

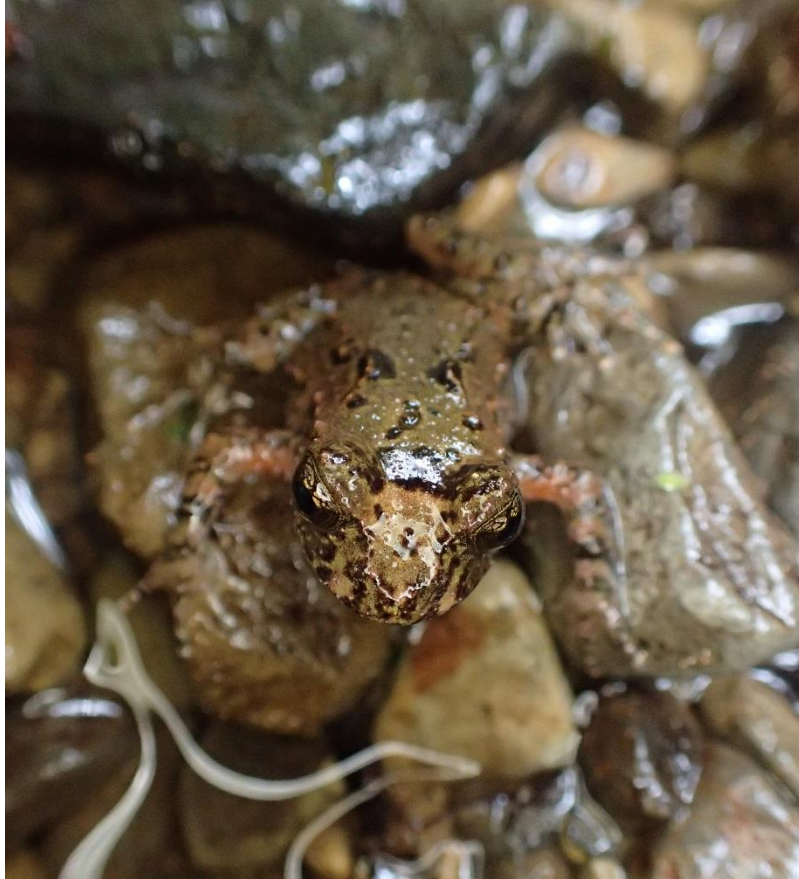
Determining the feasibility of a translocation by
investigating the ecology and physiology of the
threatened Hochstetter's frog (*Leiopelma hochstetteri*)

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at the University of Otago, Dunedin, New Zealand

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*In loving memory of Ian Jamieson,
Thank you for all of your support. We will miss you always.*



Adult Hochstetter's frog (*Leiopelma hochstetteri*). Photo: Anastasia Dula

“Zealandia’s story of life before human arrival has come to an end, but now there is a new beginning and we are the authors. It is up to us to write the future. The question is: What will we write next?”

Luke Easton 2014

Abstract

Habitat modification is one of the largest threats to amphibians worldwide, yet research investigating habitat modification impacts and management responses is often limited. Consequently, there is a necessity to address such issues, particularly for rare Hochstetter's frog (*Leiopelma hochstetteri*) populations that inhabit mature pine plantations in New Zealand. Fortunately, small populations at Torere Forest (Bay of Plenty, North Island) have received conservation attention following concerns over future pine harvesting. Possible management options are still in their infancy, but it is likely that a mitigation translocation via assisted colonisation will be required, even though a large-scale translocation for Hochstetter's frogs has not occurred before. Orokonui Ecosanctuary (Dunedin, South Island) was selected as a potential translocation site primarily because future global warming scenarios suggest that southern regions may become more favourable for Hochstetter's frogs than in their northern current distribution. However, the current cool climate at Orokonui Ecosanctuary is a concern as studies have concluded that Hochstetter's frog populations are strongly associated with warm climates that frequently reach 20°C or more. Therefore, the aims of this thesis were to investigate how Hochstetter's frog populations and individuals are influenced by a modified environment and to assess whether a translocation to Orokonui Ecosanctuary is indeed feasible regarding identifying suitable areas of habitat and the effect of a cool climate on frogs.

In order to address these aims, this study examined population parameters and individual fitness, and the resource selection of Hochstetter's frogs between mature pine plantations and native forests, followed by identifying suitable areas of habitat in Orokonui Ecosanctuary. The quality of the thermal environment at Torere Forest and Orokonui Ecosanctuary was also measured, along with the thermal preference and physiology of captive frogs exposed to cool temperatures. Overall, there were no differences in population parameters and individual body condition between the habitats, which suggested that mature pine plantations may not negatively affect populations and might even provide essential habitat. As for resource selection, the most important resources used by Hochstetter's frogs were cobble habitat and logs, particularly in pine plantations. These resources were available in Orokonui Ecosanctuary, thus suitable areas of habitat were predicted to be present. However, results from the lab suggested that the thermal environment at Orokonui Ecosanctuary may be thermally challenging for Hochstetter's frogs, particularly considering captive frogs mainly preferred temperatures between 15.3 - 20.9 °C (central 50%) and were unable to digest slaters in cool conditions. Digestion of crickets and locusts did occur however, whilst temperatures were reduced during the acclimation period. Furthermore, gut retention times and weights increased

in cool conditions, which highlighted that temperature largely influences these physiological responses. Nevertheless, studies have shown that Hochstetter's frogs may exhibit thermoregulatory behaviour to optimise the thermal environment. Such behavioural responses are useful as Hochstetter's frogs often inhabit shallow substrata where thermal conditions are possibly near or at equilibrium with cold temperatures during winter. Moreover, given their generalist diet and often low proportions of slaters ingested, results from this study suggest that energy uptake may occur during winter and that digestion of major dietary components might not be largely affected by cold temperatures.

A translocation to Orokonui Ecosanctuary therefore seems feasible, but further investigations are necessary. Further, management tools such as long-term monitoring, trial transfers, and continued stakeholder support are essential for conserving the Hochstetter's frog populations in Torere Forest. In doing so, the management of these populations will provide a foundation for the future conservation of this threatened species, especially regarding translocations that are yet to occur.

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Chapter One

General introduction

Background

Habitat modification and global amphibian declines

Global amphibian conservation faces a paradox. Whilst 32.5% of described amphibian species are threatened globally (Stuart *et al.* 2004), amphibian research receives disproportionately less attention compared to other animal groups (Hazell 2003; Stuart *et al.* 2004). However, many causes of amphibian declines have been identified, with habitat modification being one of the most significant threats (Alford & Richards 1999; Stuart *et al.* 2004). Furthermore, habitat clearance-induced amphibian declines are well documented in the United States (deMaynadier & Hunter 1995). Yet studying habitat modification is complex due to multiple local effects (Alford & Richards 1999) such as: inbreeding and reduced genetic variation (Andersen *et al.* 2004), reduced growth rates and timing of metamorphosis (DiMauro & Hunter 2002), inhibited migration (Todd *et al.* 2009), reduced survival (Raymond & Hardy 1991), and decreased abundance (deMaynadier & Hunter 1995). Moreover, given amphibians often live in meta-populations, understanding how threats affect local populations can be difficult to determine, particularly to discriminate whether local population extinctions and declines are natural or anthropogenic-induced events (Alford & Richards 1999). In addition, responses to clear-felling varies between species (Lemckert 1999; Schlaepfer & Gavin 2001; Cushman 2006; Perkins & Hunter 2006) as different species are affected by different processes (Marsh & Pearman 1997). Responses and processes (both inter- and intraspecific) also collectively change spatially and temporally, depending on the rate of re-forestation and seasonal influences (deMaynadier & Hunter 1995; Schlaepfer & Gavin 2001; Perkins & Hunter 2006).

Unfortunately, there is very little research addressing clear-felling impacts on amphibians in Australia (Hazell 2003) and especially in New Zealand. According to Hazell (2003), one reason for this under-representation is the difficulty to collect data of rare amphibian species. Indeed, studies frequently obtain inconclusive results for rare species (e.g. Goldingay *et al.* 1996; Karraker & Welsh 2006). Conversely, studies that investigate abundant species often conclude that clear-felling does not negatively impact populations because generalist species are more tolerant to disturbance (e.g. Gascon 1993; Lemckert 1999; Baker & Lauck 2006; Lauck 2006). Such conflicting results may depend on the scale of the study, yet researching at multiple scales can be beneficial. On one hand, landscape-scale research is recommended to determine meta-population status and dynamics in response to habitat modification (Alford & Richards 1999;

Cushman 2006). On the other, local-scale research is also stressed as an important approach (Alford & Richards 1999; Cushman 2006). Translating general understandings of conservation to species-specific management recommendations is difficult, as recommendations need to be tailored to the species' ecology and situation for effective conservation management (Cushman 2006). Nevertheless, it is clear that until there is a better understanding of how amphibian ecology is influenced by habitat modification, amphibians are unlikely to receive adequate conservation attention (Hazell 2003).

Exotic plantations in New Zealand

Establishing exotic plantations in New Zealand was the leading cause of native forest clearance since the 1950s (Ewers *et al.* 2006). Exotic plantations consist primarily of *Pinus radiata* (~89%) (Anon. 2007, cited in Pawson *et al.* 2010) which covers approximately 1.8 million hectares of New Zealand's total landscape (MAF 2009) and roughly 20% of New Zealand's total forest area (Pawson *et al.* 2010). The upper North Island has been affected the most, as Ewers *et al.* (2006) recorded that in 2002 the Waikato region had the largest exotic plantation coverage (778,618ha), whereas the second largest coverage was in the Bay of Plenty (655,813ha). Consequently, many threatened New Zealand species are exposed to habitat modification. At least 118 threatened species, including Archey's frog (*Leiopelma archeyi*) and Hochstetter's frog (*L. hochstetteri*), have been observed to inhabit plantations or native remnants surrounded by plantations (Shaw 1993; Douglas 1997-2001b; Norton 1998; Maunder *et al.* 2005; Allen 2006; Black 2010; Pawson *et al.* 2010; Hutchings 2011; Newman *et al.* 2013; Bishop *et al.* 2013). Yet major land use decisions appear to be made with little consideration of the contributions plantations provide to indigenous biodiversity because scant information is available (Maunder *et al.* 2005). Such lack of information has thus fuelled a long-standing debate over the value of plantations to conservation (Norton 1998; Pawson *et al.* 2010). In particular, Norton (1998) illustrated three main benefits plantations may provide: 1) habitat provision, 2) buffering of native forest remnants, and 3) increasing connectivity between native forest remnants. Indeed, Pawson *et al.* (2010) suggested that conflicting views of plantation benefits to conservation may be because some plantations were established following native forest clearance.

As for conserving threatened species in plantations, the Conservation Act (1987) does provide legal protection, but it has little relevance for indirect threats such as habitat modification during tree harvesting. Limited information and irrelevant policies thus render conservation effort for threatened species inhabiting plantations (Maunder *et al.* 2005). Fortunately, traditional perceptions that harvesting has little or no impact on indigenous biodiversity have changed as

developing pressures ensure that foresters adhere to the sustainable management guidelines (i.e. Forest Stewardship Council certification, FSC 2013). Such guidelines include approaches such as monitoring, pest control, habitat protection, research, altered harvesting practices, and animal translocations (FOA 2003; Maunder *et al.* 2005, FSC 2013). Research is especially important as it may provide crucial information into refining harvesting plans whilst maximising indigenous biodiversity protection without compromising economic gain (Maunder *et al.* 2005).

Hochstetter's frogs in pine plantations

Approximately 10% of the current distribution of Hochstetter's frog consists of modified habitat (5% in exotic plantations and 5% in pasture) (Allen 2006). Specifically, areas where Hochstetter's frogs inhabit plantations include: Northland, Coromandel, and east of Opotiki (Maunder *et al.* 2005). Observations of apparent population persistence in modified environments therefore imply that Hochstetter's frogs can adapt to moderate local habitat disturbance (Green & Tessier 1990; Shaw 1993; Towns & Daugherty 1994; Douglas 1997-1999; Whitaker & Alspach 1999; Ziegler 1999; Douglas 2000; Parrish 2004; Hutchings 2011). In contrast, potential negative effects of habitat disturbance on Hochstetter's frog populations have been identified by extensive population surveys (Newman 1982; Green & Tessier 1990; Glaser & Dobbins 1995; Douglas 1997, 1998b, 1999; Ziegler 1999; Douglas 2001a; Crossland *et al.* 2005; Hutchings 2011). For instance, the study by Crossland *et al.* (2005) in Mahurangi Forest detected fewer frogs in mature pine plantations compared to mature native forests, but even less in harvested areas. Local extinctions along the west coast of the North Island have also occurred and are likely due to habitat modification (Fouquet *et al.* 2010a). Disturbances to local habitats are therefore considered a major threat to the long-term survival of this species (Newman 1982; Newman *et al.* 2013; Bishop *et al.* 2013). Planned harvests of exotic plantations are thus likely to negatively impact resident frogs over many decades (Newman *et al.* 2013). Accordingly, careful riparian management during harvesting is essential to protect this species (Maunder *et al.* 2005). Setting habitat aside from harvesting has also been implemented in the past (e.g. sanctuary in Rodney District, Northland [Pawson *et al.* 2010]), but voluntary protection is rare (Maunder *et al.* 2005) as it can be economically detrimental to forestry companies. Lastly, mitigation translocations of Hochstetter's frogs from pine plantations prior to harvesting are also considered an option (Maunder *et al.* 2005), although large-scale translocations have not been done before. Despite such adaptive management actions, to what extent harvesting affects Hochstetter's frogs currently remains uncertain (Maunder *et al.* 2005; Bishop *et al.* 2013).

Translocation research

Translocations are becoming increasingly important for amphibian conservation to eliminate threats to local populations (Germano & Bishop 2009; Bishop *et al.* 2013; Miller *et al.* 2014), even though only 8.1% of New Zealand herpetofauna translocations are considered successful (Miller *et al.* 2014). Indeed, the establishment of additional self-sustaining populations for all *Leiopelma* species at new managed sites is an essential objective in the Native Frog Recovery Plan (Objective 4.1, Bishop *et al.* 2013), despite Ziegler (1999) suggesting that Hochstetter's frog translocations are not required given their widespread distribution. To date, only 10 translocations involving *Leiopelma* species are known to have occurred, of which included two small local translocations of Hochstetter's frogs. Both translocations were unsuccessful, although the causation of failure remains uncertain (Parrish 2004, 2005; Sherley *et al.* 2010). One leading cause of translocation failure, however, is a lack of knowledge regarding habitat quality in potential translocation sites (Griffith *et al.* 1989; Germano & Bishop 2009).

Unfortunately, identifying suitable areas of habitat is very complex, as the current locations of species' populations may not reflect optimal habitat (Osborne & Seddon 2012). Long-lived species, like *Leiopelma*, may persist in non-suitable areas for a long time, which incorrectly leads to the impression of optimal habitat (Osborne & Seddon 2012). Furthermore, the historical range of a species may not indicate suitable areas of current habitat because of natural or anthropogenic changes (Osborne & Seddon 2012). Many other limitations to gain such crucial knowledge exists (see Osborne & Seddon 2012), particularly when managing rare species that often inhabit modified or remnant habitat and lack research regarding their ecology (Cook *et al.* 2010; Bishop *et al.* 2013). Despite these set-backs, the identification of habitat for Hochstetter's frogs have been carried out in potential translocation sites such as Zealandia (Douglas 2001b), Windy Hill Rosalie Bay Catchment on Great Barrier Island (Herbert *et al.* 2014), and Orokonui Ecosanctuary (Egeter 2009).

Nonetheless, habitat does not strictly consist of available vegetation and resources required for population survival and persistence (Johnson 2007). Ecological constraints such as predation and competition intensity may also need to be controlled as they can reduce accessibility to resources provided (Johnson 2007). For ectothermic animals, like amphibians, extreme temperatures additionally act as an ecological constraint as body temperature influences their behaviour and physiology (Wells 2007). Extreme temperatures are thus likely to restrict resource accessibility in ectotherms more so than the constraints mentioned by Johnson (2007). Herpetofauna translocations must therefore involve investigations into the physiological responses of translocated individuals to the local climate of release sites (Besson & Cree 2011).

Fortunately, conservationists are increasingly including physiology into conservation programmes; a discipline now defined as “conservation physiology” (Wikelski & Cooke 2006). Importantly, conservation physiology enables an overview of both the causes of conservation issues and the consequences of conservation actions such as translocations (Wikelski & Cooke 2006; Besson & Cree 2010, 2011; Besson *et al.* 2012). However, whilst some studies have addressed behavioural responses of *Leiopelma* to the thermal environment (Cree 1989; Bell 1995; Dewhurst 2003; Haigh *et al.* 2010), none have investigated physiological responses. Despite the limited research, researchers have made inferences specifically about the thermal preference in Hochstetter’s frogs based on their current distribution (e.g. Fouquet *et al.* 2010a,b). This knowledge gap needs to be addressed especially regarding any proposed translocations of *Leiopelma* species back into the South Island, particularly considering climates are significantly cooler than what they currently experience.

Native Frog Recovery Plan 2013-2018

The Native Frog Recovery Plan 2013-2018 (Bishop *et al.* 2013) identified a multitude of issues that require urgent investigation, including the necessity to address the uncertainty regarding habitat modification effects on Hochstetter’s frogs. In the Recovery Plan, it recognised that the current distribution of native frogs may not reflect optimal ecological conditions, especially within modified habitat. Understanding species’ ecology and physiology is critical for species management, particularly with regards to habitat quality assessment and the identification of factors restricting population growth (Bishop *et al.* 2013). Yet knowledge of ecological and physiological requirements for native frogs is limited (Bishop *et al.* 2013). This lack of knowledge largely constrains assessing the suitability of potential new translocation sites. The Recovery Plan thus recommended that an assessment of land use effects on frog populations (Action 14.9) and the facilitation of research regarding species ecology and biology (Action 16.1) be made “high” and “essential” priority respectively.

Study species

The Hochstetter’s frog is one of four recognised threatened and endemic *Leiopelma* species (which includes: Hamilton’s frog *L. hamiltoni*, Maud Island frog *L. pakeka*, and Archey’s frog *L. archeyi*) in New Zealand (Newman *et al.* 2013; Bishop *et al.* 2013). The genus *Leiopelma* is a lineage dating back to the Triassic (~225 mya) (San Mauro *et al.* 2005; Roelants *et al.* 2007) and all *Leiopelma* species are ranked within the top 60 most Evolutionarily Distinct and Globally Endangered (EDGE) amphibian species (ZSL 2012). Two new *Leiopelma* species (*L. miocaenale* and *L. acricarina*) have even been identified from early Miocene (19-16 mya) fossil deposits in Central Otago, South Island, which highlights the diversity of the genus during this

period (Worthy *et al.* 2013). Seven species were known to exist during the beginning of the Holocene period (10,000 BP), of which three have become extinct since human arrival, likely because of kiore rat (*Rattus exulans*) predation and significant range reduction of the remaining *Leiopelma* species (Worthy 1987; Towns & Daugherty 1994). The actual historical agents of native frog decline, however, are largely unidentified (Issue 14.1, Bishop *et al.* 2013). Interestingly, the southern-most sub-fossil distribution of Hochstetter's frogs is Punakaiki, on the West Coast, South Island, whereas sub-fossils of the extinct Markham's frog (*L. markhami*) and Aurora frog (*L. auroraensis*) have been found in Te Anau, Fiordland (Worthy 1987). Furthermore, estimated snout-vent lengths (SVLs) of sub-fossils indicate a negative correlation with temperature (i.e. southern populations were larger) (Worthy 1987). In particular, Hochstetter's frogs may have reached 56 mm in the north-western parts of Nelson (Worthy 1987), far larger than the standard observed size range of ≤ 50 mm today (Crossland *et al.* 2005), apart from the exception made by Glaser and Dobbins (1995) who measured frogs up to 54 mm SVL in the Motu River (East Cape).

The Hochstetter's frog is the most widespread species, currently distributed in scattered parts of the upper North Island from the East Cape to southern Northland and Coromandel Peninsula, northern Great Barrier Island, and to the Whareorino region (Bell 1978a; Green & Tessier 1990; Bell *et al.* 2004a; Bishop *et al.* 2013) (Figure 2), sometimes in sympatry with *L. archeyi* (Bell 1978a; Worthy 1987; Bell *et al.* 2004a; Bishop *et al.* 2013). A small population was also discovered in 2004 within the Maungatautari Scenic Reserve (Baber *et al.* 2006) and even an anecdotal report of a possible sighting in the Tararua Ranges dates back to the early 1960s (Parrott 1967, cited in Robb 1973). The sub-fossil distribution of Hochstetter's frogs, however, indicates that this species was historically more widespread than it is today (Worthy 1987) (Figure 2). Presently, streams in central Coromandel and of the southern Waitakere Range are apparently the most densely populated sites (Green & Tessier 1990), although there is great uncertainty of the actual status and occupancy for many meta-populations, especially in the East Cape (McLennan 1985; Green & Tessier 1990; Newman *et al.* 2013; Bishop *et al.* 2013).

