Monitoring strategies for the giant land snail *Powelliphanta traversi tararuaensis* (Gastropoda: Pulmonata: Rhytididae): an assessment and exploration of current and future techniques.

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Rachel Lynn Turner

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Abstract

The current monitoring strategy employed in the management of *Powelliphanta traversi tararuaensis,* a threatened species of giant carnivorous land snail from the Manawatu region of New Zealand, was used to assess the state of two remaining population strongholds – Shannon Forest and Ohau. Conservation targets were found to be amiss in the Shannon Forest population. Average abundance of live *P. t. tararuaensis* there measured well below the recovery goal set by the *Powelliphanta* Recovery Plan. A decline in recruitment was also noted for the Shannon population, with the average size of snails found increasing between the surveys, and a significant drop in numbers of smaller individuals. *P. t. tararuaensis* populations in Ohau were found to be healthier with respect to conservation goals, with two study areas within the site having live *P. t. tararuaensis* numbers well above the target for recovery.

Questions were then asked about the current monitoring program for *Powelliphanta,* in particular concerning the apparent destructive nature of the methodology and the lack of collection of detailed data on life history parameters and population dynamics. I thus tested the effect of a monitoring event on the short-term behaviour of *P. t. tararuaensis* using a mark-recapture study design. The disturbance to the area associated with monitoring had an effect on the re-sighting probability of marked snails, with individuals less likely to be encountered in the days following the monitoring event.

New techniques for monitoring *Powelliphanta* snails were then explored to address the short-fall in methods of gaining life history data in the current program. Attaching tags to the shells of *P. t. tararuaensis* for individual identification using certain adhesives was found to affect the foraging behaviour of wild rats. Loctite and Araldite glues should be used with caution in a field setting, as they may predispose marked snails to depredation by rats. An alternative method for individual snail recognition was then trialled, utilising natural marks on snail shells and a photographic database. It was discovered that individuals of *P. t. tararuaensis* could be recognised by naturally occurring shell variation, but the accuracy decreased over a six month time-frame as new marks were gained and old ones evolved.

This thesis concludes that the current monitoring system for *Powelliphanta* could be improved, both in the type of data gained for assessing management and conservation goals, and in the lessening of impact on snail behaviour. Monitoring strategies for land snails would benefit from incorporation of a non-invasive mark-recapture approach, such as photographic identification. Such techniques would allow for more directed conservation action, without potentially negative impacts on *Powelliphanta* behaviour.

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Contents

List of Figures

List of Tables

1 Introduction

Monitoring Vertebrate and Invertebrate Populations

Monitoring animal populations serves several purposes. It is crucial in the maintenance of sustainable harvest quotas (Martell & Walters, 2002), and can be used to track changes in populations regarding declines, invasions and distributions (Marsh & Trenham, 2008). Monitoring vertebrates is an increasingly advanced field of research. Specialised equipment is now readily accessible to the vertebrate biologist, including devices capable of recording heart rate (Kreeger *et al.* 1989; Johnsson *et al.* 2001) and body temperature (Kreeger *et al.* 1989), as well as tags able to track animal movement by satellite (Graham *et al.* 2006). The implications of monitoring on animal behaviour and welfare are also routinely assessed for vertebrates (Murray & Fuller, 2000; Mellor *et al.* 2004), and researchers strive to limit the effect of their activities on study populations (Ortega *et al.* 1997; Carney & Sydeman, 1999).

Comparatively, monitoring methodologies in the invertebrate taxa are frequently crude. Umbrella-like techniques which lump a diverse range of taxa together in a single survey are frequently employed, for example Malaise traps (Brown, 2005; Neville & Yen, 2007) and pitfall sampling (Brennan *et al.* 1999; Ward *et al.* 2001; Neville & Yen, 2007). The equipment used in such surveys may be no more advanced than a set of rinsed take-away meal containers (Neville & Yen, 2007). Effects of surveys on the behaviour of invertebrates are rarely considered (Henry & Jarne, 2007), highlighting a distinct difference in attitude between the monitoring of vertebrates and invertebrates. Comprehensive monitoring programs are commonly employed with commercially valuable invertebrate species such as rock lobster (Frusher *et al.* 2009) and sea cucumber (Purcell *et al.* 2008). Large species of invertebrates are also comparatively more represented in monitoring studies, as techniques developed in vertebrate research are more applicable to large bodied invertebrate species (Naef-Daenzer *et al.* 2005).

Land Snail Conservation

The monitoring of gastropod taxa is a fundamental endeavour, as many species serve as intermediate hosts for parasites which affect humans (Brown, 1994) and other animals (Jabbour-Zahab *et al.* 1997; Hechinger & Lafferty, 2005), act as important biological models for ecological systems (Charbonnel *et al.* 2002; Henry *et al.* 2005; Regoli *et al.* 2006) or are of economic importance (Henry & Jarne, 2007). Monitoring of land snails is becoming imperative, as the group is currently facing serious worldwide declines (Wells, 1995; Lydeard *et al.* 2004). Lydeard *et al.* (2004) noted that only a minute portion (<2%) of molluscan species known to science have received sufficient assessment of their conservation status; a worrying notion considering molluscs have suffered the highest number of extinctions recorded for any major taxonomic group overall (Lydeard *et al.* 2004). Common themes in land snail decline include habitat loss and degradation (Hadfield, 1986; Stringer *et al.* 2003; Trewick *et al.* 2008) the effects of introduced predators (Meads *et al.* 1984; Murray *et al.* 1988; Hadfield *et al.* 1993; Parrish *et al.* 1995; Bennett *et al.* 2002), overexploitation (Bouchet *et al.* 1999; Pokryszko, 2003) and reduced dispersal capabilities (Solem, 1984; Cameron, 1999). Data gathered through monitoring programs can be used to scrutinise the effectiveness of management strategies (Campbell *et al.* 2002), thus monitoring is an important detail in land snail conservation.

Monitoring programs, however, may hold some failings. Sólymos & Fehér (2005) noted that geographical zones not completely covered by their study of Hungarian land snails may hold rare taxa. Therefore, further monitoring may be required to correctly identify biodiversity hotspots, and effectively target conservation focus (Sólymos & Fehér, 2005). A comprehensive summary of native land snail populations of the Society Islands (Coote & Loeve, 2003) stressed the importance of regular population monitoring surveys for their protection. Many declines in the endemic land snail fauna of the Society Islands are attributed to depredation by *Euglandina rosea,* a carnivorous snail from Florida brought into the Society Islands to control another exotic snail *Achatina fulica,* which acts as a crop pest (Coote & Loeve, 2003). Punctuated monitoring surveys missed certain incursions of *E. rosea,* allowing the spread of the predator and putting populations of the native snails at risk (Coote & Loeve, 2003). Shortcomings of monitoring programs may, therefore, put a region's endemic snail fauna in jeopardy.

New Zealand Land Snails with an Emphasis on Powelliphanta

The Rhytididae (Mollusca: Gastropoda: Pulmonata) are a family of relatively large land snails distributed throughout the Southern Hemisphere (Powell, 1979). New Zealand is home to several genera of these carnivorous snails, including *Wainuia, Rhytida* and *Powelliphanta* (Powell, 1979; Efford, 1998). The group holds a fascinating range of carnivorous habits, including cannibalism, carrion feeding, and capture of highly mobile arthropod prey (Efford, 1998; Efford, 2000). *Rhytida* possess a prehensile tail which they use to carry prey about, and some feeding traits have been suggested to be unique to New Zealand (Efford, 1998). *Wainuia* currently contains four described species from eastern central New Zealand, and an undescribed species from Fiordland (Efford, 1998). The genus *Rhytida* is presently recognised as containing ten species which range from Auckland to Stewart Island, with at least one further undescribed species from the Marlborough region (Efford, 1998). Neither group is classed as protected, nor has there been much advancement in determining the conservation status of *Wainuia* or *Rhytida* species (Efford, 1998).

Powelliphanta is found in the lower North Island and throughout the South Island. The group is thought to have ancestral associations with the "proto New Zealand" land mass which separated from the Gondwanan supercontinent (Walker, 2003), thus representing an ancient facet of New Zealand's natural heritage. There has been considerable review of the taxon since its initial description by Powell in the 1950's (Bennett, 2001), and the genus is currently recognised as containing ten species and 34 subspecies (Walker, 2003). The Department of Conservation currently bases population management decisions on a draft taxonomy created using allozyme data (Walker, 2003). Recent work using mitochondrial DNA has revealed new species within *Powelliphanta* (Figure 1.1; Trewick *et al.* 2008), and further revisions of taxonomy and changes of management plans may take place as more molecular data become available.

Powelliphanta are nocturnal and carnivorous, subsisting on a diet composed largely of earthworms supplemented by slugs, millipedes and other snails (Powell, 1979). *Powelliphanta* snails usually live in the deep, moist, non-acidic leaf mould that accumulates under some types of forest and scrub, but now have an increasingly reduced range as a result of forest clearance and predation by exotic animals (Yeates, 1991). They exemplify the K-selected traits frequently seen in New Zealand endemics: long lived with

a relatively large body size and low fecundity (Walker, 2003). These qualities make them particularly susceptible to population declines, and like many other New Zealand endemics, *Powelliphanta* bear the yoke of exotic mammalian predators. Rats (*Rattus rattus, R. exulans,* and *R. norvegicus*), mice (*Mus musculus*), hedgehogs (*Erinaceus europaeus*), pigs (*Sus scrofa*), and possums (*Trichosurus vulpecula*) are all culprits in land snail predation (Meads *et al.* 1984; Bennett *et al*. 2002; Standish *et al*. 2003; Stringer *et al*. 2003). Exotic ground-foraging birds like the song thrush (*Turdus philomelos*) and blackbird (*T. merula*) frequently depredate small size classes of *Powelliphanta,* and their effect is particularly noticeable where rodent populations are low (Bennett *et al.* 2002). Pigs and exotic birds have also been suggested as competitors for earthworm prey (Bennett *et al*. 2002).

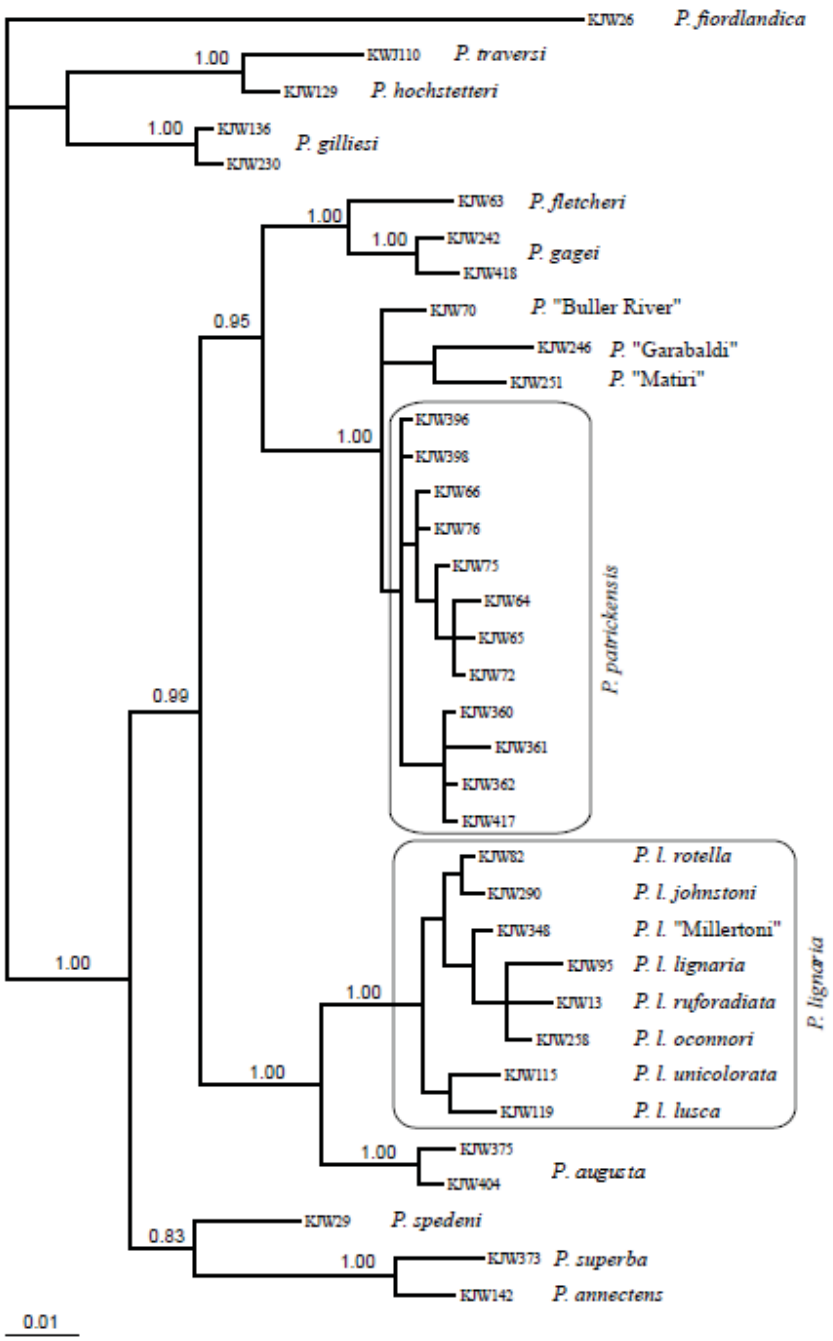

Figure 1.1. Hypothetical phylogeny of Powelliphanta based on Bayesian analysis of 36 mtDNA COI sequences. Numbers at nodes are Bayesian credibility values, with maximum support indicated by the highest value (1.0). Reproduced with minor changes from Trewick et al. (2008).

