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A comparison of approaches for estimating Hochstetter's frog (*Leiopelma hochstetteri*) abundance

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

**Master of Science
in
Conservation Biology**

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This thesis is dedicated to the memory of my grandad, Allen Johnson.
For always encouraging me to pursue my education, this is for you.



Adult *Leiopelma hochstetteri* in Te Paparahi, Aotea, New Zealand. Photo: C. Johnson.

Abstract

The Hochstetter's frog (*Leiopelma hochstetteri*) population of Aotea / Great Barrier Island is an evolutionarily distinct unit of a nationally 'At Risk – Declining' species. The Te Paparahi region of Aotea is this species' stronghold on Aotea. However, it is unknown whether the population is temporally stable. I used a range of hierarchical models on data collected from this population between 2012 and 2021 to assess both temporal and spatial patterns in abundance in this population.

Population data were collected from 15 100-m stream transects using a double-observer protocol in 2012 and 2015 and a triple-observer protocol in 2021. Frogs were not marked, but the 2021 survey tentatively identified individuals from their body size and position within a transect. The relative occurrence of waterfalls, selected plant species, and rat tracking within each transect was recorded to examine spatial correlation with frog abundance. I compared the efficacy of capture-mark-recapture (2021 only), N-mixture, occupancy models, and Poisson regression of single-count data for inferring patterns in abundance. Occupancy was modelled at the level of 10 m segments, and the occupancy probability in each transect used to derive abundance. All models were Bayesian formulations constructed in OpenBUGS.

Single-year capture-mark-recapture and N-mixture models, and multi-year N-mixture models, yielded sensible abundance estimates. The estimates of abundance generated by the single-year CMR model ranged from 0 – 118 frogs across the 15 transects, whereas estimates generated by the single-year N-mixture model ranged from 0 – 98 frogs. The estimates generated by the CMR and N-mixture models were strongly correlated, with N-mixture estimates 83% as large as CMR estimates. Abundance estimates derived from single- or multi-year occupancy models were neither sensible nor precise. The multi-year N-mixture model and Poisson regression of single counts suggested a ca. 5% decrease in Hochstetter's frog abundance between 2012 and 2021. However, the possibilities of a stable or increasing population were not discounted by the 95% credible intervals for the effect of time. The relative abundance of kanono (*Coprosma grandifolia*) was the only habitat variable positively correlated with variation in Hochstetter's frog abundance among transects.

Although highly uncertain, the estimated decrease in abundance is of concern, and continued monitoring of this population is recommended. Furthermore, this pattern reflects the gradual declines displayed by other long-lived New Zealand herpetofauna in mammal-invaded environments. Although no correlation between Hochstetter's frog abundance and rat tracking rates was identified, this result may be due to the small sample size of 45 tunnels which were only run on a single occasion. Therefore, it is recommended that the rat tracking surveys be repeated and expanded to include environments other than stream-gully margins.

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Table of Contents

1.1	Background	1
1.2	Overview of population survey and monitoring techniques and analytical frameworks used in the conservation of <i>Leiopelma</i> and related genera.....	4
1.3	Study system	10
1.3.1	Study species: Hochstetter's frog.....	10
1.3.2	Study site.....	11
1.4	Research objective and thesis outline	12
1.4.1	Research objectives.....	12
1.4.2	Chapter outline	13
1.4.3	Permits and ethics	14
2.1	Introduction.....	15
2.2	Methods	19
2.2.1	Study site.....	19
2.2.2	Transect establishment and previous double-observer frog surveys (2012-2015)....	20
2.2.3	Triple-observer frog survey (2021).....	22
2.3	Results.....	32
2.4	Discussion	48
2.4.1	Performance of single-year models	49
2.4.2	Performance of unconstrained multi-year models.....	50
2.4.3	Performance of time-trend multi-year models	51
2.4.4	Population trend between 2012 and 2021	51
Chapter 3: An investigation of the drivers of abundance in Hochstetter's frog populations in northern Aotea		54
3.1	Introduction.....	54
3.2	Methods	55
3.2.1	Collection of habitat data	56
3.2.2	Rodent-tracking field methods.....	56
3.2.3	Statistical analysis.....	60
3.3	Results.....	62
3.4	Discussion 67	
4.1	General Discussion.....	72
4.2	Limitations and future research directions.....	73
4.2.1	Rodent tracking research.....	73

4.2.2 Hochstetter's frog population research and model design.....	73
4.3 Conclusions and Implications for the future.....	75
<u>References</u>	77
<u>Appendix</u>	86
1a: OpenBUGS script for the single-year capture-mark-recapture model.....	86
1b: OpenBUGS script for the single-year N-mixture model.....	87
1c: OpenBUGS script for the single-year Site occupancy model.....	88
2a: OpenBUGS script for the multi-year unconstrained N-mixture model.....	89
2b: OpenBUGS script for the time-trend N-mixture model.....	90
2c: OpenBUGS script for the multi-year unconstrained site occupancy model.....	91
2d: OpenBUGS script for the multi-year time-trend site occupancy model.....	92
2e: OpenBUGS script for the multi-year single-count index model.....	93
3a: Example field habitat characteristics record sheet for habitat variables taken every 20-m along the transect.....	94
3b: OpenBUGS script for the multi-year time-trend N-mixture model with habitat covariates.....	95

Chapter 1 – General Introduction

1.1 Background

Amphibians are a class of animals suffering rapid population declines worldwide due to several threats, many of which are not well understood (Grant et al., 2019; Green et al., 2020). Habitat degradation, invasive species, and other undefined processes are leading agents of decline for amphibians, and the combined extent to which these factors are influencing population declines can be difficult to determine (Falaschi et al., 2020; Stuart et al., 2004). Population declines since the 1980s have been so severe that it is now estimated that 41% of amphibian species worldwide are either extinct or at high risk of extinction (Bishop et al., 2012; Romero-Zambrano et al., 2021). Rising global temperatures and climatic changes have been linked to direct and indirect consequences for many populations, likely exacerbating amphibian diversity loss (Carey & Alexander, 2003).

The unprecedented species declines are being met with increased conservation efforts to investigate threats and improve the monitoring of vulnerable species. Monitoring is extremely important in conservation as it allows scientists to document fluctuations in population abundance and estimate if these are changing over time (Goldsmith, 2012; Rohr et al., 2018). Collecting abundance and distribution data is essential for assessing whether human intervention is needed (e.g., predator control). With finite conservation resources, these assessments are necessary tools for environmental planning and funding allocation (Nichols and Williams, 2006; Possingham, 2012).

The anuran family Leiopelmatidae comprises five extant species as of 2022, three of which are native to New Zealand (*Leiopelma*) and two to North America (*Ascaphus*). In New Zealand, the three extant native frog species are the Archey's frog (*Leiopelma archeyi*), Hamilton's frog (*Leiopelma hamiltoni*), and Hochstetter's frog (*Leiopelma hochstetteri*). A fourth species of *Leiopelma* was formerly recognised, the Maud Island frog (*Leiopelma pakeka*). In recent years this species has been reclassified as *Leiopelma hamiltoni* due to the similar morphologies and geographically distributions of the two formerly recognised species (Bell et al., 1998; Easton

et al., 2018). Fossil evidence indicates that three additional species of *Leiopelma* previously existed in New Zealand (Worthy, 1987). Since the discovery and classification of New Zealand endemic frog species in the mid-19th century by Fitzinger, there has been a desire in the scientific community to understand the distributions and frequencies of *Leiopelma* populations (Stephenson and Stephenson, 1957). The ranges of each extant *Leiopelma* species as of 2013 have been mapped (Fig. 1.1).

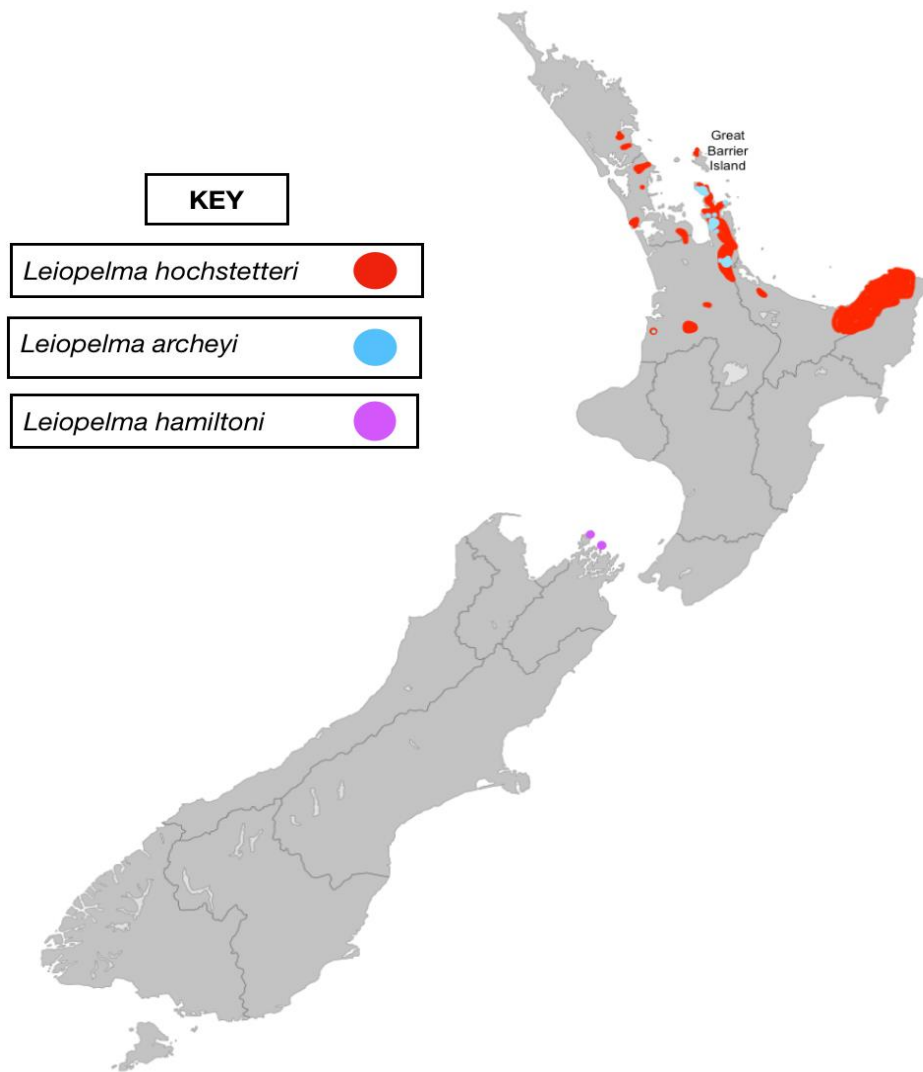


Figure 1.1: *Leiopelma* species distribution ranges throughout New Zealand (including both natural and translocated populations). Map outline provided by Wikimedia Commons (https://commons.wikimedia.org/wiki/File:New_Zealand_location_map_transparent.svg). Figure information derived from the Native frog (*Leiopelma* spp.) recovery plan, 2013–2018 (Bishop et al., 2013). <https://www.doc.govt.nz/documents/science-and-technical/tsrp63entire.pdf>

Throughout the 19th and early 20th centuries, the majority of literature on *Leiopelma* focused on classification and documenting the distributions of the extant species (Bell, 1978). It wasn't until the 1980s that amphibian abundance estimates began to be seriously considered, and a study in 1987 discussed the possible consequences that mammalian predators might have for New Zealand frogs (Worthy, 1987). Of the extant *Leiopelma* species, numbers are believed to have been declining since the 1980s, and all endemic amphibian species in New Zealand are currently classified under the New Zealand Threat Classification System (NZTCS) as either at risk and declining, threatened or extinct (Burns et al., 2018). New Zealand's native frog species are managed in accordance with goals outlined in the 2013 – 2017 Native frog recovery plan (Bishop et al., 2013). The recovery plan outlines monitoring, translocation and habitat restoration as some of the major aspects needed for sustainable management of native frogs.

Two of the three endemic frog species are terrestrial. Only the Hochstetter's frog is semi-aquatic, creating challenges for robust and efficient long-term monitoring of the species (Bishop et al., 2013). The survey techniques and statistical methodology used in the conservation of terrestrial amphibians often vary from the methods used for semi- and fully-aquatic amphibians, although there is often overlap.

There are also disparities in the monitoring efforts for each *Leiopelma* species. For Hamilton's frog, all insular populations are now legally protected through reserves and sanctuaries that are free of mammalian pests and have restricted public access (B. Bell & Bishop, 2018). Long-term monitoring is also conducted regularly for populations of the Archey's frog in the Waikato and Coromandel region of New Zealand (Thorsen, 1999; Bell et al., 2004; Haigh & Pledger, 2007). Monitoring of the mainland Hochstetter's populations has been more sporadic, with no consistent long-term monitoring protocols recognised for the species, although Hochstetter's indices continue to be collected as secondary information in the long-term monitoring of some *L. archeyi* populations in the Coromandel region (per comms. B. Bell). Research into translocation options for *L. hochstetteri* has been considered to reduce population decline, but in 2022, there are no imminent plans for Hochstetter's frog translocations (Herbert et al., 2014; Easton, 2015; Bell & Bishop, 2018).

Because of the cryptic nature of *Leiopelma* species, even in regularly surveyed frog populations, it is unlikely we understand the true abundance of each *Leiopelma* species, and it can be speculated that threat classifications may not necessarily be complete. Consistent and long-term monitoring is needed to understand the extent of the decline in Hochstetter's frog populations.

1.2 Overview of population survey and monitoring techniques and analytical frameworks used in the conservation of *Leiopelma* and related genera

Despite being the most widely dispersed and the least threatened of the four species, a current lack of abundance data for the Aotea Hochstetter's population can make detecting and reacting to abundance fluctuation trends difficult. This chapter will outline some of the monitoring techniques used in conservation monitoring of terrestrial *Leiopelma spp.* and their practicality for monitoring the Hochstetter's frog before discussing the statistical protocols that will be compared in this thesis. A discussion on spatial sampling, modelling and detection methods used in terrestrial *Leiopelma* and the related *Ascaphus* will provide context for comparing four data protocols considered promising options for future Hochstetter's monitoring.

1.2.1 Artificial Cover Objects for Frogs

Artificial cover objects (ACOs) are a monitoring technique implemented in 2003 for the monitoring of Archey's and Hochstetter's frog (Wakelin et al., 2013). ACOs are installed within the natural ranges of frog species, and data are collected on the number of frogs of each species found inside each ACO at the time of sampling. The monitoring technique is time and labour-efficient and has low material costs. The ACOs in this study were composed of plastic, fabric, light and dark trays and smooth plastics such as lunch boxes. Wakelin et al. (2013) study found the most significant issue with this monitoring technique was low occupancy rates, with an estimated occupancy uptake of only 0-20% of the frogs expected to be in the surveyed area. This monitoring technique may also not be feasible for Hochstetter's frogs as ACOs can be damaged or lost in flood-prone areas.

1.2.2 Environmental DNA Detection

The use of Environmental DNA (eDNA) detection is increasingly used in international amphibian conservation. It is being implemented in some New Zealand cryptic species for its effectiveness in detecting species that may have low abundances. This monitoring technique is an alternative to manual searching. It implements a qPCR tool and TaqMan primers from the target species to identify species in collected water samples from survey sites. This makes it helpful in researching species distributions and estimating occupancy. In 2021, research into the use of eDNA in all aspects of conservation was considered a research priority for scholarships distributed by The New Zealand Department of Conservation (DOC, 2021).

A 2019 study on the North American coastal tailed frog (*Ascaphus truei*) introduced an efficient method of monitoring that may provide promise for implementation in New Zealand's *Leiopelma* species (Hobbs et al., 2019). The life history of the coastal tailed frog is similar to that of the Hochstetter's frog, with this species also belonging to the family Leiopelmatidae (Figure 1.2). The study uses a quantitative qPCR tool and TaqMan qPCR primers developed using mitochondrial gene sequences derived from coastal tailed frog specimens and the DNA of any other species that may act as confounders of the detection tool. This technology may be useful for detection and distribution studies of cryptic species such as the Hochstetter's frog, but at this stage, it is not viable for abundance quantification of individual frogs (Beng & Corlett, 2020).

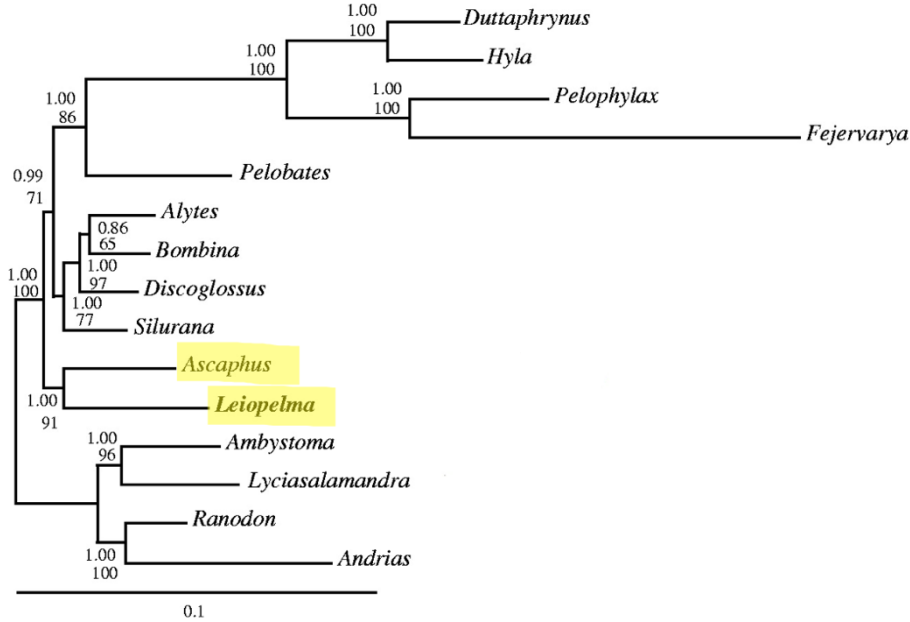


Figure 1.2: Anuran phylogeny (maximum likelihood phylogram) derived from mitochondrial genetic sequences. *Ascaphus* and *Leiopelma* genera have been highlighted to demonstrate phylogenetic relatedness. Adapted from (Irisarri et al. 2010).

While this methodology is promising for monitoring *Leiopelma* in New Zealand, limitations may arise when implementing this technique in Hochstetter's frog studies. Smith (2017) noted that eDNA might have seasonal limitations in detectability, as pH, water turbidity and temperature may influence the concentration of eDNA collected. Possibly the most significant limitation of the use of this technique in the monitoring of species such as the Hochstetter's frog is ensuring a reasonable amount of samples are taken in the field to be taken to a laboratory environment. This is an issue as currently, there is an inability to process DNA samples in remote areas. There are ongoing studies to improve the accessibility of eDNA filtration devices and qPCR tools in the field (Thomas et al., 2019). Still, at this stage, further research is needed to consider the method's viability for monitoring Hochstetter's frog populations.

1.2.3 Manual search surveying

Manual search surveying is a traditional monitoring technique widely used in terrestrial and semi-aquatic *Leiopelma* monitoring (Herbert et al., 2014; Bell et al., 2004; Bell and Bell, 1994). Search surveying is a viable long-term monitoring solution for *Leiopelma* as it is simple and easily

standardised, with many methodology options that can be adapted for specific study regions and populations (Thorsen, 1998). The monitoring technique employs one or multiple surveyors to manually search for individuals of the target species along a line of pre-determined length or a survey plot. The abundance, frequency and location of individuals are recorded. Limitations of this method are centred mostly around potential observer bias and low or variable detection probabilities. Observation biases can potentially be accounted for by using multiple surveyors in the same area, and detection probabilities can potentially be estimated through replicate samples (Herbert et al., 2013). However, these issues cannot be resolved without careful sampling designs and replicating surveys.

1.2.4 Population indices

Studies that conduct one survey or sample to generate population indices are referred to as single-survey searches and are common in ecological research where budget, time or labour resources may be limited (Johnson, 2002). Single-survey methods or surveys of population indices are often critiqued for lack of statistical robustness, with many researchers believing survey replicates to be an essential component in research design (Johnson, 2002). Single-survey counts are always biased if treated as censuses (i.e., the number present). When monitoring visually cryptic species such as the Hochstetter's frog, there is an increased likelihood of not detecting individuals truly present (Miller et al., 2012). Miller et al. (2012) discuss the use of model-based approaches for countering false positives and false negatives. Because of the frequent use of this technique and its ease of applicability in amphibian conservation, I will calculate and evaluate single counts in this thesis to consider the technique's practicality for monitoring a cryptic species.

1.2.5 Capture-mark-recapture

A commonly implemented monitoring technique in the ecological monitoring of threatened species, including *Leiopelma* spp., is capture-mark-recapture (Lettink and Armstrong, 2003). Individuals of a species are located by manually searching an area and captured by surveyors. The surveyors will 'mark' the individual with a pre-determined method before releasing it. At a later sampling time, marked individuals can be recorded as recaptures to avoid mistakenly counting them as additional individuals. In the 1990s, capture-mark-recapture (CMR) became an established practice for use in *Leiopelma* studies and was recommended for its efficiency in Department of

Conservation (DOC) monitoring protocols (Newman 1996). Many variations of CMR methodology have been used in *Leiopelma* monitoring, although in the 21st century, non-invasive methods are favoured to reduce stressing the individuals. In 1998, a Department of Conservation study on the use of capture-mark-recapture (CMR) monitoring in Hamilton's frog took place within the frog pit population on Stephen's Island (Pledger, 1998). The study design used toe-clipping as the method of marking individual frogs, and at the time, this was deemed to be an effective way to differentiate between individuals for repeated surveys. It is currently unclear whether toe-clipping is an appropriate marking methodology due to its invasive nature and the possible adverse effects it can have on frog survival (Clarke, 1972) and recapture rates (Whitaker & Alspach, 1999). The detrimental effects of toe clipping could include reducing locomotive activity and increasing stress hormone levels which in turn can lead to increased morbidity rates (Schmidt and Schwarzkopf, 2010; Narayan et al., 2011).