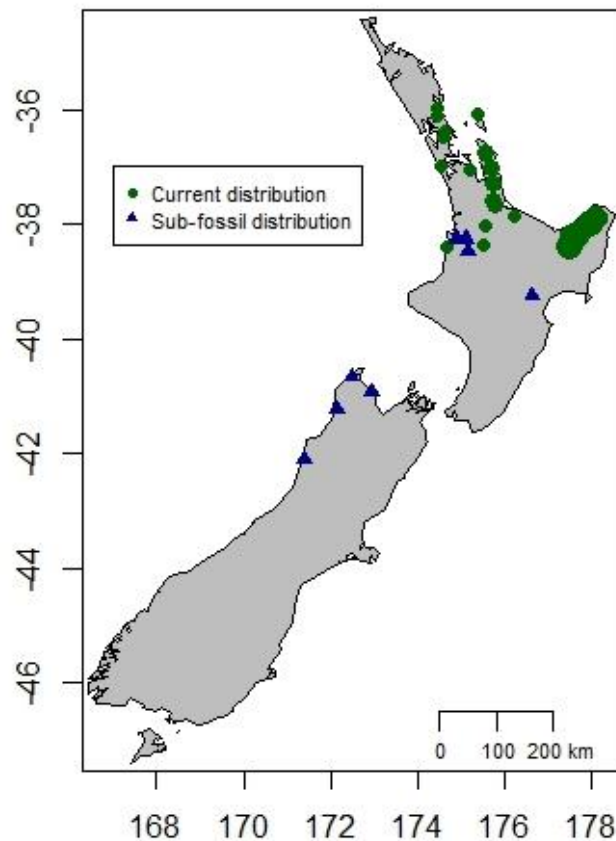


Figure 2. Map of the current (green circles) and sub-fossil (blue triangles) distributions of Hochstetter's frog. Modified from Worthy (1987) and Bishop *et al.* (2013).

The Hochstetter's frog has a threatened status of “At Risk: Declining” (estimated population size: $\leq 100,000$, Bishop *et al.* 2013; Newman *et al.* 2013) but the species entity encompasses 13 Evolutionary Significant Units (ESUs) (i.e. isolated populations of evolutionary significance, Gemmell *et al.* 2003) of the 21 meta-populations known (Fouquet *et al.* 2010b; Newman *et al.* 2013). Given the high population structure at the genetic level and low genetic diversity compared to the other *Leiopelma* species, it has been recommended that the meta-populations be managed as separate ESUs and not as a single species entity (Daugherty *et al.* 1981; Gemmell *et al.* 2003; Fouquet *et al.* 2010b; Newman *et al.* 2013). The phylogeographic population structure observed in Hochstetter's frogs is a result of the species' small localised populations and high site fidelity habits (Daugherty *et al.* 1981; Green & Tessier 1990; Tessier *et al.* 1991; Bell 1996) which were accentuated via anthropogenic, past climatic, or past geological events (Newman 1982; Gemmell *et al.* 2003; Fouquet *et al.* 2010a,b).

Compared to its congeners, the Hochstetter's frog differs ecologically and morphologically. Firstly, the Hochstetter's frog is semi-aquatic, where it inhabits rocky substrata and plant debris

within forested streams and seepages (Bell 1978a; Green & Tessier 1990; Newman 1996). This semi-aquatic lifestyle also apparently enables Hochstetter's frogs to coexist with introduced mammalian predators (Newman 1982, Daugherty *et al.* 1994; Newman 1996; Ziegler 1999 [but see Mussett 2005; Longson 2014; Egeter 2014]). Secondly, the Hochstetter's frog is structurally more robust with shorter snout and digits, along with slight webbing on its hind feet (Bell 1978a; Newman 1982). In contrast, the Hochstetter's frog is similar to its congeners as it has a generalist invertebrate diet, primarily nocturnal and sedentary behaviour, longevity, cryptic nature, and a slow rate of maturity (Bell 1978a; Green & Tessier 1990; Tessier *et al.* 1991; Eggers 1998; Ziegler 1999; Bell *et al.* 2004a; Bishop *et al.* 2013).

Conservation and study rationale

To date, conservation management of Hochstetter's frogs has mainly been through advocacy and habitat protection (Pawson *et al.* 2010; Bishop *et al.* 2013). An *ex situ* outdoor captive breeding facility at Hamilton Zoo was set up in 2006 to develop husbandry techniques and for potential population security (Bishop *et al.* 2013) but these individuals are still yet to breed successfully (Beauchamp *et al.* 2010; Kudeweh *et al.* 2011). University of Otago has the only other captive population in New Zealand held by an institution (Shaw 2013). These too are still yet to breed. Suitable areas of habitat are difficult to replicate in captivity, thus it is possible that unfavourable habitat may be a reason for the unsuccessful breeding so far (Bell 1978b; Shaw 2013).

In the last five years, concerns regarding the harvesting of pine plantations in Torere Forest (Bay of Plenty, North Island) that contain Hochstetter's frog populations (Figure 3) have stimulated discussions amongst stakeholders about the feasibility of a mitigation translocation via assisted colonisation (i.e. the intentional movement and release of animals beyond their indigenous range to avoid population extinction, Seddon 2010; IUCN/SSC 2013). The translocation of individuals to neighbouring extant ESU populations was not deemed appropriate as the genetic structure of the Torere Forest populations is not known. Furthermore, the absence of frogs in local areas may be a consequence of uncertain historical extinction agents. It is still too early to confirm whether a translocation will actually take place given the logistics and negotiations amongst stakeholders that would be required. Nevertheless, wild-to-wild translocations to other regions have not yet occurred for Hochstetter's frogs, thus the opportunity to study translocation feasibility became the main focus of this study. For the purpose of this study, Orokonui Ecosanctuary (Dunedin, South Island) (Figure 3) was investigated as a potential translocation site, bearing in mind other sites may also have essential habitat present (e.g. Zealandia). Although *Leiopelma* are not known to have historically

occurred in Dunedin (Worthy 1987), Orokonui Ecosanctuary was selected because of multiple reasons such as extensive pest control and the apparent presence of relatively high quality habitat (Egeter 2009). The primary reason was that climatic conditions of northern North Island sites (e.g. Northland and Great Barrier Island) may not be optimal for Hochstetter's frogs in the future (Fouquet *et al.* 2010a), thus selecting a climatically cooler region was preferable. In saying that, concerns were raised over the current climate of Orokonui Ecosanctuary by Egeter (2009) and were thus addressed in the present study. It is important to reiterate, however, that Orokonui Ecosanctuary is a *potential* translocation site. This term simply means that Orokonui Ecosanctuary is a model release site and that a translocation to this area is not final, if a translocation occurs at all.

Study sites

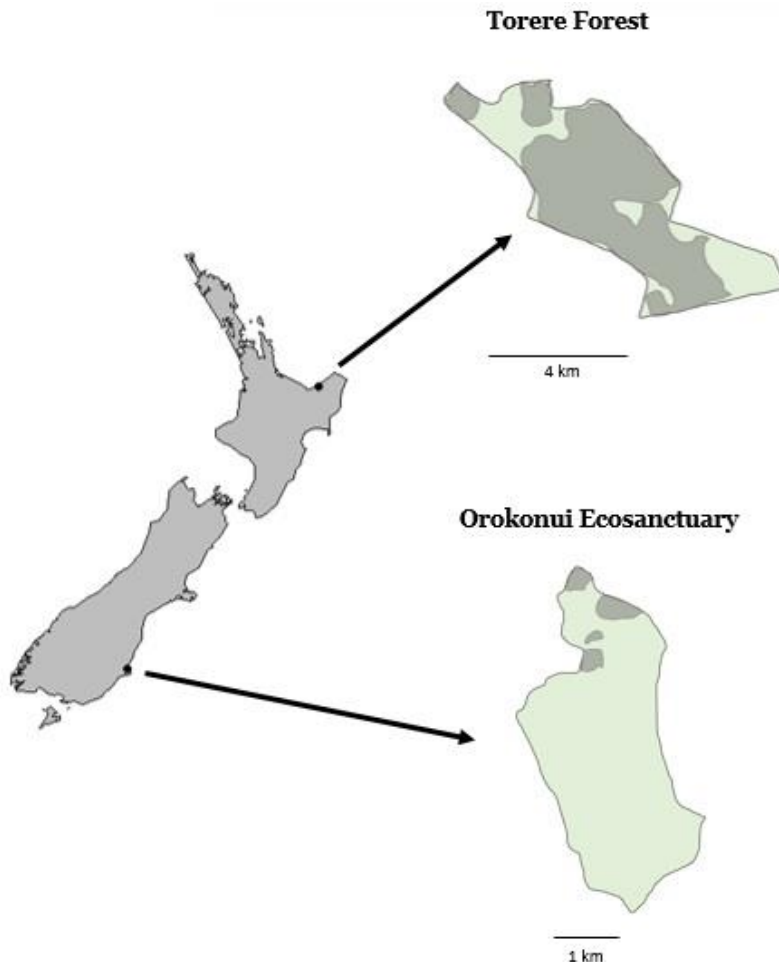


Figure 3. Map of New Zealand showing locations of Torere Forest and Orokonui Ecosanctuary. The enlarged areas of Torere Forest and Orokonui Ecosanctuary show the extent of pine plantations (dark shaded). Scale bars are shown. Modified from figures by Phill Collins (Hancock Forestry Management) and Schadewinkel (2013).

Torere Forest

Torere Forest (38°00.62'S; 177°30.78'E) is located on the northern boundary of the Raukumara ranges, just south of Torere, on the East Cape, North Island, New Zealand. Pine (*Pinus radiata*) plantations were established in the 1980s (Black R, pers. comm.; Shaw 1993) following large scale burning and clearance of native forest. Selective logging of native timber also occurred during this time (Shaw 1993). Regeneration of native understory along the Rawea catchment and other tributaries has since occurred and consequently set aside as reserves, including a large area on the western slopes. Torere Forest consists of two main blocks: Torere 64 and 65, the former being currently leased to Hancock Forest Management Ltd (HFM) by Torere 64 Incorporated. Approximately 2700 ha (2400 ha in Torere 64 and 300 ha in Torere 65) of pine plantations are planned to be harvested over the next decade or so. The terrain is predominantly steep (>36°) (pers. obs.; Black R, pers. comm.) and many tributaries consist of waterfalls, gorges, fallen pine tree debris, and erosion (pers. obs.; Hutchings 2011). Streams and seepages are generally small (<1 m in width) and are both perennial and ephemeral (pers. obs.; Shaw 1993; Black 2010). Furthermore, riparian zones vary from regenerating native forest species such as tree ferns (*Cyathea* spp. and *Dicksonia* spp.) and māhoe (*Melicytus ramiflorus*) to mixtures of native and pine (pers. obs.; Hutchings 2011). Inhabiting these areas are seemingly healthy populations of Hochstetter's frogs, more so in areas with wider riparian zones that provided protection from historical habitat clearance (Black 2010; Hutchings 2011). Nonetheless, Hochstetter's frog populations in Torere Forest are located between two ESUs; the "Western Raukumara" and "Eastern Raukumara", both of which are currently considered "At Risk: Declining" (Newman *et al.* 2013). It is likely that the Torere Forest populations have a similar threatened status. Surveys have thus been carried out by DOC, Total Backcountry Solutions Ltd and HFM to establish 1) a baseline understanding of the potential impacts that pine plantations have had on the frogs and, 2) their presence in areas destined for harvesting (Shaw 1993; Black 2010; Hutchings 2011). Surveys were carried out first in 1993, then again in 2010 and 2012. The main conclusions from these surveys were that Hochstetter's frogs in Torere Forest mostly inhabit native vegetation in areas of high substrate stability (Black 2010) and that they utilise a vast range of resources such as pine debris (Hutchings 2011). Nevertheless, as habitat loss and direct impacts to the frogs are inevitable in some cases, HFM follow strict guidelines to minimise negative impacts of tree removal (Black R, pers. comm.; Hutchings 2011). For instance, potential or confirmed frog habitat is identified and designated as protected areas during harvest planning so that they are preserved when harvesting commences (Black 2010). Despite Hutchings (2011) expecting the overall harvesting impact

on frogs in Torere Forest to be minimal, a mitigation translocation may occur to avoid some populations from becoming locally extinct because of future harvesting.

Orokonui Ecosanctuary

Orokonui Ecosanctuary (45°45.95'S; 170°35.74'E) is a fenced reserve located ~20 km north-east of Dunedin, Otago, South Island, at about 30 - 370 m above sea level (Egeter 2009). The 'pest-resistant' fence spans 8.7 km around approximately 307 ha of regenerating forest (of similar age to Torere Forest), which includes ~25 ha of broadleaf-podocarp and ~213 ha of mixed kānuka (*Kunzea ericoides*) forest/scrub (Schadewinkel 2013). Only about 48 ha of exotic plantations remains (Schadewinkel 2013). Many seepages and small streams feed the main north-flowing Orokonui stream but only several of these flow through mature broadleaf-podocarp forest, particularly in "Marie Gully" (northern most section of the sanctuary). The riparian zone in "Marie Gully" consists of emergent kahikatea (*Dacrycarpus dacrydioides*) and kāpuka (*Griselinia littoralis*) with a dense canopy of broadleaf species such as tarata (*Pittosporum eugenioides*) and māhoe (*Melicactus ramiflorus*). Other sites are similar in species composition except that emergent trees are not present. Streams in most sites consist largely of loose rock substrata where there are abundant communities of mosses, liverworts and small fern species. Since the sanctuary was declared "pest-free" in 2008, many rare species have been translocated into the valley as part of restoration or conservation efforts (Peat 2013). These translocations have occurred as a result of the strong relationship that exists between Orokonui Ecosanctuary and Kati Huirapa (Mana whenua of the region), along with Memoranda of Understandings (MOUs) signed between Kati Huirapa and other iwi (Peat 2013). Orokonui Ecosanctuary is also a potential translocation site for *Leiopelma* species, despite no evidence (i.e. sub-fossils) of *Leiopelma* historically inhabiting the region (Worthy 1987).

Aims and objectives

Population monitoring, identifying suitable areas of habitat, and investigating how temperature influences the physiological responses of ectotherms, such as the ability to digest, are three key components of ectotherm translocations. However, translocation research for *Leiopelma*, particularly Hochstetter's frogs, is still in its infancy. The aims of this research (which address some recommended actions in the Native Frog Recovery Plan) were therefore addressed by means of the following questions:

1) *How do population parameters and individual fitness compare between pine and native habitats in Torere Forest?*

This question is addressed in Chapter Two in order to achieve a baseline indication of population parameters and individual fitness prior to harvesting or potential translocation, and to assess whether pine plantations negatively impact populations such as reducing population density.

2) *What resources do Hochstetter's frogs require in pine and native habitats? How does resource use compare between pine and native habitats?*

These questions are addressed in Chapter Three in order to identify suitable areas of habitat and assess how modified habitat influences resource use.

3) *What temperatures do Hochstetter's frogs prefer? How do preferred temperatures compare to temperatures at Torere Forest and Orokonui Ecosanctuary? What are the effects of temperature on the physiology of Hochstetter's frogs?*

These questions are addressed in Chapter Four in order to identify the preferred temperature range for Hochstetter's frogs, measure the quality of the thermal environment at Orokonui Ecosanctuary and Torere Forest, and assess what impact temperatures at Orokonui Ecosanctuary may have on individuals.

4) *Is Orokonui Ecosanctuary a suitable translocation site?*

This question is addressed in Chapters Three and Four and is summarised in Chapter Five.

As *Leiopelma* species are protected under the New Zealand Wildlife Act (1953), a DOC permit was required for permission to handle frogs *in situ*. DOC approved permission (Authorisation Number: 38123-FAU) commencing on 1/2/2014 and ending on 31/12/2016. Furthermore, an application for the University of Otago Animal Ethics Committee (71/13) to enable work on wild frogs in the Torere Forest and captive frogs held in the Department of Zoology was successfully granted. This work was carried out in collaboration with Torere 64 Incorporated, Ngaitai Iwi Authority, Hancock Forestry Management, Department of Conservation, and Orokonui Ecosanctuary.

Chapter Two

Population parameters and individual fitness of Hochstetter's frogs in different habitats

Introduction

Population parameters (e.g. population growth) and individual fitness (e.g. body condition) are informative for conservation biology in many aspects, including the understanding of: human impacts, species' biology and ecology, and consequences of habitat use (Pullin 2002). Measuring population parameters is particularly important for studies that investigate amphibian population responses to habitat modification (deMaynadier & Hunter 1995; Alford & Richards 1999; Stuart *et al.* 2004). For example, Ash (1997) demonstrated that population declines of plethodontid salamanders ranged from 30-50% one year after harvesting, whilst Karraker & Welsh (2006) recorded that the size of amphibian populations inhabiting clear-cuts were almost half those in unmodified areas. Furthermore, population recovery of plethodontid salamanders was estimated by Ash (1997) to take at least two decades, although Petranka (1999) suggested that recovery would take longer. Hochstetter's frogs are no exception to habitat modification threats (Newman 1982; Green & Tessier 1990; Ziegler 1999; Newman *et al.* 2013; Bishop *et al.* 2013). Although there is no published literature on the management or population status of Hochstetter's frogs in exotic plantations (Maunder *et al.* 2005), some unpublished surveys highlighted population crashes and poor population recovery following pine harvesting (Shaw 1993; Douglas 1998a, 1999, 2001a). For instance, Douglas (2001a) observed one population that declined almost 50% over four years since harvesting occurred in the Brynderwyn Hills, in Northland. Such observations therefore imply that Hochstetter's frog populations in Torere Forest are likely to be similarly affected during harvesting, although Hutchings (2011) considered the overall impact to be minimal. Providing a baseline understanding of population status (e.g. stable, increasing, or decreasing) prior to harvesting or potential translocation is therefore critical for the management of these populations.

Equally important is understanding how habitat influences population parameters or individual fitness. Specifically, body condition (which is an index of body weight accounted for body size) is arguably one of the most important individual fitness indices to measure (Peig & Green 2009) as it is sensitive to factors such as competition and habitat quality (Tyrell 2000; Gebauer 2012). Both population parameters and individual fitness can therefore act as habitat quality indicators (Gray & Smith 2005; Karraker & Welsh 2006) provided that they are treated with caution,

especially when long-term data are unavailable (van Horne 1983; Hobbs & Hanley 1990; Johnson 2007; Ayers *et al.* 2013). Assessing how habitat affects population parameters and individual fitness is useful to know as it ultimately highlights how sensitive animals are to inhabiting modified environments.

In order to address the question of how do population parameters and individual fitness compare between pine and native habitats in Torere Forest, population parameters and body condition in both habitats were investigated. Population parameters and body condition were compared so that a baseline indication of population status and individual fitness prior to harvesting or potential translocation can be provided and to determine whether mature pine plantations negatively impact populations. Given the sensitivity of amphibian populations to habitat modification, it was predicted that population density, body condition, and the number of adults (i.e. possible breeders) would be lower in mature pine plantations than in native forests. Findings from this study are intended to aid the management of these Hochstetter's frog populations and will hopefully form part of a long-term monitoring programme.

Methods

Frog surveys

In order to investigate the population parameters of Hochstetter's frogs in modified and largely unmodified habitats, three native forests and three mature pine plantation sites were surveyed within Torere Forest (Figure 4). Populations densities of Hochstetter's frogs often vary monthly (Douglas 1999) and although the recommended time period for surveying Hochstetter's frogs is January-February (Bell 1996; Newman 1996), sampling occurred during September 25th and October 2nd 2014 because of logistical reasons. Nevertheless, reasonable frog numbers have been found during these months in other regions (Douglas 1999). As Hochstetter's frogs are linearly distributed along streams, transect sampling was used, which is essentially a strip count that assumes 100% detectability regardless of site features. Although 100% detectability is unlikely because of the cryptic habits of *Leiopelma*, strip counts are the most effective sampling method for Hochstetter's frogs (Bell 1996). Additionally, considering their dispersal distances are small (~1 m, Tessier *et al.* 1991), only 2 m either side of the stream transect was surveyed. Surveys were carried out by searching all potential cover objects (e.g. logs, rocks, etc.) for frogs. Upon finding a frog, they were captured and carefully placed in a snap-lock bag with stream water. Point of capture was marked by placing numbered brightly coloured flagging tape at ground level and by taking GPS coordinates. Snout-vent length (SVL) was measured (to the nearest 0.01 mm) using dial callipers and weight measured using an electronic balance (Model

HH 120D, Ohaus Corporation, USA) (to the nearest 0.1 g). Frogs were then returned to where they were found. Surveys stopped when no further frogs were found after around 15 minutes of searching. All field equipment was cleaned with Virkon® disinfectant between sites to minimise the potential spread of parasites or pathogens.