Powelliphanta traversi tararuaensis (Powell, 1938) (Gastropoda: Pulmonata: Rhytididae; Figure 1.2) is one of the five subspecies of *Powelliphanta traversi*, a lowland species which occupies the Horowhenua region (Figure 1.3). This taxon once resided throughout most of the basin of the Kahuterawa Stream headwaters, with a second discrete population found in a basin between the Mangaore Stream and the Makahika Stream (Walker, 2003). Both of these locales lie on a western outlier of the Tararua Range. Now, however, the original distribution is both greatly reduced and fragmented as a result of habitat modification and destruction (Walker, 2003). It is this factor, in conjunction with pressure from introduced predators, which has lead *P. t. tararuaensis* to be classified as "nationally endangered" in the most recent New Zealand Threat Classification List (Hitchmough *et al.* 2007).

Walker (2003) described *P. t. tararuaensis* as being a snail of medium size, with a maximum diameter of 53mm and a maximum height of 25mm. The shell is olive green, with a russet brown colouration on the top (Figure 1.2). Fine pale spiral lines, along with a few distinct lines around the periphery decorate the shell; and individuals possess a smooth, grey parietal callus.

Figure 1.2. An individual of P. t. tararuaensis, clearly showing the colouration and banding patterns of the shell. Photo by the author.

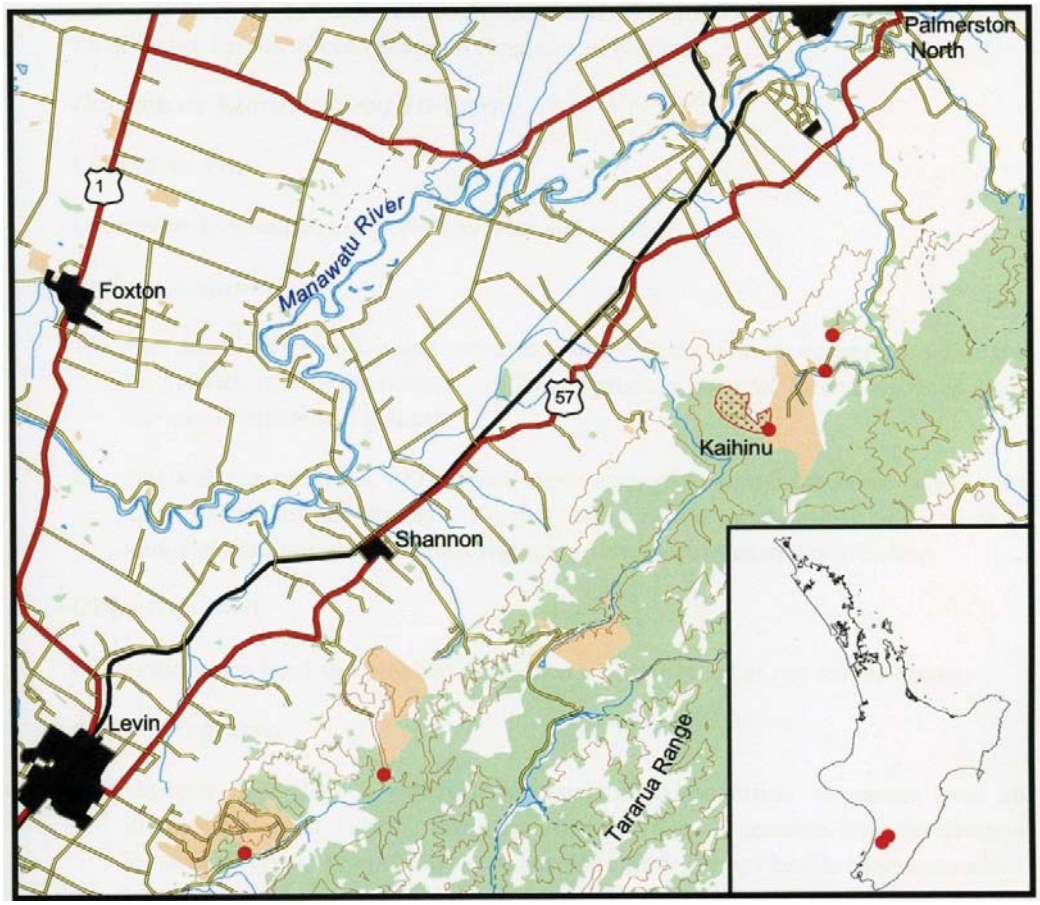

Figure 1.3. The current locales of P. t. tararuaensis. Red dots represent sites from where shells have recently been collected indicating living populations; red stippling indicates the known or reliably presumed range. Figure edited from Walker (2003).

The sedentary lifestyle of *Powelliphanta* snails together with New Zealand's biogeographic history has led to a sizeable level of radiation within the taxon (Walker, 2003; Trewick *et al.* 2008; Walker *et al.* 2008). Most groups within *Powelliphanta* are threatened and occupy small ranges. Many populations are understudied, and the crux of the issue lies in the vastness of the task due to the large number of genetically distinct groups and limited conservation resources (Walker, 2003). Additionally, the threatened nature of most taxa affords immediate conservation action at the expense of ecological research.

The current recovery plan for *Powelliphanta* snails (see Walker, 2003) recommends that:

- Accurate data on current population trends need to be obtained.
- Remaining habitat for *Powelliphanta* populations needs long-term legal protection.
- Known predators of the snails need to be controlled, and the effectiveness of control should be gauged.
- Public participation in *Powelliphanta* conservation should be encouraged, and partnerships between the Department of Conservation and groups interested in snail conservation should be supported.

Walker (2003) noted that our understanding of the ecology of *Powelliphanta* at the community, population and individual levels is poor. There is a notable paucity of information concerning basic life history traits, and the current techniques for monitoring *Powelliphanta* populations focus on abundance estimates (Walker, 1997). The current monitoring methodology may also be destructive to the snails' habitat (Walker, 1997). Without exploration of appropriate monitoring techniques and management protocols capable of gleaning life history knowledge, the shortfall is likely to remain. We cannot determine if *Powelliphanta* are threatened with extinction or just becoming very rare, as it is impossible to model the survival of threatened *Powelliphanta* taxa at very low densities due to the lack of detailed information on population dynamics (Walker, 2003). This kind of uncertainty around the fate of *Powelliphanta*, coupled with the fact that many populations exist in very large remote forest blocks as small and widely scattered clusters of snails, means that research on this taxon can be difficult. The current long-term recovery goal, as outlined in the Department of Conservation's recovery plan for *P. t tararuaensis,* aims to have "*dense (> 12 snails/100 m²) snail populations that are either stable or increasing, in at least 100ha of secure habitat at both Shannon Heights and Kaihinu*" (Walker, 2003). However, to know if we have achieved this goal we require information regarding the rates of recruitment, productivity and survival of *Powelliphanta* populations in the absence and presence of introduced predators. Currently this knowledge is lacking.

These failings have posed an immediate risk to *Powelliphanta* land snails, recently highlighted by the plight of *Powelliphanta augusta* (Trewick *et al.* 2008; Walker *et al.*

2008). In 1996 the shells of six *Powelliphanta* were collected from Mt Augustus on the Stockton Plateau north of Westport, South Island, New Zealand (Walker *et al.* 2008). These specimens were originally thought to be *Powelliphanta patrickensis*, a taxon which occupies the Stockton Plateau. Then in 2003 the shells were examined in greater detail in conjunction with a survey of the range of *P. patrickensis,* and found to be significantly different in morphology. The variations in shell shape, colour and size were enough to indicate that the shells could be from a new species (Trewick *et al.* 2008). Yet by the time this was recognised, Solid Energy mining operations had already destroyed the site where the shells were collected. A small population was discovered on about 5ha of the Mount Augustus ridgeline, but this habitat too was in the process of being mined (Trewick *et al.* 2008). Following the discovery that this was, in fact, a distinct taxon, 6139 individuals residing within the proposed mining site were taken into captivity. In 2006 and 2007 most of the remaining habitat for the newly discovered species of snail was demolished by coal mining (Walker *et al.* 2008). A portion of the snails were released into the last remaining strip of habitat, although this habitat was considered sub-optimal (Trewick *et al.* 2008). The Department of Conservation still has several thousand *P. augusta* in captivity, and has been holding them in Hokitika for over three years now (K. Weston, pers. comm.). Lack of information surrounding natural rates of recruitment, productivity and survival for *P. augusta* has the potential to hinder its recovery.

Thesis Focus

In order to address issues put forward by the current *Powelliphanta* recovery plan, a monitoring program for *Powelliphanta* snails is required, a program which has no detrimental effects on the animals, whilst being capable of amassing data for insight into population dynamics and life history traits. The majority of the questions addressed by this thesis initially arose as a result of my involvement with the *P. t. tararuaensis* monitoring work in Ohau and Shannon (Chapter Two). I was prompted to ponder, whether the methods we currently use to monitor *Powelliphanta* and other genera of Rhytididae are providing the information we need to effectively protect New Zealand's land snail fauna? Is there a chance that this monitoring technique is negatively impacting the behaviour of the snails, and thus are the population estimates reliable? Could there be a better way? These rudimentary queries lead to the study presented here.

The aim of this thesis was to review and assess several facets of the current monitoring strategies commonly employed in the management of *Powelliphanta* land snails, using populations of *P. t. tararuaensis* as a model. The potential for new techniques and methods was explored, in light of the need for conservation of this distinctive New Zealand land snail genus. The specific objectives of this study, by chapter, were:

- To utilise the current monitoring system for assessment of the status of two *P. t. tararuaensis* populations, and to consider the potential for failings in the existing methodology (Chapter Two).
- To scrutinise the effect of the current monitoring scheme on the short-term behaviour of *P. t. tararuaensis*, and the likelihood of any negative effects of the employed methodology on monitored populations (Chapter Three).
- To assess the potential for application of radio frequency identification (RFID) techniques to the monitoring of *Powelliphanta* snails, and to examine the role this method could play in predisposing snails to rat depredation (Chapter Four).
- To explore the possibility of using photographic identification for individual snail recognition by means of natural marks (Chapter Five).
- To summarise the findings and provide some recommendations for the practitioners in snail conservation (Chapter Six).

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2 The monitoring of a giant land snail (*Powelliphanta traversi tararuaensis*) in two remaining population strongholds.

Introduction

As the area occupied by humans continues to expand, and subsequently more endemic species inch toward the realm of extinction, the role played by private land owners in conservation is almost certain to become more important. Over the millennium or so that people have been in New Zealand, the natural environment has undergone high levels of modification at the hands of humans. Around 70% of the native forest cover and 90% of New Zealand's wetlands have been lost, and the destruction of habitat and introduction of exotic pests have contributed to the extinction of over 50 endemic species (Cocklin & Davis, 2001). With so much of the country's heritage at risk, the need to protect our native ecosystems and wildlife is becoming more recognised, and now over 8 million ha of land is under legal protection for conservation purposes (Cocklin & Davis, 2001). Most of this land is publicly owned and under the management of the Department of Conservation. However, there is a distinct lack of certain forest types in the public conservation estate, particularly the lowland forests which are typical of the more accessible and fertile areas. Most of these remaining natural habitats are on private land and have no formal protection, even though they may be refuges for threatened and endangered wildlife (Cocklin & Davis, 2001).

Privately owned *Pinus radiata* plantation forests have been shown to be of significant importance to a range of wildlife species. These include the brown kiwi (Colbourne & Kleinpaste, 1983), South Island robin (Clout & Gaze, 1984), kakapo (Walsh *et al.* 2006), native carabid beetles (Berndt *et al.* 2008), and the New Zealand falcon (Seaton *et al.* 2009). Many forestry companies are beginning to recognise the effect the industry can have on indigenous flora and fauna. In response to research and the demand for eco-labelled products, there has been a global move towards more

"sustainable" forestry practices in the forestry industry (Turnbull & Vanclay, 1999). This vision shift has seen many companies adopt more environmentally responsible practices in order to protect wildlife and the environment (SGS, 2006). Ernslaw One Ltd. and Rayonier New Zealand Ltd. administer a significant proportion of New Zealand's pine plantations. The companies are currently committed to sustainable forestry management programs. To maintain certification, both companies are required to protect the endangered carnivorous land snail *Powelliphanta traversi tararuaensis* which resides within the greater Shannon and Kohitere Forests managed, respectively, by Ernslaw One Ltd. and Rayonier New Zealand Ltd.

The Powelliphanta Snail Monitoring Program

A well designed monitoring program is essential for the conservation management of *Powelliphanta*, acting as a valuable tool for following population changes (Marsh & Trenham, 2008). Historically, most surveys of *Powelliphanta* snails have involved searching the litter for empty shells while walking through an area for a set time period (Meads *et al.* 1984). This allowed for presence/absence data to be gained, and an indication of proportions of empty shells damaged by certain predators (Meads *et al.* 1984; Walker, 1997). However, the surface collection of shells does not provide a reliable means to estimate the live population, as empty shells can persist in the environment for a number of years and *Powelliphanta* populations can experience rapid declines (Walker, 1997). Walker (1997) described a methodology which is currently the standard system employed in the *Powelliphanta* monitoring program. The technique involves detailed searching of permanent monitoring plots for live snails, and provides a means for estimating abundance (Walker, 1997). The method was developed to ensure the Department of Conservation obtained quantitative density measures comparable over time and between locations, allowing for assessment of trends in population size and structure (Walker, 1997).

Two of the last remaining strongholds for *P. t. tararuaensis* lie within private forestry estates, situated in the Ohau and Shannon areas. The *P. t. tararuaensis* monitoring programs for these sites are run with the assistance of Massey University postgraduate students, overseen by Dr Isabel Castro, as part of a Wildlife Management course. The Ohau and Shannon *P. t. tararuaensis* monitoring programs employ the methodology outlined by Walker (1997). The aim of the monitoring is to identify trends

in population density, age structure, and predation dynamics in the hope that the data gathered can be applied to achieve the long term goal outlined in Walker's (2003) Threatened Species Recovery Plan for *P. t. tararuaensis*. This goal states that in order to halt declines and facilitate *Powelliphanta* recovery, *"dense (>12 snails/100m²) snail populations that are stable or increasing, in at least 100 ha of secure habitat at both Shannon Heights and Kaihinu"* are required (Walker, 2003). *P. t. tararuaensis* populations in the Ohau area have been monitored since 1996, with surveys conducted in 1996, 2004 (by DoC), and the most recent survey performed in September 2008 (Castro et al. 2008). *P. t. tararuaensis* populations in the Shannon area have been monitored since 2007 (Castro *et al.* 2007), with the most recent survey conducted in August 2009.