Modern studies of *Leiopelma* that use capture-mark-recapture methodologies often use a photographic record of individuals. A 2004 DOC study demonstrated the effectiveness of photographic identification CMR in Archey's frog (*Leiopelma archeyi*) (Bradfield, 2004). The study aimed to implement a monitoring program for Archey's frogs that would be sensitive enough for researchers to detect even small changes to population densities. Due to distinctive markings found on individual frogs, a photographic record enables researchers to assess whether individuals have previously been counted or not. This is particularly useful when conducting repeat surveys over several days and also in long-term monitoring schemes. However, markings can change over time, e.g., the colouration of some lizard species changes in different life stages, temperatures, or surrounding habitats (de Velasco & Tattersall, 2008). Studies recording individuals through their natural colouration have also been conducted on Hamilton's frog, where markings along the upper lip were noted to differentiate individuals (Newman, 1982). This method is not feasible in species that do not have distinguishable markings, such as the Hochstetter's frog.

Another capture-mark-recapture technique that has been used effectively in terrestrial *Leiopelma* monitoring is non-toxic paint or powder application. This is demonstrated in a paper that focussed on short-term tracking of a population of Hamilton's frogs, which were previously classified as Maud Island frogs (Ramírez et al. 2017). A non-toxic fluorescent powder is applied to the ventral

surface and feet of the captured frog before releasing the individual. The study found that rainy nights did cause the powder to fade faster than in dry conditions, indicating this method may only be viable for short-term monitoring of terrestrial amphibians and would not be suitable for the semi-aquatic Hochstetter's frog. The use of powder is likely unsuitable for aquatic species such as the Hochstetter's frog. Beausoleil et al. (2004) discuss the methods of marking amphibians and the possible outcomes of marking. The use of non-invasive marking techniques for amphibian monitoring is still being investigated, and more research is needed before recommendations can be made for regular practice

1.2.6 Site-occupancy models

One of the earliest monitoring methodologies in New Zealand's native frog monitoring, occupancy modelling remains a keystone in monitoring Hochstetter's frogs due to the robustness of its detection probabilities and the lack of need for individual identification. The Native Frog Recovery Plan (Bishop et al., 2013) highlighted the lack of statistically robust monitoring techniques currently available for the Hochstetter's frog and outlined site-occupancy models as one of the methods they believed provided biologically sensible data. To this effect, the calculations for detection probability used in site occupancy models are often recommended in other forms of monitoring techniques due to their robustness (Hobbs et al., 2019; Pellet and Schmidt, 2005). This technique does not estimate frog abundance but rather what proportion of sites in each area shows evidence of occupying the target species.

A possible drawback of this technique in long-term monitoring is that the method does not provide estimates of abundance. Occupancy models do not make use of individual data that may underpin heterogeneity in detection probabilities and cannot offer detection-weighted information on demography (in the way that CMR models can), which can be limiting for understanding population dynamics (Chaloupka & Musick, 2017). Additionally, it is important to consider the biases that can arise using this method. Absence data collected from a segment or transect does not always indicate a species' absence in that particular space; instead, it can only state that the species was not detected. This bias can be countered by accounting for non-detections rather than absence/presence data solely. As with single-count surveys, if single occupancy surveys are conducted without the knowledge of detection probabilities, the findings may be misleading.

1.2.7 N-mixture modelling

An alternative to traditional sampling techniques that will be discussed in this comparison is N-mixture modelling. Developed by Royle (2004), N-mixture allows researchers to estimate population sizes from repeated counts over either space or time, making the model applicable for long-term monitoring programs. Unlike capture-mark-recapture, N-mixture modelling can be performed without the need for individual identification. The modelling technique has previously been implemented to estimate the abundance of Hochstetter's frogs in the Waitakere ranges (Puig, 2009). N-mixture models are expected to perform better with larger sample sizes and numbers of sample sites (McCaffery et al., 2016).

1.3 Study system

1.3.1 Study species: Hochstetter's frog

The Hochstetter's frog is a cryptic, semi-aquatic species found near and in freshwater river streambeds and catchments. The species has the most extensive distribution range of New Zealand's three extant native frog species (Figure 1.3), with populations clustered around the top of the North Island in isolated and typically mature native forest regions (Bell et al., 2004; Longson et al., 2017). Only one known population is located off the mainland of the North Island on Aotea/ Great Barrier Island. The population is considered one of 13 evolutionarily significant units (ESUs) of Hochstetter's frog and is genetically distinct from mainland populations due to allopatric speciation (Fouquet et al., 2010). As of 2017, the Hochstetter's frog was classified as 'At Risk – Declining' under the NZTCS, though without a regular monitoring scheme, it is challenging to gauge population increases or declines.

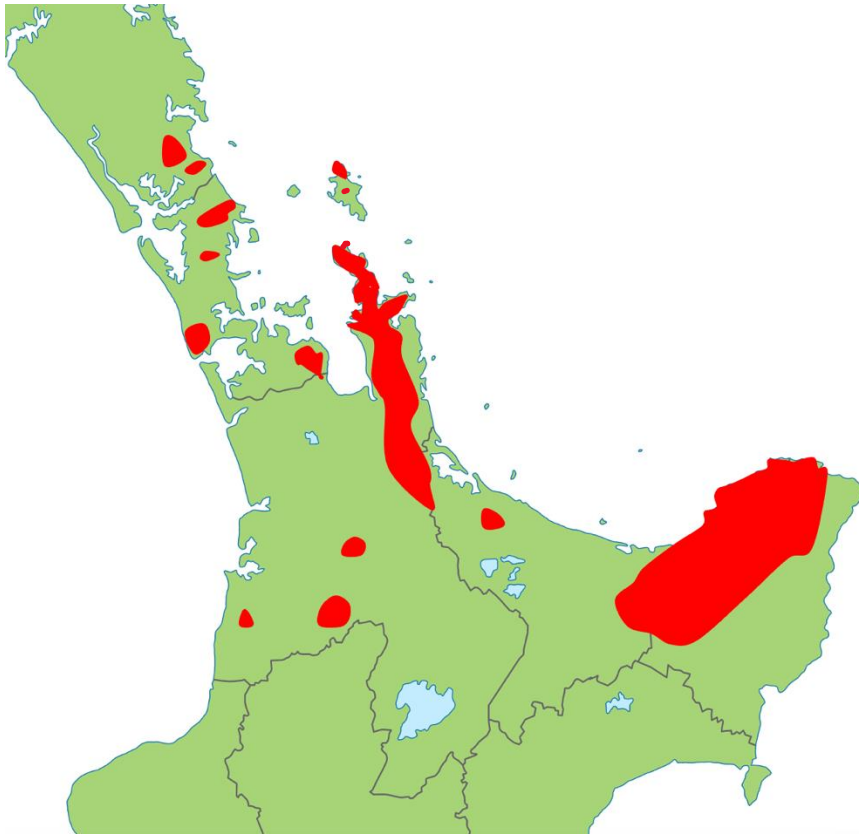


Figure 1.3: Approximate *Leiopelma hochstetteri* distribution as of 2013. Figure information derived from the Native frog (*Leiopelma spp.*) recovery plan, 2013–2017 Map outline provided by Wikimedia Commons.

(https://commons.wikimedia.org/wiki/File:New_Zealand_location_map_transparent.svg).

1.3.2 Study site

The Hochstetter's frog monitoring surveys were conducted on Aotea/Great Barrier Island in the northern Te Paparahi Region. The 15 transect locations were selected in 2012 by Herbert et al. (2015) in their initial surveys to gather information on the abundance of Hochstetter's on Aotea. These survey locations encompass five river catchments (A, B, C, D and E), and the 15 transects are named corresponding to the catchment they feed into (Figure 1.4). Specific transect locations on the catchments were selected opportunistically rather than randomly due to the region's rugged and densely forested terrain and time and budgetary constraints. Further details of study site selection are included in Herbert et al. (2014).

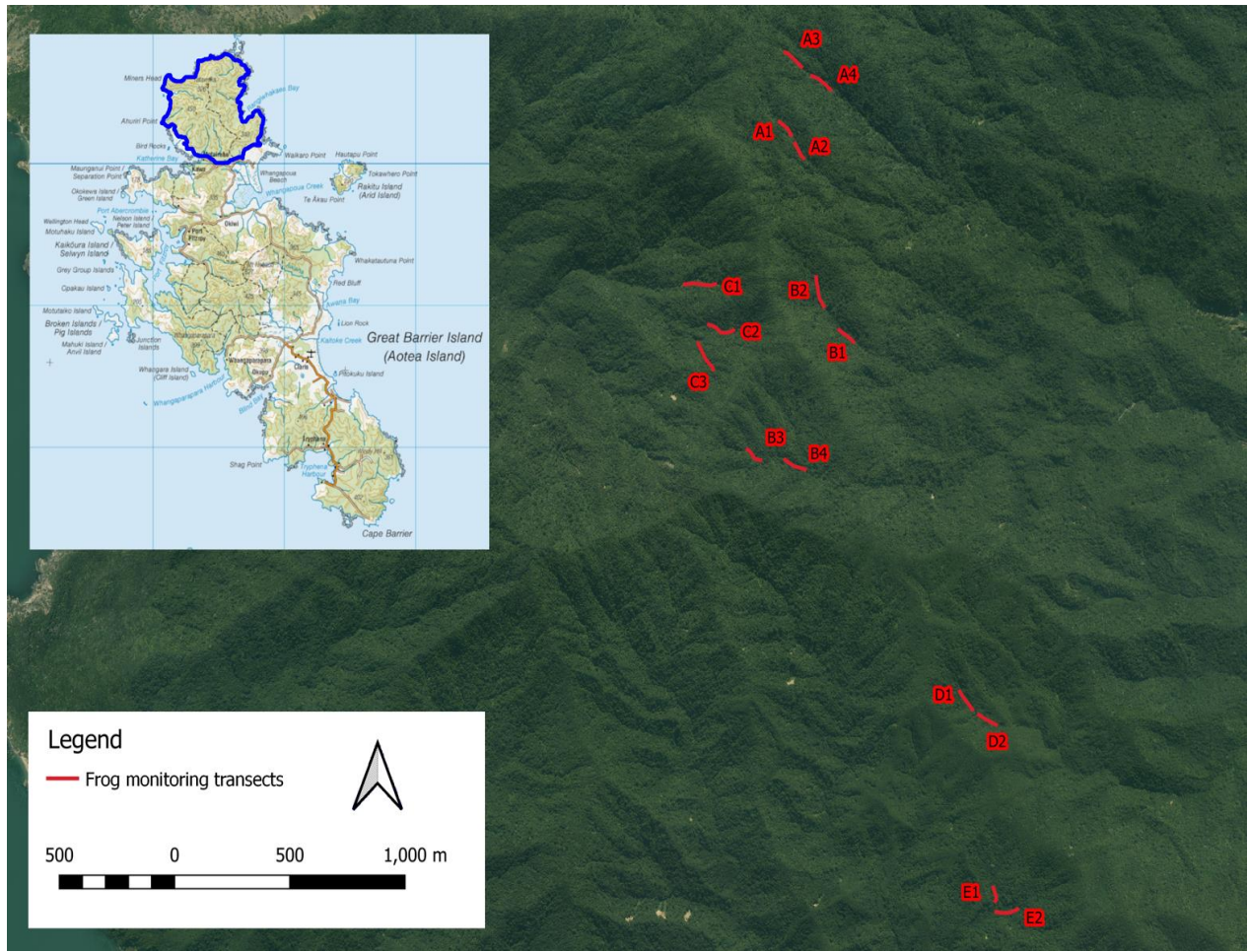


Figure 1.4: Topographical map of the 15 Hochstetter's frog survey transect locations in Te Paparahi, Aotea/Great Barrier Island and their proximity. The red lines represent the approximate locations of transects used in Hochstetter's frog monitoring, and the blue line on the map of Aotea shows the location of the Te Paparahi region where frog surveying took place.

1.4 Research objective and thesis outline

1.4.1 Research objectives

The literature surrounding population monitoring of amphibians is vast, but in the case of the Hochstetter's frog, there is still a lack of definitive long-term monitoring techniques (Burns et al., 2018). This study will investigate four data protocols that have been used in the monitoring of the Hochstetter's frog to further the pursuit of implementing a 'best practice' monitoring analysis that may be beneficial for an industry standard of Hochstetter's frog monitoring. I compare capture-mark recapture, site occupancy, N-mixture, and a single-count index. Because of limitations previously encountered with frequentist formulations of these models applied to the Aotea data

(Herbert et al. 2014; Herbert & Gilbert 2015), I used a Bayesian formulation of these models throughout this thesis. The issues that arose in the 2012 and 2015 studies were likely due to limiting the number of replicates to two per transect to ensure minimal habitat disturbance due to manual searching (per comms. S. Herbert). Bayesian inferencing may provide more robust estimates of population abundance than frequentist modelling, as even with small sample size and limited prior informative, qualitative information from past studies and comparisons is usually readily available and can be utilised when deciding on distributions for the data (Western & Jackman, 1994). Generally, Bayesian modelling is more flexible about the distributions data are considered to be sampled from than frequentist modelling.

The primary aims of this thesis are to:

- 1.) Generate and evaluate estimates of abundance and a single-count index of abundance from single-year and multi-year datasets.
- 2.) Determine the long-term (9-year) trend in abundance and/or occupancy of Hochstetter's frogs within the sampled area of Te Paparahi.
- 3.) Examine the effects of spatial heterogeneity in habitat covariates, including rodent tracking rate, on Hochstetter's frog abundance.

1.4.2 Chapter outline

In **Chapter 1**, I introduce the thesis material and review the existing literature on monitoring protocols used in the monitoring of New Zealand amphibians.

In **Chapter 2**, I compare capture-mark-recapture, N-mixture and site occupancy protocols to discuss the inferences obtained from each in reference to the Aotea data from the 2012, 2015 and 2021 surveys.

In **Chapter 3**, I analyse new data on rodent tracking rates at each transect to evaluate possible drivers of differences in abundance among transects.

In **Chapter 4**, I discuss the general conclusions and the implications of the results for future research.

1.4.3 Permits and ethics

The 2021 research was conducted under a Department of Conservation permit for 'Wildlife Act Authority for wildlife located on public conservation land'. Authorisation Number: 82606-RES 9. This permit was issued to Windy Hill Rosalie Bay Catchment Trust on April 7th 2021.

Chapter 2 – A comparison of single-year and multi-year models in the estimation of Hochstetter's frog abundance in Aotea

2.1 Introduction

Informed decision-making is needed for effective species management and requires anticipating outcomes concerning specific objectives. Predicting those outcomes, in turn, requires confidence in analytical models used and regular estimates of the system's state through monitoring (Nichols & Williams, 2006). Unfortunately, many survey techniques are not viable for cryptic species, as standard visual count techniques are less effective in species that use camouflage as an anti-predator defence (Arbuckle & Speed, 2015). Auditory surveying is also limited to monitoring vocal species and is not a viable option for New Zealand's frog genus, *Leiopelma*. The term 'cryptic species' can be misleading in ecology. Many definitions exist, such as its reference to species with indistinguishable morphologies whose evolutionary history is distinctly different (Struck et al., 2018). This thesis will use the term 'cryptic' to refer only to a visually cryptic species, both morphologically (camouflaged/indistinct body markings, small size) and behavioural (non-vocalising, hiding under refugia).

Monitoring methods that are non-invasive, cost-efficient, labour-efficient and statistically robust for cryptic species exist. However, the range of techniques available for visually cryptic amphibians is limited (Lambert & McDonald, 2014). Since the 1970s, amphibian population declines have been a growing concern globally, and approximately one-third of the recognised amphibian species globally are threatened with extinction (IUCN, 2022). Various monitoring techniques and statistical methods have been implemented to understand this issue better, with several becoming well-established practices in amphibian population management. Many of the frog species discussed in international monitoring literature vary from New Zealand frogs in that *Leiopelma* do not vocalise to communicate with other frogs and have only been observed to make chirping sounds when distressed or potentially as a tactile response (B. D. Bell, 1978). The effectivity of a monitoring technique varies between New Zealand's frog species, as each has distinct morphologies, distribution ranges and genetic makeup. Identifying individual *Leiopelma*

hochstetteri frogs (Figure 2.1) is challenging and can render the photographic identification technique often used in *Leiopelma archeyi* monitoring ineffective (Bradfield, n.d.). Manual marking methods are often invasive and pose ethical issues for the Hochstetter's frog, e.g. toe clipping and PIT tags (Ramírez et al., 2017). It is also possible that stream-dwelling species may also be more susceptible to habitat degradation if surveying is repeated too frequently. Future monitoring frameworks should consider this when deciding how frequently surveying is needed.



Figure 2.1: An adult *L. hochstetteri* blending into surrounding refugia. Photo by: C. Johnson.

Many different monitoring protocols are used in semi-aquatic amphibian monitoring. However, there is still a need for a comparison of methods recommended for the Hochstetter's frog, as the only comparisons to date are those provided by Puig (2009) using data from the Waitakere Ranges in one field season. Count indices, distance sampling, capture-mark-recapture (CMR), site occupancy, and, more recently, N-mixture and eDNA sampling have become techniques used in Hochstetter's frog abundance monitoring. CMR involves replicating sampling sessions to estimate

abundance by explicitly accounting for detection probability (Lukacs, 2009). This means that abundance can be estimated from a CMR protocol, making it more meaningful and, therefore, more widely accepted than reliance on indices of relative abundance (Crossland & MacKenzie, 2005). In addition, estimation of detection probability makes it possible to consider spatial or temporal variation in detection probability. Because detection is rarely constant or perfect, failure to account for this variation can introduce bias if observation error, environmental conditions and other confounding factors are not considered (Kellner & Swihart, 2014).

When discussing capture-mark-recapture analyses, it should be noted that the methodology in my research did not involve marking or handling the frogs. Past literature has found marking semi-aquatic amphibians like the Hochstetter's frog through translucent powder to be relatively ineffective, and both toe clipping and radio-tracking may be detrimental to the locomotive function of the individual (Ramírez et al., 2017; Schmidt & Schwarzkopf, 2010). The terminology throughout this chapter will classify individuals found on the first survey as 'captures', and individuals found on surveys 2 and 3 who meet the recapture criteria from Puig (2009) will be referred to as 'recaptures' henceforth.

Exploring more effective post-survey data analyses could be the way forward to improve statistical power and robustness in Hochstetter's monitoring. The use of Bayesian inference is growing in conservation for its flexibility in dealing with incomplete survey information and other data limitations (Wilson et al., 2008; Williams et al., 2002). All models compared in this analysis will be generated using the Bayesian updating software, OpenBUGS (Spiegelhalter et al., 1996). OpenBUGS is freely available software that enables researchers to build models that can be adapted to any dataset(s), and the code can be used with slight modification in related software such as JAGS (Plummer, 2003), MultiBUGS (Goudie et al., 2020) and NIMBLE (de Valpine et al., 2017).

Site occupancy modelling is often recommended as a monitoring metric for cryptic species due to a reduced sampling effort compared to that required for abundance estimation (Royle, 2006; Crossland & MacKenzie, 2005). It is also a less invasive technique for monitoring a target species. Occupancy monitoring can be conducted without the need for handling/markings individuals or

even at a distance without sighting individuals, for example, through eDNA or auditory detection in vocalising species (Lele et al., 2012). This thesis will also explore occupancy models with abundance derived to assess the capacity to give reliable estimates of abundance and their power for detecting population abundance trends over time. A multi-year site occupancy model estimates the proportion of sites in a given area (in this thesis, segments of a transect) occupied by a target species to estimate distribution, colonisation and extinction possibilities (MacKenzie et al., 2002; MacKenzie et al., 2003). Single-season occupancy models assume that the system is closed for the survey replicates and that there is independence between these replicates (Rota et al., 2009). N-mixture modelling is another promising approach for monitoring cryptic amphibians (Royle, 2004). It uses repeated counts from sites to make abundance estimates that account for detection probability without needing to mark individuals (Ficetola et al., 2018) or alternatively treats adjacent sites as replicates on the assumption that they have the same density (Royle, 2004). N-mixture is less labour-intensive than capture-mark-recapture and distance sampling techniques, as N-mixture does not require the identification of individuals or measurement of distances. Detection probabilities are estimated solely from the marginal likelihood of obtaining the observed numbers of captures (Royle, 2004). Whereas site occupancy models estimate the probability of detecting a species within a given area, CMR and N-mixture models estimate the probability of detecting an individual entirely.

This thesis aims to build on previous comparisons of monitoring techniques by Puig (2009). Whereas Puig's (2009) research implemented a frequentist modelling approach that required different frameworks for each protocol, my research will adopt a Bayesian approach with greater flexibility that allows models for the various protocols to be constructed in a unified framework. In addition, my study involved estimating Hochsetter's frog abundance across a nine-year survey period in 15 100-m transects on Aotea. In contrast, Puig's (2009) research involved estimating abundance in 50 40-m transects over one season, necessitating differences in the models used.