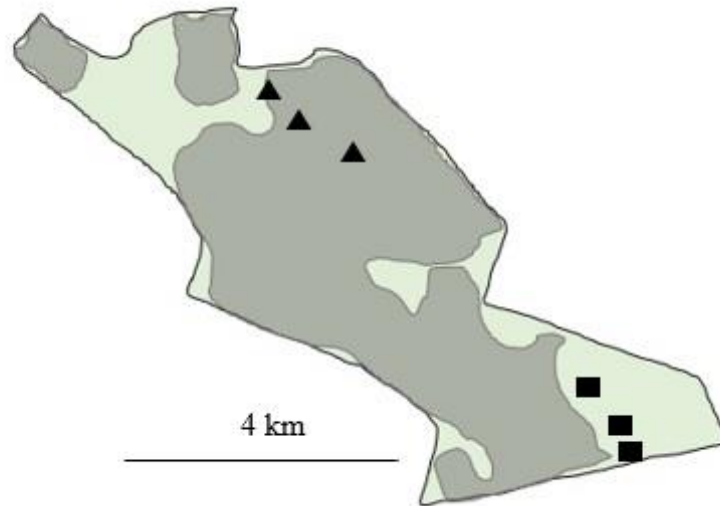


Figure 4. Map of Torere Forest showing the three sampling sites in mature pine plantations (triangles) and three sampling sites in native forests (squares). Scale bar shown.

Population parameters and individual fitness

Three main parameters and indices were measured. These were: size-class distribution, body condition, and density. Size-class classifications (based off SVLs) vary in the literature (Moreno 2009), but for the purpose of this study sizes were grouped following Whitaker & Alspach (1999): <18 mm SVL for juveniles, 18 - <24 mm SVL for sub-adults, and >24 mm SVL for adults. As for body condition, techniques that calculate these indices are highly debated (Gebauer 2012). In this thesis, the scaled mass index proposed by Peig & Green (2009) is used as it accounts for growth effects and potential variability caused by measuring weight and SVL on different scales. The scaled mass index was thus calculated as follows:

$$\hat{M}_i = M_i [L_0 / L_i]^{b_{SMA}}$$

where \hat{M}_i is the predicted weight for individual i when SVL is standardised to the arbitrary mean SVL of the sample (L_0), M_i and L_i are weight and SVL measurements for individual i respectively, and b_{SMA} is the scaling exponent which is the slope value estimated by the standardised major axis regression (SMA) of the ln-transformed data M_i against L_i . SMA was calculated using the R package “*smatr*” (Warton *et al.* 2012).

Density was estimated by dividing the number of frogs found by the total distance sampled (+2 m either side of each stream). For both habitats, the number of frogs found in each stream were pooled.

Statistical analyses

As the body condition data was normally distributed, a generalised linear model (GLM) for Gaussian data with ‘scaled mass index’ as the response and ‘habitat’ as the predictor variable was used. In addition, a Chi-squared test was carried out to compare size-class proportions between habitats. Significance was tested at $p < 0.05$ level.

All analyses were carried out in R version 3.0.2 (R Core Team 2013).

Results

The length of reach for the six streams surveyed ranged from approximately 69 m to 251 m. In total, 96 frogs were found, which included 50 in native forests and 46 in pine plantations. However, some escaped prior to handling or during measuring. Eighty-five frogs were therefore measured, and 75 frogs were both measured and weighed. Frogs were sighted within groups more often in pine plantations ($n = 7$) than in native forests ($n = 3$). A maximum of four and two individuals were found within a group in pine plantations and native forests, respectively. In pine plantations, the average density of frogs per metre² was 0.05 (range= 0.03 - 0.06), similar to the average density of 0.04 (range= 0.01 - 0.09) recorded in native forests (Figure 5).

There was no significant difference in the scaled mass index for the frogs between native forests and pine plantations ($est. = -0.02 \pm 0.12, p = 0.85$) (Figure 6), nor were there any significant differences in scaled mass index amongst size-classes between habitats ($F_{2,69} = 0.35, p = 0.70$) (figure not shown). Size class proportions also did not significantly differ between habitats ($\chi^2 = 1.94, df = 2, p = 0.38$) (Figure 7).

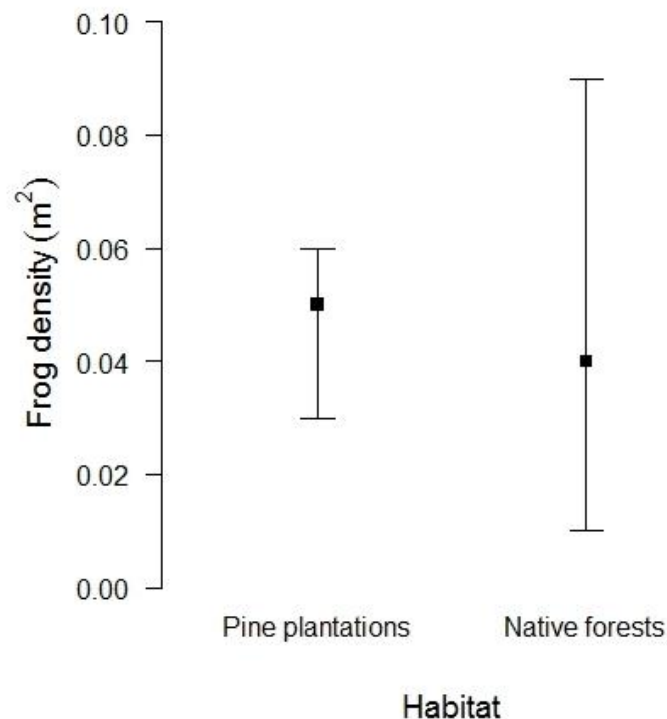


Figure 5. Mean population density of Hochstetter's frogs (with minimum and maximum) located in three surveyed streams in mature pine plantations and three streams in native forests within Torere Forest.

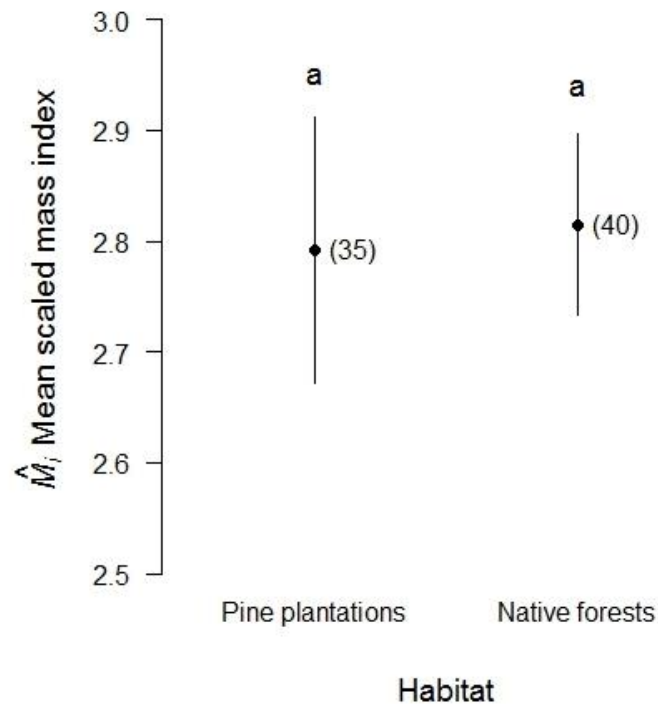


Figure 6. Mean scaled mass index with standard error bars of individual Hochstetter's frogs located in mature pine plantations and native forests within Torere Forest. Sample sizes are in brackets. There were no significant differences ($p > 0.05$).

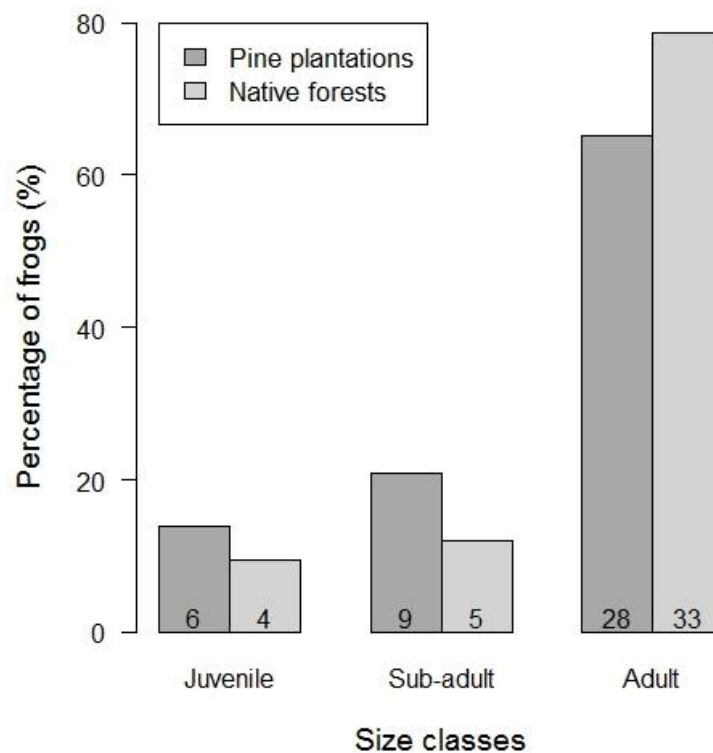


Figure 7. Size-class proportions of Hochstetter's frogs located in pine plantations and native forests within Torere Forest. Sample sizes are shown. There were no significant differences ($p > 0.05$).

Discussion

Density

Population density was not different between habitats, a finding which did not support the prediction that lower densities would be observed in mature pine plantations in relation to native forests. Overall, population densities seemed rather low, but were comparable to the relative densities indicated by Hutchings (2011). Indeed, Hochstetter's frog densities vary greatly within and between catchments, with reports such as 0.4 to 5 frogs per m² from the upper Motu River (McLennan 1985), 6.3 frogs per 100 m in the Coromandel (Whitaker & Alspach 1999), and 55 frogs per 100 m on Great Barrier Island (Herbert *et al.* 2014). Accordingly, Torere Forest seems to only support low densities of Hochstetter's frogs. However, Shaw (2013) suggested that areas with an excess of refuge sites (and therefore low densities of frogs) are considered essential habitat. Although this inference and the similar densities recorded between habitats suggest that mature pine plantations in Torere Forest may provide necessary resources for Hochstetter's frogs, previous surveys highlight conflicting conclusions. For example, Douglas (1997) initially recorded similar densities of Hochstetter's frogs in mature pine plantations and native forests but observed population declines in the pine plantations the following year (Douglas 1998a). Likewise, Shaw (1993) noted lower densities in mature pine plantations compared to native forests, of the eastern Bay of Plenty. The influence of habitat on populations, however, is not the only effect as multiple factors, whether it be current or historical, can affect Hochstetter's frog populations (Douglas 1997). For instance, Douglas (1998a) concluded that population declines observed in her study were due to flooding and storm damage, whereas it is likely that Shaw (1993) surveyed populations that were still recovering from native habitat clearance and the establishment of pine plantations in the 1980s. Furthermore, density may be influenced socially as social attraction possibly promotes clumping behaviour and therefore highly localised densities (McLennan 1985; Shaw 2013). These potential social influences on density are evident in areas of extensive retreat sites as clusters of frogs are not a consequence of intraspecific competition (McLennan 1985; Shaw 2013).

However, even if density truly does represent habitat quality, the quantity of resources in an area cannot be substituted for quality (Hobbs & Hanley 1990). Specifically, low densities may indicate the presence of low or high quality resources, depending on the carrying capacity (K) of the population. For example, in the presence of high quality resources, populations that have reached carrying capacity are often high in density, regardless of resource abundance (Figure 8a). In these circumstances, high density is a result of habitat restriction or optimal population viability. Conversely, density may remain low where only low quality resources are available

(Figure 8a). Density remains low in this case because deficiencies in those resources prevent population growth. However, considering the population status (and therefore the carrying capacity) of Hochstetter's frog populations in Torere Forest are largely unknown, and that low densities were recorded, the quality of resources is uncertain. Thus, the low densities recorded could either be an indication of low quality resources, or that the populations are still growing in areas where high quality resources occur (i.e. the carrying capacity has not yet been reached) (Figure 8b). Indeed, populations in Torere Forest may still be recovering after initial habitat clearance or native forest logging that occurred in the 1980s. It is no surprise then that density measures can be easily misinterpreted without the necessary validations such as time series (Hobbs & Hanley 1990). However, to make such validations requires long-term observations of population growth rates and size, which are then compared to resource availability (Hobbs & Hanley 1990), which was beyond the scope of this thesis. Clearly, understanding how densities are influenced and change over time is essential as snap-shot density measures must be interpreted with caution.

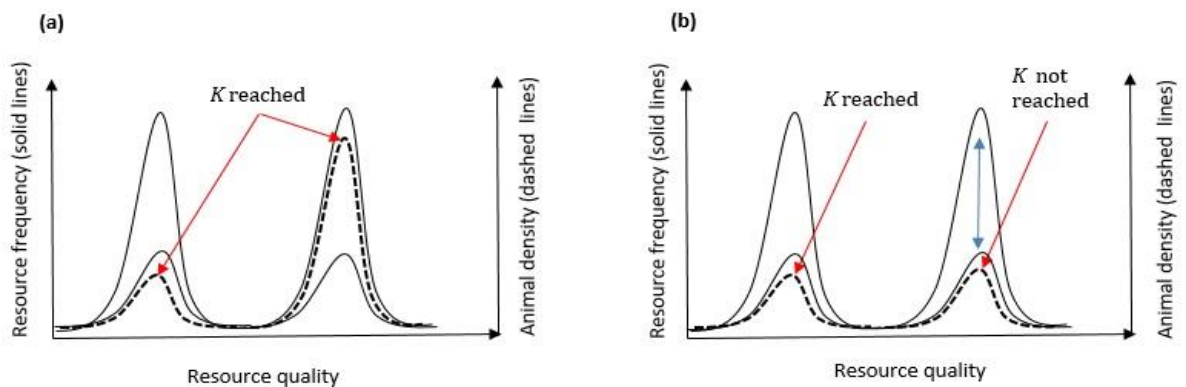


Figure 8. Schematic drawing of a theoretical distribution of density in response to resource frequency and quality for scenarios when (a) the carrying capacity (K) of the population has been met, and (b) the carrying capacity is unknown and low densities are observed (the blue double arrow indicates the growth capacity of the population). Modified from Hobbs & Hanley (1990).

Scaled mass index

There was no difference in scaled mass index between the habitats, contrary to the prediction that individuals inhabiting mature pine plantations would have lower body condition. Competition for resources in mature pine plantations was therefore not evident. Given that competition has been shown to reduce body condition of amphibians within resource-limited environments (Brown 1994; Bell 1995; Bell *et al.* 2004b; Germano 2006; Karraker & Welsh 2006), this finding indicates that necessary resources may be abundant in mature pine plantations. Furthermore, this result was congruent to the study by Chazal & Niewiarowski (1998) who investigated mole salamanders (*Ambystoma talpoideum*) that inhabited thinned and unmodified pine forests. In contrast, Lauck (2006) concluded that the body condition for wood frogs (*Crinia signifera*) inhabiting logged areas was lower compared to unlogged, although the difference was very small. Nevertheless, using body condition as an indicator of habitat quality must involve a cautious approach (Johnson 2007) as long-term data are necessary in order to validate inferences, especially for long-lived species (Hoare *et al.* 2006; Moore *et al.* 2007; Gebauer 2012).

Size-class distribution

The prediction that fewer adults would be found in mature pine plantations was also not supported. Instead, no statistical differences ($p > 0.05$) in size-class distribution between habitats were observed. In comparison, Douglas (1997) recorded a significantly lower proportion of adults in pine plantations in the Brynderwyn Hills. Likewise, Lauck (2006) concluded that body sizes of wood frogs were larger in unlogged areas compared to logged, but like for body condition, the difference was small. Conflicting results are not surprising given the variability of size-class distributions of Hochstetter's frogs over time (Douglas 1999), but habitat quality has indeed been shown to reflect population structure (Nickerson *et al.* 2003). For example, Nickerson *et al.* (2003) demonstrated that the presence of larval habitat largely influenced recruitment in a population of Ozark hellbenders (*Cryptobranchus alleganiensis*). Mature pine plantations in Torere Forest may therefore provide adequate habitat for all size-classes, but further investigations would be necessary to confirm this.

Final conclusions

The purpose of this chapter was to address the question of how population parameters and individual fitness compare between habitats in order to provide baseline parameters and to highlight habitat influences on Hochstetter's frog populations in Torere Forest. However, there were no discernible differences of any of the measured population parameters and individual fitness between habitats. These findings suggest that mature pine plantations may not negatively

affect Hochstetter's frogs. Instead, mature pine plantations may actually provide suitable areas of habitat. Even so, reasonable quality habitat in mature pine plantations is perhaps not surprising as Leiopelmatids (*Leiopelma* and *Ascaphus*) have an ancient evolutionary history adapted to inhabiting old-growth conifer forests (Reilly S, pers. comm.). Nevertheless, population parameters and individual fitness are part of natural cycles or trends that can only be determined through long-term monitoring (Lawson 1993; Moore *et al.* 2007). Furthermore, whilst population parameters and individual fitness are informative, they must be interpreted carefully, particularly when making inferences with respect to habitat quality. If there are indeed no negative effects on populations, then this might be because of behavioural adaptations to microhabitat use. As Lauck (2006) portrayed, changes in microhabitat use may mitigate environmental stressors and competition amongst certain resources may be lessened. Both the present study and Hutchings (2011) noted flexible resource use by Hochstetter's frogs inhabiting mature pine plantations, which therefore supports Lauck's (2006) conclusion, but under the condition that resources used in native forests are limited in mature pine plantations and vice versa. Whether this condition of limited used resources is actually met is investigated in the next chapter.

As it cannot be concluded that mature pine plantations do **not** have a negative impact on Hochstetter's frog populations, whether or not populations actually persist in the future remains to be seen. It is essential further monitoring takes place in order to 1) assess population status prior to harvesting, 2) assess population responses once harvesting commences, and 3) determine the actual quality of resources available. That way, monitoring will ensure that stakeholders are well informed and thus can respond rapidly and appropriately to any negative impacts on these populations.

Chapter Three

Resource selection by Hochstetter's frogs and an investigation of habitat quality in a potential South Island translocation site

Introduction

Identifying the associations between resource use and population dynamics or occurrence is necessary to evaluate the effects of habitat modification on amphibian populations (Crawford & Semlitsch 2008). Studies thus often identify used microhabitat variables that best predict population abundance (Oldham *et al.* 2000; Barr & Babbitt 2002; Crawford & Semlitsch 2008). Generally applicable conclusions from such studies are limited however, as resource variability is not uniform in nature and resource use may change as availability changes (Barr & Babbitt 2002; Manly *et al.* 2002; Johnson 2007). Used resources should therefore be compared to available or unused resources (Manly *et al.* 2002) to reach more biologically meaningful conclusions. Therefore, inferences regarding resource selection (i.e. the disproportionate use of resources in relation to its availability, Johnson 1980) (Manly *et al.* 2002) can be obtained and subsequently used to indicate habitat quality (Johnson 2007).

As previously mentioned, habitat requirements of native frogs are largely unknown (Bishop *et al.* 2013). Accordingly, habitat associations and habitat quality have been investigated for Hochstetter's frogs, such as identifying microhabitat variables associated with their presence/absence or abundance (Ziegler 1999; Nájera-Hillman *et al.* 2009a,b; Fouquet *et al.* 2010a; Nájera-Hillman 2012; Herbert *et al.* 2014). An understanding of the resource selection of Hochstetter's frogs, which can be influenced by habitat modification (Johnson 2007), is thus crucial for the management of this species. Assessing whether the necessary resources are available in potential translocation sites, such as Orokonui Ecosanctuary, is also essential (Michel *et al.* 2008). In particular, Egeter (2009) concluded that habitat quality was relatively high for Hochstetter's frogs in Orokonui Ecosanctuary by comparing habitat in areas where frogs were highly abundant in the Waitakeres (west of Auckland) to habitat found in Orokonui Ecosanctuary. Nonetheless, Egeter's (2009) results require validation to ensure the robustness of this conclusion. Therefore, the questions for this chapter aimed to identify required resources for Hochstetter's frogs through resource selection in modified and largely unmodified environments and assess how resource use compared between habitats. Additionally, resource use findings were applied to sites surveyed at Orokonui Ecosanctuary in order to address the question of whether suitable areas of habitat were available.

Based on findings from previous habitat studies of Hochstetter's frogs, it was hypothesised that rocky substrata would be an important habitat feature for Hochstetter's frog presence. Considering Hochstetter's frogs apparently utilise resources such as pine debris and that rocky habitat is often limited in pine plantations (Robertson 1999; Hutchings 2011), it was also hypothesised that Hochstetter's frogs would show flexible resource use in response to differences in resource availability. Lastly, as Egeter (2009) indicated suitable areas of habitat were available in Orokonui Ecosanctuary, it was predicted that essential resources identified in Torere Forest would also be present at Orokonui Ecosanctuary. Ultimately, these results will provide insights into management requirements regarding Hochstetter's frog ecology within a modified environment, habitat quality *in situ*, and habitat quality at potential translocation sites.