Wainuia and *Rhytida* occur in both the Shannon and Ohau areas (Castro *et al.* 2007; Castro *et al.* 2008). Neither genus is currently formally protected (Efford, 1998), and is therefore not a focus for management. However, both genera probably suffer the same hazards as *Powelliphanta* snails (Efford, 1998) and would likely benefit from threat mitigation as part of the *P. t. tararuaensis* management strategies.

This thesis Chapter compares abundance and size distribution data on live and dead snails collected in 1996, 2004, and 2008 at the Ohau sites and in 2007 and 2009 in the Shannon area. The aim was to identify any trends in abundance and predation levels for *P. t. tararuaensis* within the Ohau Operational Area and the Shannon Forest, and to assess whether the conservation goals for the species are being met. Snails of the genera *Wainuia* and *Rhytida* are also briefly considered, and an evaluation of the current monitoring techniques is offered.

Methods

Study Site

Ohau Area:

Rayonier New Zealand Ltd is a wholly owned subsidiary of Rayonier Inc., a U.S-based forest products company and real estate investment trust. The company has been active in New Zealand since 1988, and currently manages approximately 143,000 hectares of plantation forest for Matariki Forests (SGS, 2006). This includes the Kohitere Forest, a relatively small plantation forest of radiata pine (*Pinus radiata*). The forest has steep

topography and is punctuated by stands of mature and regenerating indigeneous vegetation (SGS, 2006). Kohitere Forest Scenic Reserve (66 hectares; 40.65215 S, 175.351208 E), Benton's Bush (25.26 hectares; 40.641683, S 175.374183 E), and the Makahika Scenic Reserve (50 hectares; 40.630639 S, 175.386369 E) (Figure 2.2) are all areas of native vegetation within or near this plantation forest, which support populations of *P. t. tararuaensis*. Rayonier previously managed the Kohitere Forest Scenic Reserve and Benton's Bush and was aware of the presence of *Powelliphanta* snails in this region of the forest. In their Forest Management Certification Report for the Southern North Island (which meets the Forest Stewardship Council's requirements and saw them certified for this area in 2006), they outlined their management scheme for protecting groups of rare, threatened and endangered species. This has involved ecological assessment by an ecology consultant, protection of all existing areas of natural vegetation, and forming of management plans in conjunction with specialists. With predator-susceptible *P. t. tararuaensis* in the region, some pest control is also part of Rayonier's environmental management plan (SGS, 2006). The Department of Conservation (DoC) has been involved in the management of the Kohitere, Benton's and Makahika forest blocks since 1996, and in 2007 Kohitere Forest Scenic Reserve and Benton's Bush were transferred to DoC ownership. These four patches are collectively named the Ohau Operational Area (Figure 2.1). Permanent quadrats of 100m^2 for monitoring the snails have been set up in four locations in the wider Ohau Operational Area by the Department of Conservation (Table 2.1); four in the Kohitere Forest Scenic Reserve, eight in Benton's Bush and four in the Makahika Scenic Reserve (Figure 2.3). In September 2008 an additional four quadrats were established in the Kohitere area (Castro *et al.* 2008) where pest control had only relatively recently resumed, and snail populations had not been previously monitored (Figure 2.3; Castro *et al.* 2008).

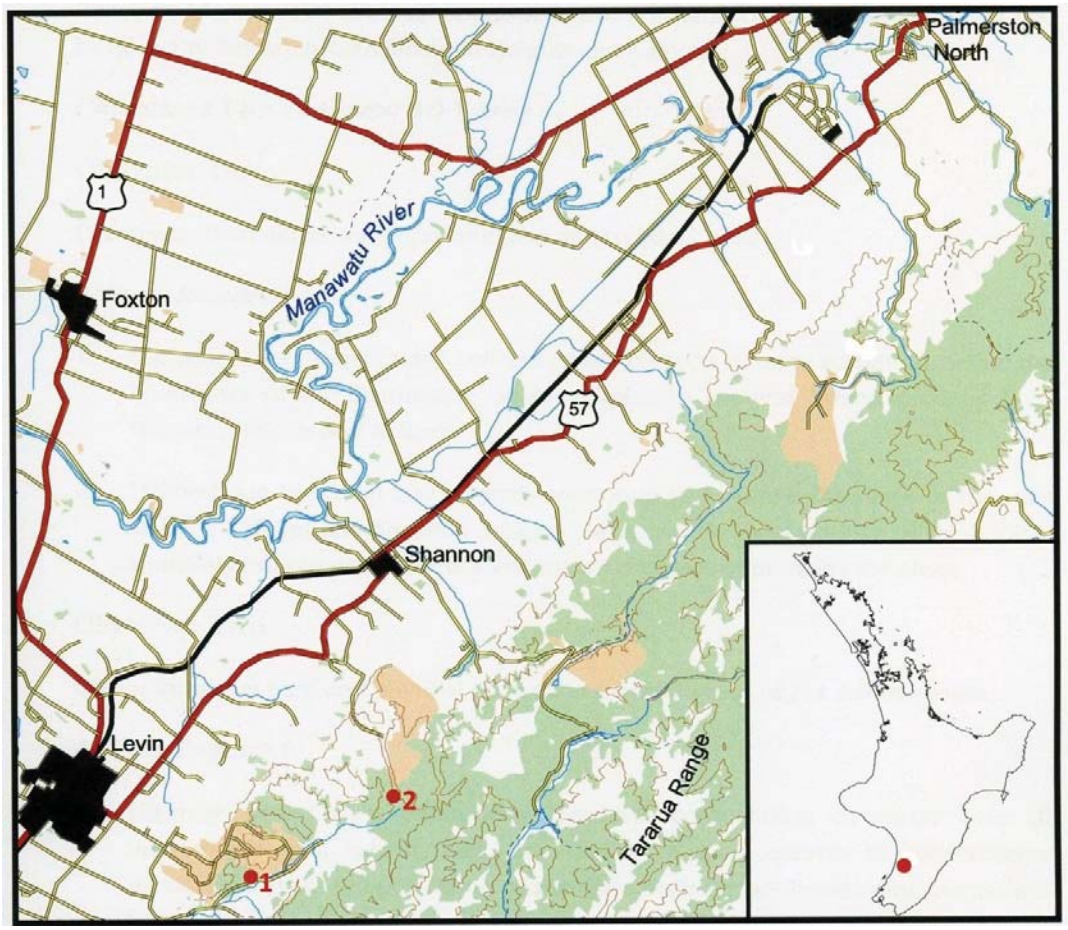

Figure 2.1. Locations of the two study sites: the Ohau site in the Ohau Operationl Area (1) and the Shannon site in the Shannon Forest (2). Map edited from Walker (2003).

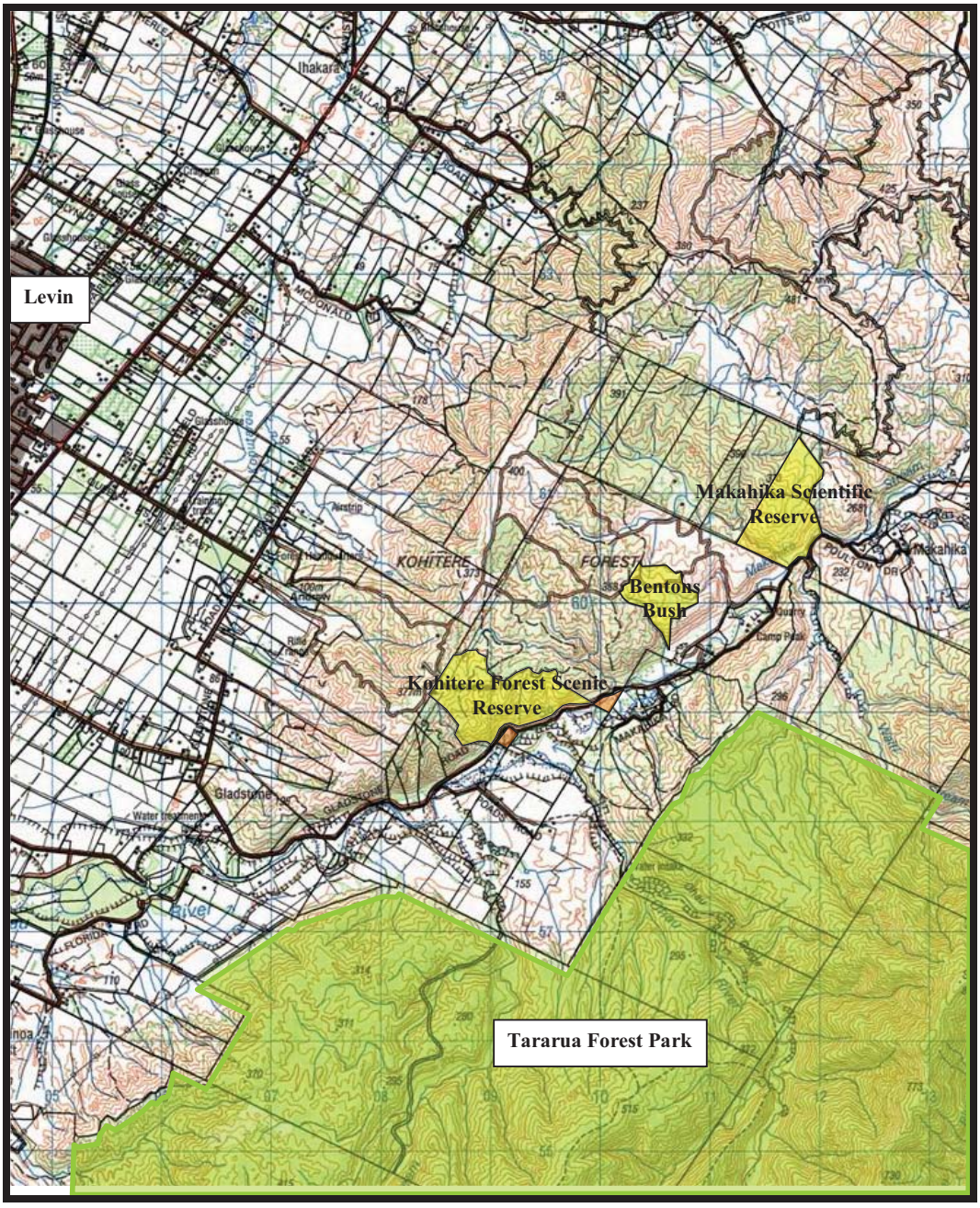

Figure 2.2. The Ohau Operational Area. The forests comprising this unit (Kohitere Forest Scenic Reserve, Bentons Bush & Makahika Scientific Reserve) have been monitored for P.t.tararuaensis since 1996, with the last operation in September 2008 (Castro et al. 2008).

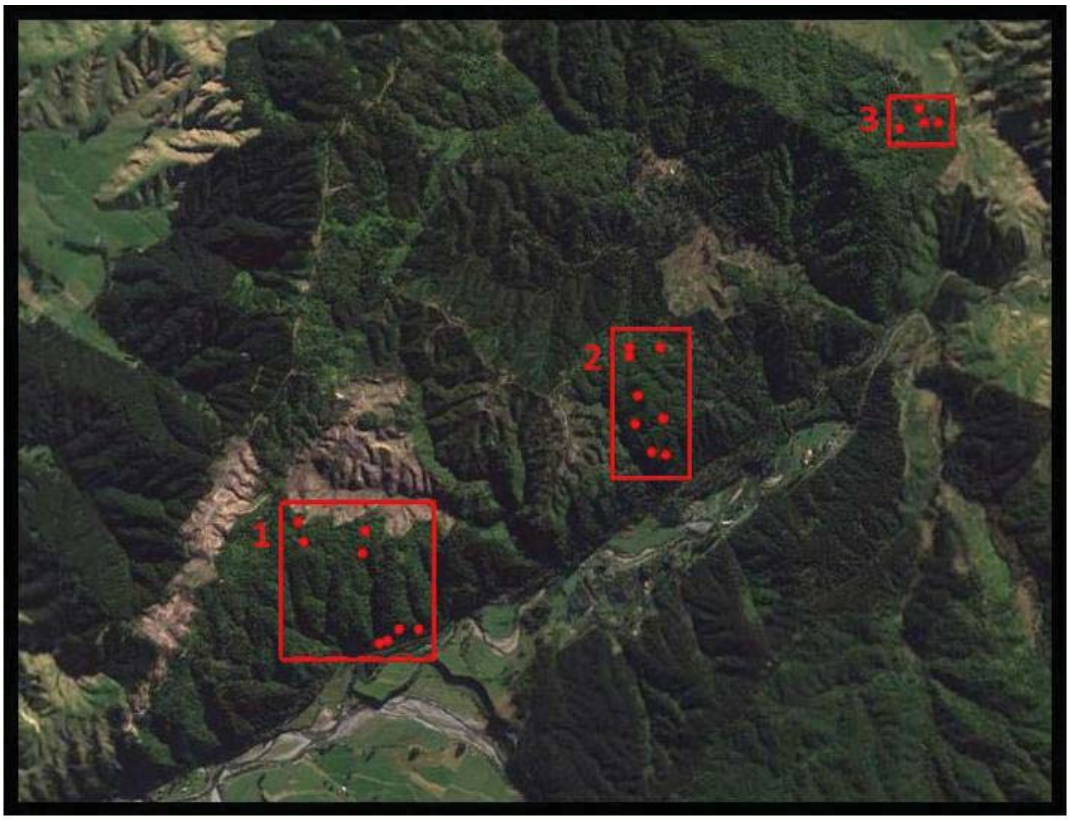

Figure 2.3. Locations of existing quadrats (red dots) within the Kohitere Forest Scenic Reserve (box 1), Benton's Bush (box 2) and the Makahika Scenic Reserve (box 3). All quadrats were established by DoC, with the exception of four northern-most Kohitere quadrats set up in 2008 by a group of from Massey University (modified from Castro et al. 2008).

