0.45	16.30	7.84	3.28	7.29	0.57	20.30
Kare kare	1	0	1	0	1	0	1	0	0	0.69	10.68	6.57	3.46	14.00	2.00	15.00	6.40	1.48	5.52	0.72	16.70
Huia	0	0	0	1	0	1	1	0	0	9.80	12.79	8.85	1.83	14.00	1.00	16.60	7.77	1.32	7.66	0.55	22.50