Methods

Sampling habitat features and weather conditions

During the Hochstetter's frog surveys in Torere Forest mentioned in Chapter Two, current and previous (up to a week prior) weather conditions were also recorded, as frog detectability is affected by heavy rainfall (Slaven 1992; Douglas 2001b). Further, general habitat was noted and any evidence of habitat disturbance along stream banks (e.g. erosion) was recorded, along with microhabitat variables measured in locations (marked by flagging tape) that were either 'used' (i.e. an area that is used by an animal or population in a fixed period of time, Manly *et al.* 2002) and 'available' (i.e. an area accessible to an animal or population during that same period of time, Manly *et al.* 2002). Surveying only ≤ 2 m from streams/seepages was particularly important, as overestimating resource use for linearly distributed species (e.g. stream inhabitants) can result in spurious estimates of resource availability (Slaght *et al.* 2013). Based on field observations and the literature, 14 habitat variables (i.e. substrate types and canopy cover) were considered important for Hochstetter's frogs and subsequently sampled (Table 1). Thirteen substrate types were measured (% cover) in an area of 1 m² marked out by an aluminium 50 cm² quadrat sequentially placed in four 'positions' surrounding the point where a frog was found (Figure 9).

Table 1. Sampled habitat features that were considered important for Hochstetter's frogs

Water	Boulder	Tree feature (e.g. root)
Canopy cover	Bedrock	Dead frond (nikau or fern frond)
Fine sediment	Moss/liverwort	Woody debris (e.g. branches/twigs)
Gravel	Leaf litter	Vegetation (≤ 50 cm height)
Cobble	Log	

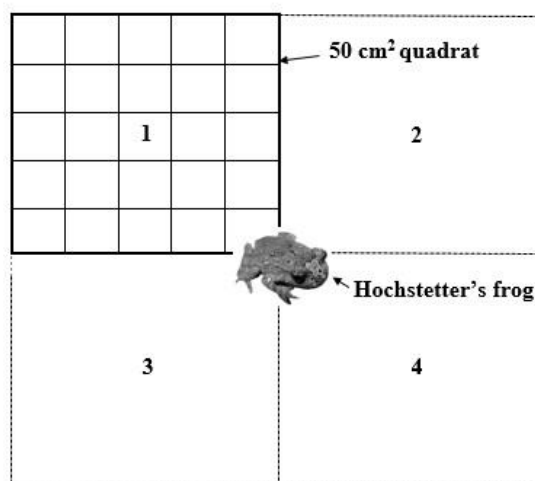


Figure 9. Layout of quadrat sampling. Habitat features were sampled using a 50 cm² quadrat placed at four positions (1 - 4) surrounding the point frogs were captured.

A modified Wentworth scale (Sagar 1993) was used to classify substrata into the following classes (measuring the longest axis): “fine sediment” = <5 mm, “gravel” = 5 - <50 mm, “cobble” = 50 - 250 mm, and “boulder” = >250 mm. Lastly, unlike the 13 substrate types, canopy cover was recorded by taking a wide-angle photograph of the canopy from the centre point of the quadrat at a height of 50 cm.

Selective sampling is common in ecological studies as more population data can be collected (Allen 1992; Gordon *et al.* 2004). Selective sampling is also arguably necessary to study cryptic and rare species like Hochstetter’s frogs. Equally important is the assumption of independency among ‘used’ variables (Manly *et al.* 2002). For the purpose of data analyses, any frogs found together in groups were thus treated as single detections following Thomas & Taylor (1990) (i.e. ‘used’ variables were only recorded once for the entire group). ‘Available’ microhabitat was sampled using a stratified sampling method to ensure that each 10 m section (i.e. stratum) was adequately represented (Harraway 1997) (Figure 10). Due to the instability of the habitat and logistical reasons, two random quadrat sites were located in each 10 m section, where the above variables were recorded within each quadrat. Flagging tape markers were collected at the end of the habitat sampling. At Orokonui Ecosanctuary, ‘available’ microhabitats were measured within three native forest sites (Marie Stream, EF 3 - 4, and EF 28) (Figure 11). Habitats at these sites were deemed likely to be adequate for Hochstetter’s frogs and were located in streams/seepages within “Marie Gully” and along the eastern slopes of the valley.

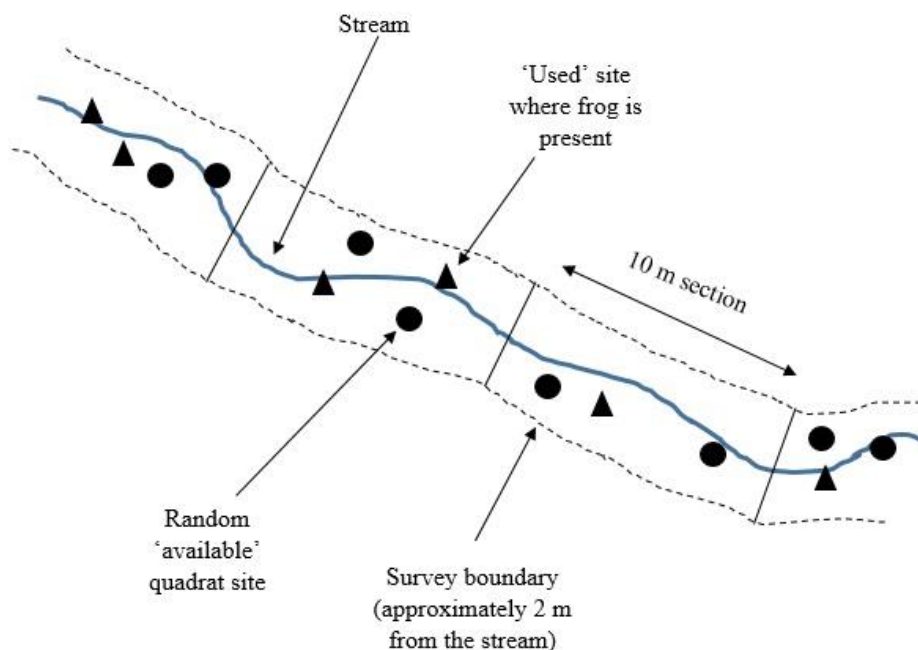


Figure 10. Schematic drawing of the 10 m stratified sampling layout of 'used' (triangles) and 'available' (circles) locations along streams in Torere Forest.

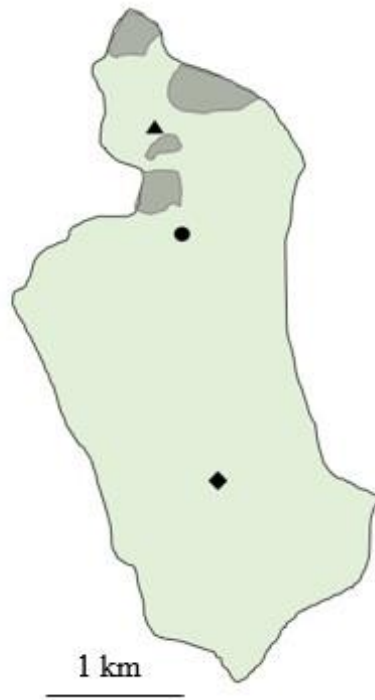


Figure 11. Map of Orokonui Ecosanctuary showing the three sampling sites: Marie Stream (triangle), EF 28 (circle) and EF 3 - 4 (diamond). Scale bar shown.

Statistical analyses

In order to address the questions for this chapter, statistical analyses were split into three components. Firstly, two additive-only models were produced to identify which resources were the most important for Hochstetter's frogs inhabiting mature pine plantations and native forests. Secondly, to investigate how resource use is influenced by habitats, resource use was compared between habitat types by producing an interaction model. Lastly, resource use in native forest was extrapolated to streams surveyed in Orokonui Ecosanctuary to predict habitat quality. Models were produced following Grueber *et al.* (2011). All analyses were performed in R version 3.0.2 (R Core Team 2013).

Resource selection

Resource selection by animals is commonly investigated using resource selection functions (RSFs), which estimate the probability of use for different resources (Manly *et al.* 2002). Resource selection was measured at the individual level, as recommended by Manly *et al.* (2002). To make inferences for the population, it was assumed that individuals captured were a random sample of the population (Manly *et al.* 2002). Generalised linear mixed-effects binomial models (GLMMs) were then used as a type of RSF. Specifically, GLMMs are used in instances where data are collected within and between multiple sites. GLMMs are useful as

they not only include random effects (such as variation between sites within a habitat) and fixed effects (i.e. predictors of interest), but they can also deal with non-normal (e.g. binary) response data (Grueber *et al.* 2011). Moreover, the inclusion of random factors is particularly important when dealing with dependent data or hierarchical study designs (e.g. response variables sampled from the same site and/or sampled from multiple sites but within the same habitat) (Grueber *et al.* 2011) as was present in this study.

Building the resource selection models

For studies that use presence/available data, ‘used’ locations must be treated as a subset of what is ‘available’ (Boyce *et al.* 2002). Treating such data this way is because ‘used’ locations are not exclusive from ‘available’, as whilst an animal may not be detected at a particular point during a survey, it does not mean that the area will never be used, particularly within a home-range (Boyce *et al.* 2002). Models were therefore produced and their performance validated as recommended by Boyce *et al.* (2002). To begin with, using the ‘*lmer*’ function in the package ‘*lme4*’ (Bates *et al.* 2014), a global (i.e. all parameters included) binomial GLMM was constructed for each habitat type, with habitat features as the predictor variables, ‘used/available’ (denoted as 1s and 0s, respectively) as the response, and ‘site’ (a three-level categorical variable; sites 1-3) as a random factor. In order to identify what variables best predicted habitat use, only additive (i.e. no interaction) terms were used for this part of the analysis. Four habitat variables (‘dead frond’, ‘bedrock’, ‘vegetation’, and ‘tree feature’) were largely absent in the data collected and were thus removed from the models before model analysis commenced. ‘Moss’ was also removed from both additive models and ‘fine sediment’, ‘log’ and ‘woody debris’ were removed from the native forest additive model for the same reason and because the data were negatively skewed. Additionally, ‘water’ and ‘canopy cover’ variables were removed from both additive models as these variables explained little variation and, once deleted, enabled the models to converge. Model diagnostics were checked and both additive models met the assumptions of normality and constant variance. Following Boyce *et al.* (2002), a *k*-fold cross-validation test was then used to evaluate the performance of the global RSF models to predict habitat use derived from the presence/available data. Model prediction performance was overall reasonable (Figure 12), particularly for the native forest additive model. The amount of variation explained by these global additive models was low ($R^2_c = 0.32$ for pine and $R^2_c = 0.28$ for native forest), but this is expected for models derived from used/available data as the classifications of predicted and observed values are not independent (Boyce *et al.* 2002).

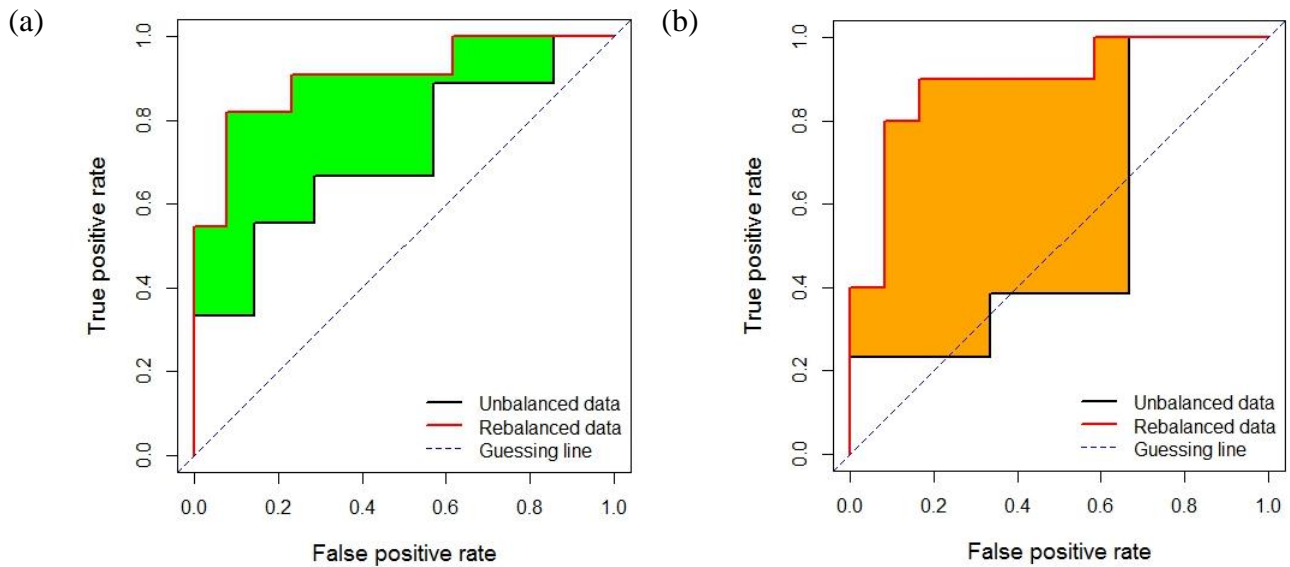


Figure 12. A receiver operating characteristic (ROC) curve showing the performance of global additive model predictions using balanced and unbalanced data for (a) native forest and (b) pine forest resource selection by Hochstetter’s frogs in Torere Forest, Bay of Plenty. Values above the blue dotted line indicate that ‘used’ locations are correctly predicted (true positives) more so than by chance (i.e. guesses) (blue dashed lines).

Next, an interaction global model was constructed to compare resource use of the frogs between habitat types. With ‘native forest’ as the reference group, interactions between habitat types (treated as a fixed factor) and habitat features (apart from the removed variables mentioned above) were computed. Variation explained by this model was similarly low compared to the two additive models ($R^2_c = 0.31$), but model diagnostics met the standard assumptions. R^2 values were calculated following Nakagawa & Schielzeth (2013) via the ‘*r.squaredGLMM*’ function in the ‘*MuMIn*’ package (Bartoń 2014).

Model standardisation and selection

Standardisation of the three global models (Table 2) was carried out using the *standardize* function in the ‘*arm*’ package (Gelman & Su 2013). Standardisation was done to improve the interpretability of the coefficients by making the predictor variables comparable once they were on the same scale (Schielzeth 2010).

Table 2. Predictor variables of the global additive and interaction resource selection models.

Global additive model- resource use in mature pine plantations
<i>Fine sediment + Gravel + Cobble + Boulder + Leaf litter + Woody debris + Log</i>
Global additive model- resource use in native forests
<i>Gravel + Cobble + Boulder + Leaf litter</i>
Global interaction model- comparing resource use in both habitats
<i>Habitat*Fine sediment + Habitat*Gravel + Habitat*Cobble + Habitat*Boulder + Habitat*Leaf litter + Habitat*Woody debris + Habitat*Log</i>

Model selection involved comparing Akaike Information Criteria that were corrected for small sample sizes (denoted as AICc) and their corresponding weights (i.e. AICc w_i), which is the relative likelihood of a model, given the data (Burnham & Anderson 2010). Using the function ‘*dredge*’ in the package ‘*MuMIn*’, a set of ‘candidate’ models with differences in AICc (i.e. ΔAICc) < 2 and that had at least four predictor variables included (minimum of two for the native forest additive model as only a few *priori* variables were left) were produced. From these sets, only those models that contained the fewest number of parameters that explained the highest proportion of variation were chosen. These represented the ‘top models’.

Model averaging

Model averaging is recommended when there is not strong support for one model over another (Grueber *et al.* 2011). Model averaging is particularly useful as it accounts for relative parameter importance and parameter estimate uncertainty, which enables more reliable inferences to be made (Burnham & Anderson 2010; Nakagawa & Freckleton 2011). In the analyses, the ‘top models’ were thus averaged using the ‘*model.avg*’ function in the package ‘*MuMIn*’ and coefficient estimates sourced from the ‘zero-method’ (i.e. with shrinkage) output, as recommended by Nakagawa & Freckleton (2011) and Burnham & Anderson (2010). The ‘zero-method’ was used because this method substitutes missing values for predictor variable estimates where the given variable is absent in certain ‘candidate’ models. Data therefore remained unbiased as missing cases were not deleted, which enabled inferences to be made for

all models (Burnham & Anderson 2010; Nakagawa & Freckleton 2011). The zero-method is particularly important if there is an underlying biological reason that may cause the absence of such data (e.g. individuals are inactive during winter) (Nakagawa & Freckleton 2011). In comparison, the ‘natural averaging method’ only infers from several models, but it can be useful if trying to detect an effect of a certain parameter that may be weak compared to other covariates (e.g. inbreeding in Grueber *et al.* 2011). Adjusted standard errors can be also sourced from the ‘zero-method’ output, as these are standard errors that account for both the error in parameter estimates and the error associated with model selection uncertainty (Burnham & Anderson 2010).

Habitat quality predictions

The averaged model for the native forest additive model was then used to predict habitat use in Orokonui Ecosanctuary. An ANOVA was used to compare predictions of habitat use between surveyed sites at Orokonui Ecosanctuary and those surveyed in mature pine plantations and native forests within Torere Forest. Significance was tested at $p < 0.05$ level.

Results

General observations

In Torere Forest, several frogs were found in areas devoid of canopy cover on the edge of native forest, but no frogs were found in pine plantation seepages with a high sediment load and/or clay stream bed. Two of the three pine plantation sites surveyed had extensive erosive disturbance as large quantities of fallen timber were recorded, including screes of sediment and gravel found below uprooted trees. Riparian zones of native vegetation were virtually absent in these sites too. Substrata in pine plantations were often unstable underfoot, which made surveying steep areas difficult. As only one day had light rain during the week of surveying, stream flow was largely unaffected. At Orokonui Ecosanctuary, there were no signs of erosion. Substrata were more stable than in pine plantations at Torere Forest, which enabled steep areas to be accessed easily. Lush vegetation along stream banks provided good riparian cover. No rain occurred during the sampling period.

Habitat features

In Torere Forest, habitat features were recorded within 157, 1 m² quadrats. Of these, 78 were recorded in pine plantations (27 used and 51 available) whilst 79 were recorded in native forests (30 used and 49 available). In Orokonui Ecosanctuary, habitat features were recorded within 70, 1 m² quadrats. The summary results of habitat features are presented in Table 3. Tree features, bedrock, dead fronds, moss/liverwort, and vegetation were all largely absent from the data and/or negatively skewed. Nevertheless, there was little vegetation recorded in Torere Forest pine plantations, compared to native forests and Orokonui Ecosanctuary which had similar proportions. Moss/liverwort cover was low in pine plantations, whereas the range was similar between Orokonui Ecosanctuary and native forests in Torere Forest, despite the average being higher in Orokonui Ecosanctuary. Leaf litter cover in native forests was lower than pine plantations, but even lower compared to Orokonui Ecosanctuary. Lowest woody debris cover was recorded in native forests and the highest in pine plantations. Logs were in similar proportions between Orokonui Ecosanctuary and pine plantations, but was much lower in native forests. Fine sediment cover was highest in pine plantations and was similar between Orokonui Ecosanctuary and native forests. Pine plantations had the highest gravel cover, whereas Orokonui Ecosanctuary had the lowest. Likewise, Orokonui Ecosanctuary had the lowest cobble cover. However, boulder cover was highest in Orokonui Ecosanctuary compared to Torere Forest. Canopy cover was overall similar between Torere Forest and Orokonui Ecosanctuary, but the average was lower in native forests due to some areas being devoid of canopy cover. Lastly, water cover was highly variable between the sites.

Table 3. Summary results of habitat features sampled in Torere Forest and Orokonui Ecosanctuary.

Habitat feature	Torere Forest pine		Torere Forest native		Orokonui	
	Mean (%)	Range (%)	Mean (%)	Range (%)	Mean (%)	Range (%)
Canopy cover	74	52 - 94	66	0 - 92	78	44 - 97
Water	25	2 - 54	36	0 - 81	4	0 - 33
Dead frond	7	0 - 47	4	0 - 67	0	0 - 24
Vegetation	0	0 - 4	2	0 - 36	4	0 - 38
Tree feature	0	0 - 7	0	0 - 5	2	0 - 16
Leaf litter	15	0 - 51	7	0 - 35	41	0 - 93
Woody debris	9	0 - 46	1	0 - 13	5	0 - 32
Log	5	0 - 39	1	0 - 21	4	0 - 38
Moss/liverwort	2	0 - 31	8	0 - 77	17	0 - 73
Fine sediment	9	0 - 46	1	0 - 15	4	0 - 17
Gravel	16	0 - 87	13	0 - 62	3	0 - 24
Cobble	9	0 - 53	23	0 - 63	6	0 - 40
Boulder	1	0 - 18	6	0 - 26	10	0 - 63
Bedrock	2	0 - 29	0	0	0	0

Resource selection

A total of eight pine plantation additive models were produced after dredging (i.e. the production of a sub-model set from the global model, Grueber *et al.* 2011). Of these, four were selected for averaging as only these models contained rock substrata variables (e.g. cobbles). Retaining these variables was important in order to test the hypothesis that rock substrata are essential resources for Hochstetter's frogs, which would be determined by an effect size that did not contain zero in the confidence interval. For the native forest additive model set, four were produced and all were selected for averaging for the same reasons. Both additive model sets, along with their associated AICc, Δ AICc and weight values, are presented in Table 4. The final averaged model for resource selection in pine plantations contained six of the original seven predictor variables included in the global model. The final model for resource selection in native forests contained all four original predictor variables. The parameter estimates for these additive models are summarised in Table 5.