Table 2.1. Powelliphanta traversi tararuaensis monitoring quadrats in the Ohau Operational Area used in this study. "NA" indicates information not available at the time of this publication.

Quadrat	Area	Altitude	Latitude	Longitude	Moisture	Slope
B1	Benton's Bush	290 m	40.63957060 S	175.37085 E	Dry	Moderate
B2	Benton's Bush	280.3 m	40.63940700 S	175.37082 E	Dry	Steep
B3	Benton's Bush	281.8 m	40.63944350 S	175.37235 E	Dry	Steep
B4	Benton's Bush	313.5 m	40.64122730 S	175.37098 E	Dry	Moderate
B5	Benton's Bush	280.3 m	40.64235030 S	175.37077 E	Dry	Steep
B6	Benton's Bush	269.5 m	40.64332750 S	175.3717 E	Dry	Flat
B7	Benton's Bush	273.6 m	40.64343510 S	175.37239 E	Slightly Damp	Flat
B8	Benton's Bush	282.5 m	40.64203620 S	175.37247 E	Dry	Slight
K1	Kohitere	128 m	40.65220150 S	175.3572 E	Damp	Moderate
K2	Kohitere	130.6 m	40.65222980 S	175.35685 E	Damp	Moderate
K3	Kohitere	141.2 m	40.65180180 S	175.35783 E	Slightly Damp	Very Steep
K4	Kohitere	133.5 m	40.65164280 S	175.35905 E	Damp	Steep
M1	Makahika	234 m	40.63014370 S	175.38792 E	Damp	Steep
M2	Makahika	237.1 m	40.63032360 S	175.38738 E	Damp	Flat
M3	Makahika	226.8 m	40.62967720 S	175.38699 E	NA	Moderate
M4	Makahika	248.1 m	40.63048230 S	175.38564 E	Damp	Moderate
K5	Kohitere New	NA	NA	NA	Damp	Steep
K6	Kohitere New	NA	NA	NA	Damp	Steep
K7	Kohitere New	NA	NA	NA	Dry	Steep
K8	Kohitere New	NA	NA	NA	NA	Steep

Shannon Area:

Ernslaw One Limited (EOL) is a privately owned softwood forestry company registered in New Zealand and currently managing 94 000 ha of stocked plantation forests (Ernslaw One Ltd., 2010). EOL has been established in New Zealand since 1990, and the company is currently certified by the Forest Stewardship Council (FSC) as being managed in a sustainable manner. This certification identifies forests as being "*environmentally sound, socially beneficial and economically viable*" (Ernslaw One Ltd., 2010). As part of their commitment to sustainable management, EOL does not allow belts of indigenous vegetation within its estate to be converted to plantation, and strives to protect native fauna residing in the area (Ernslaw One Ltd., 2010). A management strategy for *P. t. tararuaensis* snails within the Shannon Forest (Makan, 2007) was commissioned in 2007 to honour the FSC certification. This program involves protection of existing snail habitat within EOL's Shannon Forest estate, and well as targeted pest control for known predators of *Powelliphanta* snails (Makan, 2007). The Shannon forestry block lies approximately 40km southeast of Palmerston North (40.620314 S, 175.417925 E), nestled in an outlier range of the Western Tararuas (Figure 2.1). These foothills buffer the Tararua Forest Park, a vast expanse of conservation land, the largest of its kind in the North Island. The park is managed by the Department of Conservation, and plays a vital role in the protection of the indigenous biodiversity of the region. EOL currently administers 620 ha of the Shannon Forest, which consists of a 352 ha exotic pine plantation and 268 ha of native regenerating podocarp/broadleaf forest. Within the native forest patch, fifteen quadrats were set up for monitoring populations of *P. t. tararuaensis* (Castro *et al.* 2007). These were aggregated into five discrete regions (from here on referred to as Areas 1-5), with three quadrats situated within each area (Figure 2.4). As a result of a storm in 2009, quadrats 13-15 (Area 1) were lost. Three new quadrats within this area were then established during the 2009 survey conducted in August (16-18). For this reason Area 1 was excluded from the analysis. "Area 2" included quadrats 1-3, "Area 3", quadrats 4-6, "Area 4", quadrats 7-9, and "Area 5", quadrats 10-12 (Table 2.2). The five areas were considered to be one locale as they lay adjacent to each other, and the forest belt encompassing them was continuous and relatively uniform (Figure 2.5).

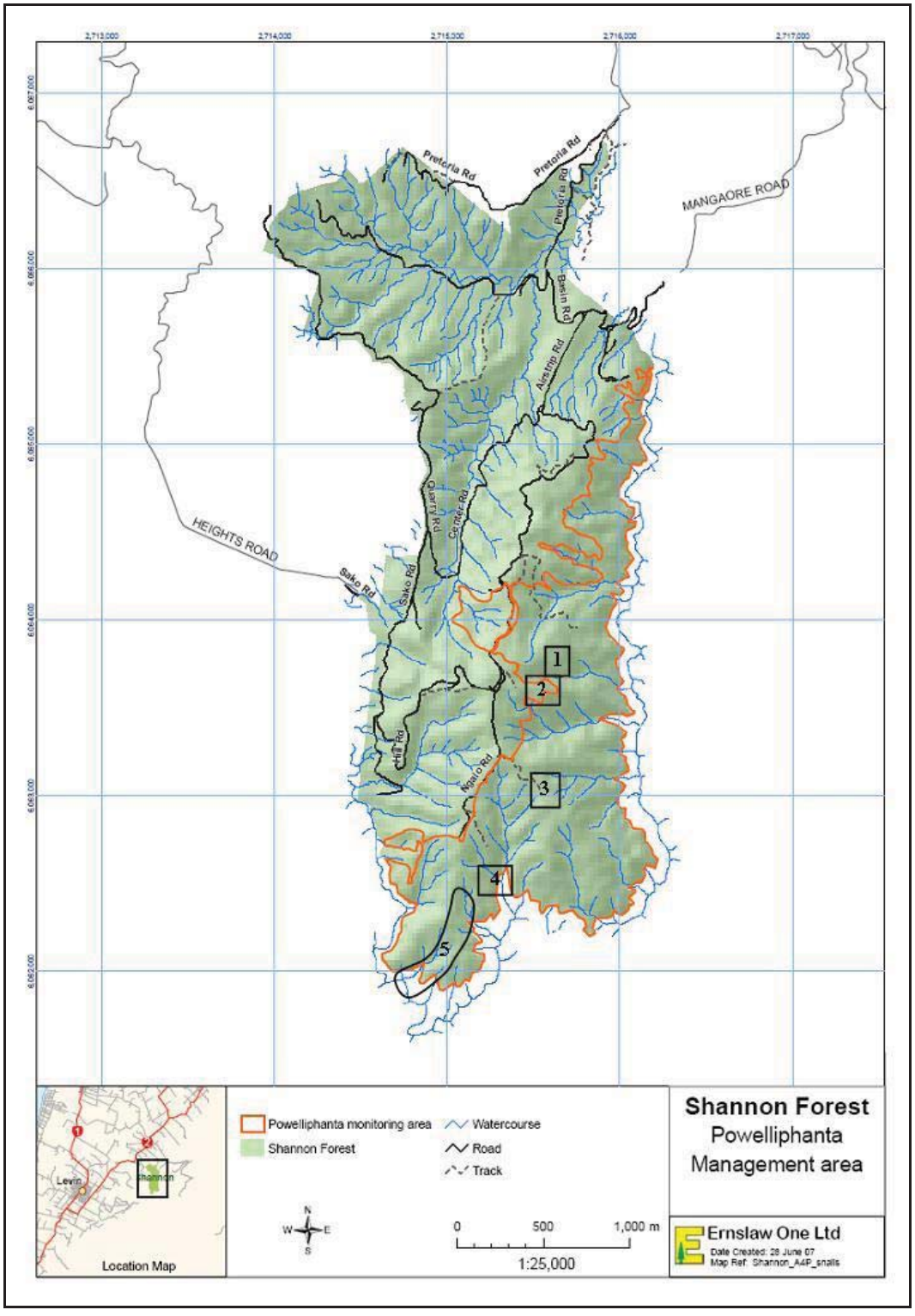

Figure 2.4. Location of the five areas (1-5) of EOL Shannon Forest containing quadrats used for P. t. tararuaensis monitoring in 2007 and 2009. Each area had three sampling quadrats (Castro et al. 2007).

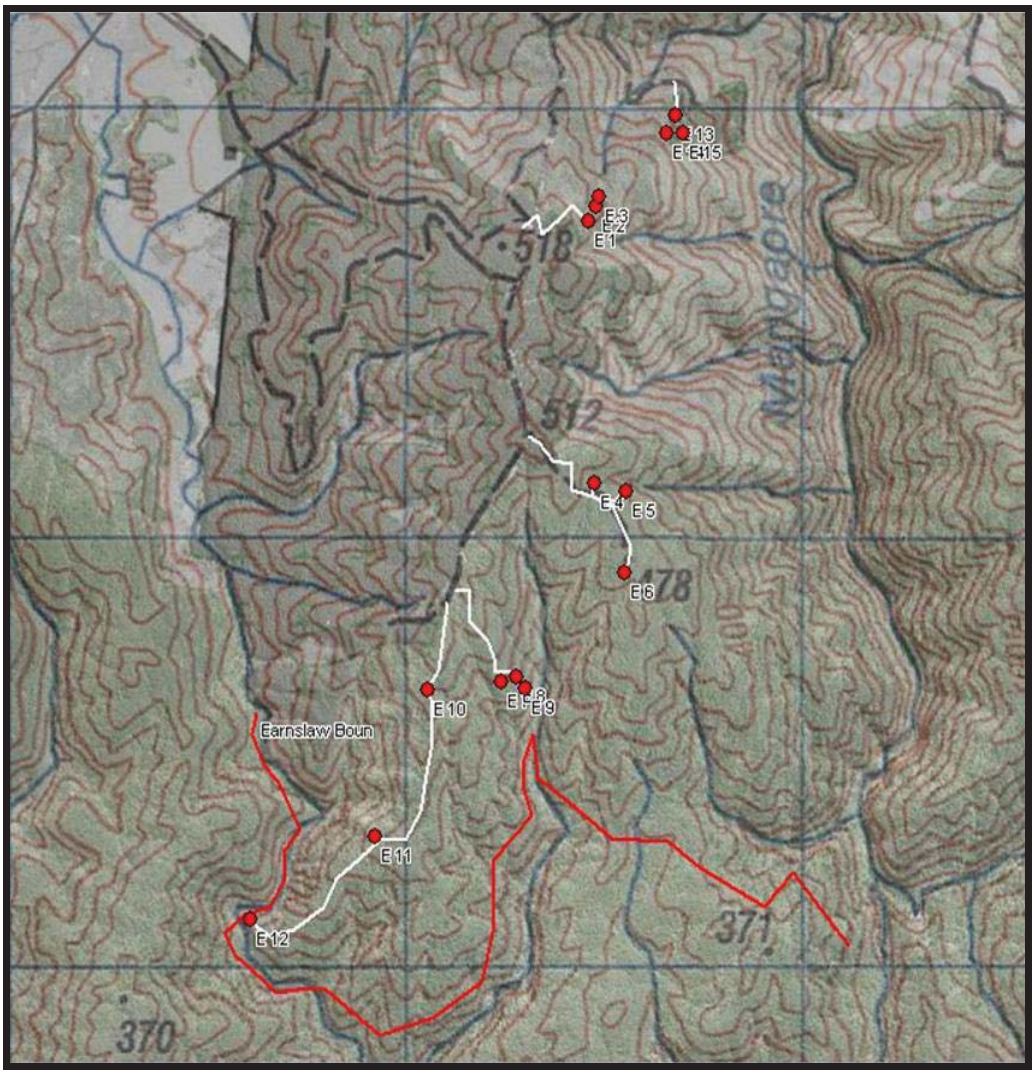

Figure 2.5. Quadrats within the Shannon Forest. The red line depicts the southern-most portion of the Powelliphanta monitoring zone boundary (Castro et al. 2007).

Table 2.2. Powelliphanta traversi tararuaensis monitoring quadrats in the Shannon Forest used in this study. "NA" indicates information not available at the time of this publication.

Quadrat	Area	Altitude	Latitude	Longitude	Dominant Vegetation
1	2	476.21521 m	40.6069708 S	175.4283621 E	*Beilschmiedia tawa*
2	2	462.2762451 m	40.6066730 S	175.4285953 E	*Dicksonia fibrosa* & *Rhipogonum scandens*
3	2	454.1049805 m	40.60643971 S	175.4286502 E	*Dicksonia fibrosa* & *Rhipogonum scandens*
4	3	470.4472656 m	40.6124497 S	175.4287564 E	*Dicksonia fibrosa* & *Rhipogonum scandens*
5	3	454.1049805 m	40.61260468 S	175.4296728 E	*Dicksonia fibrosa* & *Rhipogonum scandens*
6	3	479.3394775 m	40.61432264 S	175.4296956 E	*Beilschmiedia tawa*
7	4	406.0394287 m	40.61668801 S	175.4261129 E	*Beilschmiedia tawa*
8	4	394.5036621 m	40.61657955 S	175.4265483 E	*Beilschmiedia tawa*
9	4	NA	40.6167685 S	175.4267557 E	*Beilschmiedia tawa*
10	5	421.1801758 m	40.61689437 S	175.4239224 E	*Beilschmiedia tawa*
11	5	353.8884277 m	40.61998813 S	175.4224613 E	*Melicytus ramiflorus* & *Rhipogonum scandens*
12	5	1.00E+25 m	40.62180374 S	175.4188145 E	*Beilschmiedia tawa*

Quadrat Establishment

The monitoring quadrats each measured ten by ten metres (100m^2), and were established with the aid of a compass and measuring tape. Quadrats were laid out by placing a marker at one corner, then using a tape drawn out along the ground to the next marker. The direction was determined by a 90 degree compass heading. During quadrat establishment, special care was taken to avoid stepping within the bounds of the quadrat. This was to prevent any accidental mortality of dormant *Powelliphanta* within the study site.