This chapter aims to: (1) compare the four data protocols, CMR, N-mixture, site occupancy and a single-count index, in terms of abundance estimates obtained for single-year and multi-year datasets. (2) Determine the long-term (nine-year) trend in abundance and/or occupancy of Hochstetter's frogs within the sampled area of Te Paparahi (3) Draw conclusions about the

population status of the Aotea Hochstetter's frog population over a nine-year survey period. The abundance estimates of each model can only be compared to one another, and a discussion around the model's sensitivity is given.

2.2 Methods

2.2.1 Study site

The Hochstetter's frog surveys on Aotea took place in the Te Paparahi region, in the Northern section of the island (Figure 2.2, Map B). Surveys took place in five river catchments accessibly by foot off the Burrill Route track (Figure 2.2, Map C). Each transect was measured with a transect line and followed the stream's natural course for 100 m. The exception was Transect C3, which could only be surveyed for 80 m in 2021 due to a landslip in 2015 that partially covered the stream. The Te Paparahi region is densely forested, with large areas of coastal broadleaf forests near the eastern slopes and Kānuka (*Kunzea ericoides*) forest in patches of secondary regrowth after fires (Perry et al., 2010; Aotea Great Barrier Environmental Trust, 2018). Aotea is free of mustelids, possums (*Trichosurus vulpencula*), Norway rats (*Rattus norvegicus*), goats (*Capra hircus*) and deer (*Dama spp. and Cervus spp.*). The most problematic pest animals in the Te Paparahi region of Aotea are ship rats (*Rattus rattus*), kiore (*Rattus exulans*), mice (*Mus musculus*), feral pigs (*Sus scrofa*), and feral cats (*Felis catus*) (Great Barrier Local Board, 2017).

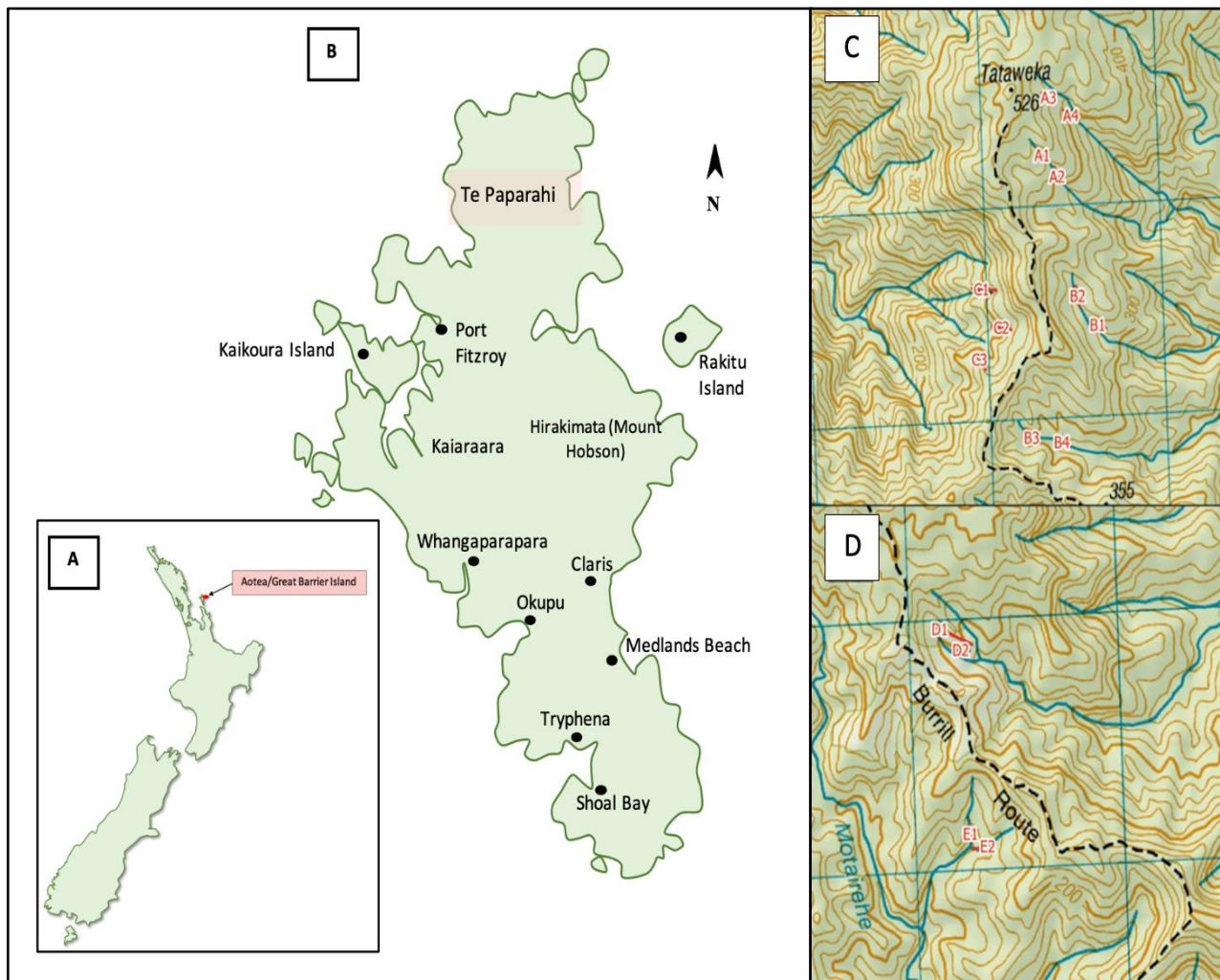


Figure 2.2: A: Location of Aotea/Great Barrier Island off the east coast of New Zealand's North Island. B: Map of Aotea, showing the Te Paparahi region in the northern part of the island (highlighted in red). C: Locations of Transects A1, A2, A3, A4, B1, B2, B3, B4, C1, C2, C3 within the Hochstetter's frog surveying area at Te Paparahi. D: Locations of Transects D1, D2, E1, D2. Map C and D are provided by Wildland Consultants Ltd.

2.2.2 Transect establishment and previous double-observer frog surveys (2012-2015)

The first survey of the Aotea Hochstetter's frog population was conducted in 2012 (Herbert et al., 2014). Fifteen 100 m transects were established and surveyed two times each over a 10-day period, with the exception of transect A1, which was used as a training transect in 2012 and excluded from data analysis. The 15 transects were within the headwaters of five catchments and at various altitudes. The transects in catchments A, B, and C were at higher altitudes (277-477 m above sea level) than those in catchments D and E (136 to 228 m above sea level). The transect locations

were not selected randomly outside of these general factors, and rather they were based on accessibility to maximise the number of sites in the rugged and densely forested terrain that could be surveyed within the 10 days. The locations were marked with flagging tape, and the GPS coordinates were recorded to become 'fixed sites' for subsequent years of sampling. The surveying followed the daytime search protocol specified by Bell (1996) and was conducted in an upstream direction. A double-surveyor method was used to reduce observer bias in the resulting counts of individual frogs. This involved one person searching under rocks and refugia (Figure 2.3) in a 0-50 m section and the second simultaneously searching the 50-100 m section of the transect before switching and repeating the search. The average time to complete a transect was approximately 4 h and depended on the number of searchable refugia available, i.e., transects with more rocks took longer to search thoroughly. The independence of repeated surveys was maintained by searchers not discussing the results of their search while other surveyors were still scanning the transect. Upon encountering a frog, the observer recorded its location as the distance along the transect in metres (i.e., 0 to 100 m) and measured the approximate snout-to-vent length (SVL in mm) by holding a ruler over the frog.

The same 15 transects were resurveyed in 2015 following a similar protocol to that used in 2012 (Herbert & Gilbert, 2015). It was decided during the 2012 surveys that subsequent sampling expeditions would only occur every 3 years approximately, as the human disruption to the habitat caused during surveying may be detrimental to the population if occurring too frequently. Notable differences between the 2012 and 2015 surveys were: 1.) the 2012 survey team consisted of five people with different pairs assigned to each transect, whereas the same two people surveyed every transect in 2015. 2.) Some of the frogs were handled in the 2015 transect surveys to photograph retinal venation, so it is likely these frogs moved more than unhandled frogs in the 2012 studies. 3.) The 2015 surveys were completed across 12 days rather than 10 days due to rain.

2.2.3 Triple-observer frog survey (2021)

The survey effort in 2021 was increased from a double-surveyor to a triple-surveyor protocol. Each survey involved three surveyors manually searching under rocks and refugia in one of three approximately equidistant sections of the transect (0-36 m, 36-67 m, 67-100 m) before moving on to the next section. Each surveyor completed all sections of the transect and all surveyors were able to search their respective sections simultaneously. In 2021, the perpendicular distance from the left or right side of the transect (in metres) was recorded in addition to the distance along the transect to provide more precise information on the position of each frog sighting. The life stages of individuals were decided based on Hochstetter's size class measurements discussed by Whitaker & Alspach (1999), where adult/sub-adult frogs (~1-year-old) have SVLs of > 18 mm and juvenile frogs (< 1 -year-old) have SVLs of < 18 mm. The terminology throughout this study will classify individuals found on the first survey as 'captures', and individuals found on surveys 2 and 3 who meet the recapture criteria from Puig (2009) will be referred to as 'recaptures' henceforth. Following these criteria, an individual was considered re-sighted (from now on, a 'recapture' despite no handling occurring) if located within 0.2 m of another recorded frog sighting and had an SVL within ± 5 mm (Puig, 2009). This assumption can be made due to the relatively sedentary nature of this species in the short-term (Green & Tessier, 1990). In 2021 the average time to complete a transect was approximately 4 h. The independence of the surveys was maintained by searchers not discussing the results of their search while other surveyors were still scanning the transect.



Figure 2.3: Claire Johnson (Left) and Henry Cookson (Right) conducting manual searches of transects for Hochstetter's frogs in April 2021. The 100-m central transect line (white) can be seen here. Photo by: S.Dwyer.

2.2.4 Analytical methods

Three datasets were used in this thesis. The datasets from 2012 and 2015 were collected by Sarah Herbert and collaborators (Herbert et al., 2013, 2015). The 2012 and 2015 surveys did not record the perpendicular positions of the frogs with respect to the transects, and this variable was added to the research design in 2021. This was revised in the 2021 research when I collaborated with Sarah Herbert and Wildland Consultants Ltd to conduct transect surveys. For this reason, the 2021 single-year analysis will compare all four statistical protocols, whereas the multi-year analysis will only compare N-mixture, site occupancy, and the single-survey index. The models assumed closed populations (i.e., no births, deaths, immigration or emigration) within the 2–3 surveys conducted in a year as the survey replicates were collected on the same day in a matter of hours. I also assume homogeneity in detection probability among frogs but not between surveys, in which the probability of finding an individual within a survey will not vary between

animals within the population, except in CMR, where the likelihood of recapturing an individual decrease after the first survey (Pollock, 1982; Pollock, 2000).

The terminology and analytical specifications used in this chapter are described here. In Bayesian inference, the relevant information about a species or environment before analysis is referred to as prior information and is summarised in prior probability distributions for the parameters in the model (Ellison, 2004). In CMR and N-mixture models, detection probability (p) refers to the probability of detecting an individual that is present. In the site occupancy model, p refers to the probability of detecting a species if it is present. The notations used in the code of the four models follow the OpenBUGS coding language. A detailed description of BUGS symbols and notations can be found in the OpenBUGS manual (Spiegelhalter et al., 2007). This thesis will discuss single-year models, unconstrained multi-year models and multi-year "time-trend" models, which refer to generalised linear models including year as a fixed factor. In the time-trend models, the spatial variation among transects is assumed to be consistent among years, whereas this is not the case in the unconstrained models.

The factors considered to potentially affect frog abundance were (1) transect (A1, A2, A3, A4, B1, B2, B3, B4, C1, C2, C3, D1, D2, E1, E2); and (2) year (in multi-year models), whereas the factors considered to potentially affect detection probability were (1) number of times a transect section had been surveyed already (first, second, or third); and (2) whether the frog had been found in a previous survey (in the capture-mark-recapture model only).

Prior to creating single-year and multi-year models for analysis, two frog observations had missing 'perpendicular distance from transect' points due to the survey sheets having water damage and becoming unreadable. These observations were Frog ID 218 and 219 (Appendix 1). For these observations, the SVL and distance along the transect ruled out the possibility of either of these observations being the same frog as any previous observation. Therefore, perpendicular distance values of 0 were arbitrarily assigned. However, accurate perpendicular distances were often essential for determining whether an observation was the same frog as a previous observation (recapture) or a newly-sighted individual.

2.2.5 Single-year models

The data from 2021 were used to investigate the feasibility of estimating single-season abundances or site-occupancy probabilities of Hochstetter's frogs from just three surveys of each transect. Three modelling approaches were used: abundance estimation via closed capture-mark-recapture (CMR) analysis (Otis et al., 1978), abundance estimation from N-mixture modelling (Royle, 2004), and occupancy estimation with single-season occupancy models (Mackenzie et al., 2002). Bayesian formulations of each model type were constructed using purpose-built code on the Bayesian updating software OpenBUGS (2014, version 3.2.3). The single-year code is available in Appendix 1. The code for multi-year unconstrained models is available in Appendix 2a and 2b, and the time-trend model code is available in Appendix 2c and 2d. I fitted each model using three Markov Chain Monte Carlo (MCMC) chains to ensure model convergence and discarded a burn-in of at least 1,000 samples (Barker & Link, 2010).

Closed-population Capture-Mark-Recapture

Closed-population capture-mark-recapture involves estimating two separate components: detection probability and abundance. Detection probability is the probability of a surveyor detecting an individual present on a transect during a survey. These detections can be divided into initial sightings or 'captures' of individuals that have not yet been detected and resightings or 'recaptures' of individuals detected in previous surveys. This model and subsequent models in this chapter were adapted from code used in Hotham (2019) to estimate the abundance of Archey's frogs.

The capture probability (c) and recapture probability (p) for survey j of any transect were given by:

$$\text{logit}(c[j]) <- a.p + re.j.p[j] \quad \text{Equation 2.1}$$

$$\text{logit}(p[j]) <- \text{logit}(c[j]) + b.B \quad \text{Equation 2.2}$$

Where $a.p$ is the intercept, $b.B$ is the effect of initial detection on subsequent detection probability, and $re.j.p[j]$ is a random effect allowing variation among the three surveys. The standard deviation

of these effects was given by the hyperparameter $s.j.p$. The priors for these parameters and hyperparameters were:

$$a.p \sim dnorm(0,1) \quad \text{Equation 2.3}$$

$$b.B \sim dnorm(0,1) \quad \text{Equation 2.4}$$

$$s.j.p \sim dunif(0,1) \quad \text{Equation 2.5}$$

Where $dnorm(0,1)$ means the parameters are believed *a priori* to fall within a normal distribution with mean 0, and precision 1 (precision = $1/SD^2$) and $dunif(0,1)$ means the parameter is believed to fall in a uniform distribution between 0 and 1. The prior for the hyperparameter was mildly informative (Banner et al., 2020), as was necessary when estimating standard deviation among just three surveys. In contrast, the other two priors were wide enough to be uninformative. These priors were used for all models discussed in this chapter.

For each survey j of transect I , the number of newly sighted frogs (u) is considered a binomial sample from the number of 'unmarked' frogs (U) present. Similarly, the number of recaptured frogs (m) found on transect i in survey j is considered a binomial sample from the number of 'marked' frogs present (M). This is represented by the code:

$$u[i,j] \sim dbin(c[j], U[i,j]) \quad \text{Equation 2.6}$$

$$m[i,j] \sim dbin(p[j], M[i,j]) \quad \text{Equation 2.7}$$

After each survey, the numbers of marked and unmarked frogs present are updated based on the number of new frogs found in that survey. This is represented by the code:

$$U[i,j+1] <- U[i,j] - u[i,j] \quad \text{Equation 2.8}$$

$$M[i,j+1] <- M[i,j] + u[i,j] \quad \text{Equation 2.9}$$

In the first survey, there are no 'marked' frogs, so $M[i,1] <- 0$, the number of 'unmarked' frogs present is the total number of the transect, i.e., $U[i,1] <- N[i]$. Consequently, the sampling process allows these abundances to be estimated as well as the detection parameters described above.

The priors for the abundances ($N[i]$) took the form of Poisson samples from expected numbers ($\mu[i]$) that were log-normally distributed. This is represented by the code:

$$a.n[i] \sim dnorm(0,0.1) \quad \text{Equation 2.10}$$

$$\log(\mu[i]) <- a.n[i] \quad \text{Equation 2.11}$$

$$N[i] \sim dpois(\mu[i]) \quad \text{Equation 2.12}$$

This form of prior could be used in all abundance models, allowing consistency. The prior distribution $dnorm(0,0.1)$ means there is a 95% prior probability that there are less than approximately 500 frogs in a transect. The same prior was used for all single-season and unconstrained multi-season models but needed to be adjusted in the time-trend models where variation among fragments was modelled as a random effect (Equation 2.16–2.20).

N-mixture

In N-mixture, there are no attempts to distinguish newly-‘captured’ frogs from ‘recaptured’ frogs, necessarily adding the constraint that capture and recapture probabilities are assumed equal. The intercept ($a.p$) parameter and random variation among surveys were kept the same as in the CMR model, meaning the detection component of the model was simplified to:

$$\text{logit}(p[j]) <- a.p + re.j.p[j]$$

Where $p[j]$ now refers to survey-specific detection probability regardless of whether a frog is believed to have been previously detected.

The binomial sampling for each of the survey occasions was therefore simplified to:

$$n[i,j] \sim dbin(p[j], N[i])$$

Where $n[i,j]$ is the number of frogs detected on the transect in the survey and $N[i]$ is the number of frogs present on the transect.

Site occupancy

With occupancy modelling, the probability of a site being occupied by the species is estimated as well as the probability of the species being detected in a survey if it is present. For each of the 15 transects, the data were divided into ten 10-m segments, and it was recorded whether the species was detected in each of the segments on each survey. The probability of a segment being occupied in a transect gives a measure of relative abundance for the transect. In the site occupancy model, the detection component is the same as for the N-mixture model (Equation 2.3-2.5), but $p[j]$ now refers to the probability of the species being detected in a 10-m segment rather than the probability of an individual frog being detected.

Whether or not a particular 10-m segment is occupied is considered to be a Bernoulli sample based on the occupancy probability for the transect. Whether or not frogs are detected within a segment in a survey depends on whether the segment is occupied and the probability of frogs being detected if present. This is represented by the code:

$$present[k] \sim dbern(p.present[transect[k]]) \quad \text{Equation 2.13}$$

$$detected[k,j] \sim dbern(p.detect[k,j]) \quad \text{Equation 2.14}$$

$$p.detect[k,j] <- present[k]*p[j] \quad \text{Equation 2.15}$$

Where $present[k]$ is the occupancy of segment k , $p.present[transect[k]]$ is the occupancy probability for the transect it belongs to, $detected[k,j]$ indicates whether frogs were detected the segment k on survey j , and $p[j]$ is the probability of frogs that are present and being detected in a segment on survey j .

The prior distribution for each transect's occupancy probability was derived from its prior distribution for abundance, which was the same as that used for CMR and N-mixture modelling (Equations 2.10 – 2.12). Assuming animals are Poisson distributed, the probability of a species occurring in a sample area is $1-\exp(-D)$, where D is the expected number (Caughley, 1977). The probability of a 10-m segment being occupied is, therefore:

$$p.present[i] <- 1-\exp(-N[i]/10)$$

Where $N[i]$ is the number of frogs on the transect divided by 10 to get the expected number of frogs in a 10-m segment. This form of prior allows abundance to be automatically derived from occupancy probability.

2.2.6 Unconstrained multi-year models

This study will incorporate three datasets collected over a nine-year period. Repeating the modelling with multiple datasets from 2012, 2015, and 2021 data increases the number of survey replicates and strengthens the models' statistical power (Goulet & Cousineau, 2019). Utilising multiple datasets collected over time also makes it possible to make inferences about any temporal trends that may be occurring. The multi-year analyses are very similar to the single-year versions of their respective models. The priors for all parameters used were the same as for the single-season models (Equations 2.3, 2.5, 2.10–2.12).

N-mixture

The intercept ($a.p$) parameter and random variation among surveys remain the same as the single-year N-mixture analysis, and so the detection component of the model is unchanged.

The abundance estimation is also unchanged. However, with the incorporation of a three-year dataset, the *n.surveys* variable in the detection component of the single-year N-mixture model is changed to *n.surveys.max* to specify that there is a maximum of three surveys per transect. The *n.transects* is also amended to *n.rows* to allow for three datasets that contain the same transects (Appendix 2a).

Site Occupancy

The code for the detection model remained the same as the single-year occupancy model (Equation 2.3 and Equation 2.4), as well as the abundance component of this model, which remained the same as the single-year site occupancy model (Equation 2.10 – 2.12). To allow this model to incorporate three datasets for a multi-year analysis, the occupancy component of the model now estimates the probability of occupancy for each transect for each of the three years. This is represented by the code *n.transect* being extended to *n.transect.year*. When estimating the

occupancy probability of each 10 m segment on the transect with a Bernoulli sample (Equations 2.13 – 2.15), the code is extended to *transect.year[k]* (Appendix 2b).

2.2.7 Time-trend models

I generated purpose-built single count, N-mixture and site occupancy models to investigate temporal abundance trends and compare their sensitivity for estimating those trends. One of the most effective ways to estimate whether a population's abundance is fluctuating over time is to conduct analyses that identify trends in the data. These models were all designed to estimate the rate of change in abundance over time and the variance among transects, assuming that all transect abundances are either increasing, decreasing or remaining stable. It is possible to statistically analyse the single counts within this framework because of the repetition of these counts among years.