There were four strong associations between predicted habitat use and habitat features observed in Torere Forest. Logs and cobble substrate were the most important resources as positive associations were observed for cobble and log in pine plantations and cobble in native forests.

In comparison, there was a strong negative association for gravel in native forests. All other habitat features were deemed statistically unimportant due to small effect sizes.

A total of 10 interaction models were produced after dredging, of which two were selected and subsequently averaged. These interaction models, along with their associated AICc, Δ AICc and weight values, are presented in Table 6. The final averaged model for comparing resource selection between pine plantations and native forests contained five of the original seven predictor variables included in the global model. The parameter estimates for this model are summarised in Table 7.

There was a strong interaction effect between log cover and habitat type. This indicated that Hochstetter's frogs inhabiting pine plantations used logs as a resource more often as log cover increased, compared to native forests. All other interactions were statistically unimportant due to small effect sizes.

Habitat quality predictions

Relatively high habitat quality was identified in Orokonui Ecosanctuary as no significant differences in predicted habitat use were observed between any sites surveyed within and between Orokonui Ecosanctuary and Torere Forest ($F_{4,222} = 1.15$, $p = 0.33$) (Figure 13). At Orokonui Ecosanctuary, the EF 28 site scored the highest predictions of habitat use, as 38.5% of quadrats (10/26) had estimates higher than 0.5. In comparison, Marie Stream had 12.5% of quadrats (3/24) with estimated probabilities greater than 0.5. Lastly, EF 3 - 4 had 25% of quadrats (5/20) with estimated probabilities higher than 0.5.

Table 4. Ranking of candidate additive models for Hochstetter’s frogs’ resource selection in mature pine plantations and native forests located within Torere Forest, Bay of Plenty. Columns from left to right are predictor variables included in the model, K (number of parameters in the model, including the random factor and intercept), AICc, Δ AICc and AICc w_i .

Resource selection in mature pine plantations	K	AICc	ΔAICc	AICc w_i
<i>Cobble + gravel + log + woody debris</i>	6	95.31	0	0.38
<i>Fine sediment + cobble + gravel + log</i>	6	96.26	0.95	0.24
<i>Cobble + gravel + leaf litter + log</i>	6	96.40	1.09	0.22
<i>Fine sediment + cobble + gravel + log + woody debris</i>	7	96.99	1.68	0.16

Resource selection in native forest	K	AICc	ΔAICc	AICc w_i
<i>Cobble + gravel</i>	4	99.65	0	0.35
<i>Boulder + cobble + gravel</i>	5	100.08	0.43	0.29
<i>Cobble + gravel + leaf litter</i>	5	100.77	1.12	0.20
<i>Boulder + cobble + gravel + leaf litter</i>	6	101.25	1.61	0.16

Table 5. Summary results for averaged additive models representing Hochstetter’s frogs’ resource selection in mature pine plantations and native forests located within Torere Forest, Bay of Plenty. Columns from left to right are variable names, effect sizes, adjusted standard errors and relative variable importance. Variables are ranked by their weights. Large effect sizes and their corresponding 95% CI that do not contain zero are highlighted in bold.

Variables (pine plantations)	Effect size	Adjusted SE	95% CI	w_i
<i>Cobble</i>	1.86	0.75	0.39 – 3.33	1
<i>Gravel</i>	-1.06	0.84	-2.71 – 0.59	1
<i>Log</i>	1.48	0.61	0.28 – 2.68	1
<i>Woody debris</i>	0.38	0.53	-0.66 – 1.42	0.54
<i>Fine sediment</i>	0.20	0.45	-0.68 – 1.08	0.40
<i>Leaf litter</i>	-0.12	0.41	-0.92 – 0.68	0.22

Variables (native forests)	Effect size	Adjusted SE	95% CI	w_i
<i>Cobble</i>	1.63	0.58	0.49 – 2.77	1
<i>Gravel</i>	-1.36	0.69	-2.71 – 0.008	1
<i>Boulder</i>	0.31	0.49	-0.65 – 1.27	0.44
<i>Leaf litter</i>	0.20	0.41	-0.60 – 1.00	0.36

Table 6. Ranking of candidate interaction models for comparing Hochstetter’s frogs’ resource selection between mature pine plantations and native forests located within Torere Forest, Bay of Plenty. *Habitat* is a 2-level categorical fixed factor with native forest as the reference group (i.e. native= 0 and pine= 1). Columns from left to right are predictor variables included in the model, K (number of parameters in the model, including the random factor and intercept), AICc, Δ AICc and AICc w_i .

Variables	K	AICc	Δ AICc	AICc w_i
<i>Habitat*fine sediment + habitat*cobble</i> <i>+ habitat*leaf litter + habitat*log</i>	6	208.27	0	0.55
<i>Habitat*fine sediment + habitat*gravel</i> <i>+ habitat*leaf litter + habitat*log</i>	6	208.65	0.38	0.45

Table 7. Summary results for averaged interaction models comparing Hochstetter’s frogs’ resource selection between mature pine plantations and native forests located within Torere Forest, Bay of Plenty. *Habitat* is a 2-level categorical fixed factor with native forest as the reference group (i.e. native= 0 and pine= 1). Columns from left to right are interaction parameters, effect sizes, adjusted standard errors, 95% confidence intervals and relative variable importance. Variables are ranked by their weights. Large effect sizes and their corresponding 95% CI that do not contain zero are highlighted in bold.

Variables	Effect size	Adjusted SE	95% CI	w_i
<i>Habitat*Fine sediment</i>	0.17	0.88	-1.55 – 1.89	1
<i>Habitat*Cobble</i>	-0.35	0.72	-1.76 – 1.06	1
<i>Habitat*Leaf litter</i>	-1.34	0.84	-2.99 – 0.31	1
<i>Habitat*Log</i>	1.67	0.84	0.02 – 3.32	0.55
<i>Habitat*Gravel</i>	0.13	0.52	-0.89 – 1.15	0.45

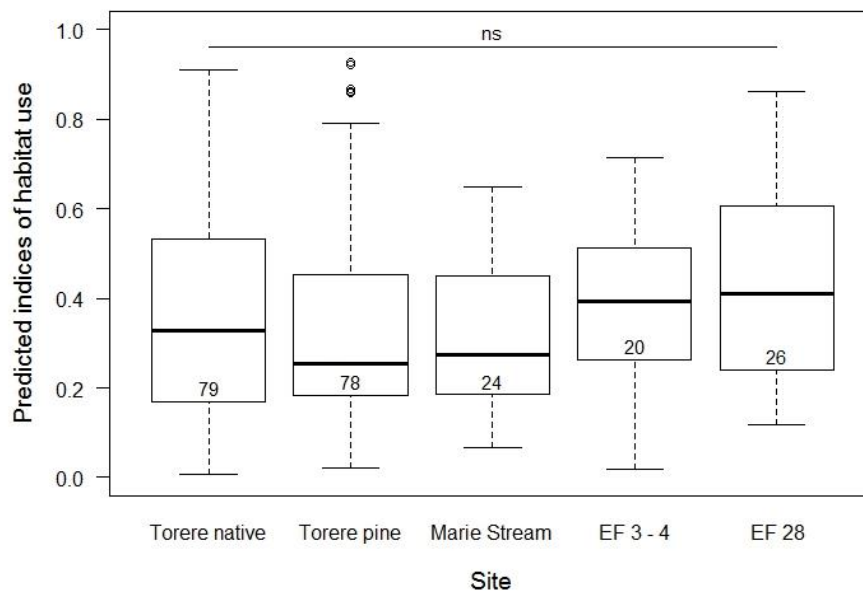


Figure 13. Predicted habitat use indices for Hochstetter’s frogs in surveyed streams in Torere Forest and Orokonui Ecosanctuary (Marie Stream, EF 3 - 4, and EF 28). Predicted habitat use for the three surveyed streams were combined for native forests and also for pine plantations in Torere Forest, but not for Orokonui Ecosanctuary. Numbers presented denote the number of quadrats sampled. There were no significant differences ($p > 0.05$).

Discussion

Resource selection

Rock substrata

Positive associations were recorded between predicted habitat use and cobble cover in both habitats at Torere Forest, which supported the hypothesis that rock substrata would be an important habitat feature for Hochstetter's frogs. Furthermore, in comparison to native forests, the effect size of cobble use in mature pine plantations was slightly higher as cobble habitat was more limited. These results supported other studies that have highlighted the strong affiliation between Hochstetter's frog presence/abundance and rock substrata in particular (McLennan 1985; Tessier *et al.* 1991; Shaw 1994; Glaser & Dobbins 1995; Glaser 1996; Eggers 1998; Ziegler 1999; Nájera-Hillman *et al.* 2009a,b; Shaw 2013; Herbert *et al.* 2014). This association is also observed in the sister taxon *Ascaphus* from north-west USA (Adams & Bury 2002; San Mauro *et al.* 2005).

Notably, the composition of cobbles that frogs were found under in pine plantations were predominantly unconsolidated (i.e. 'brittle') clay or mudstone, as opposed to the consolidated (i.e. 'solid') sedimentary greywacke observed in native forests. The distinction between unconsolidated and consolidated cobbles and the potential effect cobble composition may have on frog distribution were also highlighted by Glaser (1996). Whilst the present study could not (and did not) test for this composition effect as mainly unconsolidated substrata were located in pine plantations, other studies have demonstrated that the percentage occupancy of stream amphibians is generally higher in streams with consolidated substrata compared to unconsolidated (Diller & Wallace 1999; Adams & Bury 2002). Adams & Bury (2002) inferred that consolidated rock habitat is more optimal, but disproportionate sampling was evident. Nevertheless, Wilkins & Peterson (2000) concluded that unconsolidated microhabitat should be regarded as a low conservation priority for protection during harvesting, given the rarity or absence of frogs inhabiting unconsolidated substrata in pine plantation streams (Adams & Bury 2002). However, as Adams and Bury (2002) illustrated, no studies have yet examined the interaction effect of rock composition and harvesting on occupancy. Indeed, as Robertson (1999) and the present study have shown, there are often decreases in the proportions of consolidated cobbles and boulders as forestry impacts intensify. Unconsolidated substrata may therefore become utilised by frogs more in harvested areas as the availability of consolidated substrata decreases. Additionally, as observed in this study, if consolidated substrata are largely unavailable, then frogs will utilise unconsolidated substrata instead. Considering frogs were observed to inhabit unconsolidated substrata in both the present study and by Adam & Bury

(2002), unconsolidated substrata do provide habitat for frogs and may therefore require higher conservation priority for protection. This protection is particularly necessary in steep areas where coarse substrata are unstable.

Size and shape are also features that make cobbles an important resource for Hochstetter's frogs. Smooth rocks are apparently not optimal as these provide few retreat sites (Shaw 2013) and as Glaser (1996) pointed out, substrate size greatly determined the likelihood of frogs inhabiting the areas he surveyed. Results from the present study support Glaser (1996) as there were strong negative associations with gravel substrate, which were also congruent to observations made by Herbert *et al.* (2014) and Nájera-Hillman *et al.* (2009b). High gravel cover, like that observed in pine plantations, is therefore non-suitable for Hochstetter's frogs. As for boulder cover, this was not considered statistically important for Hochstetter's frogs in the final models, but as Glaser (1996) highlighted, boulders are difficult to search for frogs as they are often too large to lift carefully. Boulders may therefore still provide adequate cover for Hochstetter's frogs (Glaser 1996; Nájera-Hillman *et al.* 2009b; Herbert *et al.* 2014), but the importance of this resource remains largely unknown due to the logistics of surveying boulder habitat.

Substrate size and shape are particularly important as small interstitial spaces aid in the protection of frogs, especially from predators. For instance, Barr & Babbitt (2002) demonstrated that densities of larval two-lined salamander (*Eurycea bislineata*) were higher in boulders in the presence of the predatory brook trout (*Salvelinus fontinalis*) compared to streams where the trout were absent. Furthermore, Towns (1996) noted that shore skinks (*Oligosoma smithi*) which inhabited small interstitial spaces between rocks were not negatively affected by rat predation, whereas skinks that inhabited boulders were. Whether cobble substrate actually mitigates the predation pressure of introduced mammals on Hochstetter's frogs is still uncertain, as there are contrasting views regarding population responses to predator control (Mussett 2005; Nájera-Hillman *et al.* 2009b; Longson 2014). Research into whether resource selection differs between streams targeted for predator control and those that are not, would provide a more comprehensive understanding of how predation impacts and habitat associations interact.

Fine sediment

Given that interstitial spaces may mitigate predation pressure, the prevention of individual frogs accessing these refuges would therefore be considered a threat. The high sediment cover recorded in pine plantations may therefore threaten Hochstetter's frogs as it is a major characteristic of pine streams and increases as forestry impacts intensify (Robertson 1999;

Thompson 2001). This impact was particularly obvious in the present study as streams that had high sediment loads were all devoid of frogs. Glaser & Dobbins (1995) and McLennan (1985) also observed the same pattern. Moreover, several studies have identified negative associations between frog abundance/presence and increasing sedimentation (Nájera-Hillman *et al.* 2009a,b; Herbert *et al.* 2014). Douglas (1997), however, demonstrated that Hochstetter's frogs are able to withstand moderate levels of sedimentation, particularly if frogs can shelter in waterfalls with crevices that are situated nearby. Likewise, frogs were often found near water cascades in areas with moderate sedimentation in the present study, which was specifically noticeable in pine plantations. It is likely that no strong negative associations between sedimentation and predicted habitat use were estimated by the final models because of frogs selecting these waterfall microhabitats.

Logs and coarse woody debris

Another major characteristic of pine plantations is the large amount of woody debris and fallen logs that are produced (Thompson 2001). Logs and woody debris in native forest streams were therefore low in availability but logs were found to be highly associated with predicted habitat use in the mature pine plantations. The importance of logs as a habitat feature was further supported by the positive interaction effect between log cover and habitat type, which indicated that the use of logs in pine plantations became more prominent as log cover increased, in relation to native forests. Furthermore, considering there was no strong interaction effect in cobble use between mature pine plantations and native forests, this infers that frogs utilised cobbles similarly regardless of habitat. As cobble cover was lower in pine plantations than in native forests, logs may be utilised to compensate for the limited cobble habitat. Considering frogs were not restricted to cobble habitat in pine plantations, this positive association with logs may explain why the use of cobbles was similar between the habitat types. The hypothesis that frogs would select different resources based on availability between the habitat types was therefore supported.

Indeed, as streams in pine plantations are more susceptible to scouring during flooding (Douglas 1997) and if cobbles are limited, then logs may provide adequate protection in otherwise low quality microhabitat surroundings. In particular, Evans (1992) highlighted that surrounding substrate may become finer due to the presence of fallen logs and coarse woody debris. Notably, Beschta (1979) also showed that substrate scouring increased after woody debris removal. Such impacts on the physical characteristics of streams undoubtedly influences resource availability and may explain the strong affiliation Hochstetter's frogs have with logs in mature pine plantations, given the negative associations with fine substrata.

Strong affiliations with woody debris have also been observed in the mole salamander (*Ambystoma talpoideum*) (Moseley *et al.* 2004). In this study they examined the effects of coarse woody debris and leaf litter manipulations on salamander microhabitat use. When leaf litter was present in low levels, coarse woody debris was utilised more. Moseley *et al.* (2004) concluded that coarse woody debris may have been utilised more to compensate for inadequate conditions because of reduced leaf litter. It is possible a similar interaction may therefore be present regarding cobble availability and the use of logs as a resource.

Habitat quality predictions

Predicted habitat use was not different between Orokonui Ecosanctuary and Torere Forest, which supported the prediction that suitable areas of habitat were available in Orokonui Ecosanctuary. In addition, the EF 28 site was considered the most optimal of the three sites surveyed at Orokonui Ecosanctuary. Although there was less cobble cover recorded in Orokonui Ecosanctuary than in Torere Forest, the proportion of other certain resources indicate provision of reasonable habitat quality. For instance, boulder and gravel cover were higher and lower in Orokonui Ecosanctuary than in Torere Forest, respectively, whilst log cover was similar to pine plantations.

Many other studies have already predicted habitat quality for Hochstetter's frogs in novel areas (Allen 2006; Egeter 2009; Fouquet *et al.* 2010a; Nájera-Hillman 2012; Herbert *et al.* 2014), but the scale and type of modelling approaches were often different. For example, Allen (2006) and Fouquet *et al.* (2010a) predicted habitat quality for the entire North Island, whereas Nájera-Hillman (2012) and Herbert *et al.* (2014) did so only for the Auckland region and for a site on Great Barrier Island respectively. In particular, Fouquet *et al.* (2010a) identified warm temperatures and forest cover to be the most important features associated with Hochstetter's frog population presence, thus the majority of the North Island was deemed suitable in simulated future scenarios. Allen (2006) predicted a similar distribution to Fouquet *et al.* (2010a) using GIS, but also extrapolated to the northern portion of the South Island near where Hochstetter's frogs were historically found. In contrast, Herbert *et al.* (2014) compared habitat features that were more than 50% correlated with frog abundance and deemed habitat quality to be high if provisions could potentially support moderate to high frog abundance. Particularly, Herbert *et al.* (2014) predicted habitat quality as part of translocation feasibility research for the intra-island reintroduction of Hochstetter's frogs to the Windy Hill Rosalie Bay Catchment. Contrary to the conclusion regarding habitat quality in Orokonui Ecosanctuary however, Herbert *et al.* (2014) considered habitat at Windy Hill inadequate for Hochstetter's frogs.

Interestingly, there was no difference in habitat quality between mature pine plantations and native forests in Torere Forest. Mature pine plantations may therefore be considered reasonably adequate for Hochstetter's frogs. However, Nájera-Hillman (2012) predicted low habitat quality for the Rodney Ecological District (an area modified by forestry and agriculture) using a spatial decision support system. Nevertheless, although these contrasting results are not entirely comparable given the different modelling approaches and scales used, the microhabitat scale used for the present study was more biologically relevant as habitat quality was derived from resources used at the individual level.

Model considerations

Although resource selection models are highly useful, there are some limitations and important features that must be considered to ensure that appropriate biological inferences are reached (Beyer *et al.* 2010). Firstly, resource selection models are often site-specific, thus extrapolating information to other areas can be difficult to achieve (Boyce *et al.* 2002; Beyer *et al.* 2010; Nájera-Hillman 2012). For example, lower cobble and gravel cover were recorded in Orokonui Ecosanctuary compared to native forests in Torere Forest. Given the differences in resource availability, potential resource use in Orokonui Ecosanctuary may therefore deviate somewhat from resource use measured in Torere Forest.

Secondly, as Hochstetter's frogs are highly cryptic (Bishop *et al.* 2013), detectability can be an issue (Thomas & Taylor 1990; Hobbs & Hanley 1990; Boyce *et al.* 2002; MacKenzie 2006). As already mentioned, the correct classification of 'used' locations may be low when using presence/available data (Boyce *et al.* 2002), but even more so if a species is cryptic (MacKenzie 2006). These factors may explain why the prediction performance of the pine plantation additive model was lower than the native forest model, especially considering the unstable and erosive pine habitat made searching difficult. Nonetheless, to account for underestimating used resources, occupancy models have been established to estimate detectability and have even used to monitor Hochstetter's frogs (Crossland *et al.* 2005; Moreno 2009). Such models require multiple surveys of an area within a certain time period (Crossland *et al.* 2005; MacKenzie 2006; Moreno 2009), but multiple surveys can be risky to frogs that inhabit steep areas where substrata are unstable. This risk, along with logistical reasons, was why occupancy models were not used in this study.

Lastly, coefficients that represent the absence of an effect (i.e. the 95% CI contains zero) do not indicate that individuals are unresponsive to particular habitat features (Beyer *et al.* 2010). Instead, zero effects may be a result of sampling bias because of undetected individuals or that habitat features were not or could not be searched (e.g. amongst boulders). Moreover, zero

effects indicate selections or responses are possibly made at other levels of availability (Beyer *et al.* 2010). For instance, strong negative responses to gravel cover were observed in both habitats, yet only the native forest additive model estimated a 95% CI that did not include zero for this particular coefficient. Considering gravel cover was highest in pine plantations than in native forests, it would be expected that strong ‘avoidance’ of gravel cover would be less likely in pine plantations and thus reflected in the coefficient estimate.