P. t. tararuaensis Sampling

Data from 1996 and 2004 at the Ohau site were collected by DoC as part of their own monitoring scheme (C. Puches, pers. comm.). DoC established 200m² permanent quadrats in the Ohau area as follows: one each in Kohitere and Benton's Bush, and two in Makahika. In 1996 each of these quadrats was monitored, while in 2004 only quadrats in Makahika were monitored. Furthermore, quadrat two was reduced to 100m². In 2007 DoC and Rayonier delegated the monitoring of these sites to I. Castro from Massey University (I. Castro, pers. comm.). To ensure the sites conformed to the *Powelliphanta* Recovery Plan recommendations, the number of quadrats per area as well as the size of the quadrats was revamped. Therefore, the monitoring data from 2008 at Ohau were collected by Massey University postgraduate students, as part of the Wildlife Management course. In Shannon, EOL also entrusted the monitoring to I. Castro; therefore, the monitoring of the quadrats in 2007 and 2009 was carried out by Massey students.

There is no detailed information on how the sampling was done in 1996 and 2004, although the search method would have followed Walker (1997). Monitoring in 2007 and 2009 was done by groups of seven to eleven Massey University students. These started in a row along the downhill side of a quadrat and searched uphill. This technique allowed each sampler to have a defined transect line and width (~1 to 1.5 m/person), which maximised the area surveyed within the quadrat. Searching was done following Walker (1997) and consisted of combing through the leaf litter on hands and knees collecting any species of snail, alive or dead, encountered along the transect line.

Upon discovery of a live snail, the location was marked with a numbered peg and the animal placed in a plastic sealable box (approx. 300mm length x 250mm width x 50mm depth) with a corresponding numbered compartment (approx. 50mm length x 50mm width x 50mm depth). Damp leaf litter lined the partitions of the box to prevent desiccation. Marking the collection site allowed the resident snail to be returned to the place where it was found.

Once the entire quadrat had been scoured, all live snails and intact dead snails were measured with Vernier callipers across the widest part of the shell. Due to the fragmented nature of a significant number of shells, some dead snails could not be

measured using this method. The sizes of these individuals were estimated and clustered into size categories: small (<30mm), medium (30-40mm) and large (>40mm). These size classes were based on those used in similar surveys conducted by the Department of Conservation (C. Purches, pers. comm.). The shells of the deceased individuals were also scrutinized for any tell-tale signs of predation. Rat predation is characterised by jagged shell edges. Bird predation is often diagnosed by holes punched into the shell, while possums usually take a bite out of the back of the shell and may peel it open. Pig predation is characterised by a distinct flattening of the shell, and the shells are often split laterally along the whorl (Figure 2.6). Snails with intact shells with no signs of predation were assumed to have died of natural causes, probably due to desiccation. Where cause of death could not be determined, it was labelled as unknown.

Live snails were returned to the area from where they were found, and the dead snails were placed outside of the quadrat in an area located near the bounds of the downward slope of the quadrat. This ensured that these individuals would not be recounted in future surveys, but the stockpiled calcium in the shells was still available to the immediate environment.

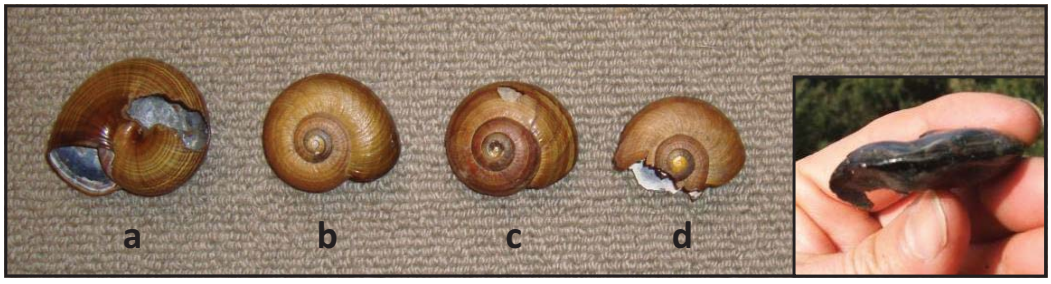

Figure 2.6. Examples of causes of death in Powelliphanta (a = rodent, b = natural, c = bird, d = possum and inset = pig). Photo by the author.

Statistical Analysis

Ohau Site:

Due to the lack of detailed data available from the 1996 and 2004 surveys, I compared the population densities between the three years graphically based on the average values for each site. A generalized linear model (GLM) was constructed with the 2008 survey data using the live *P. t. tararuaensis* abundance (total snails per quadrat) as the dependent variable, and area (Kohitere (n= 4 quadrats), Benton's Bush (n = 8), Makahika (n = 4) and Kohitere New (n = 4)) as the factor. Pairwise comparisons between the four areas of Ohau were carried out using sequential Sidak tests (outputs from these tests can be found in Appendix A). Numbers of *Wainuia* and *Rhytida* were too low for GLM analyses. The cause of death of the three genera of Rhytididae snails in 1996 and 2004 was not recorded and therefore this information was not examined.

Shannon Site:

For the Shannon site, a GLM was constructed with the 2007 and 2009 survey data using the live *P. t. tararuaensis* abundance (snails per quadrat) as the dependent variable, and quadrat (1-12) and year (2007 and 2009) as the factors; the factorial model was selected to include the interactions between factors. Pairwise comparisons between the years and quadrats at the Shannon site were carried out using sequential Sidak tests (outputs from these tests can be found in Appendix A). Numbers of *Wainuia* and *Rhytida* were too low for the building of a GLM. Mann-Whitney tests were performed on the size distribution data of live snails using Minitab (Version 14) in order to determine differences in snail size between the two survey years (2007 and 2009).

GLM's were run in SPSS (version 17.0.1, Dec. 1, 2008). A GLM test was selected because it is recommended when analysing count data, and when the numerical data is not normally distributed. Snail abundance was measured as number of snails in an area (quadrats) which were independent from each other, and it was assumed that snails were randomly distributed within the area. Both models assumed that the data followed a Poisson distribution with a log link function as this is the most common case for count data.

Results

Ohau: Live Snails

In 2008, seven eggs were found in the Kohitere area, fifteen in Benton's Bush, and four in the Kohitere New block. Abundance of live *P. t. tararuaensis* (number of snails per 100m^2) visibly increased since 1996 in all areas that were surveyed, with highest numbers found in Kohitere and Makahika (Figure 2.7). There was a significant effect of area on the numbers of *Powelliphanta,* with Kohitere (mean = 26.75, SE = 2.58) and Makahika (mean = 23.50, SE = 2.42) having significantly higher numbers of snails on average than both Benton's Bush (mean = 0.50, SE = 0.25) and Kohitere New (mean = 0.25, SE = 0.25) ($\chi 2$ = 193.624, df = 3, p = 0.000; Table 2.3). Live *Wainuia* also increased in abundance between surveys for the Kohitere and Benton's Bush areas, but remained similar in the Makahika area (Figure 2.7). Numbers of live *Rhytida* were very low in all areas.

When the size distribution of live snails found in the 2008 survey was examined, most live *Wainuia* fell into the 20.01-30mm category, with fewer animals belonging to the smallest size classes, and very few falling into the larger size classifications (Figure 2.8). For *P. t. tararuaensis,* most of the snails found belonged to the larger size classes, with much lower numbers of small individuals found (Figure 2.8).

Table 2.3. P-values from the sequential Sidak post hoc test comparing the four study areas in the Ohau site. Significant values are in bold.

	Kohitere	**Benton's Bush**	**Makahika**	**Kohitere New**
Kohitere	-	**0.000**	0.359	**0.000**
Benton's Bush	-	-	**0.000**	0.480
Makahika	-	-	-	**0.000**
Kohitere New	-	-	-	-

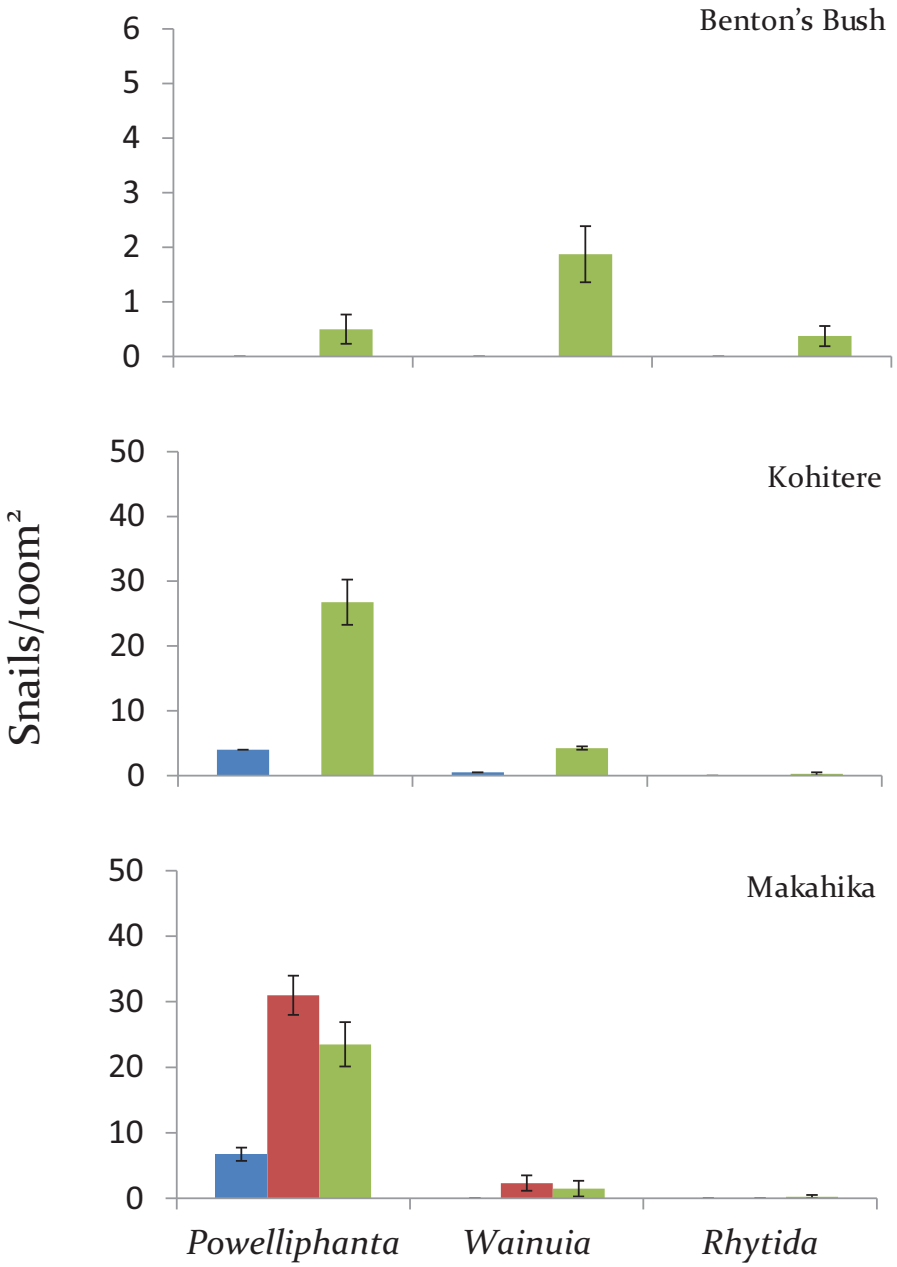

Figure 2.7. Average abundance of live snails (number per 100m²) in the Ohau site for the years 1996 (blue), 2004 (red), and 2008 (green). Error bars = standard error.

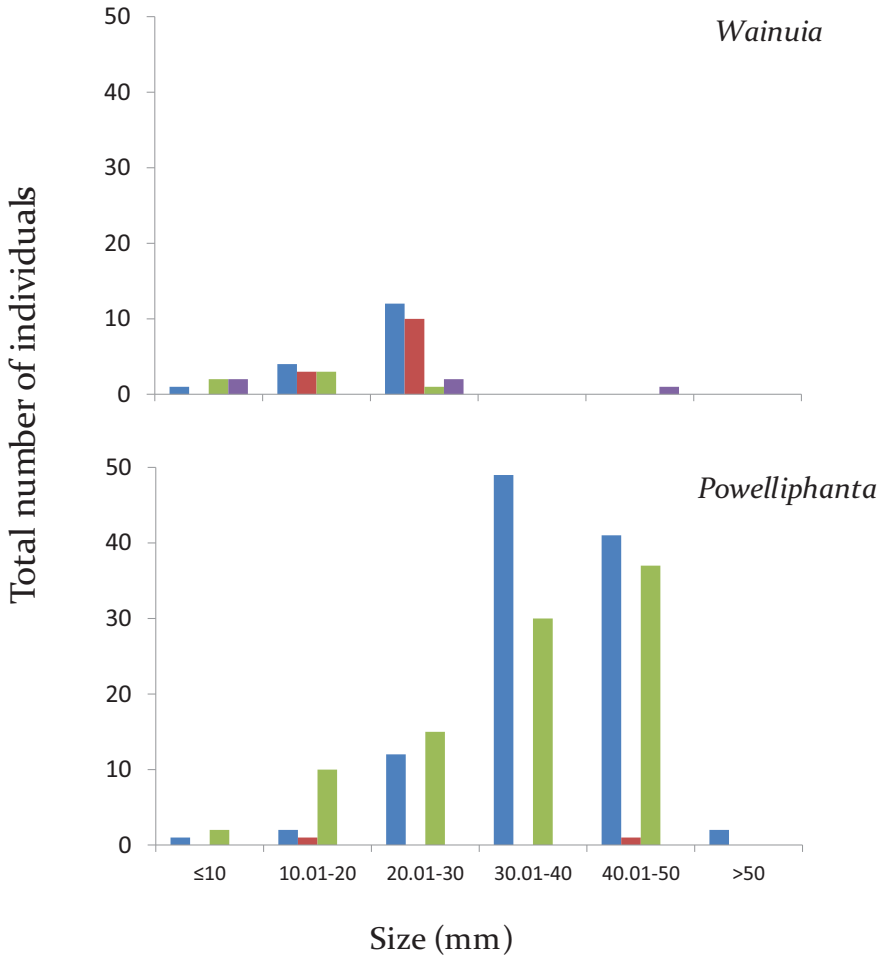

Figure 2.8. Size distribution of live snails found in the Ohau sites during the 2008 survey (blue = Kohitere, red = Benton's Bush, green = Makahika, purple = Kohitere New).