N-mixture

The detection component of this model remained the same as the unconstrained N-mixture model. The abundance component is adjusted so there is a log-linear relationship between abundance and year, with variation among fragments modelled as a random effect. This means that changes over time are assumed to take the form of exponential growth or decline. The log-linear relationship between abundance and time is represented by the code:

$$\log(\mu[i]) <- a.n + b.year*(year[i]-2012) + re.trans.n[transect[i]] \quad \text{Equation 2.16}$$

$$N[i] \sim dpois(\mu[i]) \quad \text{Equation 2.17}$$

Where *a.n* is the intercept and *b.year* is the slope (which is multiplied by the number of years elapsed since 2012), and *re.trans.n[transect[i]]* is the random effect of the transect. The priors for the parameters were:

$$a.n \sim dnorm(0,1) \quad \text{Equation 2.18}$$

$$b.year \sim dnorm(0,1) \quad \text{Equation 2.19}$$

$$s.trans.n \sim dunif(0,5) \quad \text{Equation 2.20}$$

Here the prior knowledge about the possible number of frogs in any fragment is determined by the intercept ($a.n$) and the random variation among fragments ($s.trans.n$). The combination of priors used here gives a similar level of diffuseness to the prior used for individual fragments in the single-season and unconstrained multi-season models (i.e., $a.n[i]$ in Equation 2.10).

The parameter $b.year$ is equivalent to the intrinsic rate of increase (r) in an exponential growth model. The derived finite rate of increase (λ) over one year nine yearsars is represented by the code:

$$lambda <- exp(b.year) \quad \text{Equation 2.21}$$

$$lambda9 <- pow(lambda,9) \quad \text{Equation 2.22}$$

The parameter $lambda9$ is the $lambda$ raised to the power of 9, as the study ran over nine years.

Single-count Index

A regression model was generated to compare abundance counts over time in this analysis. This model was adapted from the time-trend N-mixture Poisson linear regression (Appendix 2b). There are no survey replicates for single counts, so a detection model cannot be used. Therefore the model is simplified to include only the estimation of the mean count, which is similar in form to the estimation of abundance. The priors in this model remain the same as in the N-mixture time-trend model (Equation 2.18 - 2.20).

Site occupancy

This model was also adapted from the N-mixture time-trend model. The detection component of this model remained the same as the unconstrained multi-year site occupancy model (Equation 2.3 – 2.5). The occupancy component of this model is the same as the abundance component of the N-mixture time-trend analysis. This model includes the segment level code (Equations 2.13 – 2.15). The derived parameters to estimate the change in abundance (Equations 2.18 and 2.19) also remained the same in this model as in the N-mixture time-trend model.

2.2.8 Comparing the precision of estimates

To consider statistical power in the comparison of models, the coefficient of variation (CV) will be used as a measure of precision in abundance estimation. The coefficient of variation for the parameter of interest is given by:

$$CV = \frac{SD}{\mu} \quad \text{Equation 2.23}$$

2.3 Results

The total number of frog observations recorded across the three datasets for Te Paparahi (2012, 2015 and 2021) was 1,068 (Table 2.1). The year with the highest number of frog observations was 2021, which may have been due to the addition of a third survey, whereas in previous years, a double-survey method was used. The 1,068 observations of frogs are not representative of the number of frogs present on these transects, as some were counted more than once (recaptures), and some of the frogs were present on the transects would not have been found (Wildland Consultants, 2021). The transect with the highest number of recorded frog observations across all years was transect A3, totalling 234 observations. The A-catchment had the highest number of frog observations of the five catchments, with a total of 561 of the 1,068 frog observations (52%) found in this catchment alone, despite it containing four of the 15 transects (27%).

Table 2.1: Summary of the total Hochstetter's frog observations over multiple surveys of each transect in the survey expeditions in 2012, 2015, and 2021. These observations may include 'recaptures' and are not the true number of frogs likely to be present on each transect. Two survey replicates were conducted in 2012 and 2015, and three replicates were conducted in 2021.

Transect	2012	2015	2021	Total
A1	-	50	74	124
A2	57	68	78	203
A3	63	99	72	234
A4	25	23	41	89
B1	36	26	21	83
B2	16	25	44	85
B3	12	6	1	19
B4	0	4	3	7
C1	21	35	16	72
C2	19	21	55	95
C3	4	6	24	34
D1	5	0	3	8
D2	0	2	0	2
E1	2	5	1	8
E2	1	0	4	5
Total	261	370	437	1068

2.3.1 2021 Single-year results

In the 2021 survey expedition, 437 frog observations were recorded over the 15 100-m transects. Of this total, 72 observations (17%) were classified as juveniles. The number of frogs recorded in the first of the three surveys is the minimum number of frogs I would know were in each transect if just one survey had been conducted, i.e., there are no recaptures, and all observations in the first survey are newly sighted. These first counts of frogs ranged from 0 in Transects D1 and D2 to 30 in Transect A3 (Table 2.2).

Capture-mark-recapture and N-mixture

Abundance estimates generated in the CMR model ranged from 0 to 118 frogs across the fifteen transects, with the estimate of 118 on both transect A2 and transect A3 (Table 2.2). Abundance estimates generated using N-mixture modelling ranged from 0 to 98 frogs across all transects, with the highest estimate on transect A2 (Table 2.2). The mean, medians and credible interval

summaries of detection and abundance parameters used in the CMR and N-mixture models are outlined in Table 2.3.

In the CMR model, the probability of detecting a previously undetected frog (c) on one of the three respective surveys is represented by $c[1]$, $c[2]$ and $c[3]$. The probability of recapture (p), i.e., detecting a previously detected frog, on one of the three respective surveys is represented by $p[1]$, $p[2]$ and $p[3]$. The estimated probability of detecting a previously undetected frog across the three surveys was 0.23–0.29, with the third survey having the highest probability. The estimated recapture probability was 0.10–0.13. The variation across the three surveys is supported by the parameter $s.j.p$ being evidently > 0 (Table 2.3). Table 2.3 shows the different detection patterns of p in the CMR and N-mixture models.

Despite differences in detection probability specificity, there was a strong correlation between the estimates generated using CMR and N-mixture ($R^2 = 0.996$; Figure 2.4). The figure shows that under N-mixture, abundance (N) estimates were 83% as large as CMR estimates of N . The higher abundance estimates under CMR result from an apparent behaviour effect, with recapture probabilities estimated to be significantly lower than initial capture probabilities.

Table 2.2: Estimated abundance (N) and occupancy probability ($p.present$) for Hochstetter's frogs on each 100-m transect on Aotea in 2021 compared to the first count done on each transect. Here occupancy probability refers to the probability of a 10-m segment being occupied on a transect rather than the occupancy of the transect as a whole. Abundance was estimated using closed-population capture-mark-recapture (CMR) and N-mixture and was also derived from the occupancy probabilities (see Table 2.4 below). SD, 2.5% and 97.5% refer to the standard deviation and 95% credible limit around each estimate.

Transect	Count	CMR			N-mixture			Occupancy		
		Mean N	SD	97.5%	Mean N	SD	97.5%	Mean $p.present$	SD	97.5%
A1	29	104.10	24.79	164	92.93	29.35	166	0.98	0.04	1.00
A2	28	118.20	28.06	186	97.61	30.92	175	0.98	0.04	1.00
A3	30	118.20	27.90	185	91.00	28.6	163	0.94	0.08	1.00
A4	10	67.66	16.84	108	51.77	16.8	94	0.98	0.04	1.00
B1	8	29.42	8.12	49	25.86	9.313	49	0.93	0.09	1.00
B2	28	69.47	17.06	111	59.58	17.66	104	0.49	0.15	0.79
B3	0	1.73	1.21	5	1.66	1.138	5	0.15	0.08	0.39
B4	1	3.42	1.80	8	3.19	2.19	9	0.29	0.13	0.59
C1	3	24.17	6.97	41	19.92	7.429	38	0.29	0.13	0.59
C2	24	79.89	19.4	127	69.27	22.03	124	0.94	0.08	1.00
C3	9	34.58	9.26	57	29.76	10.44	56	0.84	0.14	1.00
D1	0	5.13	2.28	11	3.90	2.11	9	0.21	0.11	0.50
D2	0	0.17	0.53	2	0.15	0.50	2	0.01	0.04	0.18
E1	1	1.73	1.22	5	1.66	1.13	5	0.15	0.08	0.39
E2	1	3.41	1.77	8	4.70	2.59	11	0.29	0.13	0.59

Table 2.3: Mean, median, standard deviation (SD) and 95% credible intervals (2.5% and 97.5%) for detection and abundance parameters in the single-year capture-mark-recapture and N-mixture model. c is the detection probability for previously undetected frogs, and p is the detection probability for frogs found in one or more previous surveys. $p[1]$ is not included in the CMR model as there cannot be any previously detected frogs in the first survey.

	Parameter	Parameter definition	Mean	Median	SD	2.5%	97.5%
CMR	a.p	The intercept which represents the logit of initial detection probability for an average survey	-1.00	-0.99	0.40	-1.83	-0.23
	b.B	Effect of initial detection on subsequent logit detection probability	-0.89	-0.94	0.41	-1.66	-0.05
	c[1]	Probability of detecting a frog in the first survey	0.26	0.27	0.05	0.16	0.36
	c[2]	Probability of detecting a previously undetected frog in the second survey	0.23	0.23	0.05	0.123	0.35
	c[3]	Probability of detecting a previously undetected frog in the third survey	0.29	0.28	0.08	0.14	0.46
	p[2]	Probability of detecting a previously detected frog in the second survey	0.10	0.10	0.01	0.07	0.14
	p[3]	Probability of detecting a previously detected frog in the third survey	0.13	0.13	0.01	0.10	0.17
	s.j.p	Standard deviation in logit detection probability among the three surveys	0.33	0.27	0.23	0.035	0.90
N-mixture	a.p	The intercept which represents the logit of detection probability for an average survey	-0.91	-0.91	0.44	-1.78	-0.04
	p[1]	Probability of detecting a frog in the first survey	0.32	0.32	0.08	0.17	0.51
	p[2]	Probability of detecting a frog in the second survey	0.24	0.24	0.06	0.12	0.38
	p[3]	Probability of detecting a frog in the third survey	0.27	0.27	0.07	0.14	0.43
	s.j.p	Standard deviation in logit detection probability among the three surveys	0.40	0.34	0.22	0.08	0.92

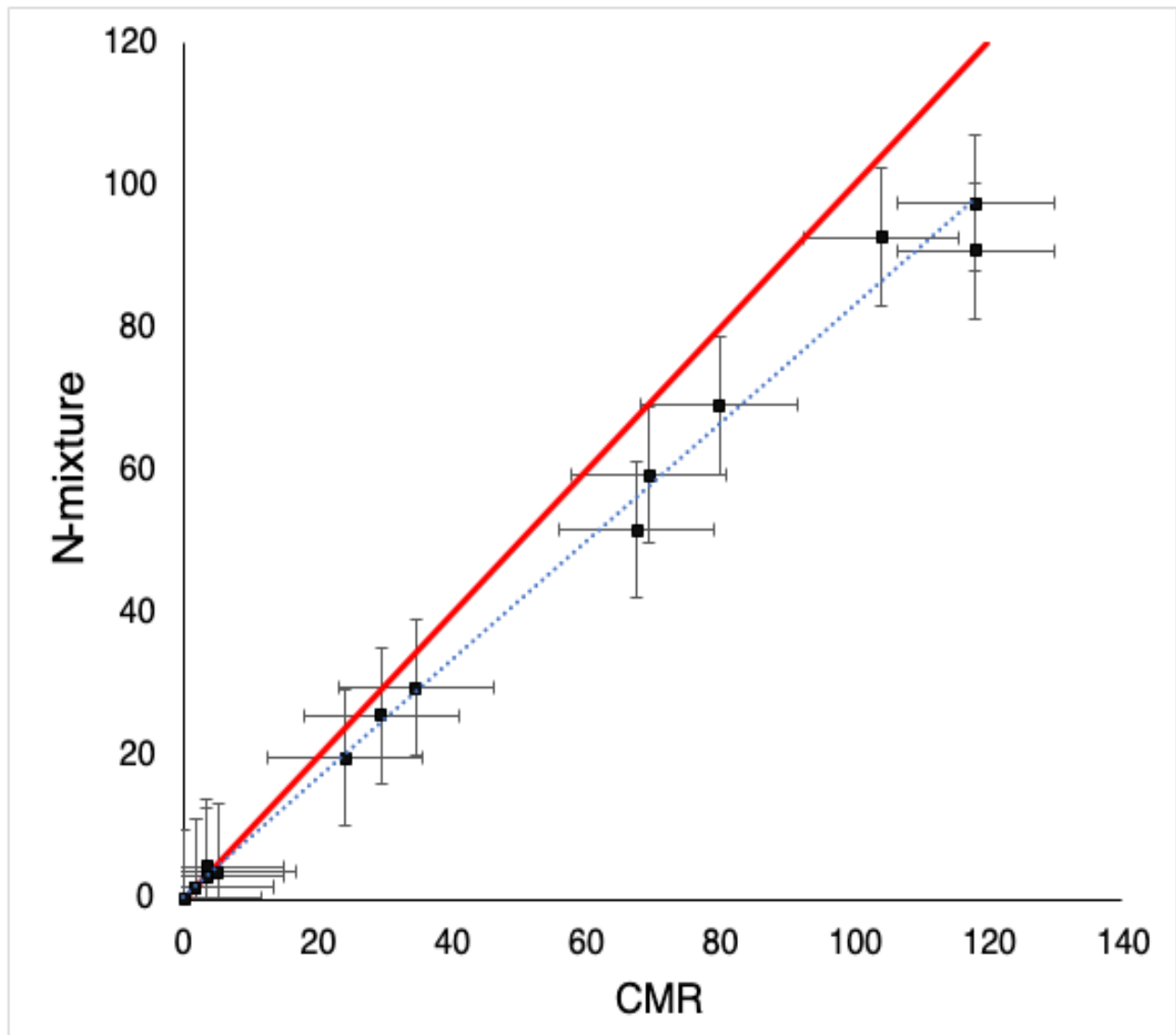


Figure 2.4: Relationship between capture-mark-recapture (CMR) and N-mixture estimates for the abundance of Hochstetter's frogs in 15 100-m transects on Aotea in 2021. The blue dotted line shows the fitted relationship indicating that N-mixture estimates were 83% as large as CMR estimates (the red line shows a 1:1 relationship). Error bars show 95% credible intervals around estimates.

Site Occupancy

All transects were occupied with at least one frog in 2021 except for Transect D2, where no frogs were observed. The estimates of probability of occupancy reported in this thesis are based on occupancy probabilities at the segment level of transects (10 segments per transect). This allows the capacity to make inferences about the probability of occupancy at the individual segment level rather than broadly across the entire transect.

The probability of a 10-m segment being occupied was estimated to vary across transects from 1% to 98% in 2021 (Table 2.4). Catchment A transects had the highest probability of occupancy (*p.present*). The highest probabilities of occupancy were 98% on transects A1, A2, and A4. Transects in catchments D and E have the lowest *p.present* in 2021, with the lowest probability of occupancy being on transect D2, where no frogs were found. As the segment occupancy data are a sample and not representative of the entire stream, the occupancy model will never estimate a 100% or 0% probability of occupancy but will include 0% or 100% in the credible intervals.

For abundance estimates derived from occupancy, the upper credible interval will not be considered as when occupancy is close to 100%, the upper limit for abundance does not have any constraint except that imposed by the prior. The median estimate of N and the lower credible interval will be used when discussing these derived abundance estimates, as means are highly affected by large upper credible limits, so the means for each transect can be misleading. The highest median abundance derived from the occupancy model is 101 frogs on Transect A2, and the lower credible interval for this estimate is 19 frogs (Table 2.4). The lowest median estimate of frogs was 1 frog in Transect E1. The 2.5% credible limit for this estimate is also 1 frog.

Table 2.4: Median and lower credible limit (2.5%) from the posterior distribution for the abundance of Hochstetter's frogs on each 100-m transect on Aotea in 2021 derived from occupancy estimates. These values are compared to the first count done on each transect.

Transect	First count	Median	2.5%
A1	29	98	19
A2	28	101	19
A3	30	48	12
A4	10	83	18
B1	8	42	11
B2	28	7	2
B3	0	1	1
B4	1	3	1
C1	3	3	1
C2	24	50	12
C3	9	20	7
D1	0	2	1
D2	0	0	0
E1	1	1	1
E2	1	3	1

2.3.2 Unconstrained multi-year results

Unconstrained N-mixture and site occupancy models were conducted for multi-year analysis. Single counts cannot be statistically modelled for a single year because there is no replication.

N-mixture

For all years of surveying, the mean estimates of Hochstetter's abundance and their credible limits are shown in Figure 2.5. Catchment A had the highest estimates of abundance across the three datasets, with transect A3 having the highest estimated number of frogs in both 2012 (92 frogs) and 2015 (144 frogs) (Figure 2.5). The lowest N-mixture estimates of frog abundance were in catchment D. The largest estimate of frogs for a single transect in catchment D was 7 frogs in transect D1 in 2012. The detection probability for each of the three surveys was very similar,

ranging from 0.31-0.39 (Table 2.6). The s.j.p value is clearly >0 (0.36) for this model, indicating some variation in detection probability between surveys 1, 2 and 3.

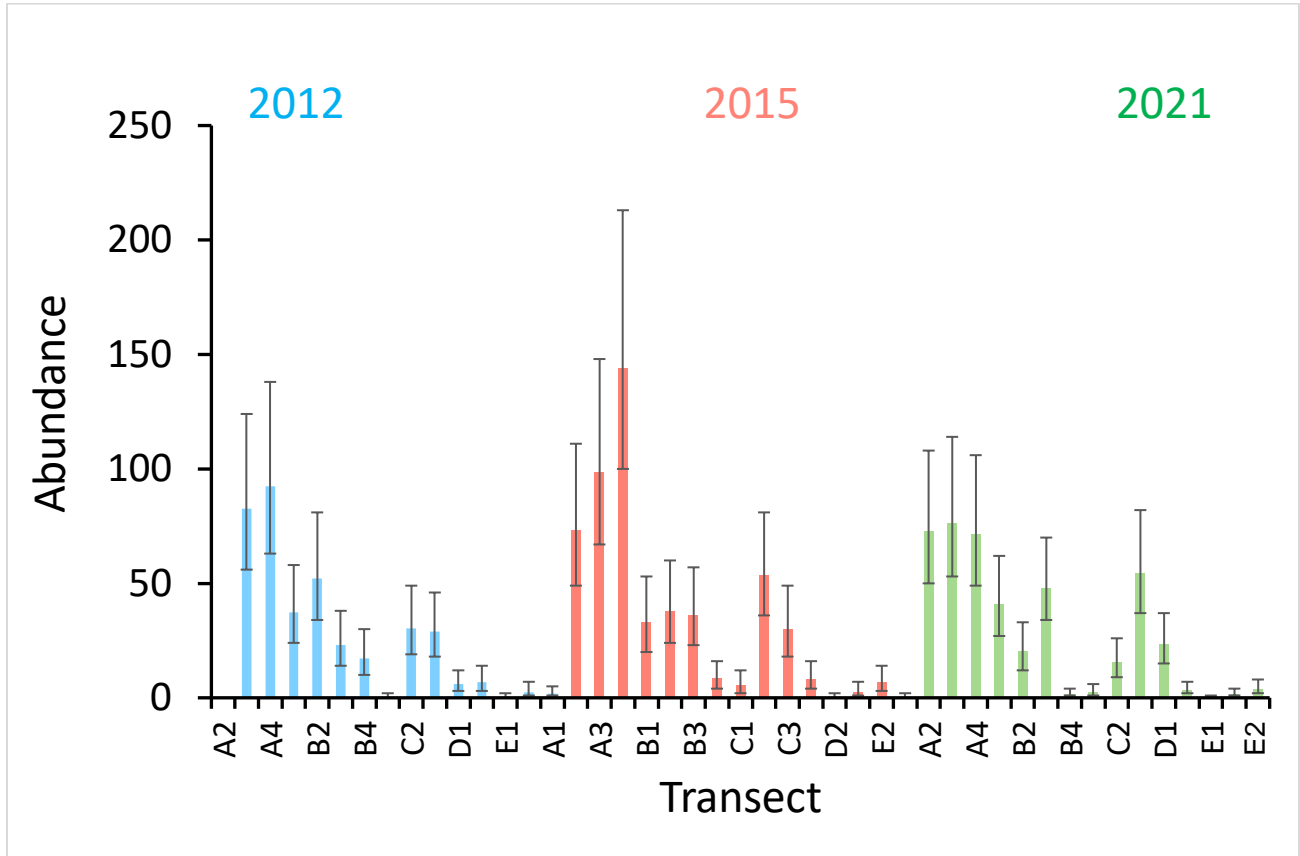


Figure 2.5: Estimates of Hochstetter's frog abundance for each transect on Aotea in 2012, 2015 and 2021 generated using an unconstrained N-mixture model.

Site occupancy

For all years, there was only one transect where no frogs were observed. All transects had at least one frog recorded in one of the three survey years. The highest estimated probabilities of segment occupancy were 98% for transect A2 in both 2015 and 2021.

The highest estimate of occupancy was in catchment A transects for all three years. Transects A1, A2 and A3 had *p.present* estimates of $> 95\%$ for all three years (Table 2.5). The catchments with the lowest estimated probability of segment occupancy were D and E, with the *p.present* estimates

for all catchment D transects < 29% across all three years and the *p.present* estimates for all catchment E transects < 22% across the three years.