Final conclusions

In this chapter, the first two questions aimed to identify important resources for Hochstetter’s frogs within modified and largely unmodified environments and to assess how resource use is influenced by habitats. Consequently, these results have built upon the spectrum of landscape to local-scale research necessary for amphibian conservation. Moreover, findings from this local-scale study were congruent with the landscape-scale, presence/absence research carried out by Nájera-Hillman *et al.* (2009a), which reinforces the established perception of essential habitat for Hochstetter’s frogs. However, observations in the present study did not support Nájera-Hillman’s (2012) assumption that mature pine plantations and native forests provide similar habitat as disturbance was a major characteristic in pine plantations. The main findings in this thesis research were that Hochstetter’s frogs predominantly used cobble habitat as suitably sized interstitial spaces may provide protection from predators. In comparison to native forests, logs were also important in the mature pine plantations, which was emphasised by the increased use of logs as log cover increased. In addition, cobble habitat was more limited in pine plantations than in native forests, thus the use of other resources, such as logs, may be a compensatory response by Hochstetter’s frogs. In hindsight, as indicated by Hutchings (2011), the findings that other resources are utilised and that there is reasonable habitat quality in mature pine plantations suggest that Hochstetter’s frogs have some degree of adaptability to modified habitat. The final question for this chapter was to determine whether a potential translocation site was suitable based on the provision of required habitat. Encouragingly, suitable areas of habitat were available in Orokonui Ecosanctuary. Despite lower cobble cover recorded in Orokonui Ecosanctuary when compared to Torere Forest, the composition of other important resources enabled suitable areas of habitat to be available. Overall, resource selection models provide multiple insights into the ecology of Hochstetter’s frogs and should thus be implemented as a tool for the conservation management of this rare species.

Chapter Four

Thermal preference and physiological responses to a simulated cool climate of a South Island potential translocation site

Introduction

Ectotherm behaviour and physiology are profoundly influenced by the environmental conditions in which these animals live (Wells 2007). Behavioural and physiological responses also vary considerably between and within species (Sinsch 1984; Wilson 2001; Freidenburg & Skelly 2004; Wells 2007). In particular, latitudinal differences in species' tolerances to global warming is of global conservation concern (Deutsch *et al.* 2008). Consequently, translocations of species to more suitable areas in response to global warming are an important conservation tool (Hoegh-Guldberg *et al.* 2008; Besson & Cree 2011). Yet studies that predict the physiological performance of individuals translocated to new environments are relatively limited for most taxa (Besson & Cree 2011). Fortunately, conservation programmes have recently placed more emphasis on physiology (Wikelski & Cooke 2006). For example, prior to the recent translocation of tuatara (*Sphenodon punctatus*) to Orokonui Ecosanctuary (Dunedin) (Peat 2013), the ecophysiology of tuatara and egg incubation exposed to cooler conditions were intensively investigated in both the lab and wild (Besson & Cree 2010, 2011; Besson *et al.* 2012).

Similarly, the present study assessed the feasibility of translocating an ectothermic frog species sourced from the northern site of Torere Forest (Bay of Plenty) to Orokonui Ecosanctuary. Cool temperatures, however, are apparently not favourable for Hochstetter's frogs. According to Fouquet *et al.* (2010a,b), cool temperatures during the Last Glacial Maximum (LGM, 19 - 26,500 BP) restricted population dispersion, when average annual temperatures were ~2.5 - 4°C cooler than today (Drost *et al.* 2007). In addition, Fouquet *et al.* (2010a) highlighted strong associations between present-day Hochstetter's frog occurrence and temperatures $\geq 20^{\circ}\text{C}$. Findings such as these imply cool sites like that of Orokonui Ecosanctuary might not be suitable for Hochstetter's frogs.

Nevertheless, as mentioned in Chapter One, behavioural and physiological responses of *Leiopelma* to the thermal environment have not been studied in great detail, thus inferences regarding preferred temperatures of Hochstetter's frogs currently remain untested. The present study followed Besson & Cree (2011) in order to address the questions regarding thermal preference, the effects of temperature on the physiology of captive Hochstetter's frogs, and the

quality of the thermal environment (i.e. the difference between environmental and preferred temperatures, Hertz *et al.* 1993) at Torere Forest and Orokonui Ecosanctuary. Although many interspecific differences between frogs and reptiles exist, general temperature effects on ectotherm physiology and behaviour ensures that amphibian and reptile studies are somewhat comparable. As ectotherm studies generally highlight temperature effects on responses such as digestion ability and body temperature (Wells 2007), the present study focused on three main physiological and behavioural responses: 1) gut retention times, 2) scaled mass index (i.e. body weight accounted for SVL), and 3) thermal preference.

Cool climates restrict amphibian activity (Sinsch 1989), thus it was predicted that the scaled mass index and gut retention times would increase under cool temperatures. Moreover, as many ectotherms exhibit temperature acclimation (Wells 2007), it was predicted that thermal preference in captive frogs would not greatly differ from the temperatures they currently experience and also not differ over time. Overall, studying whether the cooler southern climate may restrict the outcome of frog translocations will provide conservation managers a better understanding of the feasibility of reintroducing *Leiopelma* species into the South Island. Furthermore, should this study provide informative results like the studies for tuatara, then this would be a major stepping stone for the conservation of New Zealand native frogs.

Methods

Animal husbandry

There are 18 adult Hochstetter's frogs (8 males; 10 females) held in captivity at the Department of Zoology, University of Otago. These individuals were sourced from Pukeamaru (East Cape, North Island) in September 2009 for an earlier study (Ohmer *et al.* 2013). In the present study, frogs were housed in individual plastic containers (29 cm x 20 cm x 9 cm) containing three moist paper towels in a frog husbandry room which was maintained at approximately 14.5-15.5°C. Relative humidity inside the containers was at or near 100%. The light cycle was set at 8L:16D, but the frog containers were partially covered by blackout material, simulating light conditions on a dense forest floor. Every week individuals were weighed to the nearest 0.01 gram, paper towels were changed, and individuals were fed *ad libitum* insects such as: *Tenebrio obscurus* larvae (mealworms), *Gryllus bimaculatus* (pinhead crickets), and *Porcellio scaber* (slaters). The SVL of individuals have been measured at least five times since the frogs have been in captivity.

Environmental conditions

HOBOWare® Pro data loggers (HOBO U23-001 Temp/RH and HOBO UTBI-001 TidbiT v2) were used to record climatic data in the field. In order to gain an adequate representation of the microclimate, two of each data logger were placed at the Marie Stream site at Orokonui Ecosanctuary (Figure 11) on the 18th June 2013. Data loggers measuring air temperature and relative humidity were tied to a tree trunk and under a tree root within ~5 m distance of each other and ~1 m above stream level to avoid damage by potential flooding. Water temperature data loggers were placed within ~5 m distance of each other in the stream. On the 21st June 2014, data was downloaded using a HOBOWare® Shuttle. Data loggers were placed at Torere Forest on the 19th November 2013. One of each model was placed in one native forest and one mature pine plantation site. These loggers were retrieved and the data downloaded on the 25th and 26th September 2014. Data were averaged by season and time of day to get the mean daily cycle of temperature and relative humidity for each season. The average daily air temperature for Orokonui Ecosanctuary during the winter months between 18th June 2013 and 21st June 2014 cycled from approximately 6 - 7.5°C. On the basis of these temperatures, conditions were simulated in the lab to represent an 'Orokonui winter' treatment for the gut retention and scaled mass index experiments.

Thermal preference

Thermal preference (i.e. preferred body temperature) was tested in a Department of Zoology environmental lab (light cycle 8L:16D) between 26th November and 2nd December 2014. To do

so, a thermal gradient (Figure 14) was constructed. Six stainless steel runways (1270 mm x 80 mm x 80 mm) were placed over an aluminium backing (1270 mm x 740 mm), which extended 125 mm in height and a farther 200 mm at the cooling end. Underneath the aluminium backing were two heating panels (Nu-Klear, Auckland, New Zealand) (500 mm x 300 mm) running at 80 watts/m² which were connected to a proportional temperature controller. Each runway had an acrylic plastic lid (1 mm thick) and a piece of acrylic (660 mm x 70 mm x 3 mm) was placed at the cool end with 6 mm diameter holes spaced 20 mm apart to allow ventilation and ease of cooling. A double-glazed glass panel (1270 mm x 600 mm x 17 mm) overlaid the runways, which aided insulation, along with polystyrene packing between the runways and the wooden frame (1330 mm x 825 mm x 20 mm) and between the heating panels and the wooden base. Moist paper towels were laid along the bottom of the runways and also scrunched up evenly to provide some cover. Paper towels were changed between frog groups.

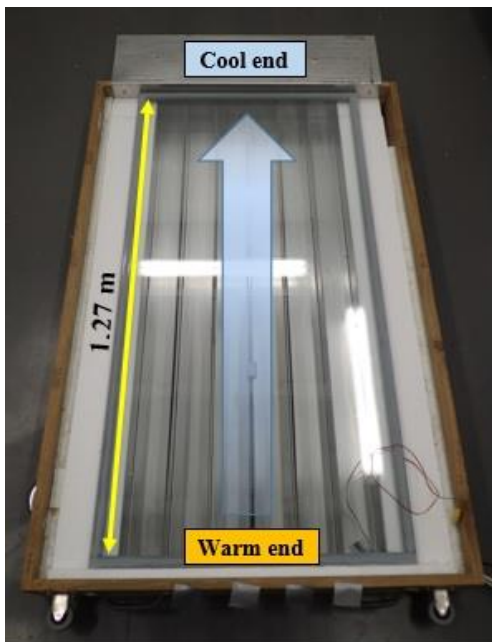


Figure 14. Thermal gradient set up indicating the warm and cool ends of the six runways. Scale provided.

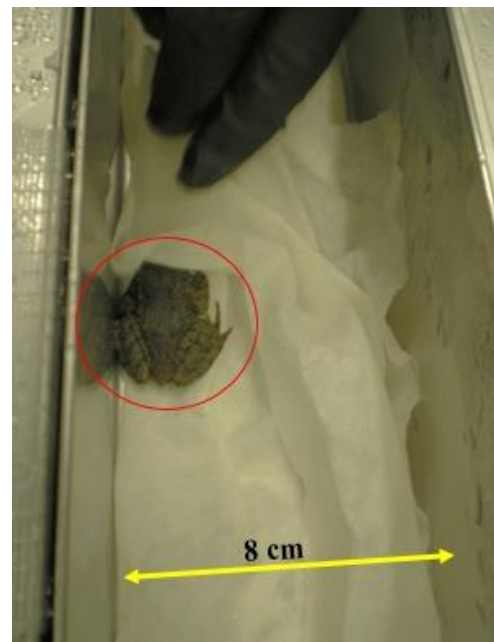


Figure 15. Captive Hochstetter's frog (circled) in one of the six runways. Scale provided. Photo: Sally Wren.

As Hochstetter's frogs have a higher susceptibility to dehydration than the other *Leiopelma* species (Cree 1985, 1988), paper towels were sprayed with water every six hours. Even so, paper towels at the warm end of the gradient often dried out, thus the temperature gradient was kept at a conservative ~10 to 20°C. Six frogs (one in each runway, Figure 15) were placed into the thermal gradient at a time, thus three recording sessions were required to measure the thermal preference of all 18 frogs. Each frog was placed in the centre of the runway and allowed to explore the environment for at least five hours prior to the experiment commencing. Thermal

preference was represented by ‘selected’ skin temperatures (T_{sel}). Skin temperature (T_{sk}) was measured using an infrared thermometer (IRT) (Model: Q1370, DickSmith Electronics) as previous studies have shown that T_{sk} measured by an IRT accurately indicates internal body temperature (T_b) in lizards, tuatara (Hare *et al.* 2007) and amphibians (Rowley & Alford 2007). IRTs are also a non-invasive tool that minimises disturbance, which is advantageous when repeating measurements and reducing the error of unrepresentative T_b as a result of handling animals (Hare *et al.* 2007; Rowley & Alford 2007). As recommended by Hare *et al.* (2007), T_{sk} was recorded using the IRT at a distance of approximately 100 mm, in line with the body axis, and pointed to the abdomen. For each individual, three T_{sk} measurements (which were averaged) were recorded at 12 am, 6 am, 12 pm, 6 pm, and 12 am the following morning. Individuals were only exposed to one recording session of 25 hours in the thermal gradient. Environmental air temperatures in Torere Forest and Orokonui Ecosanctuary were also compared to the preferred temperature range of the captive frogs to determine the quality of the thermal environment.

Gut retention and scaled mass index

In order to assess the temperature effects on the physiological responses, frogs were left in the frog husbandry room for four weeks (13th July - 11th August 2014) at a relatively constant temperature of 14.5 - 15.5°C to serve as the control. After four weeks, the frogs were gradually acclimatised to cooler temperatures for a week. Firstly, air temperatures in the frog husbandry room were decreased by ~2°C a day until they reached ~9°C, which is the minimum temperature setting capable for this room. Secondly, the frogs were transferred into an environmental lab so that air temperatures could be reduced farther for the ‘Orokonui winter’ treatment of ~6 - 7.5°C. The light cycle remained at 8L:16D. Frogs were allowed to adjust to the cool temperatures for several days before commencing the treatment, where the frogs were left for another four weeks (17th August - 15th September 2014). During the acclimation period, frogs were monitored approximately every six hours by checking their righting responses. After about nine hours exposure to ~6 - 7.5°C, 11 out of the 18 frogs were not able to right themselves when turned over onto their backs and were thus removed from the environmental lab back into the frog room which was still held at ~9°C. This necessity under animal ethic protocols reduced the power of the treatment as it can be inferred that the seven ‘hardier’ individuals were left in the treatment. After a week, the 11 individuals that were removed were returned to the environmental lab held at ~6 - 7.5°C. All frogs were then able to right themselves, which meant that they were all able to withstand the treatment conditions.

After four weeks (three weeks for 11 of the individuals), temperatures were increased again to ~14.5 - 15.5°C. Scaled mass index and gut retention times were then compared between the two

temperature regimes. As there were no differences in responses between those that initially righted themselves and those that did not with the cold temperatures, both groups were pooled to increase the sample size of the treatment group. As the 11 individuals were not fed slaters during their additional week in acclimation however, gut retention times could only be investigated in the seven individuals that remained in the treatment. The sample sizes were thus $n=18$ for the control and treatment groups for investigating the temperature effects on scaled mass index, and $n=18$ and $n=7$ for the control and treatment groups respectively for investigating gut retention times.

Gut retention times were assessed by feeding each frog five slaters (*P. scaber*) (marked using polyester string) once a week for two weeks. Slaters were used as they are readily eaten by the frogs and markers, such as polyester strings, can be tied easily and securely between their segmented dorsal plates. During the week prior to this experiment, 83% (15/18) of the frogs had defecated, thus it was assumed that previous feeding would not largely influence gut retention times. Polyester strings were used as markers as they are indigestible, do not harm animals that ingest them, and have been successfully used before (Hailey 1997; Shaw 2013). Slaters were tied with coloured strings (<1 mm width, ~15 mm length) around their carapaces (Figure 16) so that strings could be observed in the frogs' faeces following defecation. String colours varied so that prey items could be traced from the relative day of ingestion to defecation (days were relative as the exact time of ingestion and defecation were not known). Containers were checked daily to record when prey had been eaten and when string had been defecated. Any dead slaters, or those that had freed themselves from the string, were removed (including the loose string) and replaced with newly marked individuals. During the acclimation week between temperature regimes each frog was fed two to three small *Locusta migratoria* (locusts) and ~15 *G. bimaculatus* (pinhead crickets). In concurrence with their weekly feed, frogs were weighed as per usual to measure the scaled mass index. Five weighing sessions were carried out for each temperature regime.

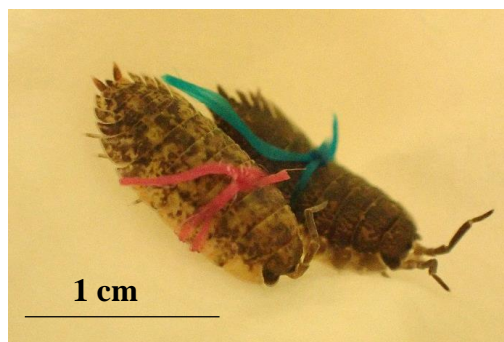


Figure 16. Slaters (*Porcellio scaber*) tied with coloured polyester string. Scale bar shown.

Statistical analyses

A discriminant function analysis was used to compare environmental conditions between Torere Forest and Orokonui Ecosanctuary using the environmental data retrieved (n=8039 recordings for Orokonui Ecosanctuary and n=7386 for both the native forest and pine plantation in Torere Forest).

In the lab experiments, the same individuals were exposed to all treatments thus the physiological response data was obviously non-independent. Whilst there are cons to using this experimental design, one benefit is the reduction of variation by taking into account between-individual effects (Harraway 1997; Logan 2010). In addition, fewer individuals are needed (Harraway 1997; Logan 2010), which is preferable when working with threatened species.

Thermal preference was analysed using a repeated measures ANOVA with ' T_b ' as the response, 'time' as a fixed factor and 'individual ID' as a random factor. Significance was tested at $p < 0.05$ level. Gut retention times between temperature regimes were compared using a generalised linear mixed-effects Poisson model using the '*lme4*' package (Bates *et al.* 2014) with 'days to defecation' as the response variable, 'treatment' (treated as a factor) and 'time in treatments' as fixed effects, and 'individual ID' as the random factor. To obtain the scaled mass index estimates (M_i), the four most recent SVL measurements were averaged for each individual. These averaged SVLs and the corresponding weights for each individual were then scaled (following methods by Peig & Green (2009); see Chapter Two) for each week commencing on the 13th July 2014 (assuming that SVLs would remain constant over the 11 week study period). Temperature effects on scaled mass index were assessed using a linear mixed-effects model using the '*nlme*' package (Pinheiro *et al.* 2014), but instead with 'scaled mass index' as the response variable. All analyses were performed in R version 3.0.2 (R Core Team 2013).

Results

Environmental conditions

Environmental temperatures in Orokonui Ecosanctuary during 2013 - 2014 were similar to the long-term average for the region, as the mean air and water temperatures were $\sim 8.9^{\circ}\text{C}$ (range = $-0.3 - 17.2^{\circ}\text{C}$) and $\sim 9^{\circ}\text{C}$ (range = $1.6 - 14.2^{\circ}\text{C}$), respectively (Figure 17). Relative humidity was generally high (mean = $\sim 99\%$), but the minimum values were 23.1% in the more 'exposed' site (recorded from the tree trunk) and 52.7% in the more 'sheltered' site (under the tree root) (Figure 18). Environmental temperatures in Torere Forest were also similar to the long-term average for the region. However, air temperatures at above ground were generally cooler in the pine plantation compared to the native forest (mean = 10.5°C [range = $-2.2 - 19.1^{\circ}\text{C}$] and 12.0°C [range = $1.6 - 22.2^{\circ}\text{C}$], respectively). Water temperatures averaged 12.2°C (range = $6.2 - 26.8^{\circ}\text{C}$) in native forest, whereas in the pine plantation the mean was 10.3°C (range = $-0.3 - 16.2^{\circ}\text{C}$) (Figure 17). Relative humidity was similar between the native forest and pine plantation (mean = 96.2% and 99.8%, respectively), but the minimum was lower in native forest (57.7%) compared to the pine plantation (70.6%) (Figure 18). The discriminant function analysis correctly allocated 59.4% of temperature and relative humidity recordings to those observed in Orokonui Ecosanctuary, but misclassified 34.1% as Torere Forest pine plantation and 6.5% as native forest cases instead. As for the Torere Forest pine plantation recordings, 39.9% were correctly assigned, but 37.5% were misclassified as Orokonui Ecosanctuary and 22.6% as native forest cases. Only 1.7% of native forest cases were misclassified as Orokonui Ecosanctuary, with 10.9% misclassified as pine plantation cases. Water temperature was considered the most important discriminating factor for the primary discriminant loading, followed by air temperature and relative humidity (LD1 = 1.00, -0.46 and -0.14 respectively). Relative humidity was the most important discriminating factor for the secondary discriminant loading, followed by air and water temperature (LD2 = 0.21, 0.15 and 0.11, respectively).