<u>*Ohau: Dead Snails*</u>

The number of dead *P. t. tararuaensis* and *Wainuia* (number of snails per 100m^2) found increased from 1996 to 2008 in Kohitere and Benton's Bush, with a large increase in dead *Wainuia* for the Kohitere area (Figure 2.9). In Makahika, dead snail abundance declined for *P. t. tararuaensis* (Figure 2.9). Numbers of *Rhytida* were comparatively low in all areas (Figure 2.9).

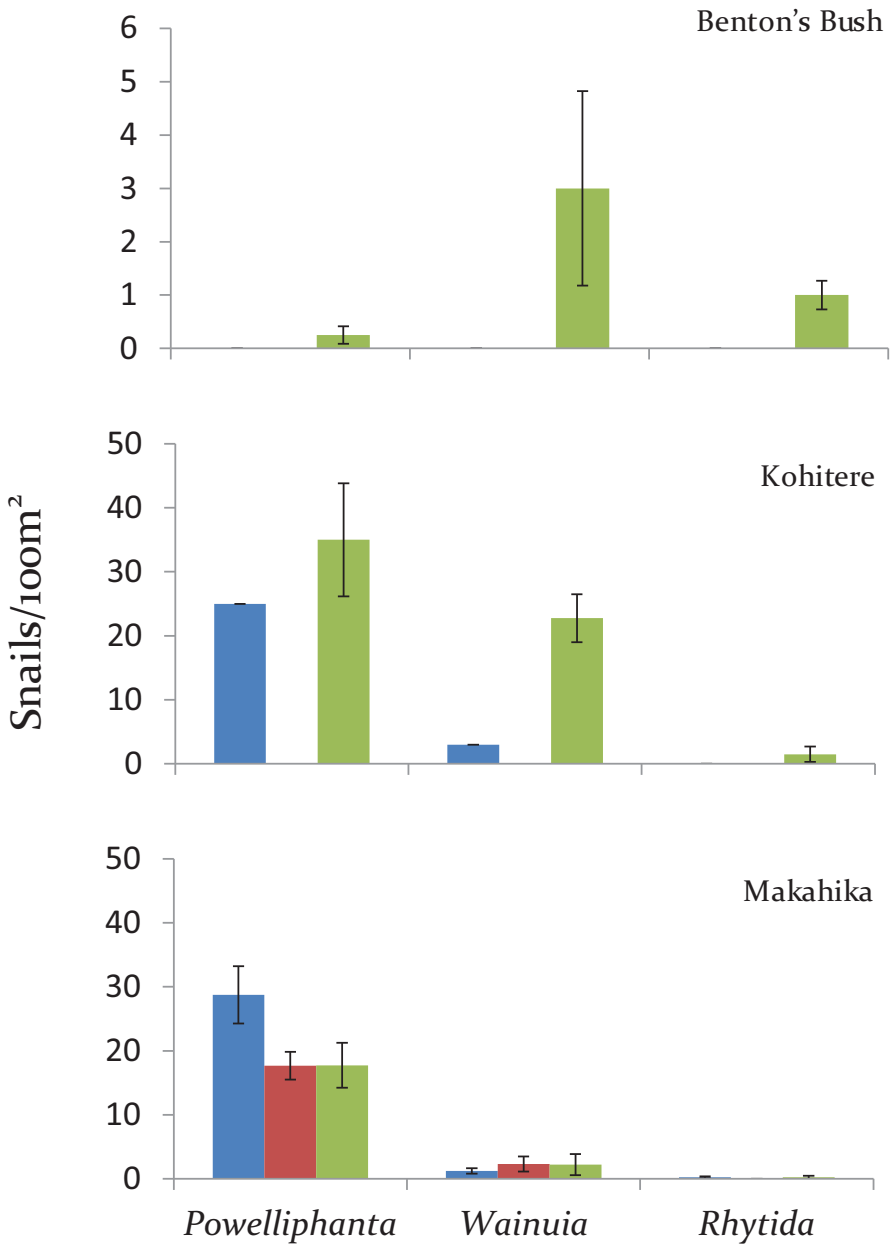

Figure 2.9. Average abundance of dead snails (number per 100m²) in the Ohau site for the years 1996 (blue), 2004 (red), and 2008 (green). Error bars = standard error.

Shannon: Live Snails

No snails' eggs were found in either year for the Shannon site. On average, significantly more snails were found in 2007 (mean = 4.67, SE = 0.66) than 2009 (mean = 3.00, SE = 0.50) ($\chi 2 = 5.542$, df = 1, p = 0.020; Figure 2.10). There was also a significant effect of quadrat ($\chi 2 = 51.785$, df = 11, p = 0.000) on the abundance of live *Powelliphanta,* with quadrats 7 and 11 holding the lowest numbers of snails (Figure 2.11).

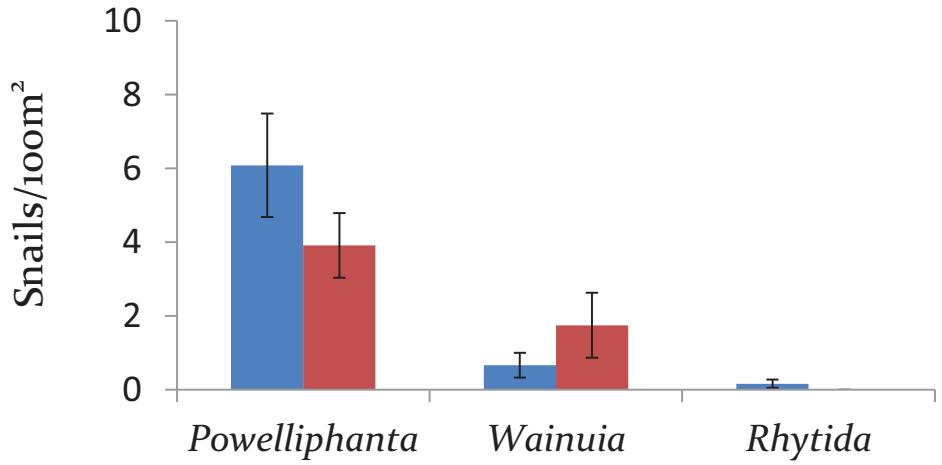

Figure 2.10. Average abundance of live snails (number per 100m²) in the Shannon site for the years 2007 (blue) and 2009 (red). Error bars = standard error.

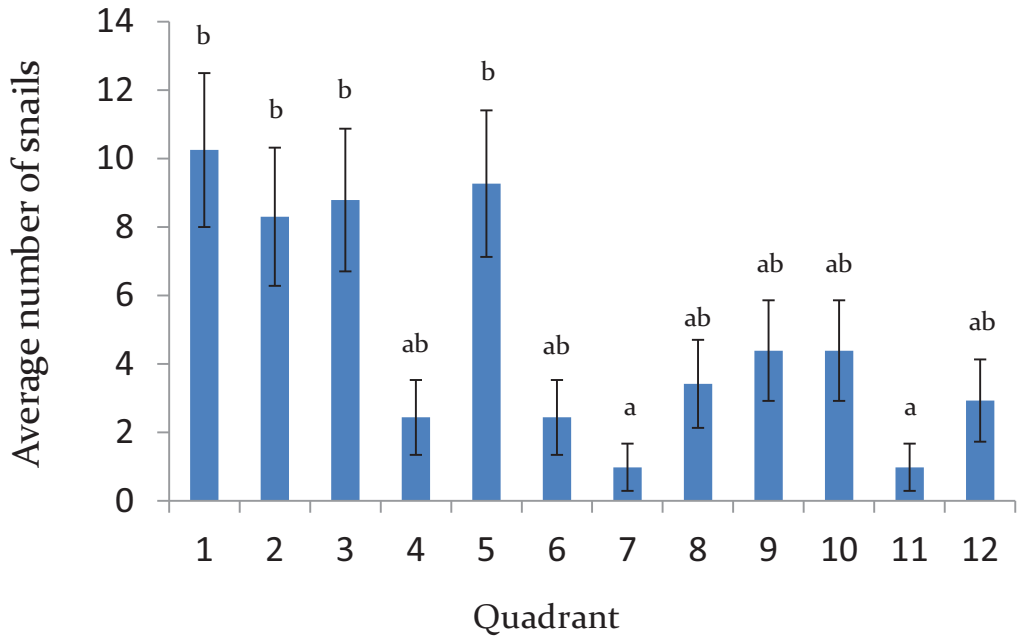

Figure 2.11. Average number of live snails for the 12 quadrats in the Shannon site. Error bars = standard error. Letter groupings indicate significant differences (sequential Sidak test, $\alpha = 0.05$).

No significant difference was found between the sizes of *Wainuia* from the 2007 (median = 22.45 mm, range = 13.20 - 30.10 mm) and 2009 (median = 25.85 mm, range = 6.80 - 37.90 mm) surveys (W = 141.5, p = 0.9676). For the *P. t. tararuaensis* population however, the distribution of snail sizes appeared to shift towards larger snails, with drops in numbers for all size classes below 30mm (Figure 2.12). There was a significant increase in median snail size between the 2007 (median = 37.00 mm, range = 3.40 - 55.90 mm) and 2009 (median = 39.25 mm, range = 12.46 - 56.40 mm) surveys (W = 9078.0, p = 0.0306).

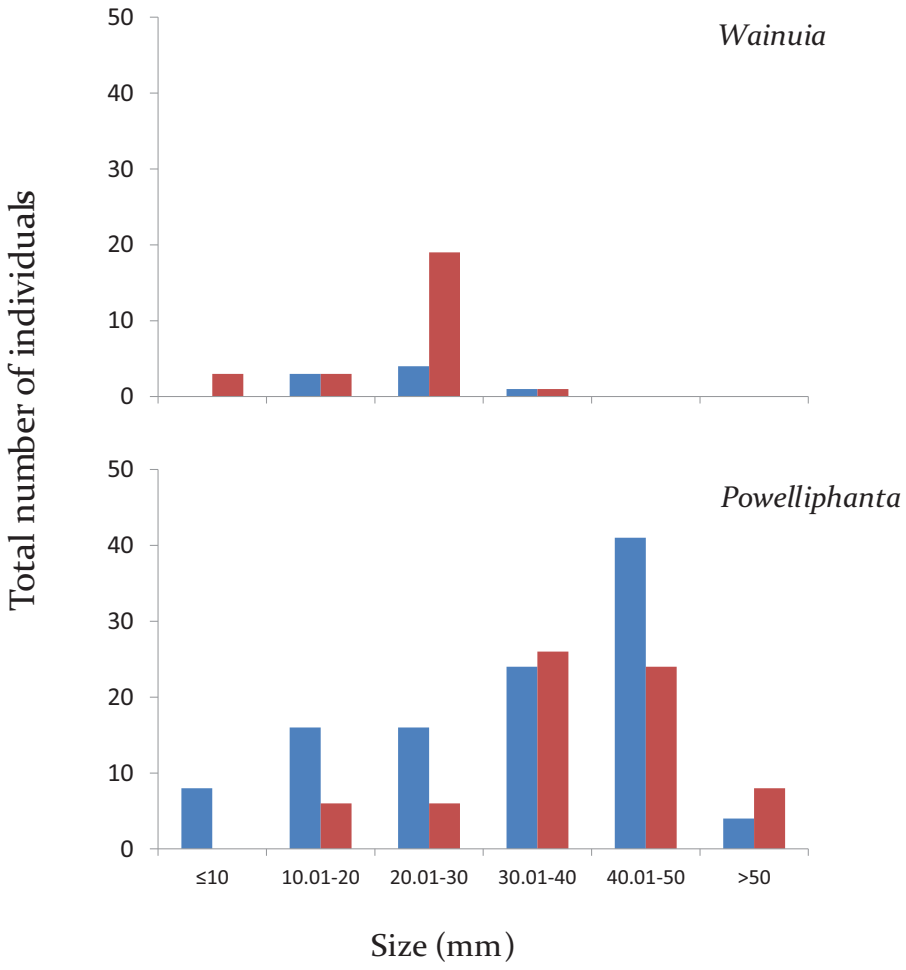

Figure 2.12. Size distribution of live snails found in the Shannon site in the 2007 (blue) and 2009 (red) surveys.

Shannon: Dead Snails

There were no changes in dead snail abundances between 2007 and 2009 in Shannon (Figure 2.13).

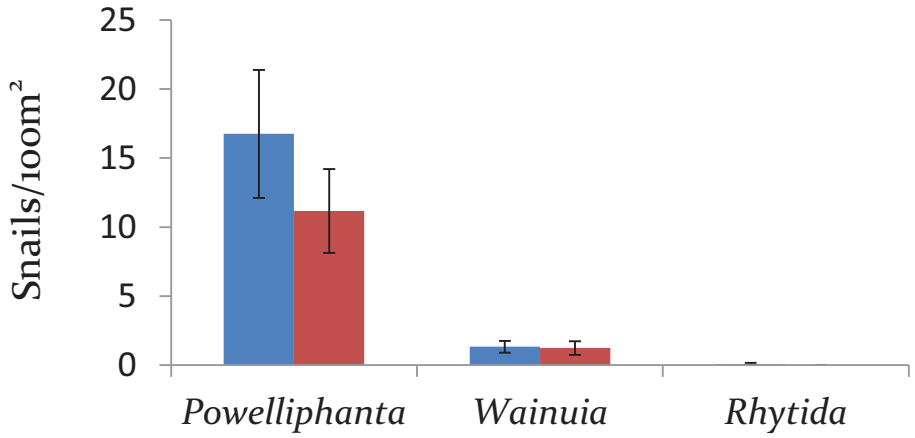

Figure 2.13. Average abundance of dead snails (number per 100m²) in the Shannon site for the years 2007 (blue) and 2009 (red). Error bars = standard error.