As with the single-year occupancy model, the derived medians from the *p.present* estimates will be discussed. Transects in catchment A had estimates of the median number of frogs on a transect (N) of > 90 frogs for all years (Table 2.5). The highest median abundance of frogs was 95 frogs in transect A2 in 2015. Transects in catchments D and E had consistently low estimates of median frog abundance in all three surveyed years, with median estimates of < 5 frogs in each of the catchment D and E transects. The mean s.j.p value in this model was 0.51, indicating some variation in the detection probability between surveys 1, 2 and 3. The detection probability of finding frogs in the three respective surveys ranged from 0.66-0.79, with the lowest probability of detecting frogs in survey 3 (Table 2.6).

It is likely that the probability of occupancy estimates are less precise when segment occupancy is close to 100% or 0%, which can be seen in catchment A and catchments D and E transects (Table 2.5). In turn, this lowers the precision of median N estimates as these are derived from the probability of occupancy estimates.

Table 2.5: Unconstrained estimates of the probability of occupancy (*p.present*) median frog abundance (*N*) and lower credible limit (2.5%) for Hochstetter's frogs on each 100-m transect on Aotea in 2012, 2015 and 2021. Here occupancy probability refers to the probability of a 10-m segment being occupied on a transect rather than the occupancy of the transect as a whole. Transect A1 in 2012 was used as a training transect for new surveyors, so estimates of *p.present* and median frog abundance were not included in this analysis.

Transect	2012			2015			2021		
	Mean <i>p.present</i>	Median N	2.5% N	Mean <i>p.present</i>	Median N	2.5% N	Mean <i>p.present</i>	Median N	2.5% N
A1				94.5%	50	12	98.2%	100	19
A2	98.1%	87	19	98.2%	95	19	98.0%	87	18
A3	98.0%	88	18	98.1%	87	19	98.1%	89	18
A4	71.8%	13	5	71.4%	13	5	78.8%	16	7
B1	95.2%	66	12	49.5%	7	2	57.4%	9	3
B2	49.4%	7	2	71.8%	13	5	67.3%	12	5
B3	39.5%	5	1	39.6%	5	2	14.7%	1	1
B4	1.3%	0	0	39.5%	5	2	14.8%	1	1
C1	84.9%	21	7	84.3%	20	7	20.4%	2	1
C2	39.6%	5	2	72.7%	13	5	91.6%	31	10
C3	39.4%	5	1	29.6%	3	1	67.5%	12	5
D1	21.1%	2	1	1.4%	0	0	28.6%	3	1
D2	1.3%	0	0	15.1%	1	1	1.3%	0	0
E1	15.1%	1	1	21.1%	2	1	14.8%	1	1
E2	15.0%	1	1	1.3%	0	0	14.8%	1	1

Table 2.6: Mean, median, standard deviation (SD) and credible limits of detection and abundance parameters under the unconstrained multi-year N-mixture and site occupancy models. 2.5% is the lower credible limit and 97.5% is the upper credible limit for the estimates of each parameter. p is the detection probability of frogs for each respective survey, 1, 2 and 3.

	Parameter	Parameter definition	Mean	Median	SD	2.5%	97.5%
N-mixture	a.p	The intercept which represents the logit of detection probability for an average survey	-0.60	-0.61	0.35	-1.28	0.11
	p1	Probability of detecting a frog in first survey	0.39	0.38	0.06	0.26	0.52
	p2	Probability of detecting a frog in second survey	0.31	0.31	0.05	0.21	0.42
	p3	Probability of detecting a frog in the third survey	0.34	0.33	0.06	0.22	0.46
	s.j.p	Standard deviation in logit detection probability among the three surveys	0.36	0.30	0.21	0.09	0.90
Site Occupancy	a.p	The intercept which represents the logit of detection probability for an average survey	0.98	0.98	0.32	0.22	1.55
	p1	Probability of detecting a frog in the first survey	0.79	0.79	0.02	0.73	0.84
	p2	Probability of detecting a frog in second survey	0.75	0.75	0.02	0.69	0.80
	p3	Probability of detecting a frog in third survey	0.66	0.66	0.05	0.54	0.76
	s.j.p	Standard deviation in logit detection probability among the three surveys	0.51	0.49	0.24	0.08	0.96

2.3.3 Temporal trends

Single-count Index

Based on the Poisson regression model fitted to the first counts for all years, transects in Catchment A had the highest mean first count (Figure 2.6).

Changes to the relative abundance of the population over time are calculated through the variables *b.year* and lambda (λ). The variable *b.year* gives us the expected change in relative abundance in a year, where a *b.year* value of 0 would indicate population stability. The *b.year* value estimated in this model was -0.006. This value alone is very close to 0, but population stability cannot be assumed from this value alone. The estimate of λ in this model was 0.993. To estimate the change in abundance over the duration of the study (nine years), λ is raised to the power of 9 (λ^9), giving 0.95, with a 95% credible interval ranging from 0.76–1.16. The population is therefore estimated to have declined 5% from 2012 to 2021, with a possible decline of up to 24% but also a potential increase of up to 16%.

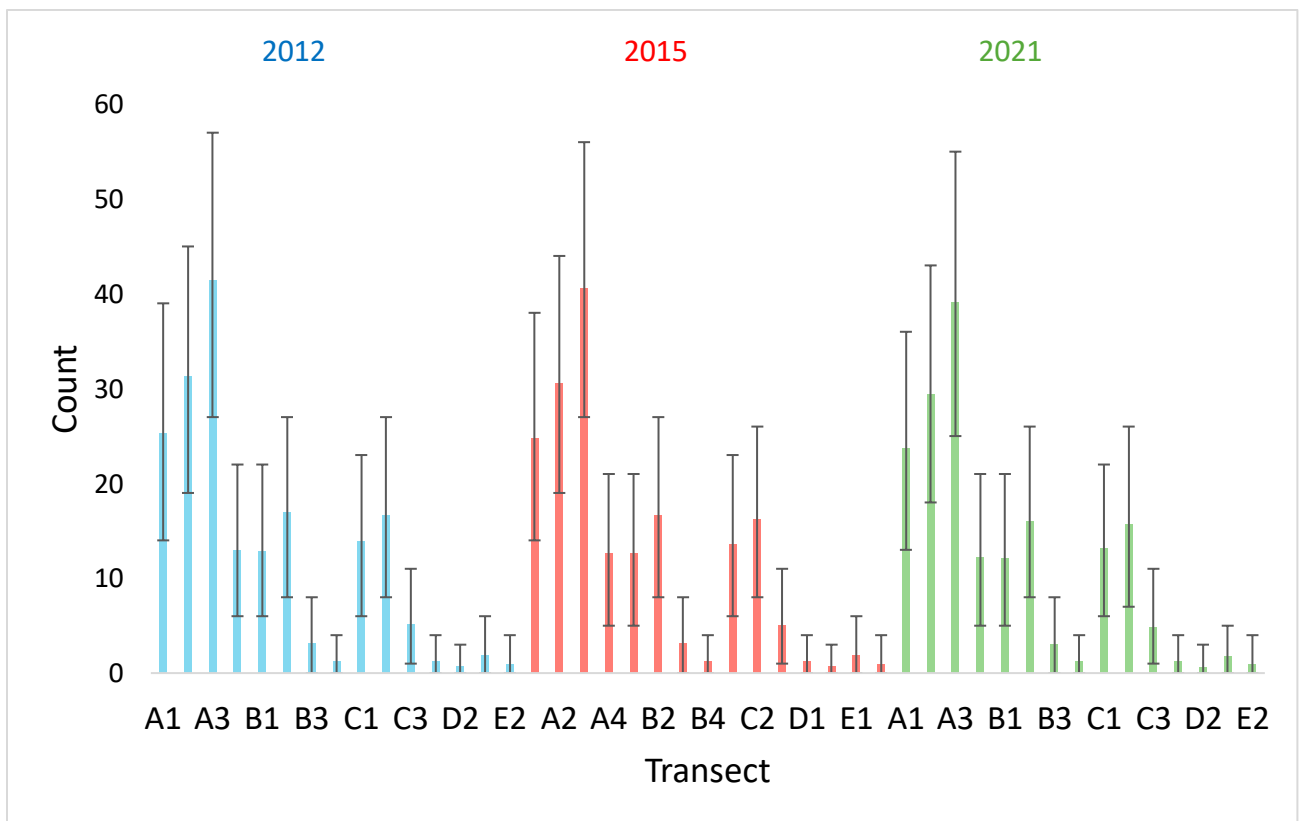


Figure 2.6: Mean first counts of Hochstetter's frogs-for each transect at Te Paparahi in 2012, 2015 and 2021 generated using a log-linear model with year as a fixed effect and transect as a random effect.

N-mixture

The abundance estimates generated by the time-trend N-mixture regression model closely matched the unconstrained N-mixture estimates (Figure 2.5), indicating that the variation in abundance is captured by a log-linear year effect and log-normal random effect.

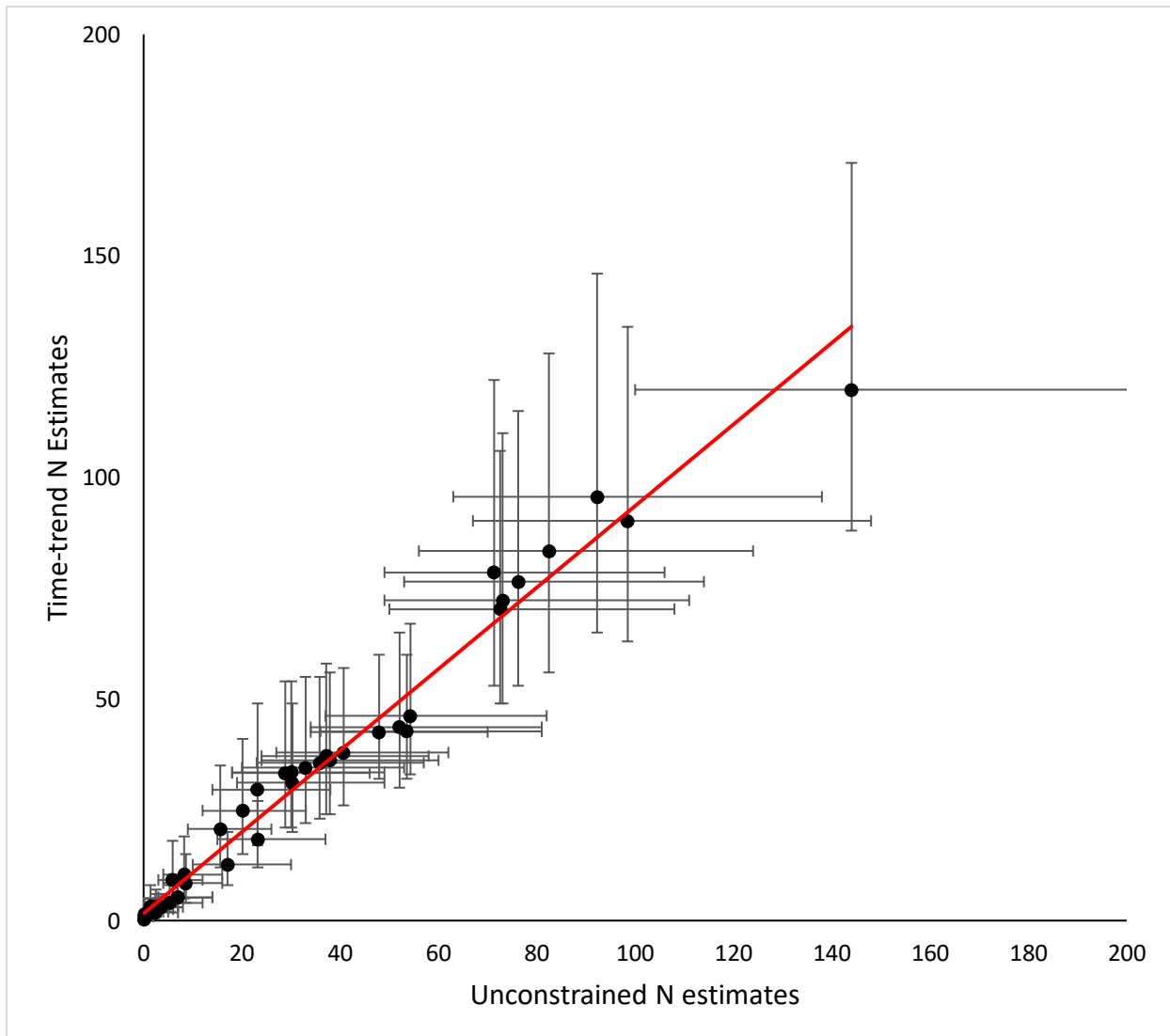


Figure 2.7: Comparison between unconstrained N-mixture estimates of abundance (Figure 2.5) to N-mixture estimates of abundance (N) fitted to a log-linear function with year as a fixed effect and transect as a random effect. The red line shows a 1:1 relationship. The error bars represent the 95% credible intervals around the estimates.

The *b.year* value generated by the N-mixture regression model is -0.009, which corresponds to a λ of 0.990 and λ^9 of 0.92 over the nine years, with a 95% credible interval from 0.76 to 1.10. Therefore, the estimated change under this model is very similar to that inferred from single counts and only slightly more precise.

Site occupancy

Changes to abundance over time (*b.year*, λ , λ^t) could not be estimated using this model, with the posterior distribution for *b.year* matching the specified prior information rather than being updated based on the data. This is likely because λ is derived from estimates of N and the estimates of N generated in this model were unreliable.

2.3.4 Comparing the precision of estimates generated by CMR, N-mixture, and single count index models

Excluding transects where the number of frogs was estimated to be < 10 , where the CV rapidly inflates, the range of CVs for abundance estimates from the single-year CMR model is 24 to 29% (Table 2.7). CVs for the time-trend site occupancy model will also not be considered, as the estimates from segments where occupancy is close to 100% are biased. This is evident in several of the estimates' 95% credible intervals, where the number of frogs is clearly below the minimum number of frogs present. The precision of a model is redundant if the estimates are inaccurate. The range of CVs from the single-year N-mixture model for the same transects is 32 to 37%. The single-year abundance estimates derived from the site occupancy model had much larger CVs, ranging from 59% to 413%. This is a result of the poorer precision in general of N estimates derived from occupancy probability estimates, but especially where occupancy approaches 100%, so there is little or no upper constraint on the likely abundance.

Table 2.7: Comparison of Coefficient of Variation (CV) for abundance estimates obtained using single-year CMR and N-mixture models and multi-year time-trend-models for single -counts and N-mixture estimates. CVs are excluded for transects where the abundance estimate is < 10 frogs, as CVs rapidly inflate as estimates approach zero.

		Single-year models			Multi-year time-trend models	
Year	Transect	CMR	N-mixture	Site occupancy	Single-count index	N-mixture
2021	A1	0.24	0.32	2.85	0.25	0.21
2021	A2	0.24	0.32	2.29	0.22	0.21
2021	A3	0.24	0.31	2.41	0.19	0.23
2021	A4	0.25	0.32	2.39	0.34	0.21
2021	B1	0.28	0.36	2.39	0.34	0.28
2021	B2	0.25	0.30	0.52	0.29	0.17
2021	B3					
2021	B4					
2021	C1	0.29	0.37	0.59	0.32	0.29
2021	C2	0.24	0.32	2.30	0.30	0.19
2021	C3	0.27	0.35	4.13	0.52	0.21
2021	D1					
2021	D2					
2021	E1					
2021	E2					
2015	A1				0.25	0.22
2015	A2				0.21	0.20
2015	A3				0.18	0.18
2015	A4				0.33	0.25
2015	B1				0.33	0.23
2015	B2				0.28	0.23
2015	B3					
2015	B4					
2015	C1				0.31	0.17
2015	C2				0.29	0.26
2015	C3				0.51	0.36
2015	D1					
2015	D2					
2015	E1					
2015	E2					
2012	A1				0.26	0.26
2012	A2				0.21	0.22
2012	A3				0.19	0.22
2012	A4				0.32	0.23
2012	B1				0.33	0.20
2012	B2				0.29	0.28
2012	B3				0.65	0.24
2012	B4					
2012	C1				0.31	0.24
2012	C2				0.29	0.26
2012	C3					
2012	D1					
2012	D2					
2012	E1					
2012	E2					

2.4 Discussion

The majority of approaches investigated in this chapter for modelling single- and multi-year repeated survey data from Hochstetter's frogs proved capable of producing abundance estimates from a very low number of repeated surveys (i.e., 2-3) within a year. However, the models varied in performance; therefore, some appear better suited to this system than others. In particular, abundance estimates derived from occupancy models performed poorly because abundance is difficult to estimate when occupancy is close to 100%. When considering the fitted relationship of the CMR and N-mixture models generated in the single-year analyses comparison (Figure 2.4), N estimates are approximately 20% larger when modelled using CMR than when modelled with N-mixture. The N-mixture model is likely underestimating abundance compared to the CMR single-year model. Overall, the abundance estimates generated in the single-year and multi-year site occupancy models performed poorly compared to the other models. The estimates were unreliable, with the highest mean probability of occupancy approximately 36% lower than the highest mean estimate from the CMR model and 56% lower than the highest mean for the N-mixture model. The large standard deviations of the site occupancy derived N estimates also render calculating a coefficient of variance to estimate the model's power ineffective (Reed et al., 2002). Therefore, I do not recommend using site occupancy modelling to estimate the abundance of Hochstetter's frog populations. One of the key advantages of conducting a time-trend analysis is that the model allows us to quantify how confident we are that the population is stable. This is not possible in unconstrained multi-year models, where population stability can only be assumed if there is no obvious change. The 95% credible interval of λ in the time-trend N-mixture model is 0.76 to 1.10, indicating that gradual population decline cannot be ruled out.

In the following sections, I discuss the performance of the various single-year, unconstrained multi-year, and time-trend multi-year models separately, followed by the apparent nine-year trend in abundance of Hochstetter's frogs in Te Paparahi.

2.4.1 Performance of single-year models

Of the single-year models conducted in this chapter, capture-mark-recapture and N-mixture were the only single-year models that generated biologically reasonable and precise estimates of abundance. Single-count index models are well-established practices but do not provide estimates of a population's abundance. The probability of occupancy estimates generated in the single-year site occupancy model are good indicators of distribution, but when estimating abundance is the key objective, capture-mark-recapture and N-mixture models provide more reliable estimates than derived estimates of N from occupancy probabilities. This model is particularly susceptible to large numbers skewing the average. Median estimates of N derived from the probability of occupancy estimates are not easily compared to other models, so they cannot be recommended as an effective technique for estimating abundance with single-year datasets. Both CMR and N-mixture models estimated a similar pattern in the abundance of frogs in 2021, though the CMR model estimated abundance to be slightly higher than was estimated in the N-mixture model. I cannot be sure whether CMR is a more accurate estimator of abundance than N-mixture. However, as both models produced biologically sensitive and precise estimates (Table 2.7), I would recommend these as the preferred models for estimating the abundance of Hochstetter's frogs in future studies conducted in the Aotea region. A critical advantage of using a CMR model over N-mixture modelling was the incorporation of detection probabilities for newly-sighted and recaptured frogs. In both models, detection probability is imperfect. Still, no differentiation between the detection probability for recaptures and newly-sighted frogs can be seen as a limitation in the N-mixture model (Joseph et al., 2009).

In contrast, it not clear how effective the classification of recaptured individuals was because, under the CMR model, the estimated recapture probabilities were significantly lower than the initial capture probabilities. Behavioural changes such as the frogs moving or swimming away as a result of surveying are a possible source of variation that is likely to affect the probability of recapturing individuals between surveys (Fegatelli & Tardella, 2013). After being measured, some frogs jumped under rocks or into water pools which may have obscured them from view partially and made it harder to accurately measure them in subsequent surveys. Another implication of using capture-mark-recapture in future Hochstetter's monitoring research in the Te Paparahi region is that it is challenging to conduct many survey replicates. The three repeated surveys used in the single-year analyses are a relatively low sample size compared to studies with similar aims

(Ficetola et al., 2018), but with limited daylight hours and rugged survey terrain, only three surveys per transect were feasible. The third repeat survey is still likely to have been beneficial in improving the precision of analyses with a larger sample size.

2.4.2 Performance of unconstrained multi-year models

For the multi-year analyses, unconstrained N-mixture and site occupancy models were conducted to estimate abundance with a multi-year dataset of nine-years. The unconstrained multi-year N-mixture model is the model I recommend for estimating abundance in future Hochstetter's monitoring studies. The estimates generated in this model were both biologically feasible and precise. The N estimates derived from the unconstrained multi-year site occupancy model were unreliable, as was the case with the single-year equivalent of this model's estimates. Despite issues with unreliable derived N estimates in the site occupancy model, the probability of occupancy estimates generated in this model may prove helpful in research focusing on Hochstetter's distribution throughout the Te Paparahi region. The segment occupancy methodology in this model may also provide insight for population dynamics studies. A comparison between the abundance estimates generated in a multi-year unconstrained N-mixture model and a CMR model would be of great interest for future Hochstetter's frog surveys to assess whether a similar relationship to that of single-year models occurs.

The assumptions of the N-mixture (where p is derived from temporal replicates) and site occupancy models outlined by Royle (2004) and MacKenzie et al. (2002) were violated in this study to some extent. Both models assume an absence of unmodelled heterogeneity in abundance and detection, which was likely violated despite the best efforts of all surveyors. The complexity of the stream and surrounding riparian environment, coupled with the visually cryptic nature of Hochstetter's frogs, means there will likely be some variation that was not accounted for in the models. It is also possible that the closed population assumption was violated because at least one frog jumped and was carried downstream during surveying. It is possible this frog swam outside the 100 m transect boundary, which would classify as emigration.