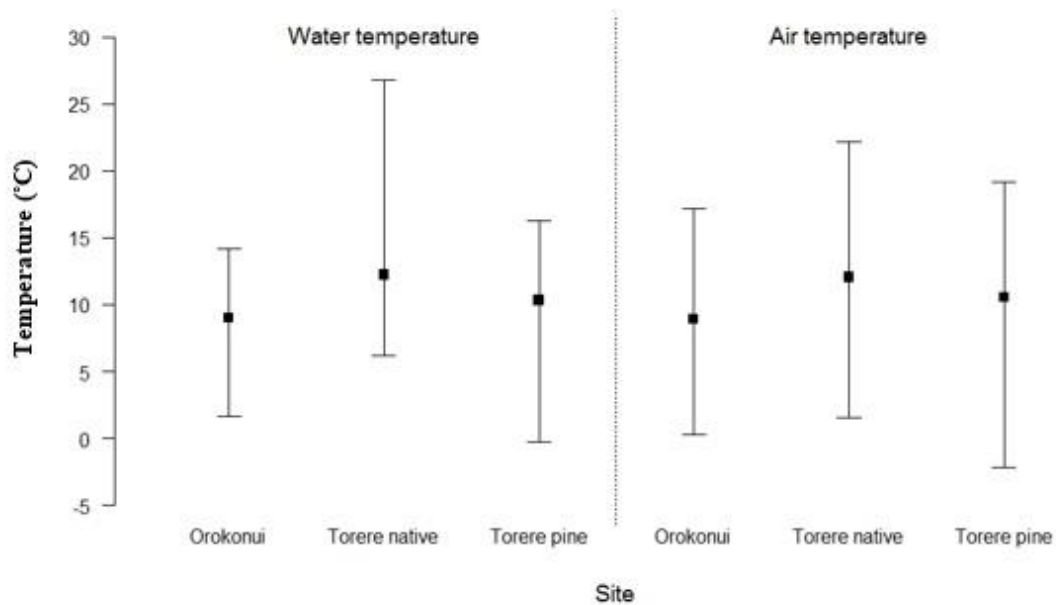


Figure 17. Environmental water and air temperatures (minimum, mean and maximum) recorded at Orokonui Ecosanctuary (June 2013 - June 2014) and in a native forest and pine plantation at Torere Forest (November 2013 - September 2014).

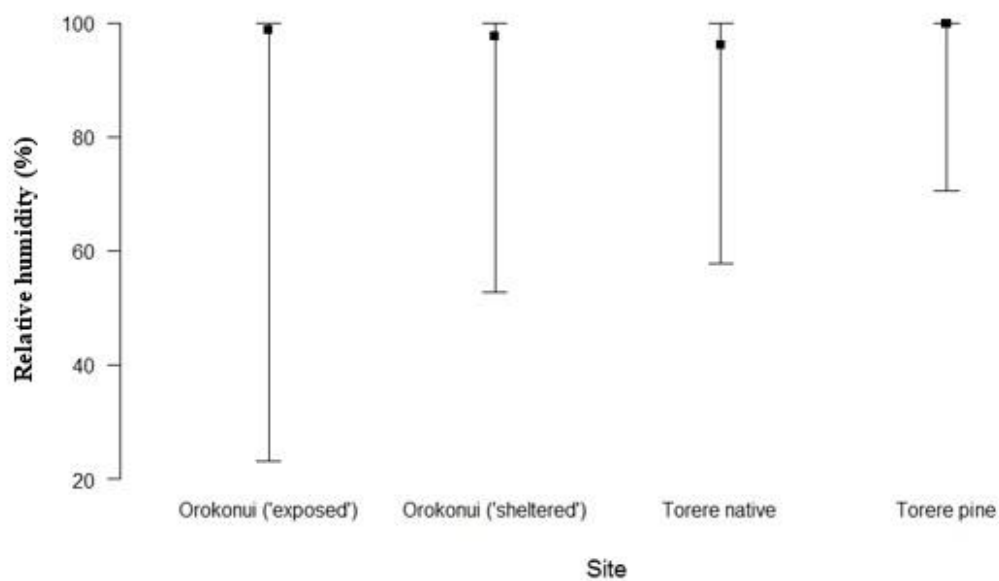


Figure 18. Environmental relative humidity (minimum, mean and maximum) recorded at Orokonui Ecosanctuary ('exposed' and 'sheltered' sites) (June 2013 - June 2014) and in a native forest and pine plantation at Torere Forest (November 2013 - September 2014).

Thermal preference

Captive frogs generally selected warm temperatures, as their preferred body temperatures ranged from 12.1 to 25.4°C (mean= 18.6°C, 50% interquartile range= 15.3 - 20.9°C) and did not significantly differ over time ($F_{1,71}= 1.59$, $p = 0.21$) (Figure 19). During winter, air temperatures recorded in Orokonui Ecosanctuary and Torere Forest did not reach the lower limit of the preferred temperature range (15.3°C) (Figure 20a). During summer, air temperatures in Orokonui Ecosanctuary exceeded the lower limit only 2.8% of the time, whilst in Torere Forest temperatures exceeded the limit 27.3% and 44.7% of the time in the pine plantation and native forest respectively (Figure 20b). The quality of the thermal environment at Orokonui Ecosanctuary was therefore lower than Torere Forest, especially during summer.

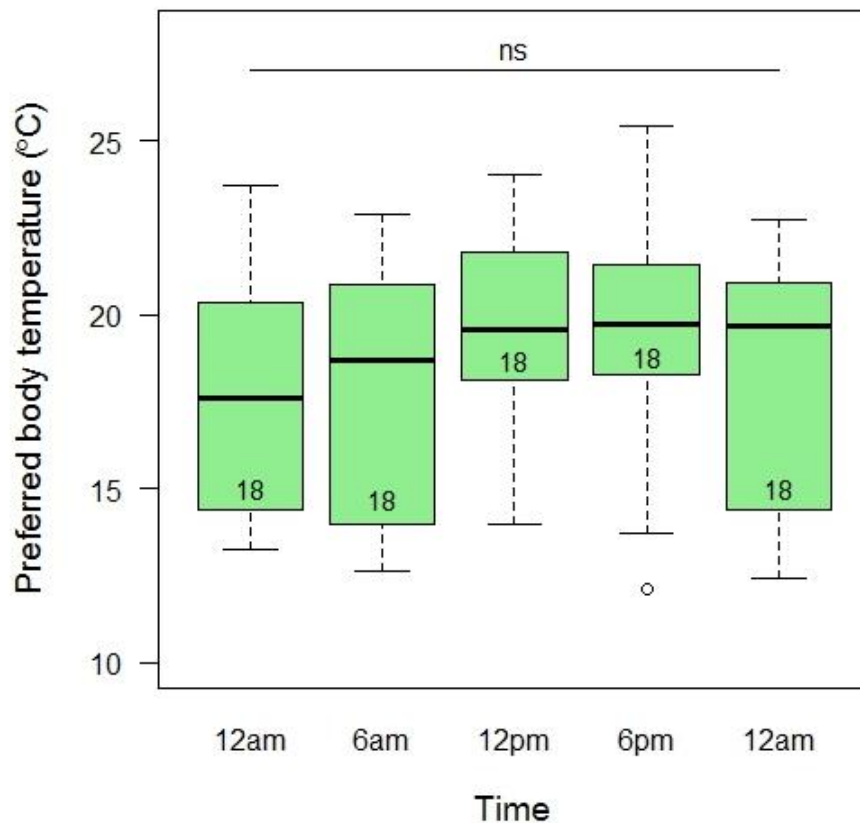


Figure 19. Preferred body temperature of captive Hochstetter's frogs (n=18) over a 24 hour cycle. There were no significant differences in temperatures selected ($p > 0.05$).

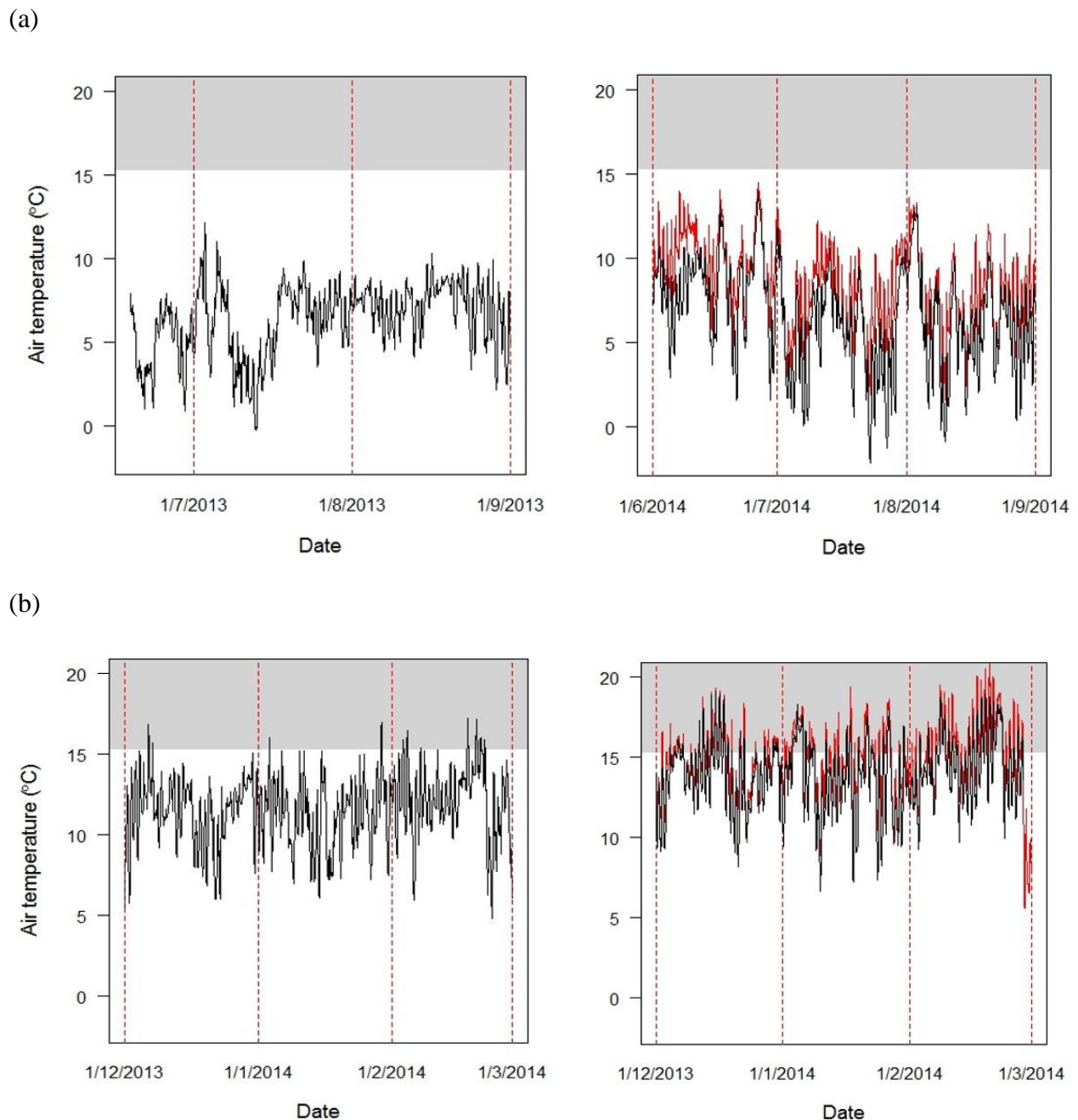


Figure 20. Air temperatures recorded during (a) winter and (b) summer 2013 - 14 at Orokonui Ecosanctuary (left) and at Torere Forest (right) for the pine plantation (black) and native forest (red). Vertical dashed lines correspond to the beginning of each month. Grey filled areas denote the central 50% preferred temperature range (15.3 - 20.9°C) based on the thermal preference of captive Hochstetter's frogs recorded in the present study. The smaller the deviation between air temperatures and the preferred temperature range minimum (i.e. 15.3°C), the higher the quality of the thermal environment (Hertz *et al.* 1993).

Gut retention and scaled mass index

In the 14.5 - 15.5 °C control, 17 frogs ingested 122 strings tied to slaters and defecated 121 strings within the time frame of the treatment (the remaining string was not accounted for). In the 6 - 7.5°C treatment, six frogs ingested 24 strings and defecated 23, of which 9 were defecated during the time frame of the treatment (by two frogs) and 14 were defecated afterwards (by six frogs, including those that defecated during the treatment [7 strings within 24 hours of warming up and 7 one week later; the remaining string also being unaccounted for]). The 9 strings defecated during the treatment were all found in faecal pellets containing undigested matter (slater bodies were observed in their entirety) (Figure 21), but all remaining strings defecated after the treatment were found in faecal pellets containing normal digested matter (Figure 22). Several faeces containing digested locust and presumably pinhead cricket remains were collected during the acclimation period between treatments. The minimum and maximum gut retention time in the control was 2 and 16 days respectively. For the treatment, the minimum was 7 days and the maximum 24 days. As for the pellets with digested matter defecated after the experiment, the minimum was 18 days whilst the maximum reached 41 days (mean= 31.3 days). Gut retention times increased under cool conditions (*est.* = 0.26, 95% CI = 0.04, 0.48) whereas time in treatments had a small effect (*est.* = 0.06, 95% CI = 0.04, 0.08). The estimated number of days to defecation was 8 (\pm 0.1 SE) days for the control and 10.6 (\pm 0.6 SE) days for the treatment (Figure 23). Scaled mass index also increased under cool conditions (acclimation: *est.* = 0.27, 95% CI = 0.17, 0.37 and treatment: *est.* = 0.47, 95% CI = 0.35, 0.59) (Figure 24) but again the effect of time spent in the treatments was small (*est.* = -0.004, 95% CI = -0.006, -0.002).

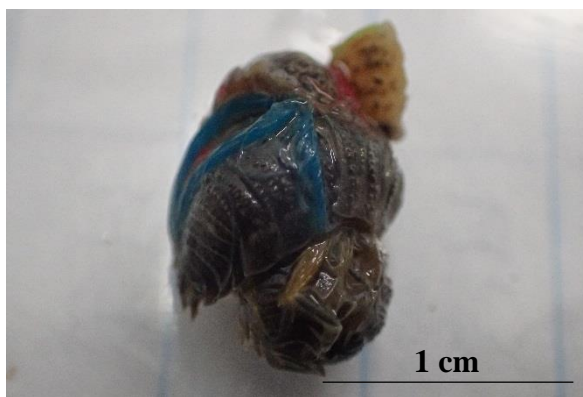


Figure 21. Undigested slaters in faecal pellet.
Scale bar provided.

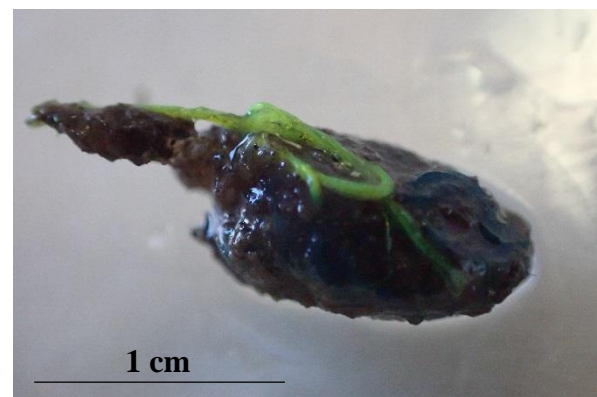


Figure 22. Digested slaters in faecal pellet.
Scale bar provided.

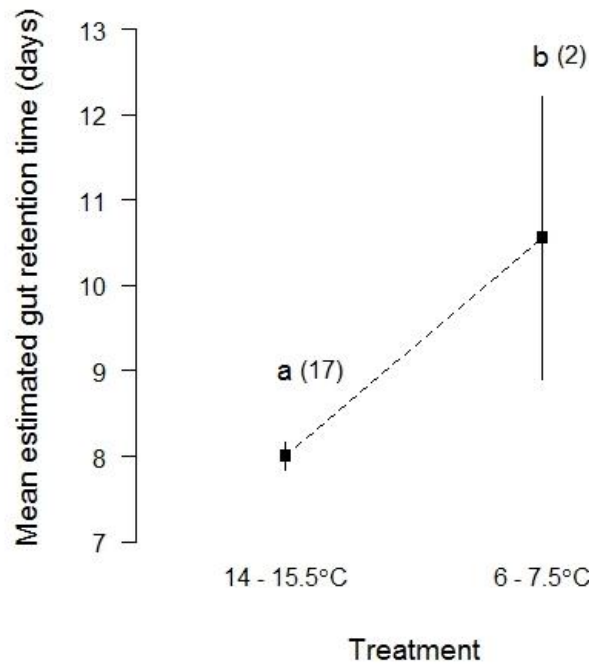


Figure 23. Mean estimated gut retention times of captive Hochstetter's frogs (in days) with standard error bars under control (14.5 - 15.5°C) and treatment (6 - 7.5°C) temperatures. Sample sizes are in brackets. Different letters correspond to significant differences. The dashed line denotes dependency between the treatments.

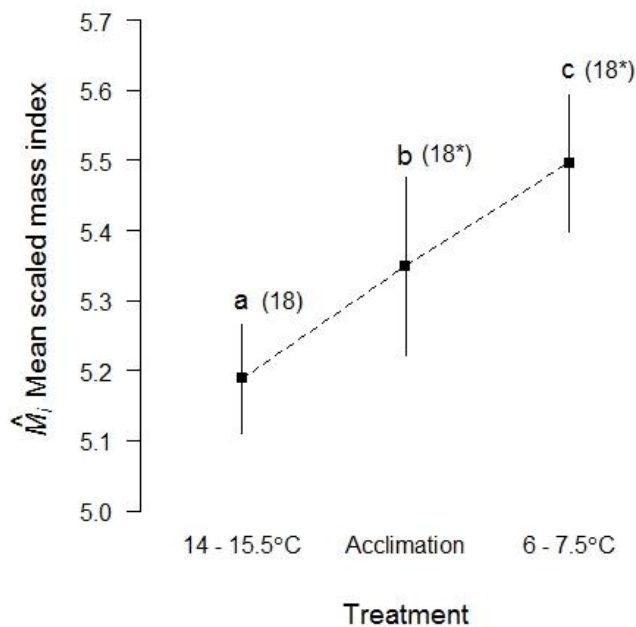


Figure 24. Mean scaled mass index of captive Hochstetter's frogs with standard error bars under control (14.5 - 15.5°C), acclimation (decrease of 2°C per day) and treatment (6 - 7.5°C) conditions. Sample sizes are in brackets. Asterisks indicate that some individuals had a longer time period in acclimation and therefore less time in the treatment. Different letters corresponds to significant differences. The dashed line denotes dependency between the treatments.

Discussion

Environmental conditions

Although Orokonui Ecosanctuary temperatures were cooler overall than those recorded in Torere Forest, the overlap of thermal conditions between the Torere Forest pine plantation and Orokonui Ecosanctuary suggest that these locations have relatively similar microclimates. This finding is important as considering Hochstetter's frogs often inhabit shallow cobble substrate, it seems that Hochstetter's frogs are frequently exposed to cold conditions in the pine plantation and hence may tolerate similar minimum temperatures experienced in Orokonui Ecosanctuary. This inference is based on the assumption that shallow substrate is less thermally regulated, compared to habitat that consists of rock substrata that can continue metres underground, such as where Hamilton's frog (*Leiopelma hamiltoni*) live (Bell 1982). Interestingly, the overall temperatures recorded in the native forest were even warmer than those in the pine plantation and at Orokonui Ecosanctuary. The reason for the discrepancy in overall temperatures between the Torere Forest pine plantation and native forest is uncertain, but it may be due to the extent of riparian zone cover which apparently acts as a thermal buffer (Thompson 2008). Considering riparian zones were not extensive in the pine plantation compared to native forest, this indeed may have been a contributing factor. On the other hand, average relative humidity was similar between Orokonui Ecosanctuary and Torere Forest. The minimum relative humidity measurement for the Torere Forest pine plantation was higher than in native forest, but higher humidity was probably due to a small water cascade situated near the data logger. At Orokonui Ecosanctuary, the highest relative humidity minimum was recorded in the sheltered site (i.e. under the tree root), which supports Seebacher & Alford (2002) who observed lower desiccation rates in sheltered versus non-sheltered areas. What is more, high humidity in refuge retreats may provide access to somewhat higher temperatures than in exposed sites.