When the cause of death of *P. t tararuaensis* snails was examined for the two survey years, the most common was death by natural causes (Figure 2.14). Declines in rodent and pig predation were noted from 2007 to 2009, and no possum predation was recorded at all in 2009. There were a high proportion of dead shells in both years that I was unable to classify (Figure 2.14).

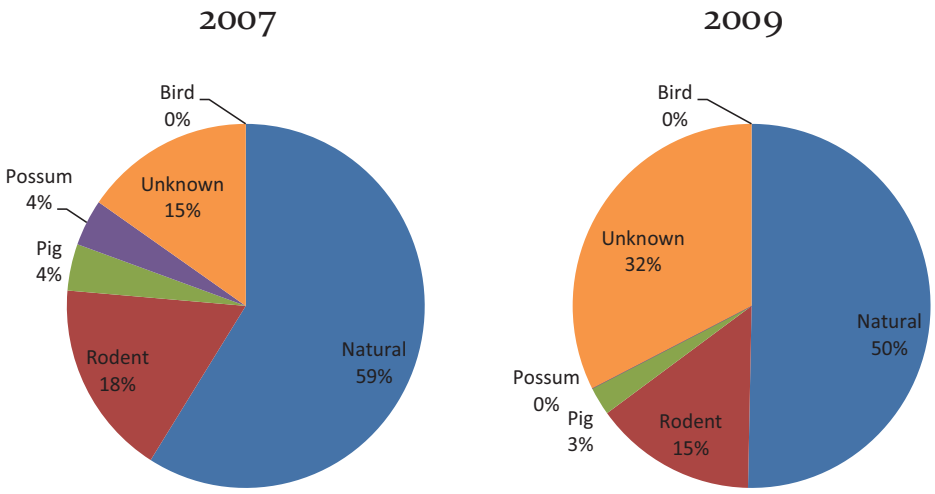

Figure 2.14. Causes of death for Shannon P. t tararuaensis snails.

Discussion

The Ohau snail populations appear to have increased over the survey period, with all sites boasting significantly higher numbers of live *P. t. tararuaensis* in the later surveys. *Wainuia* numbers remained low for both live and dead snails in all sites, although a large increase in dead snail abundance for Kohitere was notable. *Rhytida* remained at very low numbers in all areas surveyed. In contrast, the Shannon population seems to have declined from 2007 to 2009. Some quadrats in Shannon were found to have very low numbers of snails. The mean diameter of the shell in *P. t. tararuaensis* population increased significantly from 2007 to 2009, due to a decline in the numbers of smaller snails in the population. *Wainuia* and *Rhytida* numbers in Shannon remained at low levels for both years surveyed.

The findings for the Shannon site should be of concern as the population of *P. t. tararuaensis* in the Shannon Forest is currently well below the *>12 snails/100m*^{2} target for recovery set by Walker (2003) in the *Powelliphanta* Recovery Plan. Declines in the smallest snail size classes as well as the lack of live eggs and higher levels of natural mortality may be of future concern. It is possible that this drop in smaller snails in the population is indicative of habitat failings, with certain environmental facets potentially making the area no longer suitable for eggs or the smallest *P. t. tararua*ensis snails. However, eggs may not have been found in Shannon as a result of seasonal effects. *Powelliphanta* produce eggs in the spring (October to December) (O'Connor, 1945; Walker, 2003), and the 2009 survey was conducted in the final week of August. It may be possible that snails were not producing eggs at the time of survey in Shannon. Although, eggs take between two and six months to hatch (Walker, 2003), thus one would still expect to find hatchling and small sized snails. Kohitere and Makahika, on the other hand, appear to be supporting a much healthier population of *P. t. tararuaensis,* with the most recent abundance measures above target, and live eggs were located in the Kohitere, Benton's Bush and Kohitere New areas.

There is a possibility that the sampling method for *Powelliphanta* monitoring is negatively altering the habitat for the snails. The turning of leaf litter has the potential to affect humidity, light intensity and temperature, possibly at levels detrimental to *P. t. tararuaensis.* By combing through the leaf litter and lower vegetation to the extent required to find hidden *Powelliphanta* snails in the daylight hours, the microhabitat

could be altered to levels unfavourable to the smallest snails. The lack of physical adaptations to retard desiccation (such as an operculum or epiphragm) restricts *Powelliphanta* to damp microhabitats (Yeates, 1991). This, coupled with the lack of any intimate understanding of habitat requirements (Walker, 2003), could mean that regular monitoring procedures are contributing to the decline of *Powelliphanta* snails. The effects of the monitoring event could be viewed as mimicking a disturbance, and thus hold a risk of mortality. This could cause snails to redistribute amongst sites according to the decrease in perceived survival rate in the disturbed area (Gill & Sutherland, 2000). This process has been acknowledged in the snail *Cepaea nemoralis,* with the handling and marking of snails being found to increase dispersal rate (Cameron & Williamson, 1977). If something similar is happening in the Shannon Forest population because of monitoring practises, then any inferences drawn about the state of the population may be incorrect. The repeated alteration of the sampling quadrats may mean the survey zones are not accurate representations of the true favoured habitat by *Powelliphanta* snails. Thus any conclusions drawn may be inaccurate. The potential for this must be evaluated, and sampling events may need to be separated by a time lapse greater than two years, or may require a complete overhaul of methods. Walker (1997) commented briefly on the possibility of using night-time surveys for abundance estimates, but the technique has not been explored further.

While mortality through predation appears to have dropped from 2007 to 2009 in the Shannon Forest, there is still some loss of *Powelliphanta* through depredation by exotic mammals. In a population at risk of decline, any reduction of mortality is of benefit, and so it is important that any mammalian pests known to depredate snails are controlled. It could be of value to establish some form of predator monitoring within the patches of *P. t. tararuaensis* habitat. This would allow for assessment of introduced mammal numbers, and therefore evaluation of the feasibilities of different control methods. The gauging of control method suitability holds special importance for the snails considering some techniques can hold ramifications for *Powelliphanta* populations. 1080 use for the control of introduced mammals could harm snails through episodes of secondary poisoning (Booth *et al.* 2003); and the use of brodifacoum for the control of rodents can lead to a rise in exotic bird predation (Bennett *et al.* 2002). The case of bird predation should be especially considered as there is currently none documented in the Shannon Forest for the two survey years of this study. Birds are also known to target

young snails (Meads *et al.* 1984; Bennett *et al.* 2002), and in this case, there may be no evidence of predation as avian predators could presumably swallow small snails whole. This could be especially damaging in a population already experiencing low juvenile numbers.

In Ohau, DoC has been involved in the management of the Kohitere, Benton's and Makahika forest blocks since 1996, and in 2007 Kohitere Forest Scenic Reserve and Benton's Bush were transferred to DoC ownership. The work conducted in the native forest blocks has mostly been centred on the control of exotic mammalian pests, with the majority of focus on the possum (*Trichosurus vulpecula*) and the rat (*Rattus spp.*). Brodifacoum poison baits have been the primary control method, and the poison is considered low risk for invertebrates so is safe for use around *Powelliphanta* snails (Hare & Hoare, 2006; Booth *et al.* 2003). The current predator management scheme employed by the Department of Conservation may be helping to promote population growth in the Ohau site, and the Shannon land snail populations may benefit from a similar approach.

The current monitoring program employs no means by which to gather data on population dynamics or life history parameters. Shells of dead snails found may also be an accumulation from several years, as there is lack of detail surrounding methodologies which were in place before Massey University's involvement in the monitoring programs. This means that while the existing system can identify declines, the nature of those declines cannot be well understood or combated without information on birth rates, death rates, emigration and immigration. In order to better address declines in *Powelliphanta* snails, and ways with which to mediate them, it is vital that some method of estimating demographic parameters is incorporated into the monitoring. This could be as simple as upon the location of live animals, uniquely marking each snail in some form to allow for mark-recapture data to be gathered.

Neither *Wainuia* nor *Rhytida* currently possesses protected status, although they are probably vulnerable to many of the threats recognised for *Powelliphanta* (Efford, 1998). The low numbers of both taxa in Ohau and Shannon should be of concern, as both groups of snails represent little known genera which could become at risk in the near future (Efford, 1998). A notable finding of this study is the very high number of dead *Wainuia* snails found in the Kohitere site with concomitant low numbers of live animals

in the same area, as well as the extremely low numbers of *Rhytida* in both Ohau and Shannon. This suggests that death rates for *Wainuia* may be proportionally high in Kohitere, and that populations of *Rhytida* in both Ohau and Shannon are faltering. There could be factors of the current *Powelliphanta*-targeted monitoring program which is failing both *Wainuia* and *Rhytida*. It may be of great value to establish a rigorous monitoring program for both genera now, allowing for development of management techniques in anticipation of population declines. Efford (1998) recommended the establishment of a series of "mini-reserves", approximately 0.5 to 5ha in size, around viable populations of *Wainuia* and *Rhytida* in order to glean information surrounding population monitoring and management for these taxa. I feel such a program could be simply incorporated into that of the current *Powelliphanta* monitoring scheme, and could provide a vital indicator of changes in population structure and dynamics.

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3 What lies beneath: the effect of monitoring on the short-term behaviour of *Powelliphanta traversi tararuaensis*.

Introduction

The use of permanent plots for sampling and monitoring populations is often employed in studies of land snails (Sherley *et al.* 1998; Mand *et al.* 2002; Hylander *et al.* 2004; Hylander *et al.* 2005). Permanent sampling units hold certain advantages over temporary ones for relatively sedentary animals (Elzinga *et al.* 2001). If monitored over long periods, permanent quadrats can allow the assemblage of enough data for a comprehensive analysis of change in a population (Austin, 1981). Permanent quadrats are also particularly effective at identifying lack of variation from year to year (Elzinga *et al.* 2001), and require fewer experimental units to detect a certain degree of change in comparison to temporary quadrats (Elzinga *et al.* 2001). Since a large portion of the global land snail fauna is now threatened (Lydeard *et al.* 2004), efficient monitoring systems capable of detecting annual variation in populations are particularly valuable for targeted conservation action.

The sampling method for land snails is usually a relatively uniform process, and involves establishing permanent monitoring quadrats of a given size and combing through surface leaf litter searching for live individuals (Baur & Baur, 1990; Walker, 1997; Sherley *et al.* 1998; Mand *et al.* 2002; Hylander *et al.* 2004; Hylander *et al.* 2005). However the technique results in significant modification of the plot's surface. The structure of the soil is altered by being turned over, plant material and leaf litter is relocated, and vegetation is often damaged (Baur & Baur, 1990). As a consequence of this, certain environmental conditions may be affected and the microclimate altered (Baur & Baur, 1990).

Select aspects of microclimate have been recognised as being particularly important for populations of land snails, including temperature (Boag, 1985; Prior, 1985; Chen *et al.* 1993; Devine, 1997) and moisture (Prior, 1985; Chen *et al.* 1993; Devine, 1997). Change to the microclimate of survey plots caused by methods used for snail sampling was reported to affect the behaviour of land snails (Cameron & Williamson, 1977). Cameron & Williamson (1977) suggest that the searching procedure for marked *Cepaea nemoralis* may damage vegetation and alter microclimate, which in turn may alter the behaviour of the snails. White & Pickett (1985) defined a disturbance as "*a relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment*". Thus monitoring a quadrat could be considered a disturbance event for a snail population. Because land snails are fairly sedentary, they cannot easily avoid a disturbance or the subsequent change in environmental surroundings (Strayler *et al.* 1986). Hot and dry conditions may adversely affect or even kill snails in extreme cases (Hylander *et al.* 2004), and juveniles of many species are particularly vulnerable to desiccation (Asami, 1993).

Powelliphanta is a group of large carnivorous snails endemic to New Zealand. Various species in the group are thought to be in danger of extinction, and a great effort is being made to monitor population trends. The current monitoring practise for *Powelliphanta* is similar to the method described above, involving the modification of the habitat, and is utilised to obtain an estimate of density per area. Quadrats are recommended to be surveyed every year to detect population trends at a fine level (Walker, 1997). Devine (1997) recognised that temperature and humidity are principal components in *Powelliphanta* distribution. In her description of the current *Powelliphanta* monitoring techniques, Walker (1997) remarked that the methodology may degrade the habitat for the snails, or cause direct mortality through desiccation. Disturbance of the habitat as a result of routine monitoring practises could therefore have detrimental effects on populations of *Powelliphanta,* as well as influencing the results of the survey (Walker, 1997). It is therefore important to assess any change in behaviour of *Powelliphanta* snails following a monitoring event, and to examine any potential for negative effects of disturbance on populations of *Powelliphanta.*

In this study I investigate the effect of a typical monitoring procedure on the short term behaviour (one week) of *Powelliphanta traversi tararuaensis* in order to gauge

the likelihood of any long-term implications for *Powelliphanta* populations and management plans.

Methods

Experimental Design

I used an experimental design involving mark-recapture. I chose three sites with *Powelliphanta* populations and treated each site as a replicate. I built two quadrats at each site, one acting as a control and one subjected to the treatment (disturbance/monitoring simulation). In total there were three control and three experimental quadrats which were used to gather data to build a parent (control) model for snail re-sighting probability. Because the data were collected at different times at different sites, due to a single observer, these additional quadrats were also used to explore a possibility of incorporating temperature and humidity data into the model in a consistent manner. *Powelliphanta* snails were tagged, and the quadrats were searched seven subsequent nights for marked animals. Following disturbance of the quadrat, an additional seven nights of recapture data was gathered. Re-sighting histories of individual snails were then used to fit a range of re-sighting probability models. The best fitting models were used to make predictions about changes in re-sighting probability of marked *Powelliphanta* snails.

The mark-recapture data gathered allows for examination of the movements of *Powelliphanta* snails both prior to and following a disturbance event; and should enable insight into the extent to which monitoring may be affecting the movements and behavioural patterns of *P. t. tararuaensis*.

Study Sites

The three study sites used in this project are located the foot of the Tararua Ranges (Figure 3.1). Raw weather data with associated dates are presented in Appendix B. For the description of the first two study sites (Ohau and Shannon) see Chapter Two.