2.4.3 Performance of time-trend multi-year models

The single-count index and N-mixture models had similar levels of precision, which were reflected in the models' estimates of the parameters $b.year$ and λ . When comparing these two models, the N-mixture model could produce abundance estimates, whereas temporal trends from single counts give an index of relative abundance.

I recommend using N-mixture models to estimate the abundance of the Hochstetter's frog population over time. The site occupancy model could not generate estimates for these parameters. The derived N estimates in this model were unreliable, as was the case with the single-year and unconstrained multi-year site occupancy models. Therefore, this model is unsuitable for a multi-year dataset that investigates temporal trends in abundance. Considering a capture-mark-recapture model for modelling population abundance over time would be valuable in future Hochstetter's frog monitoring research to investigate its precision compared to the N-mixture model used in this analysis.

2.4.4 Population trend between 2012 and 2021

The parameters $b.year$ and λ estimated in the single-count index and N-mixture models do not show a clear trend differing from 0. This is to say that when looking at the 95% credible interval, the population may be increasing, stable or decreasing. However, the λ estimate suggests that, like the mainland populations of Hochstetter's frogs (Bishop, 2013; Newman et al., 2010), the Aotea population of Hochstetter's frogs are also gradually declining. If such a decline is occurring, it may be a result of predation (rats, feral pigs or cats) or habitat degradation. The possibility of human interference caused by monitoring as an agent of decline cannot be ruled entirely either. I believe predation or another habitat degradation factor is a more likely cause of population decline than human disturbance because the surveys conducted had few replicates, and subsequent surveying infrequently occurred, once every 3-5 years. The effects of long-term gradual declines in abundance have been seen in other species in New Zealand, such as parakeets. The red-crowned parakeet (*Cyanoramphus novaezelandiae*), yellow-crowned parakeet (*Cyanoramphus auriceps*) and orange-fronted parakeet (*Cyanoramphus malherbi*) are three species of birds that were once common across mainland New Zealand in forests but have suffered gradual population declines that have reduced the species to near extinction in some areas (O'Donnell, 1996). Like the

Hochstetter's frog, mammalian predation and habitat modification are believed to be contributing factors to the decline of these species (Kearvell, 2016). Kearvell discusses preventative and reactive predator control as important actions for successfully re-introducing orange-fronted parakeets. Additionally, the possible rapid increase in the population of Hochstetter's frogs in Maungatautari has been attributed to the eradication of mammalian pest species (Longson et al., 2017). Another factor to consider is that with only three surveyed years of abundance data, the trend of population abundance is assumed to be linear, which may not be reflective. Changes in abundance often fluctuate, and these fluctuations are better reported in time-trend analyses that span multiple decades (Lester et al., 2017).

2.4.5 Conclusions

This chapter has identified that N-mixture modelling generates biologically feasible and precise estimates of Hochstetter's frog abundance in single-year and multi-year models. The single-year and unconstrained models in this analysis indicated population stability, but a temporal trend analysis has highlighted a possible slow decline in the Te Paparahi population abundance of Hochstetter's frogs. These findings stress the importance of consistent, long-term monitoring programs. The data for all three years suggests population stability, but this analysis has shown that this does not exclude the possibility of gradual decline. This level of estimate precision is possible due to a nine-year study period combined with effective analytic methodologies.



Individual Hochstetter's frog (*Leiopelma hochstetteri*) that was found under a rock in 2021 abundance surveys. Photo by: C.Johnson.

Chapter 3: An investigation of the drivers of abundance in Hochstetter's frog populations in northern Aotea

3.1 Introduction

Understanding factors that drive abundance is important for improving the precision of estimates of population parameters and for effective conservation management. In New Zealand, habitat loss and predation by invasive mammals are considered the primary causes of declines in *Leiopelma* populations (Bishop et al., 2013; Longson et al., 2017). While Aotea (/ Great Barrier Island) is free of some invasive predators, including mustelids (stoats *Mustela erminea*, weasels *Mustela nivalis* and ferrets *Mustela furo*), possums (*Trichosurus vulpecula*), hedgehogs (*Erinaceus europaeus*) and Norway rats (*Rattus norvegicus*). However, at least nine introduced mammal species are documented as being established in Aotea (Great Barrier Local Board, 2017). In the northern part of Aotea (Te Paparahi region of Aotea,) ship rats (*Rattus rattus*), kiore (*Rattus exulans*), mice (*Mus musculus*), feral cats (*Felis catus*) and pigs (*Sus scrofa*) are present and likely have a negative impact on the ecosystem. The abundance of these species in Te Paparahi is unknown, although observations suggest that the abundances of cats and pigs could be high and may have been for decades (Newman & Towns, 1985). It is assumed that ship rat abundance is high in Te Paparahi based on rat monitoring work carried out on other parts of the island (Barr, 2009; Ogden & Gilbert, 2009; Gronwald & Russell, 2020). However, there has been no attempt to date to investigate whether rat numbers are similarly high in Te Paparahi. Of the invasive predators in Te Paparahi, rodents are expected to be the most widely spread and likely to have a significant detrimental effect on Hochstetter's frog abundance (Egeter, 2014). Newman and Towns (1985) discuss the degradation of forest understory in areas of Te Paparahi by feral goats, pigs and other wandering stock. They also examine the extensive erosion and habitat deterioration in this area of Aotea and the accumulated silt in streambeds (Newman & Towns, 1985). The Hochstetter's frog occupies stream and stream adjacent habitats, usually in shaded areas of mature forest and riparian vegetation (Nájera-Hillman et al., 2009). Hochstetter's frogs are sensitive to habitat degradation, and areas with high sediment accumulation are not suitable for sustaining frog populations (Newman and Towns, 1985; Nájera-Hillman et al., 2009; Herbert et al. 2014).

This chapter will detail the outcome of rat tracking research conducted in May of 2022 and analyse the correlation between rat tracking and Hochstetter's frog abundance in combination with other habitat variables. The rat tracking was done in collaboration with the community research group Tu Mai Taonga. No mammalian predator monitoring had previously been conducted in the Te Paparahi region of Aotea, so the novel findings of this research do not have sample replicates. With time and budgetary constraints for this research, rodents were the primary focus of the predator monitoring as they were expected to be the most widely spread and likely to be having a significant detrimental effect on Hochstetter's frog abundance (Egeter, 2014).

The results of Chapter 2 suggested that the Aotea Hochstetter's frog population could be gradually declining, and an investigation into what could be driving a potential decline is needed to aid future conservation efforts. Rodent predation is a possible cause of the decline. The population shows no evidence of being affected by amphibian chytrid fungus (*Batrachochytrium dendrobatidis*), so this factor is not considered here. This disease was tested for at Te Paparahi in 2008 (Puig 2009) and is being monitored in some mainland *Leiopelma* populations but has not yet been documented in Hochstetter's frogs (Bishop et al., 2013).

In this chapter, I aim to (1) test the assumption of high rat abundance in Te Paparahi and (2) examine whether spatial variation in habitat characteristics and rodent relative abundance affected Hochstetter's frog abundance between 2012 and 2021.

3.2 Methods

In remote and isolated populations such as the Hochstetter's frog population in the Northern block of Aotea, Te Paparahi, habitat characteristics such as canopy plant species, stream condition, and the presence of rats and mice are the main factors I expect to influence abundance. Following the recommendations of Herbert et al. (2014) in their Spearman rank correlation analysis, the habitat covariates I will investigate are two tree species present in the subcanopy: patē (*Schefflera digitata*) and kanono (*Coprosma grandifolia*), and one stream

characteristic: frequency of waterfalls. Rat tracking rate was the fourth spatial covariate I investigated. Undergrowth characteristics were also recorded during sampling of this population but will not be considered in the analysis because the incidence of these undergrowth species was strongly correlated with the incidence of the subcanopy species considered.

3.2.1 Collection of habitat data

Habitat data were collected from the Hochstetter's frog transects in 2012 and 2021. The methodology for habitat data collection in 2012 is described in Herbert et al. (2014). Habitat data were not collected during the 2015 Hochstetter's frog surveys due to a reduced number of surveyors. The 2015 monitoring expedition had two surveyors, whereas five surveyors were available in 2012. With limited daylight hours and a reduced research team, the frog abundance surveys took precedence over the habitat characteristics surveys in this year. In 2021, the number of habitat variables recorded was reduced to those previously indicated to be important for the relative abundance of Hochstetter's frogs and the presence of juveniles (Herbert et al., 2014). These five habitat variables were: stream condition, stream substrate, undergrowth plant species, canopy/subcanopy plant species, water clarity, and stream depth in centimetres (Appendix 3a).

3.3.2 Rodent-tracking field methods

The 2022 rodent tracking research was conducted in collaboration with Tū Mai Taonga at the end of April / May in 2022. The predator tracking research was conducted at each of the Hochstetter's frog monitoring transects (Figures 3.1 and 3.2).

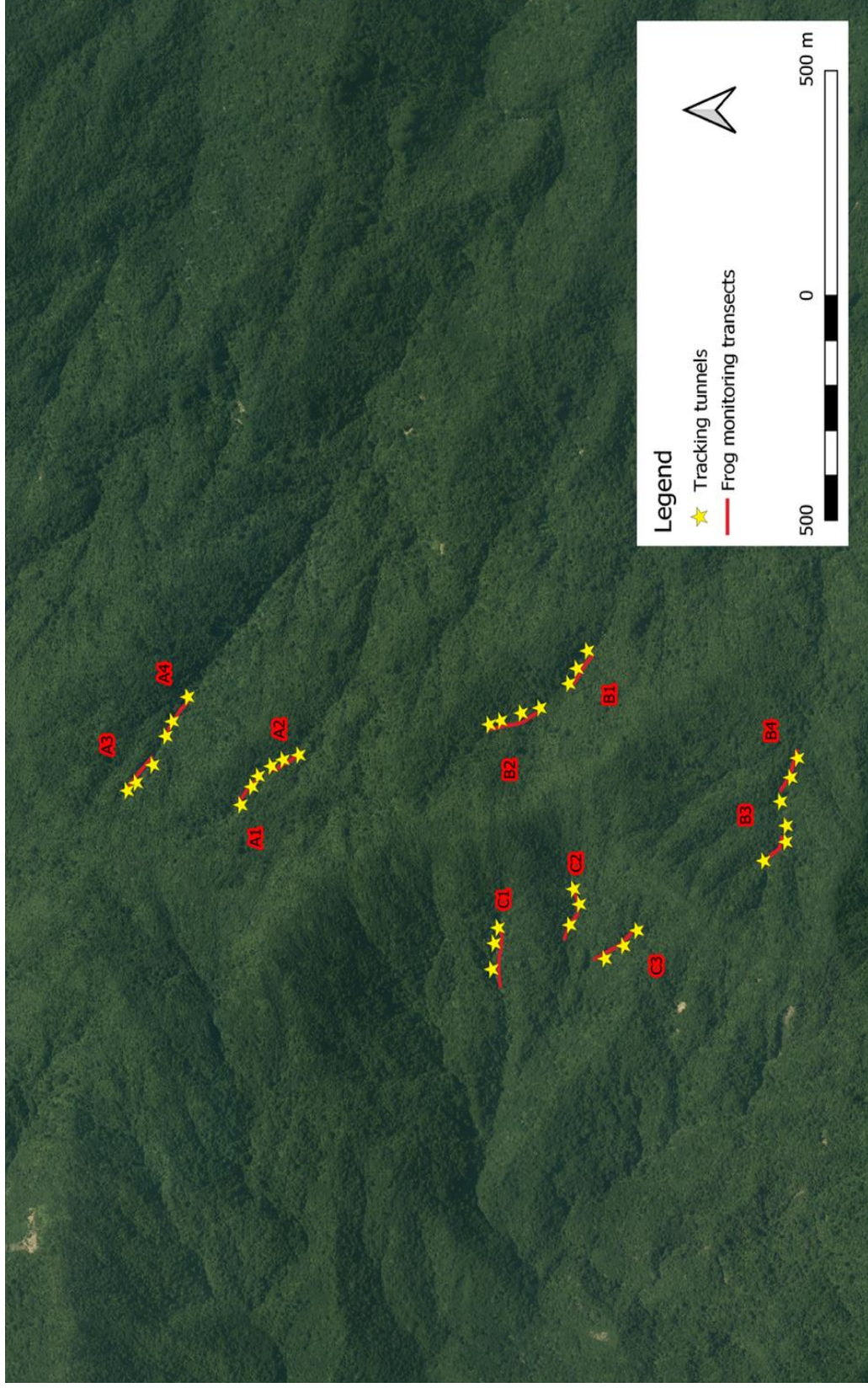


Figure 3.1: Transects A1, A2, A3, A4, B1, B2, B3, B4, C1, C2 and C3, where Hochstetter's frogs were monitored, vegetation and stream characteristics were recorded, and rat tracking was conducted. The red lines represent the approximate locations of transects used in Hochstetter's frog monitoring, and gold stars represent the locations of tracking tunnels used in rodent tracking in 2022. Map produced by S.Herbert.

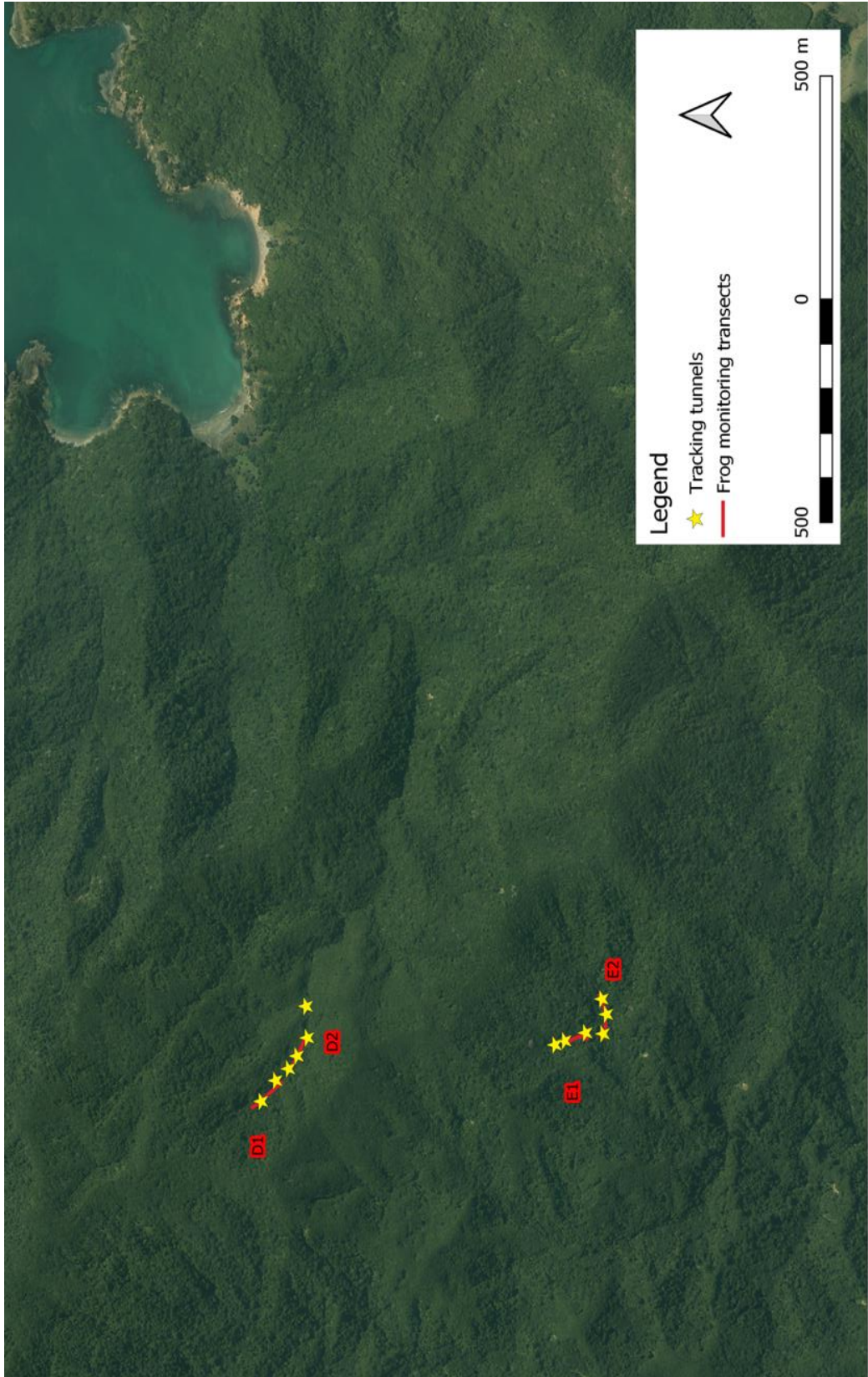


Figure 3.2: Transects D1, D2, E1 and E2 where Hochstetter's frogs were monitored, vegetation and stream characteristics recorded, and rat tracking was conducted. The red lines represent the approximate locations of transects used in Hochstetter's frog surveying, and gold stars represent the locations of tracking tunnels used in rodent tracking in 2022. Map produced by S.Herbert.

Three Black Trakka tunnels were allotted to each of 15 transects (45 tunnels total). The three tunnels were placed 50m apart along the streamside at each location, as per standard procedure to reduce miscounts (Blackwell et al., 2002). The Department of Conservation (DOC) Tracking Tunnel Guide V2 was used as a guide for this research (Gillies & Williams, 2013). A tracking paper and an ink pad were placed inside each tunnel. The tunnels were pegged into the ground using wire. This prevents the tunnels from moving in intense weather or with wildlife disturbance. As neophobia (fear of novel objects, such as food) is prevalent in rats (Wilmshurst & Carpenter, 2020), the tunnels were left *in situ* for three weeks at the start of April 2022 to allow rodents to acclimatise to their presence.



Figure 3.3: Two Black Trakka Tunnels *in situ*. The photo was taken on the day of installation before the three-week acclimation period. Photos by D. Braddock

Researchers returned to the tracking tunnels three weeks later to put an ink tracking card inside each. The tracking card for each tunnel was labelled with the transect number before heading into the field. To attract rodents, the tunnels were baited with peanut butter in the centre of each tunnel. All tracking cards were placed in the tunnels at each transect in one day rather than

multiple days to reduce temporal variance when conducting the post-survey analysis. The tracking cards were left for approximately 24 hours before being collected from all tracking tunnels. The tracking cards could not be placed into the tunnels on any days when it was raining heavier than a light drizzle to prevent the ink from running or damaging rodent prints needed for identification. When the cards were collected from the tunnels, each card was photographed for rodent identification in post-survey analysis.

3.2.3 Statistical analysis

An analysis was conducted using habitat data from 2012 and 2021, the frog repeated count data from 2012, 2015, and 2021, and the rodent tracking data collected in 2022. The designated habitat surveyor noted the presence or absence of patē, kanono and waterfalls at six points along each transect: 0 m, 20 m, 40 m, 60 m, 80 m and 100 m. At each of the six measurement points, the researcher scanned the overhanging subcanopy, canopy, and understorey within ± 2 m of the stream banks for each plant species (Appendix 3a). If the plant species or a waterfall was present, it was circled on the habitat sheet. The average of each variable was taken to calculate a score from 1-0 averaged for each transect. The average of the scores from 2012 and 2021 was used in the model (Table 3.1). The pate, kanono and waterfalls scores were considered environment covariates, and rodent tracking rate was used as the rat covariate. The rodent tracking conducted in 2022 gave new data for the Te Paparahi region of Aotea; therefore, there are no survey replicates for this covariate. To ensure the drivers of abundance analysis are comparable to the abundance estimates generated in Chapter 2, I adapted the OpenBUGS code used in that chapter.

Because some transects are close together (within 100 m), rat tracking rates were calculated independently for seven clusters rather than for each of the 15 transects (Table 3.1). Because of the proximity of some transects, rats may be able to travel between the transects, impairing their independence. The home range of ship rats in a riparian environment can exceed 100 m² (Whisson et al., 2007). Some of the frog transects were less than 100 m apart and thus may not have been spatially independent for ship rats. The tracking rate for rats (*Rattus* spp.) and mice was calculated as the proportion of tunnels tracked in each cluster. No attempt was made to distinguish kiore footprints from those of ship rats.

Table 3.1: Two or more transects within 100 m of each other were grouped into seven clusters for analysing the correlation between rat tracking and Hochstetter's frog abundance.

Cluster-ID	Transects grouped	No. tunnels	Rat tracking rate
1	A1, A2	6	0.867
2	A3, A4	6	0.833
3	B1, B2	6	0.000
4	B3, B4	6	0.000
5	C1, C2, C3	9	0.667
6	D1, D2	6	0.500
7	E1, E2	6	0.333

The time-trend multi-year N-mixture model constructed in Open BUGS in Chapter 2 was adapted to incorporate the effects of the additional habitat covariates and rodent parameters. Only the rat tracking data were used in this model because no mice were detected by the tracking tunnels. The detection component of this model remains unchanged from that used in all models in Chapter 2 (Equation 2.3, Equation 2.5).