Thermal preference

Generally, individuals selected temperatures between 15.3 and 20.9°C, thus the prediction that preferred temperatures would not deviate from acclimation temperatures was not supported. Positive associations of Hochstetter's frogs with warm temperatures have previously been demonstrated in emergence surveys of captive frogs at Hamilton Zoo (Haigh *et al.* 2010) and by Fouquet *et al.* (2010a). This finding is in contrast to related species such as the tailed frog (*Ascaphus truei*) (a sister taxon to Hochstetter's frog), Archey's frog (*Leiopelma archeyi*) and the Maud Island frog (*L. pakeka*) which prefer cool conditions (Cree 1989; Bell 1995; Adams & Bury 2002; Dewhurst 2003). However, it is likely that the average selected temperature and the upper limit would have been higher if the captive frogs had the opportunity. How high the

upper limit could have been remains uncertain, but it may be similar to the critical thermal maximum for the tailed frog (*A. truei*) at approximately 28 - 30°C (Claussen 1973). Considering selected temperatures sometimes exceeded 20°C (maximum of 25.4°C) when paper towels began to dry out, this may indeed be the case. Although very few studies have investigated the thermal preference of frogs, the interquartile range of selected temperatures is often narrow (Malvin & Wood 1991; Wells 2007) and therefore similar to this study's findings. Such narrow selected temperature ranges are often because of constraints in the wild (e.g. predation) which limit amphibians from reaching preferred temperatures in certain microhabitats (Bradford 1984; Wells 2007). In addition, amphibians are generally poor thermoregulators (Wells 2007). Considering the frogs used in this study have been exposed to relatively constant temperatures since 2009, it is more likely that acclimation is the main contributing factor to the narrow range observed. Indeed, these results were similar to the selected temperature ranges of hellbender (*Cryptobranchus alleganiensis*) and mudpuppy (*Necturus maculosus*) individuals acclimated to the same temperatures as the captive frogs (Hutchison & Hill 1976). In support of the prediction, acclimation may have also prevented a diel cycle of selected temperatures from being observed, but as the captive frogs are housed in very low light conditions, this is also likely to reduce the possibility of a diel cycle from occurring. Besides these explanations, another potential factor is that the frogs were not fed during the experiment. As Witters & Sievert (2001) demonstrated, experimentally fed Woodhouse's toads (*Bufo woodhousii*) exhibited diel cycles whereas unfed individuals did not. It would be useful to investigate how feeding influences selected temperatures in captive frogs.

The quality of the thermal environment at Orokonui Ecosanctuary was substantially lower than Torere Forest, particularly during summer. Orokonui Ecosanctuary would therefore be a thermally challenging environment for Hochstetter's frogs. This finding is not surprising as the same conclusion was reached by Egeter (2009) and Besson & Cree (2010) for *Leiopelma* and tuatara respectively. That being said, cold-adapted amphibians generally alternate between nocturnal and diurnal activity, forage at a greater range of temperatures than species from warmer regions (Wells 2007), or even migrate to cool areas during summer (Adams & Frissell 2001). Likewise, Hochstetter's frogs have been observed out in the open during the day (Whitaker & Hardy 1985; this study) and also active during winter (Douglas 1997). Observations such as these suggest that Hochstetter's frogs may behaviourally adapt to an environment like Orokonui Ecosanctuary.

Gut retention and scaled mass index

Initially, many individuals responded negatively to treatment conditions as indicated by the inability to right themselves. However, once the group that did not exhibit righting responses was held for another week at temperatures slightly warmer than the treatment and subsequently returned to the experiment, all were capable of righting themselves. This experiment was the first to expose the captive frogs to temperature changes, thus having been in relatively constant conditions since 2009, this would undoubtedly contribute to the negative responses observed. Unfortunately, the reason for the initial difference in group responses remains uncertain, considering no biological (e.g. mean weight or sex) differences were apparent at any stage between the groups. Therefore, it can only be attributed to individual variation. For future reference, acclimation over two weeks, instead of one, seems more appropriate for these captive frogs.

As predicted, cool conditions largely influenced the physiological responses of the captive frogs. Specifically, cool conditions reduced the feeding performance and the number of faeces produced. Consequently, although frogs ingested fewer prey than in the control, scaled mass index increased as food was retained in the gut for longer. Incidentally, many laboratory studies have noted these responses to cool conditions in other ectothermic species (Lillywhite *et al.* 1973; Gossling *et al.* 1980; Stevens 1988; Jiang & Claussen 1993; McConnachie & Alexander 2004; Besson & Cree 2011). Time in treatment effects for scaled mass index and gut retention times were virtually zero, thus these physiological responses did not greatly change over time regardless of treatment. Similarly, Besson & Cree (2010) detected no changes in body weight over time for juvenile tuatara. The reasons for no change in body weight could be that there was truly no effect or that the duration of treatments were not long enough to detect any. Particularly for scaled mass index, the latter is more likely as biological responses of long-lived species are generally slower (Moore *et al.* 2007). As for gut retention times, ranges were wide and therefore balanced out any directional effects of time.

Interestingly, captive frogs did not digest prey in the 6 - 7.5°C treatment, but as Besson & Cree (2011) observed, neither did juvenile tuatara exposed to similar treatment conditions. Understandably, the inability to digest may raise concerns over the survival of Hochstetter's frogs in cool conditions like in Orokonui Ecosanctuary. However, digestion of locusts and pinhead crickets did occur during the acclimation period between treatments, which suggests digestibility may be dependent on what prey is ingested under certain conditions. Indeed, Shaw (2013) demonstrated that in constant conditions digestion was longer for a diet consisting entirely of slaters than a more varied diet for captive *Leiopelma*. Furthermore, Smith (1976)

noted an inability of southern toads (*Bufo terrestris*) to digest crickets at temperatures ranging between 20 - 30°C. Understanding such variation between prey digestibility and gut retention times at certain temperatures has important implications for the energy uptake of individuals. According to Bobka *et al.* (1981), energy uptake is inversely related to temperature in red-backed (*Plethodon cinereus*) and Shenandoah salamanders (*P. shenandoah*). Therefore, this conclusion implies that as a consequence of cool conditions, long gut retention times may be beneficial to amphibians given that prey can be digested. In support of this concept, Smith (1976) did not observe any differences in energy uptake in the southern toad between 20 - 30°C, although interspecific variation could not be ruled out. Studying these associations are clearly complex, as whilst gut retention times and digestion collectively influence energy uptake, such influences have as much to do with diet composition as it does temperature.

Nevertheless, the question remains regarding whether Hochstetter's frogs could digest prey and gain enough energy in a thermal environment like Orokonui Ecosanctuary. Although it cannot be concluded that adequate energy uptake could occur as this was not tested, it is likely that Hochstetter's frogs can digest some prey in cool conditions because of their generalist and seasonally variable diet (Eggers 1998; Shaw *et al.* 2012; Shaw 2013). According to Shaw (2013), slaters are generally not a major component of Hochstetter's frog diet anyway, as almost 40% of 73 faecal pellets produced by wild-caught frogs consisted of Hymenoptera (e.g. ants) and Coleoptera (i.e. beetles), compared to only ~3.5% for Isopoda. Further, Shaw *et al.* (2012) recorded that ~32% of stomach contents (dissected from nine preserved Hochstetter's frog specimens) consisted of Amphipoda (i.e. hoppers), but in contrast to Shaw (2013), roughly 22% of stomach contents were of slaters. This proportion of slaters was possibly accentuated by the smaller sample size. However, considering crickets and locusts were digested by frogs whilst temperatures were reduced during the acclimation period, and that slaters are not highly represented in Hochstetter's frog diets, this would imply that important food sources may not be affected by cold temperatures.

Additionally, sporadic peaks in temperature may enhance digestion of food, as indicated by the defecation of faecal pellets containing digested material during the week following the 6 - 7.5°C treatment. After long retention periods during cool conditions, Hochstetter's frogs may therefore rely on warmer peaks or cycles of temperatures to process food. Lastly, tuatara scat is prominent in the tuatara release area at Orokonui Ecosanctuary (pers. obs.), thus tuatara clearly digest and defecate under Orokonui Ecosanctuary thermal conditions despite the contrary recorded in the lab (Besson & Cree 2011). Even though the interspecific differences

between tuatara and Hochstetter's frogs are immense, this field observation is encouraging for the potential release of Hochstetter's frogs in Orokonui Ecosanctuary.

Study considerations

The most commonly known limitation involving studies of this nature is that multiple factors present in the field cannot be replicated in the lab (Angilletta 2009). Responses in the captive frogs may therefore differ to those in the wild (Shaw 2013). For example, Bradfield (2006) observed no differences in body weight before and during winter for Hochstetter's frogs held in outdoor enclosures at Hamilton Zoo, whereas a temperature effect was detected in the present study. Additionally, captive frogs in the present study were exposed to relatively constant conditions and had no basking opportunity. In the wild however, animals are rarely at equilibrium with their thermal environment because environmental conditions are extremely variable over time (Angilletta 2009), between microhabitats (Huey 1991), and obviously sites (Eggers 1998; Nájera-Hillman *et al.* 2009a; Beauchamp *et al.* 2010; Shaw 2013). Furthermore, the thermal environment for terrestrial habitat is more complex than water due to more avenues of heat loss and gain (Huey 1991; Wells 2007). Huey (1991) also highlighted that measured environmental temperatures are often a poor representation of microhabitats potentially used by ectotherms because of the positioning of recording equipment. Recorded environmental air temperatures were certainly not entirely representative of Hochstetter's frog microhabitat as data loggers were not placed under stream rocks. Instead, given the possibility of flooding which would damage the equipment, data loggers had to be attached to a nearby tree trunk and root above the stream. Considering there are many limitations present, it is no wonder that field data of thermoregulation and other physiological responses of amphibians are generally rare (Wells 2007).

Finally, the temperature gradient selected for the thermal preference investigation was deliberately chosen not to exceed approximately 20°C in order to mitigate the risk of the frogs dehydrating. Selected temperatures almost encompassed the entire range of gradient temperatures, thus the results were conservative. Nonetheless, as long as such limitations are considered, important biological insights can still be made.

Final conclusions

This chapter addressed the questions regarding the investigation of thermal preference, the physiological responses of captive Hochstetter's frogs to temperature, and the quality of the thermal environment at Orokonui Ecosanctuary and Torere Forest. These results suggest Hochstetter's frogs are strongly associated with warm temperatures and that cool conditions can influence physiological responses. Although there are still many uncertainties,

Hochstetter's frogs may be able to perform vital physiological processes, such as the ability to digest, by behaviourally adjusting to a thermally challenging environment like Orokonui Ecosanctuary. Certainly, given the habitat that they live in, it is likely that Hochstetter's frogs are regularly exposed to cold or subzero conditions anyway. Yet there is a clear distinction between adjustment and adaptation (Rome *et al.* 1992). As Wilson (2001) and Besson & Cree (2011) collectively pointed out, populations may be adapted to local thermal conditions, thus these underlying genetic components need to be addressed. Understanding the genetic structure of a population is especially important for potentially transferring an apparently warm-adapted species to a proposed cool site.

Equally important are the potential influences temperature have on embryonic development and subsequent growth rates. Indeed, deVlaming and Bury (1970) observed a shift in temperature preference for larval *Ascaphus* during development, which highlighted that temperatures required for successful development change over time. In addition, Brown (1975) demonstrated that thermal tolerance ranges for embryonic *Ascaphus* are relatively narrow. Unfortunately, temperature effects on development and growth rates in Hochstetter's frogs (and *Leiopelma* in general) are virtually unknown. This uncertainty is largely due to the rarity of locating egg strings in the wild and the difficulty of breeding the frogs in captivity (Bell 2002; Beauchamp *et al.* 2010). Nevertheless, successful hatching and development of Hochstetter's frogs have been observed in temperatures recorded between 9.4 and 15°C (Bell 1982; Beauchamp *et al.* 2010). Temperature has been shown to moderately affect development and growth in Archey's frogs (Eggers 1998), but it is clear that further investigations are required.

In conclusion, future research into the thermal responses of Hochstetter's frogs is essential. In particular, a trial release of acclimated Hochstetter's frogs into enclosures at Orokonui Ecosanctuary during winter is recommended. This recommendation follows the trial release of tuatara which was deemed successful for their establishment at Orokonui Ecosanctuary and thereby improving the understanding of tuatara responses to the thermal environment (Mello *et al.* 2013). Only after a trial release of Hochstetter's frogs occurs can there be confidence in deciding whether a translocation may or may not be feasible regarding the management of Torere Forest populations threatened by pine harvesting.

Chapter Five

General discussion

Summary

The purpose of this thesis was to investigate how Hochstetter's frog populations are influenced by a modified environment in Torere Forest and assess whether a translocation to Orokonui Ecosanctuary might be feasible. To achieve this, this study firstly examined population parameters and resource selection between mature pine plantations and native forests in Torere Forest, followed by identifying suitable areas of habitat in Orokonui Ecosanctuary. Secondly, this study assessed the quality of the thermal environment at Orokonui Ecosanctuary and Torere Forest and measured the thermal preference and physiological responses of captive frogs to cool conditions.

For Chapter Two, it was predicted that the modified habitat of mature pine plantations would negatively impact frog populations, but no such effects were observed. Undetected negative effects on population parameters and body condition were possibly a reflection of resource use as frogs were observed to utilise extensive resources in mature pine plantations compared to native forests. Consequently, the use of extensive resources in mature pine plantations may have relaxed primarily intraspecific competition, particularly when cobble habitat was limited or absent. These results also suggest that Hochstetter's frogs are somewhat tolerant to living in modified environments, but further investigations are warranted. Whilst there was no evidence to suggest that populations inhabiting mature pine plantations were negatively affected by modified habitat, there remain uncertainties about population structure, specifically whether founder populations were re-colonisers or survivors of initial habitat clearance (Douglas 1998b). The extent of impacts harvesting pine will have on population persistence in the long-term is unclear.

Although identifying important resources is crucial because resource preservation is necessary for population sustainability (Manly *et al.* 2002; Ayers *et al.* 2013), threatened species often inhabit entirely modified environments (e.g. Brockerhoff *et al.* 2005). Investigations like the present study that have the opportunity to compare between modified and predominantly unmodified habitats therefore offer rare insights into what resources are important for certain species. Specifically, in support of the hypothesis that rock substrata were important for Hochstetter's frogs, the investigation of resource selection in Chapter Three highlighted that

cobble habitat is a necessary resource. Interestingly, logs were also an important resource in mature pine plantations. Furthermore, cobble habitat was extensive in native forests whereas logs were not, compared to both pine plantations and Orokonui Ecosanctuary. In the context of Hobbs & Hanley's (1990) proposed model (see Chapter Two) and the low population densities recorded in Torere Forest, the actual quality of these resources cannot be determined without long-term monitoring to see whether densities increase over time. Nonetheless, priority should be given to the protection of cobble and log habitats, particularly in pine plantations, in order to conserve Hochstetter's frog populations.

Based on the resource selection models produced in this thesis, habitat quality was predicted for several streams at Orokonui Ecosanctuary. Predicted habitat use indices were similar to those obtained for inhabited streams in Torere Forest, thus suitable areas of habitat were available at Orokonui Ecosanctuary. This finding supported the prediction that suitable areas of habitat were present, which is important as translocations will fail if required habitat at release sites is absent or very limited (Armstrong & Seddon 2008). Clearly, cobble and log cover are important habitat features that should be considered when identifying essential habitat in novel areas. Lastly, surveying for suitable areas of habitat in other mainland sanctuaries (e.g. Zealandia) is another investigation that is required.

Whilst habitat quality can be inferred from studying resource selection, it is important to remember that habitat varies spatially and temporally (Osborne & Seddon 2012). Possible seasonal movements between habitats must also be considered (Osborne & Seddon 2012), along with breeding habitat (Beauchamp *et al.* 2010) and potential differentiation in habitat use as individuals develop to maturity (Ziegler 1999; Manly *et al.* 2002). In particular, ontogenetic shifts in habitat use for Hochstetter's frogs are largely unknown (Tessier *et al.* 1991) although the lack of a relationship between rock sizes and frog SVL observed by Shaw (2013) infers that there may be none - at least for cobbles. Nevertheless, Ziegler (1999) and Shaw (2013) suggested that low-growing vegetation, leaf litter and logs are important juvenile habitat. Given the cryptic nature of Hochstetter's frogs and green colouration of juveniles observed in the present study, the colouration and structure of vegetation may indeed be important resources to consider. By far the most critical component that defines habitat quality, however, is connectivity (Douglas 2001b; Harris *et al.* 2014; Dade *et al.* 2014). Specifically, ensuring connectivity of juvenile habitat is essential for population recruitment as movement patterns have been shown to decrease with age in *Ascaphus* (Daugherty & Sheldon 1982), which is likely to be similar for Hochstetter's frogs. Considering the life cycle ecology of Hochstetter's

frogs was not addressed in the present study, future research on specific habitat requirements during development is essential.

The laboratory study, highlighted in Chapter Four, demonstrated that temperature strongly influences the physiological responses of captive Hochstetter's frogs. Notably, the results supported the prediction that the scaled mass index and gut retention times would increase as a consequence of cool temperatures. The initial negative response exhibited by many frog individuals and the fact that digestion of slaters was not observed when exposed to cool conditions does raise concerns, however these responses may be attributed to a combination of laboratory, individual variation, and dietary effects. In addition, thermal preference indicated an association with warm temperatures, contrary to the prediction that the frogs would select acclimated conditions, although these results were conservative given the designed temperature gradient. Re-doing this experiment with modifications (such as having water along the bottom of each runway and increasing the temperature gradient) would be useful. Needless to say, Orokonui Ecosanctuary conditions are thermally challenging compared to Torere Forest, but Hochstetter's frogs may be able to exhibit compensatory behavioural thermoregulation to optimise the thermal environment. Such behavioural responses are likely to occur as Hochstetter's frogs often inhabit shallow substrata where thermal conditions are possibly at equilibrium or close to environmental temperatures that regularly reach near freezing levels during winter. Moreover, their generalist diet should enable individuals to digest and uptake energy for some food sources during winter months, especially considering the digestion of major dietary components may not be largely affected by cold temperatures. This study did not test for energy uptake in cool conditions, but it would be interesting to do so in the near future. Another necessary study is the investigation of temperature impacts on Hochstetter's frog development. To carry out such research, however, will be challenging given the rarity of locating egg-strings in the wild and the difficulty of breeding these frogs in captivity. A trial transfer during winter is therefore recommended as this would confirm whether Hochstetter's frogs sourced from Torere Forest could survive in Orokonui Ecosanctuary conditions.

Future implications

Ultimately, based on this study's preliminary results, a translocation of Hochstetter's frogs to Orokonui Ecosanctuary does seem feasible, but further research is needed. Translocations require thorough assessments (Seigel & Dodd 2002; Armstrong & Seddon 2008; IUCN 2013), including scenarios of potential translocation outcomes. For example, assuming that the extensive log habitat in Orokonui Ecosanctuary is actually of low quality, the density of a hypothetical established population is likely to be low. In addition, the cool thermal

environment may further reduce population density, thus the carrying capacity may be lower than the source population. These ‘worst-case’ scenarios are rather pessimistic, but this cautious approach must be implemented into conservation that requires translocations as management tools.

In response to global warming, and the likelihood of environmental conditions (particularly thermal) becoming less optimal for Hochstetter’s frogs in the northern regions of the North Island (Fouquet *et al.* 2010a), southern potential translocation sites will increasingly require investigation. Most importantly, the genetic structure and the prioritisation of certain populations need to be considered during translocation feasibility research. At least 13 Evolutionary Significant Units (ESUs) have been identified (Fouquet *et al.* 2010b; Newman *et al.* 2013), thus maintaining this phylogeographic structure would require very strict translocation regulations. For instance, if the genetic structure of one translocated population is different to another that requires translocating, then the release site of the previously released individuals would be “off-limits”. Hence, another potential release site would need to be identified. In this case, conservationists may argue that ESUs that are considered “Nationally Critical” (e.g. *Leiopelma* aff. *hochstetteri* “Otawa”, Newman *et al.* 2013) should thus be prioritised as potential source populations, rather than ESUs that are “At Risk: Declining”, which is what the Torere Forest populations are likely to be. In saying that, perhaps the initial focus should be on more ‘common’ ESUs in order to refine translocation management techniques without greatly decimating source populations. Regardless, identifying multiple potential translocation sites would ensure that the goal to maintain the phylogeographic structure of Hochstetter’s frogs is achieved.

In the meantime, pine harvesting in Torere Forest is likely to have detrimental effects on Hochstetter’s frog populations, thus establishing long-term monitoring over multiple populations is essential prior to harvesting commencing. In addition to monitoring population parameters and individual fitness, resource quality/use and temperature interactions must be addressed as harvesting also influences these factors (Rothermel & Luhring 2005; Bury 2008). Finally, investigating the possibility of riparian buffer protection, population connectivity, and whether re-colonisation occurs, should be considered. Overall, implementing investigations such as these will aid in securing frog populations, but will enable other biodiversity goals to be achieved as they are highly applicable to other species (Norton 2001; Meurk & Hall 2006). Hopefully coordinated efforts, like those seen by stakeholders associated with this project, continue to manage biodiversity in modified environments without compromising economic productivity (deMaynadier & Hunter 1995) and that foreseeable challenges are collaboratively

overcome. Namely, how rapidly management plans are established in response to the onset of harvesting is of concern, especially when harvesting in Torere Forest is expected to commence over the next two years and necessary investigations are yet to occur. Fortunately, stakeholder support is looking positive for the management of the Hochstetter's frog populations in Torere Forest. Whether stakeholders will all support the decision of a translocation to Orokonui Ecosanctuary remains to be seen, but it is encouraging that the current collaborative effort is another step forward in protecting one of the world's most evolutionarily distinct and globally endangered species.

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