The log-linear relationship used in the N-mixture time-trend model in Chapter 2 (Equation 2.12) was extended in this model to incorporate the habitat and rodent parameters. The log-linear relationship of expected abundance ($\mu[i]$) over time was modelled with the habitat parameters as fixed effects and the residual variation among transects as a random effect. This relationship is represented by the code:

$$\log(\mu[i]) <- a.n + b.year*(year[i]-2012) + re.trans.n[transect[i]] + b.pate*pate[transect[i]] + b.kanono*kanono[transect[i]] + b.waterfalls*waterfalls[transect[i]] + b.rat*rat[cluster[i]]$$

Where $a.n$ is the intercept; $b.year$ is the effect of the number of years elapsed since the initial year of sampling (2012); $b.pate$, $b.kanono$, $b.waterfalls$ and $b.rat$ are the fixed effects of patē,

kanono, waterfalls and rat tracking respectively, and *re.trans.n* is the residual random effect of the transect.

For the abundance component of this model, the priors for the intercept (*a.n*) and year effect (*b.year*) prior remain the same as in the time-trend models used in Chapter 2, Equation 2.12. The prior distributions for the habitat parameters were kept broad to ensure they were as uninformative as possible. The priors for the year, three habitat covariates and rat tracking rates were $\sim dnorm(0,0.1)$.

The incorporation of the habitat parameters in this model adds a new source of variance and therefore widens the prior distribution for the number of frogs on each transect. The prior for residual standard deviation among transects meant *s.trans.n* (Equation 2.8) needed to be narrowed to compensate and to allow model convergence. The new prior was to resolve the distributions for each habitat covariate:

$$s.trans.n \sim \sim dunif(0,3) \quad \text{Equation 3.1}$$

3.3 Results

The 45 tracking cards from the Black Trakka tunnels indicated that rat species were likely the only species to have been tracked in this research. The rat tracking rate across the 45 tunnels was 0.47 and ranged from 0–0.87 among clusters (Table 3.2).

The average number of habitat covariates in each transect (2012 and 2022) is provided in Table 3.2. The average of both years was calculated for N-mixture modelling.

In 2012, waterfalls were present in 8 of the 15 transects. Patē was observed in 11 out of the 15 transects, and kanono was observed in 9 of the 15 transects. In 2021 waterfalls were observed in 7 of the 15 transects. In 2021, patē was also recorded in 11 of the 15 transects, and kanono was found in 12 of the 15 transects.

Table 3.2: Average of binary (present / not present) habitat characteristics on each transect in 2012 and 2021, the averages between those two years which were used as the habitat covariates in the analysis, and the 2022 rat tracking rate which was also used as a covariate in the analysis.

	2012			2021			Average			2022
	Waterfalls	Patē	Kanono	Waterfalls	Patē	Kanono	Waterfalls	Patē	Kanono	Rat
A1	0.00	0.00	0.83	0.00	0.50	1.00	0.00	0.25	0.92	0.86
A2	0.66	0.33	0.33	0.16	0.66	0.83	0.41	0.50	0.58	0.86
A3	0.50	1.00	0.83	0.50	0.50	0.50	0.50	0.75	0.67	0.83
A4	0.50	1.00	0.83	0.16	1.00	1.00	0.33	1.00	0.92	0.83
B1	0.16	0.16	0.33	0.16	0.50	1.00	0.16	0.33	0.67	0.00
B2	0.00	0.16	0.50	0.00	0.83	1.00	0.00	0.50	0.75	0.00
B3	0.20	0.16	0.16	0.00	0.33	0.83	0.10	0.25	0.50	0.00
B4	0.16	0.00	0.00	0.16	0.33	0.66	0.16	0.17	0.33	0.00
C1	0.00	0.16	0.16	0.00	0.50	0.83	0.00	0.33	0.50	0.66
C2	0.33	0.33	0.00	0.16	0.33	0.83	0.25	0.33	0.42	0.66
C3	0.16	0.16	0.66	0.00	0.00	1.00	0.08	0.08	0.83	0.66
D1	0.00	0.33	0.00	0.00	0.16	0.16	0.00	0.25	0.08	0.50
D2	0.00	0.00	0.00	0.00	0.50	0.16	0.00	0.25	0.08	0.50
E1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33
E2	0.00	0.16	0.00	0.16	0.00	0.00	0.08	0.08	0.00	0.33

3.3.1 Effect of vegetation and waterfall covariates

Of the four habitat covariates investigated, kanono was the only variable with a significant effect, i.e., the 95% credible interval does not include zero (Table 3.3). The effect size for kanono is 2.98 (SD \pm 1.02), so we can be confident that kanono is positively correlated with frog abundance (Figure 3.4). The effect size for waterfalls was 1.40 (SD \pm 1.74), and for patē was 0.48 (SD \pm 1.30). The 95% credible intervals for these covariates included zero, so it is unclear whether these covariates are correlated with abundance. The estimated effect size of waterfalls and patē are also smaller, indicating that even if these covariates were correlated with frog abundance, the effects would likely not be as strong as that of kanono.

Table 3.3: Mean, median, standard deviation (SD) and 95% credible intervals (2.5% and 97.5%) for detection and abundance parameters in the time-trend N-mixture model with habitat covariates. p is the detection probability for frogs found in one or more previous surveys.

Parameter	Parameter definition	Mean	SD	2.5%	Median	97.5%
a.p	The intercept which represents the logit of detection probability for an average survey	-0.76	0.38	-1.55	-0.75	-0.02
s.j.p	Standard deviation in logit detection probability among the three surveys	0.37	0.22	0.09	0.31	0.91
p[1]	Probability of detecting a frog in the first survey	0.35	0.07	0.21	0.35	0.49
p[2]	Probability of detecting a frog in the second survey	0.27	0.05	0.16	0.27	0.39
p[3]	Probability of detecting a frog in the third survey	0.30	0.06	0.18	0.30	0.43
a.n	Intercept for log(abundance)	0.52	0.52	-0.52	0.52	1.53
b.year	The effect of year on log(abundance)	0.52	0.52	-0.52	0.52	1.53
b.waterfalls	Effect of waterfalls on log(abundance)	1.40	1.74	-2.05	1.38	4.83
b.kanono	Effect of kanono on log(abundance)	2.98	1.02	0.87	3.01	4.91
b.pate	Effect of patē on log(abundance)	0.48	1.30	-2.05	0.46	3.17
b.rat	Effect of rat tracking rate on log(abundance)	0.83	0.84	-0.80	0.82	2.54

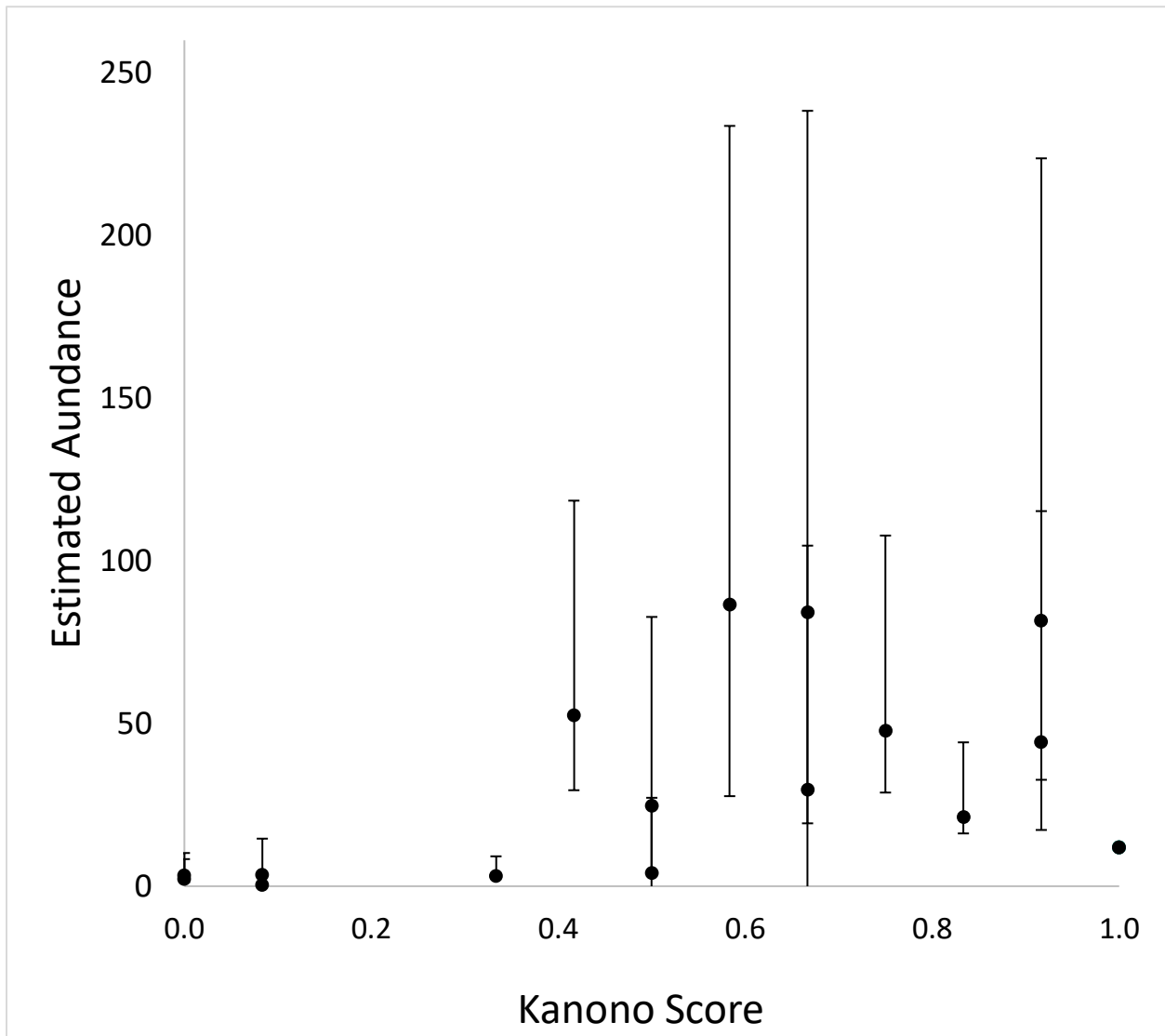


Figure 3.4: The estimated abundance of Hochstetter's frogs in 15 100-m transects on Aotea in 2021 in relation to the proportion of points with kanono present in each transect. Error bars show 95% credible intervals.

3.3.2 Effect of rat tracking

The rat tracking rates in the seven clusters in 2022 ranged from 0–87% (Table 3.2). Rat footprints (ship rat and/or kiore) were the only observed footprints on the tracking cards of the 45 tracking tunnels.

The estimated effect size of the rat tracking rate on frog abundance was 0.83 (SD \pm 0.84). This effect size was insignificant as the lower credible limit for this effect is -0.80, and the upper

credible limit is 2.54. Tunnel 108 (Transect B2) was found partially buried, likely due to disturbance from feral pigs (Figure 3.5). Rat tracking was highest in Catchment A transects, which were the transects that had the highest estimates of frog abundance (Chapter 2). Similarly, rat presence was the lowest in Catchment D and Catchment E, the two catchments with the lowest estimates of frog abundance (Chapter 2). However, catchment B was the only catchment with no detected presence of rodents, with all B transects having no recorded tracks. Frog abundance was reasonably high in catchment B transects; hence this was the exception to the otherwise positive correlation between rats and frogs.



Figure 3.5: Photograph of Tunnel 108 on Transect B2 found partially buried. Photo by: D. Braddock.

3.4 Discussion

From this investigation into the possible factors that drive Hochstetter's frog abundance, I can make inferences about whether significant relationships exist between abundance and two subcanopy species, kanono and patē, waterfall presence, and rat tracking.

The results of this study reveal possible correlations between habitat covariates and abundance and should not be misinterpreted for causation (Hilborn, 2016). Kanono was the only habitat covariate identified as having a significant relationship with abundance in this study. The data from the rodent tracking tunnels yielded a statistically insignificant positive correlation, indicating that Hochstetter's frog abundance tended to be higher in transects where rat tracking was higher but that this could have occurred by chance. Because only one survey was conducted with a small number of tracking tunnels, this result was expected and is not an unusual finding for this study.

3.4.1 Habitat covariates

Numerous *Coprosma* species are abundant throughout the Te Paparahi region, as can be expected across an area with various soil and rock types (Wright & Cameron, 1985). Kanono was the dominant *Coprosma* species near the fifteen transects in the initial 2012 Hochstetter's frog surveys (Herbert et al., 2014). Of the habitat covariates, kanono is the only covariate found to be moderately strongly correlated with abundance when modelling with a Poisson N-mixture model. The findings of this study further support the suspected correlation between kanono and abundance found by Herbert et al. (2014). In the 2014 study, this correlation had a Spearman's ρ of 0.69. A positive correlation between kanono and Hochstetter's frog abundance is not entirely surprising, as the preferred habitat of the Hochstetter's frog is shaded, cool and moist.

The insignificant correlation between frog abundance, the subcanopy species patē, and the incidence of waterfalls is surprising because of the Hochstetter's frogs habitat preferences. The Hochstetter's frog displays a preference for non-silted streams and areas of fast-flowing water (Nájera–Hillman et al., 2009), and as waterfalls are less prone to trapping sediment, they are ideal habitats for Hochstetter's frogs. This result may be because waterfall incidence is a dynamic

variable rather than a more static variable like canopy species, and flooding events or minimal rainfall may impact waterfall frequency.

The 2015 survey (Herbert & Gilbert, 2015) noted that Hochstetter's frogs might be able to persist in degraded habitats, as frogs were found in sedimented areas upstream and directly downstream of a landslide on Transect B2. For this reason, the stream conditions recorded here may not be a significant driving influence on frog abundance.

3.4.2 Rat tracking

Currently, all populations of Hochstetter's frog coexist with introduced mammalian predators, though the extent of their impact on Hochstetter's frog abundance is unclear (Nájera–Hillman et al., 2009; Longson et al., 2017). Nájera–Hillman et al. (2009) investigated a Hochstetter's population in the Waitakere Ranges concerning the effect of habitat characteristics and rodent predation. Their study was also conducted using generalised linear models with an assumed Poisson error distribution and log link function. Habitat characteristics such as percentage of boulders and percentage cover of water covering an area were significantly correlated with frog abundance, but the presence or absence of pest management operations did not significantly influence abundance. However, their study did not attempt to estimate detection as only single counts of frogs were used. A study by Crossland et al. (in press) also discusses a potentially strong correlation between the predator control history of sites and the occupancy of Hochstetter's frogs. This study indicates that predator control may be a beneficial measure for Hochstetter's frog populations, as it found that juvenile, sub-adult and adult frogs were consistently more abundant at sites where intensive predator control was undertaken.

The rat tracking rate calculated from the 2022 data was lower than expected for forested sites in close proximity to streams. Barr (2009) conducted rat tracking in the Port Fitzroy area of Aotea in 2008 and found rat tracking rates of > 0.80 in two of the four sites. I expected rat detection rates to be high because this research was conducted in Autumn, a season where rat abundance is often high (Murphy et al., 1998; Balls, 2019). Armstrong et al. (2014) noted that rat tracking rates were high in fragments with dense understorey (ca. 0.50-0.90). The low rat tracking rate calculated in this study is likely due to the research being conducted with a small sample size.

Future research should conduct rat tracking over multiple months to improve the sample size and consider seasonality.

The results of my research indicate that there may be a positive correlation between frog abundance and rat tracking rate, with an effect size of 0.82, but the 95% credible interval for this parameter indicates that I cannot be sure this parameter is correlated with frog abundance. The preferred habitat of rats is similar to that of the Hochstetter's frog in shaded, cool and moist riparian environments (Stroud, 1982; Baber et al., 2006). A likely explanation for this correlation is that the rats coexist in the same environmental niche as Hochstetter's, making detecting any effect on frog abundance difficult. This is not to say that the Hochstetter's frog is not declining as a result of rat predation, but rather that further survey replicates from these tracking tunnels are needed to make conclusions about the nature of any correlation between rat and frog abundance. The rat tracking rates in the Catchment B tracking tunnels were 0, and average/moderate estimates of frog abundance were found in this catchment (Chapter 2). It cannot be said that a lack of rat detection equals a lack of rat presence in Catchment B, and further rat tracking in this area would be beneficial. With rat tracking data from only 2022, I assumed that these results were representative of all years. It is unlikely that the tracking rates found in 2022 represent all years since 2012. Still, there are no existing historical data from this region that can be considered at this time. Repeating this tracking research in future studies would improve the reliability of this dataset.

Leiopelma can probably persist in non-ideal habitats for extended periods, sometimes leading to incorrect assumptions of population stability (Easton, 2015). This could explain a gradual decline of the Aotea Hochstetter's population over the nine-year survey period if such a decline is occurring. Rat tracking should be further investigated in this region in future monitoring efforts of Hochstetter's frog to identify whether any temporal trends are occurring and if they can be linked to the gradual decline of the Aotea Hochstetter's frog population.

3.4.3 Possible agents of decline

Identifying the agents of population decline is complex, and often numerous factors contribute to the decline in varying degrees (Beebee & Griffiths, 2005). Mammalian predation has been

discussed as a significant agent of decline for many amphibian populations. However, the research findings in this chapter do not give any evidence that variation in rat abundance among the 15 transect locations explains the observed variation in Hochstetter's frog abundance. This study does not include multiple survey replicates due to time and budgetary restraints, so it may not reflect the true correlation between rodents and Hochstetter's frogs, and further predator tracking in the Te Paparahi region would clarify the nature of the correlation. Future predator monitoring could also incorporate motion-sensitive cameras to detect feral pig and cat presence surrounding the transect locations (Anton et al., 2018). Feral pigs have been noted to contribute to riparian degradation and likely destroy frog habitats through foraging behaviours in and around the streambed (Towns & Daugherty, 1994; Baber et al., 2006; Bishop et al., 2013; Herbert & Gilbert, 2015). Baber et al. (2006) discuss that feral pigs are also likely to kill Hochstetter's frogs opportunistically, and so the Aotea population would likely benefit from pig control measures in Te Paparahi.

Chapter 4: General Discussion

4.1 General Discussion

In this thesis, I considered three statistical analyses using a Bayesian framework and a comparison of an index of abundance to estimate the abundance of the Hochstetter's frog population in 15 fixed locations in Te Paparahi, Aotea / Great Barrier Island.

These analyses were conducted using count or presence/absence data collected using a double surveyor method (2012 and 2015) or a triple surveyor method (2021) on a transect in a single day. While this method was not ideal, conducting all repeat transect surveys in one day instead of over multiple days was necessary for this study because of time and resource limitations. This method also increased surveying efficiency by reducing the time spent travelling to and from difficult-to-access transects. Conducting the multiple surveyor protocol on a transect was also safer than if researchers were to split up and rotate around transects, an important consideration when conducting surveying in remote and steep regions like Te Paparahi. The four statistical methods considered in this thesis were all shown to have practical functions for use in Hochstetter's frog abundance monitoring. Using N-mixture analyses and Bayesian inferencing was beneficial for estimating the abundance of the Aotea Hochstetter's frog population. Of the analyses conducted, capture-mark-recapture and N-mixture models yielded ecologically feasible and reasonably precise estimates of frog abundance. While the abundance estimates produced in the site occupancy models were generally unreliable, understanding occupancy at the segment level is practical for future population dynamics research on this species. A possible gradual decline (figures 2.3 and 2.4) in the Aotea population of Hochstetter's frogs over a nine-year survey period has been identified, although the cause remains speculative. Rodent tracking rates were found to be low in Te Paparahi compared to the tracking rates found in other parts of Aotea (Barr, 2009). A significant correlation between kanono (*Coprosma grandifolia*) and Hochstetter's frog abundance was identified in the habitat covariate analysis component of this research. The main limitations and research recommendations for future Hochstetter's frog abundance monitoring in Aotea are discussed in this chapter, as well as opportunities to expand on the findings of this thesis.

4.2 Summary and Conclusions

4.2.1 Rodent tracking research

Mammalian predation is considered a major factor in the decline of New Zealand amphibians, with rodents (*Rattus* spp.) likely the largest mammalian threat for *Leiopelma* frogs (Innes, 2001; Bishop et al., 2013; Egeter et al., 2016). As of June 2022, no control of mammalian predators has been conducted in the Te Paparahi region of Aotea, but the rodent tracking tunnels that we have installed in the 15 transect locations have yielded novel rat tracking data and the opportunity to further investigate rodent activity along streams that Hochstetter's frogs occupy. The 2022 tracking tunnels have been left *in situ* for continued use by Tu Mai Taonga. Repeat surveys of the tracking tunnels in this region are needed to confirm that the rodent tracking rates calculated in this study are reflective of their true abundance in Te Paparahi. The rat tracking methodology conducted in this research could be extended to include additional traps in different Te Paparahi environments (i.e. ridgelines) and in various months of the year to examine any seasonality patterns. I recommend that long-term trends of rodents should be investigated in this region through the continuation of tracking tunnels. While predator control measures such as trapping and strategically pulsed toxin baits have been implemented in other parts of the island with little success in suppressing rodent abundance, hunting may be an option for reducing feral pigs in this region (Ogden & Gilbert, 2009). The extent to which pigs are impacting Hochstetter's frog abundance is unknown. However, anecdotal evidence from hunters near Whatipu has found up to nine Hochstetter's frogs in the stomach contents of a wild pig (per comms. S.Melzer). Additionally, habitat destruction through vegetation removal and increased nitrate levels in the soil is a growing concern associated with feral pig presence around streams occupied by Hochstetter's frogs (Krull et al., 2013). This research may benefit from further investigations into the abundance of feral pigs in the Te Paparahi region.

4.2.2 Hochstetter's frog population research and model design

Future research in Hochstetter's frog population abundance in Aotea should investigate the precision of estimates generated in multi-year capture-mark-recapture analyses. I could not consider this model type in this thesis due to insufficient variables in historical datasets necessary for facilitating multi-year analysis. This model requires a binary 'side of transect' value to denote whether a frog was encountered on the transect line's left (0) or right (1) during abundance

surveying and a measure of each frog's perpendicular distance to the central transect line. These variables were necessary to distinguish between 'newly captured' frogs and 'recaptured frogs' in the data matrix. I recommend the continued collection of frog position data for use in CMR analyses. However, the frog position differentiation method should only be conducted in studies where all surveys of a transect are completed in a single day, as it is assumed that frogs do not move between surveys. As the single-year CMR analysis was found to generate meaningful estimates of abundance in a single-year dataset, future studies should consider estimating Hochstetter's frog abundance in this region by conducting a series of closed-population Capture-mark-recapture. This study has found that ecologically feasible estimates of abundance can be generated by using the position of frogs in a transect as a proxy for individual identification. This sidesteps the need for invasive 'marking' measures such as toe clipping, and further investigation into multi-year CMR studies may be promising (Baber et al., 2006)

Another potential limitation of this research was not incorporating varying detection probabilities among transects in the models. In this thesis, estimating detection probability 1.) allowed me to estimate absolute abundance as opposed to having an index and 2.) Possibly model variation in detection probability over space (among transects) and time (among years). Modelling variation spatially and temporally would be beneficial to avoid misleading inferences about the abundance that may result from variation in detection probability. The absence of varying detection probabilities meant that transect conditions were assumed to be consistent. It may be reasonable to assume that detection probability is constant spatially (among transects) and temporally (among years). Constant detection probability among transects is likely the reason the estimates of the single-count index model were similar to the estimates of the N-mixture model in the multi-year analyses. For all years of the study, streams would only be surveyed if the conditions were similar to that of the previous survey period, i.e. only 80 m of transect C3 was surveyed in 2021 due to a landslide subsequent to surveying in 2015. Additionally, at least one researcher (Sarah Herbert) was present in conducting surveying for all nine years of the study period. These factors may not be consistent for all monitoring studies, and in those cases, it is essential that spatial or temporal variation in detection probability is accounted for. In future research, adding covariates for detection probability may improve this design.

Altitude is a factor that was not considered in this research, but it may affect the local abundance of Hochstetter's frogs. The effects of altitude on Hochstetter's abundance have not been investigated in surveys of the Aotea population in Te Paparahi because two of the lower altitude fixed sites had kanuka-dominant regenerating forests; therefore, the effects of forest types cannot be separated from those of altitude. A possibility for considering altitude as a variable in future abundance monitoring of this population would be to estimate frog abundance in several transects over an altitudinal gradient that are nested within the same catchment. The forest in the lower reaches of Catchments A, B and C are likely less modified than the catchments in more accessible parts of Te Paparahi and so may make good candidates for monitoring that investigates altitude. The Archey's frog (*Leiopelma archeyi*) is sympatric with some mainland Hochstetter's frog populations and has an ideal altitudinal range of 400–1,000 m asl (Bishop et al., 2009). Hotham et al. (in press) found Archey's frog abundance was high at both ends of the altitudinal range they examined (149 m - 448 m asl), with a positive correlation between elevation and frog abundance identified. Research into the lowest altitude Hochstetter's frogs can inhabit and breed on Aotea may help inform future translocation efforts for this species. Understanding which populations on Aotea are breeding (and persisting) may also be useful for prioritising conservation efforts, such as targeting predator control in possible areas of source populations rather than habitat sinks.

4.3 Conclusions and Implications for the future

While this species remains relatively abundant in Te Paparahi, with transects in Catchment A all estimated to be inhabited by 90+ frogs, consistent monitoring should be continued. The findings from this research based on nine years of monitoring have identified that the population of Hochstetter's frogs on Aotea Great Barrier Island could be experiencing a gradual decline in abundance. The cause of this decline remains unclear, but rat presence was confirmed in all transect clusters except clusters 3 and 4 (Table 3.1) in Catchment B. The Black Trakka tunnels installed in the 2022 rodent tracking component of this research were left in place for future use in the long-term monitoring and management of mammalian predators in Te Paparahi.

Consistent and long-term monitoring of this species will play an essential role in determining the long-term trend in abundance, identifying possible agents of decline, and informing adaptive conservation management of the Hochstetter's frog population on Aotea.

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Appendix 1a: OpenBUGS script for the single-year capture-mark-recapture model

Single year - Capture-mark-recapture

```
list(N=c(29,28,30,19,8,28,1,1,7,24,9,2,0,1,2)) # initial values
```

```
Model {
```

```
  # Detection model
```

```
  a.p ~ dnorm(0,1)      # intercept of logit of detection probability (p)
  b.B ~ dnorm(0,1) #I(,0) # negative effect of capture on detection probability
  s.j.p ~ dunif(0,1)    # standard deviation among surveys in logit p
  tau.j.p <- pow(s.j.p,-2) # tau is converting SD to precision (tau = 1/sd^2)
```

```
  for (j in 1:n.surveys) {      # j = survey number (1,2 or 3)
    re.j.p[j] ~ dnorm(0, tau.j.p) # assign survey random effect on detection probability
    logit(c[j]) <- a.p+re.j.p[j] # calc. probability of first capture
    logit(p[j]) <- logit(c[j])+b.B # calc. probability of recapture
  }
```

```
  # Abundance model
```

```
  for (i in 1:n.transects) {
```

```
    a.n[i] ~ dnorm(0,0.1)      # the log transformed expected N
    log(mu[i]) <- a.n[i]      # a log normal poisson prior - expectation of number of frogs on each transect
    N[i] ~dpois(mu[i])
```

```
    U[i,1] <- N[i]           # initially all individuals are unmarked
    M[i,1] <- 0              # and no individuals are marked
```

```
    for (j in 1: n.surveys) { # for each sampling occasion
      u[i,j] ~ dbin(c[j],U[i,j]) # sample no. new found from no. unmarked present
      m[i,j] ~ dbin(p[j],M[i,j]) # sample no. marked found from no. marked present
      U[i,j+1] <- U[i,j]-u[i,j]
      M[i,j+1] <- M[i,j]+u[i,j]
    }
```

```
  }
  logit(c.ave) <- a.p      # average detection prob. for unmarked frog
  logit(p.ave) <- a.p+b.B # average detection prob. for marked frog
```

```
}
```

Appendix 1b: OpenBUGS script for the single-year N-mixture model

Single-year, N-mixture version

Model {

Capture effect uncommended; note that constraint also removed

a.p ~ dnorm(0,1) # intercept of logit of detection probability (p)

s.j.p ~ dunif(0,1)

tau.j.p <- pow(s.j.p,-2)

for (j in 1:n.surveys) {

re.j.p[j] ~ dnorm(0, tau.j.p) # assign survey random effect on detection prob.

logit(p[j]) <- a.p+re.j.p[j] # calc. prob of capture

}

for (i in 1:n.transects) {

a.n[i] ~ dnorm(0,0.1)

log(mu[i]) <- a.n[i]

N[i] ~ dpois(mu[i])

for (j in 1:3) { # for each sampling occasion

n[i,j] ~ dbin(p[j],N[i]) # sample no.of frogs found from no. of frogs present in transect (N)

}

}

logit(p.ave) <- a.p # average detection prob. for unmarked frog

Appendix 1c: OpenBUGS script for the single-year Site occupancy model

Single year - Site occupancy (with abundance derived)

```
Model {  
  
  # Detection model  
  
  a.p ~ dnorm(0,1) # logit of average detection probability.  
  s.j.p ~ dunif(0,1) # Standard deviation among surveys in logit p  
  tau.j.p <- pow(s.j.p,-2) # Tau is converting SD to precision (tau = 1/sd^2)  
  
  for (i in 1:n.transects) { #i = transects  
  
    a.n[i] ~ dnorm(0,0.1)  
    log(mu[i]) <- a.n[i]  
    N[i] ~ dpois(mu[i])  
    p.occ[i] <- 1-exp(-N[i]/10) # probability of any 10m segment on the transect being occupied  
  
  }  
  
  for (j in 1:n.surveys) { # j = survey number (1,2 or 3)  
    re.j.p[j] ~ dnorm(0, tau.j.p) # re = random effect. ~ = sampling from a distribution  
    logit(p[j]) <- a.p+re.j.p[j] # adds random effect to each transect  
  
  }  
  
  for (k in 1:n.segments) { # k = segments  
  
    occ[k]~ dbern(p.occ[transect[k]]) # p. occ of segment k idepends upon on what transect you're in.  
    for (j in 1:n.surveys) {  
      presence[k,j] ~ dbern(p.frogsdetected[k,j]) # presence = whether or not a frog was observed in  
                                                    segment k on occassion j  
      p.frogsdetected[k,j] <- occ[k]*p[j] #prob of seeing a frog depends on whether the frogs are there and  
                                           the probability of seeing the frogs that are there  
    }  
  }  
  
}
```

Appendix 2a: OpenBUGS script for the multi-year unconstrained N-mixture model

Multi-year unconstrained - Nmixture

```
list(N=c(0,29,38,17,20,10,7,0,12,14,3,3,0,1,1,30,35,54,12,16,13  
,4,2,26,11,3,0,1,3,0,29,28,30,19,8,28,1,1,7,24,9,2,0,1,2)) # initial values
```

```
Model {
```

```
  # Detection model
```

```
  a.p ~ dnorm(0,1)      # intercept of logit of detection probability (p)  
  s.j.p ~ dunif(0,1)    # standard deviation among surveys in logit p  
  tau.j.p <- pow(s.j.p,-2) # tau is converting SD to precision (tau = 1/sd^2)
```

```
  for (j in 1:n.surveys.max) {  
    re.j.p[j] ~ dnorm(0, tau.j.p) # assign survey random effect on detection prob.  
    logit(p[j]) <- a.p+re.j.p[j] # calc. prob of first capture  
  }
```

```
  # Abundance model
```

```
  for (i in 1:n.rows) {
```

```
    a.n[i] ~ dnorm(0,0.1)      # the log transformed expected N  
    log(mu[i]) <- a.n[i]      # a log normal poisson prior - expectation of number of frogs on each transect  
    N[i] ~ dpois(mu[i])
```

```
    for (j in 1:n.surveys[i]) { # for each sampling occasion  
      n[i,j] ~ dbin(p[j],N[i]) # sample no. new found from no. unmarked present  
    }
```

```
  }  
}
```

Appendix 2b: OpenBUGS script for the time-trend N-mixture model

Multi-year - Time trend N-mixture

```
list(N=c(0,29,38,17,20,10,7,0,12,14,3,3,0,1,1,30,35,54,12,16,13
,4,2,26,11,3,0,1,3,0,29,28,30,19,8,28,1,1,7,24,9,2,0,1,2)) # initial values

Model {
# Detection model

a.p ~ dnorm(0,1)          # intercept of logit of detection probability (p)
s.j.p ~ dunif(0,1)
tau.j.p <- pow(s.j.p,-2)

for (j in 1:n.surveys.max) {
  re.j.p[j] ~ dnorm(0, tau.j.p) # assign survey random effect on detection prob.
  logit(p[j]) <- a.p+re.j.p[j] # calc. prob of capture
}

# Abundance Model
a.n ~ dnorm(0,1)
b.year ~ dnorm(0,1)
s.trans.n ~ dunif(0,5)
tau.trans.n <-pow(s.trans.n,-2)

#Derived parameters

lambda <-exp(b.year)
lambda9 <-pow(lambda,9) # converts lambda to show changes to abundance over 9 year timeframe

for (i in 1:n.transects) {
  re.trans.n[i] ~ dnorm(0, tau.trans.n) # assign transect random effect on abundance
}

for (i in 1:n.rows) {
  log(mu[i] <- a.n + b.year*(year[i]-2012 + re.trans.n[transect[i]])
  N[i] ~ dpois(mu[i])

  for (j in 1:n.surveys[i]) { # for each sampling occasion
    n[i,j] ~ dbin(p[j],N[i])
  }
}
}
```

Appendix 2c: OpenBUGS script for the multi-year unconstrained site occupancy model

Multi year - Site Occupancy (with abundance derived)

```
Model {  
  
  # Detection model  
  
  a.p ~ dnorm(0,1) # logit of average detection probability.  
  s.j.p ~ dunif(0,1) # Standard deviation among surveys in logit p  
  tau.j.p <- pow(s.j.p,-2) # Tau is converting SD to precision (tau = 1/sd^2)  
  
  for (j in 1:n.surveys) { # j = survey number (1,2 or 3)  
    re.j.p[j] ~ dnorm(0, tau.j.p) # re = random effect. ~ = sampling from a distribution  
    logit(p[j]) <- a.p+re.j.p[j] # adds random effect to each transect  
  }  
  
  # Occupancy model  
  
  for (i in 1:n.transect.year) { #i = transects  
  
    a.n[i] ~ dnorm(0,0.1)  
    log(mu[i]) <- a.n[i]  
    N[i] ~ dpois(mu[i])  
  
    p.occ[i] <- 1-exp(-N[i]/10) # prob. of any 10m segment on the transect being occupied  
  
  }  
  
  for (k in 1:n.segments) { # k = segments  
  
    occ[k]~ dbern(p.occ[transect.year[k]]) # p.occ of segment k depends upon on the transect  
    for (j in 1:n.surveys) {  
      p.frogsdetected[k,j] <- occ[k]*p[j] #prob of seeing a frog depends on whether the frogs are there  
      # and the probability of seeing the frogs that are there  
      presence[k,j] ~ dbern(p.frogsdetected[k,j]) # presence = whether or not a frog was observed in  
      # segment k on occassion j  
    }  
  }  
  
}
```

Appendix 2d: OpenBUGS script for the multi-year time-trend site occupancy model

Multi year - Time trend Occupancy

```
Model {  
  
  #Detection mode{  
  a.p ~ dnorm(0,1) # logit of average detection probability.  
  s.j.p ~ dunif(0,1) # Standard deviation among surveys in logit p  
  tau.j.p <- pow(s.j.p,-2) # Tau is converting SD to precision (tau = 1/sd^2)  
  
  for (j in 1:n.surveys) { # j = survey number (1,2 or 3)  
    re.j.p[j] ~ dnorm(0, tau.j.p) # re = random effect. ~ = sampling from a distribution  
    logit(p[j]) <- a.p+re.j.p[j] # adds random effect to each transect  
  }  
  
  # Occupancy model  
  a.n ~ dnorm(0,0.1)  
  b.year ~ dnorm(0,0.1)  
  s.trans.n~dunif(0,1)  
  tau.trans.n <-pow(s.trans.n,-2)  
  
  # Derived parameters  
  lambda <- exp(b.year) #expected to be near 1 because pop. stable  
  lambda9 <- pow(lambda,9) #converts lambda to show the change over 9 year timeframe  
  
  for (i in 1:n.transects) { #at the transect level, assigning random effects  
    re.trans.n[i] ~ dnorm(0, tau.trans.n) # assign transect random effect on abundance  
  }  
  
  for (i in 1:n.transect.year) { #i = transects  
  
    log(mu[i]) <- a.n + b.year*(year[i]-2012) + re.trans.n[transect[i]]  
    N[i] ~ dpois(mu[i])  
  
    p.occ[i] <- 1-exp(-N[i]/10) # prob. of any 10m segment on the transect being occupied  
  }  
  
  for (k in 1:n.segments) { # k = segments  
  
    occ[k]~ dbern(p.occ[transect.year[k]]) # pocc of segment k idepends upon on the transect  
    for (j in 1:n.surveys) {  
      p.frogsdetected[k,j] <- occ[k]*p[j] #prob of seeing a frog depends on whether the frogs are there and  
                                           the probability of seeing the frogs that are there.  
      presence[k,j] ~ dbern(p.frogsdetected[k,j]) # presence = whether or not a frog was observed in  
                                                    segment k on occassion j  
    }  
  }  
}
```

Appendix 2e: OpenBUGS script for the multi-year single-count index model

Multi-year - Time trend (single-count index)

Initial values

```
list(a.n=1,b.year=0,s.trans.n=5)
```

Model {

```
  # Abundance model
```

```
  #priors
```

```
  a.n ~ dnorm(0,1)
```

```
  b.year ~ dnorm(0,1)
```

```
  s.trans.n~dunif(0,5)
```

```
  tau.trans.n <-pow(s.trans.n,-2)
```

```
  for (i in 1:n.transects) {
```

```
    re.trans.n[i] ~ dnorm(0, tau.trans.n)  # assign transect random effect on abundance  
  }
```

```
  for (i in 1:n.rows) {
```

```
    log(mu[i]) <- a.n + b.year*(year[i]-2012) + re.trans.n[transect[i]]
```

```
    N[i] ~dpois(mu[i])
```

```
    n[i,1] ~ dpois(mu[i])    # sample no. new found from no. unmarked present
```

```
  }  
}
```

Appendix 3a: Example field habitat characteristics record sheet for habitat variables taken every 20-m along the transect.

GBI Hochstetters frog survey April 2015 – Habitat data sheet

Date: 14/2
Transect: B2

Measurer(s): Sarah, Blair, Henry.

Section	Stream condition	Stream substrate	Undergrowth spp.	Canopy / subcanopy spp.	Water clarity	Stream depth (cm)		
0m	Waterfalls Fast flowing Slow flowing	Pools No water	Rock slabs Boulders Cobbles	Gravel Sand Mud Clay	Pate SCHDIG Taraire BEITAR Kanono COPGRA	Pate SCHDIG Kanono COPGRA Cyathea smithii CYASMI Taraire BEITAR Kanuka KUNERI	Suspended sediment in water Clear water but sediment between rocks No accumulated sediment	5
20m	Waterfalls Fast flowing Slow flowing	Pools No water	Rock slabs Boulders Cobbles	Gravel Sand Mud Clay	Pate SCHDIG Taraire BEITAR Kanono COPGRA	Pate SCHDIG Kanono COPGRA Cyathea smithii CYASMI Taraire BEITAR Kanuka KUNERI	Suspended sediment in water Clear water but sediment between rocks No accumulated sediment	10
40m	Waterfalls Fast flowing Slow flowing	Pools No water	Rock slabs Boulders Cobbles	Gravel Sand Mud Clay	Pate SCHDIG Taraire BEITAR Kanono COPGRA	Pate SCHDIG Kanono COPGRA Cyathea smithii CYASMI Taraire BEITAR Kanuka KUNERI	Suspended sediment in water Clear water but sediment between rocks No accumulated sediment	16
60m	Waterfalls Fast flowing Slow flowing	Pools No water	Rock slabs Boulders Cobbles	Gravel Sand Mud Clay	Pate SCHDIG Taraire BEITAR Kanono COPGRA	Pate SCHDIG Kanono COPGRA Cyathea smithii CYASMI Taraire BEITAR Kanuka KUNERI	Suspended sediment in water Clear water but sediment between rocks No accumulated sediment	6
80m	Waterfalls Fast flowing Slow flowing	Pools No water	Rock slabs Boulders Cobbles	Gravel Sand Mud Clay	Pate SCHDIG Taraire BEITAR Kanono COPGRA	Pate SCHDIG Kanono COPGRA Cyathea smithii CYASMI Taraire BEITAR Kanuka KUNERI	Suspended sediment in water Clear water but sediment between rocks No accumulated sediment	5
100m	Waterfalls Fast flowing Slow flowing	Pools No water	Rock slabs Boulders Cobbles	Gravel Sand Mud Clay	Pate SCHDIG Taraire BEITAR Kanono COPGRA	Pate SCHDIG Kanono COPGRA Cyathea smithii CYASMI Taraire BEITAR Kanuka KUNERI	Suspended sediment in water Clear water but sediment between rocks No accumulated sediment	8

Appendix 3b: OpenBUGS script for the multi-year time-trend N-mixture model with habitat covariates.

Habitat Model

```
list(N=c(0,29,38,17,20,10,7,0,12,14,3,3,0,1,1,30,
35,54,12,16,13,4,2,26,11,3,0,1,3,0,29,28,30,19,8,28,1,1,7,24,9,2,0,1,2))
```

```
Model {
```

```
  # Detection model
```

```
  a.p ~ dnorm(0,1)      # intercept of logit of detection probability (p)
  s.j.p ~ dunif(0,1)
  tau.j.p <- pow(s.j.p,-2)
```

```
  for (j in 1:n.surveys.max) {
    re.j.p[j] ~ dnorm(0, tau.j.p) # assign survey random effect on detection prob.
    logit(p[j]) <- a.p+re.j.p[j] # calc. prob of first capture
  }
```

```
  # Abundance model
```

```
  #priors
```

```
  a.n ~ dnorm(0,1)
  b.year ~ dnorm(0,0.1)
  b.pate ~ dnorm(0,0.1)
  b.kanono ~ dnorm(0,0.1)
  b.waterfalls ~ dnorm(0,0.1)
  b.rat ~ dnorm(0,0.1)
  s.trans.n~dunif(0,3)
  tau.trans.n <-pow(s.trans.n,-2)
```

```
  for (i in 1:n.transects) {
    re.trans.n[i] ~ dnorm(0, tau.trans.n) # assign transect random effect on abundance
  }
```

```
  for (i in 1:n.rows) {
```

```
    log(mu[i]) <- a.n + b.year*(year[i]-2012) + re.trans.n[transect[i]] + b.pate*pate[transect[i]] +
    b.kanono*kanono[transect[i]] + b.waterfalls*waterfalls[transect[i]] + b.rat*rat[cluster[i]]
    N[i] ~dpois(mu[i])
```

```
    for (j in 1:n.surveys[i]) { # for each sampling occasion
      n[i,j] ~ dbin(p[j],N[i]) # sample no. new found from no. unmarked present
    }
```

```
  }
}
```