Palmerston North Site:

The final site was within the Woodpecker Forest (40.472703 S, 175.611803 E), part of the greater Kahuterawa Outdoor Recreational Area, approximately 15km South of

Palmerston North (Figure 3.1). The reserve is comprised of both mature pine plantation and native podocarp and broadleaf forest; and contains two frequently trafficked mountain biking/walking tracks. The first, the Sledge Track, snakes through the native forest of the Kahuterawa Valley and allows access to Hardings Park (861 hectares of native bush at the southern end of the Turitea Water Reserve). A second track weaves its way along the edge of the study site; locally known as the Back Track. It forms the beginning of a network of mountain bike tracks which meander through the surrounding Woodpecker Forest pine plantation and the neighbouring farmland.

There is a substantial population of *P. t. tararuaensis* within the reserve (Walker, 2003), and DoC currently monitors a handful of permanent 100m² quadrats as part of regular abundance estimates. The last surveys in the Woodpecker Forest were conducted in June 2010 (pers. obs.).

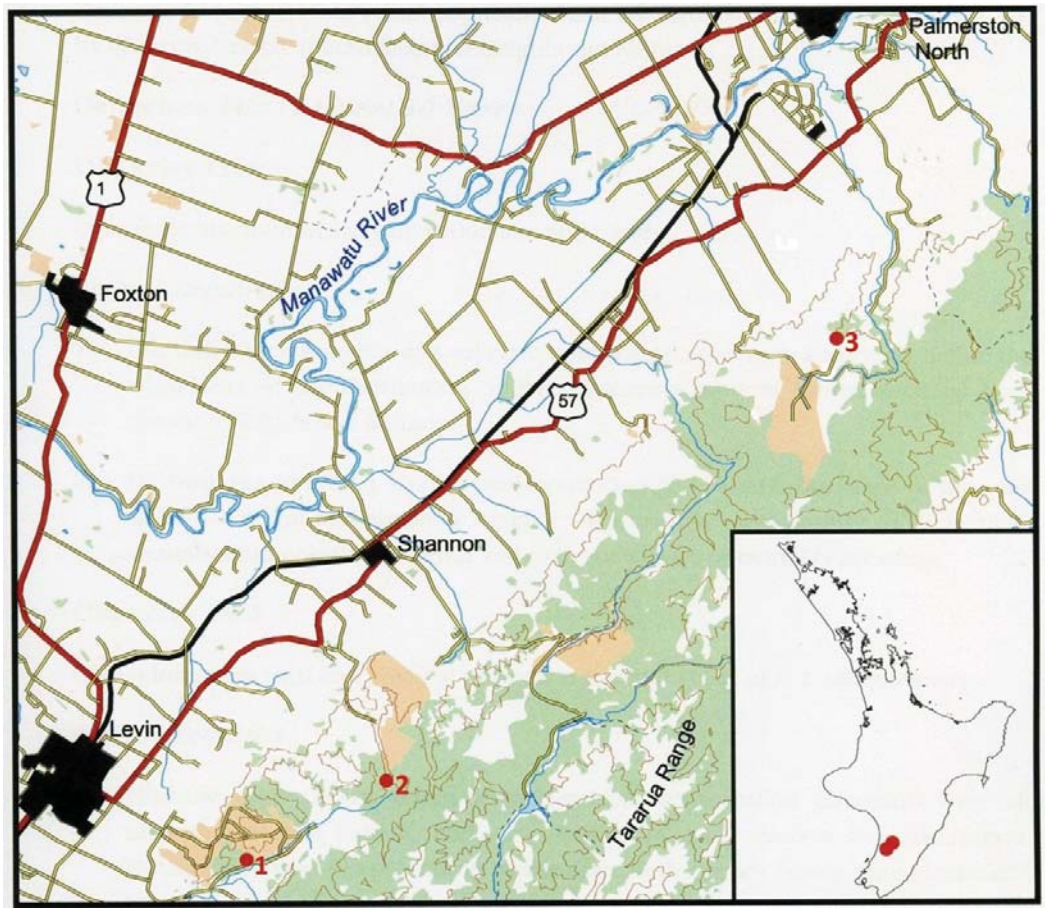

Figure 3.1. Locations of the three study sites. The Ohau site in the Ohau Operationl Area (1), the Shannon site in the Shannon Forest (2) and the Palmerston North site at Kahuterawa (3). Map edited from Walker (2003).

Quadrat Establishment

The location of the experimental quadrats was determined through an extensive spot-sampling process which lasted one month in each area (three months in total). During the night hours when *Powelliphanta* are active, compass bearings were used to walk a grid through patches of forest where *Powelliphanta* were known to be present. These patches of forest were bordering or in a similar region to the existing *Powelliphanta* abundance monitoring plots. Every five minutes, a spot sample of the immediate vicinity was conducted. A brisk count of any visible snails (live or dead) was performed in an arc limited by the field of vision. These counts were used as a rapid abundance assessment for the general area (exact positions were obtained with a handheld GPS), and locales

with the highest values were selected as the centre for the establishment of the 45m x 45m study quadrats. Locations with high abundance measures were sought to maximise the potential number of animals available to be marked.

Quadrats were created with the aid of a compass and measuring tape (50m length). A tape was run out from a set point to create a single 45m line, and the remaining sides of the quadrat were set out using a 90° compass bearing. The quadrat was then divided into a grid with 16 columns and 16 rows using a similar method, so that each grid cell measured 3m x 3m. The grid points were marked with a letter/number combination, such that the columns were labelled A-P, the rows 1-16, designating the initial corner marker as A1 (Figure 3.2).

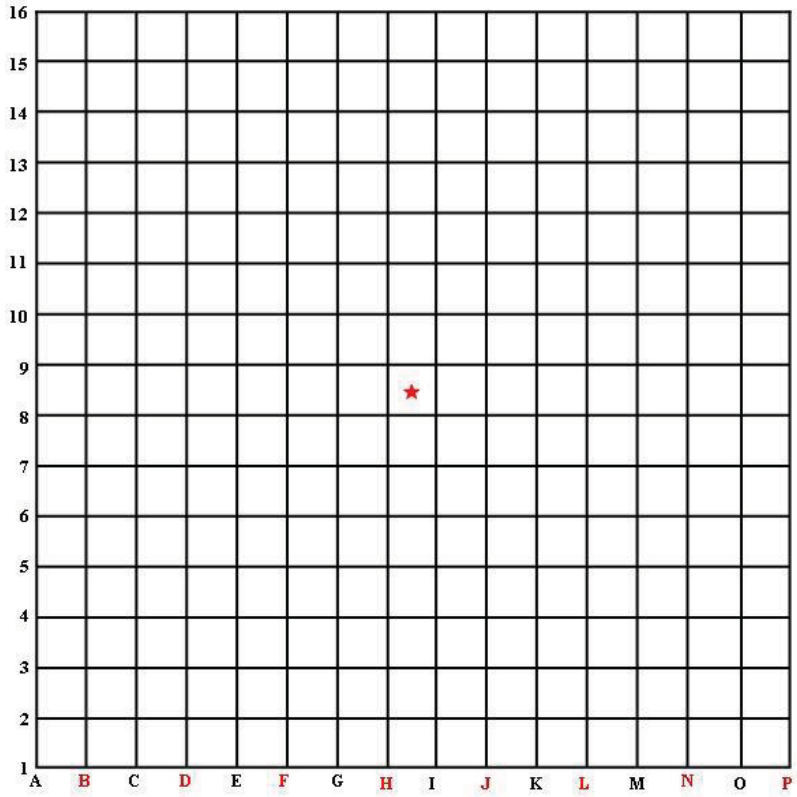

Figure 3.2. Basic setup of a study plot. The complete quadrat measured 45m x 45m, with a grid cell consisting of 3m x 3m. The grid points were named according to their associated letter column and numerical row (e.g. K9, G6, M16 etc.) and were used as reference points. Letter colours indicate the orientation of the markers, black depicting white reflective tape and red being red reflective tape. Location of the data logger is indicated by the red star.

Markers for the 256 grid points were plastic clothes pegs bearing a piece of white and red reflective tape on each of the peg's arms. The markers were attached to vegetation at eye level, and orientated such that the white reflective tape was visible when walking in one direction of the column, and the red tape visible when moving in the reverse direction (Figure 3.2). By alternating the marker orientation every second column, a system was created for consistently scanning the entire grid. By following one colour, it was possible to move up and down the grid without overlap. Once all markers were in place, the measuring tape used to position them was removed. This left a complex grid, relatively veiled by vegetation in the daytime hours, but extremely conspicuous at night with the aid of a head lamp. The nature of the marker placing meant that there was nothing at the ground level to potentially interfere with the movements of the *Powelliphanta* snails.

A data logger (HOBO® Pro v2, Onset Computer Corporation, Bourne, MA, USA) was installed at five centimetres from ground level in a central position of the quadrat (Figure 3.2) in order to record both temperature and relative humidity. Temperature and humidity data were downloaded using the HOBOware® Pro software (Onset Computer Corporation, Bourne, MA, USA).

Table 3.1. Summary of the six quadrats created for this study.

Quadrat*	Location	Latitude	Longitude
OD	Ohau	40.650656 S	175.358517 E
OND	Ohau	40.650794 S	175.357356 E
SD	Shannon	40.612183 S	175.428339 E
SND	Shannon	40.613017 S	175.428292 E
KD	Kahuterawa	40.472353 S	175.611953 E
KND	Kahuterawa	40.471825 S	175.611419 E

*OD = disturbed; OND =not disturbed; SD = disturbed; SND = not disturbed; KD = disturbed; KND =not disturbed.

Marking P. t. tararuaensis Snails

During the quadrat establishment phase, every care was taken to avoid stepping in the internal area of the grid cells and unnecessarily disturbing the habitat. In addition, prior to tagging, the area was left for a minimum of three days and nights following quadrat establishment to allow for "settling" of the area before the study commenced. It was hoped any unintentional disturbance and consequent behavioural alterations on the snails would be remedied by this "settling" phase. Marking was usually timed so that the region had recently experienced rain, as *Powelliphanta* tend to be most active in moist conditions (Devine, 1997). This ensured that there would be snails visible foraging on the surface of the leaf litter for capture and tagging.

The first night after the settling period, the entire grid of the quadrat was walked, and any snails found had their position on the grid recorded. Each snail was fitted with a passive integrated transponder (PIT) tag (Trovan® ID 100A, Identify UK Ltd., UK) which had a detection distance of approximately 30 centimetres. The tags were attached to the dorsal surface of the shell using a liquid hydrocarbon-based building adhesive (Selleys Liquid Nails®; refer to Chapter Four for information regarding the choice of adhesive). Once the adhesive had become set to a "touch-dry" state, after approximately ten minutes, the animal was released.

Recapture Data

Nights two to eight involved searching the study plot for the snails present, both marked and unmarked. The grid was walked at a slow pace from 21:00 to 04:00, and the entire surface of the leaf litter was scanned with a handheld reader (Trovan® GR-250 High-Performance portable reader, Identify UK Ltd., UK). At this search pace the quadrat was scanned once per night. When a snail was either sighted or detected by the reader, the identity (marked/unmarked), time of recapture/capture and the location with reference to the position on the grid were recorded. Control quadrats used to construct parent (control) models were searched until night eight. Treatment plots were disturbed on the eighth day to imitate a monitoring event, and recapture data were then collected for a further seven nights (Table 3.2). The entire project involved 315 hours of night searching with 105 hours at each site.

Table 3.2. Dates of survey for the three disturbed treatment quadrats (2011).

Night	Ohau	Shannon	Kahuterawa
Night 1	10/4	28/2	25/4
Night 2	11/4	1/3	26/4
Night 3	12/4	2/3	27/4
Night 4	13/4	3/3	28/4
Night 5	14/4	4/3	29/4
Night 6	15/4	5/3	30/4
Night 7	16/4	6/3	1/5
Night 8	17/4	7/3	2/5
Night 9	18/4	8/3	3/5
Night 10	19/4	9/3	4/5
Night 11	20/4	10/3	5/5
Night 12	21/4	11/3	6/5
Night 13	22/4	12/3	7/5
Night 14	23/4	13/3	8/5
Night 15	24/4	14/3	9/5

Plot disturbance simulated a typical *Powelliphanta* monitoring event (see Chapter Two). This involved a line of people abreast systematically searching through the leaf litter on their hands and knees (Walker, 1997). They were arranged so that the group moved from one side of the quadrat to the opposite side, and the entire area of the quadrat was covered thoroughly. When a snail was located, a designated scribe recorded which area of the quadrat the snail was found in, what species it was (*Powelliphanta, Wainuia, Rhytida;* see Chapter Two regarding *Wainuia* and *Rhytida*), and whether it was dead or alive. If an animal bore a mark, the tag number was also recorded. Live snails were placed in a box with numbered compartments which were filled with damp leaf litter to prevent desiccation. A peg bearing the corresponding number to the compartment the snail was housed in was then placed where the individual was found. The snails were replaced where they were found at the end of the survey. Dead snails were collected but not marked (see below).

Once the monitoring simulation was completed, all live snails and intact dead snails were measured to 0.5mm accuracy with Vernier callipers across the widest part of the shell. Some dead snails could not be measured in this manner due to shell damage, and so their sizes were estimated and grouped into size classes: small (<30mm), medium (30-40mm) and large (>40mm). Dead snails were also examined to determine the cause of death (see Chapter Two for a detailed description of causes of death classification). Live snails were then returned to where they were found and dead snails were discarded outside and downhill from the quadrat to avoid resampling the shells in subsequent surveys. For a summary of the monitoring simulations, see Appendix C.

Statistical Analysis

Re-sighting data were analysed using the program MARK (Version 6.1, White & Burnham, 1999). Because of the relatively short time frame of this investigation (maximum of 15 nights in any one study site) it was assumed that there was no mortality or emigration during the study period. Thus, a closed system was employed, and the parent (control) model used for the analysis was (Φ. p_t) where survival probability (Φ) is fixed at 1, and re-sighting probability (p) varies with time. The control model does not take into account the effect of the disturbance. This parent model was fitted to the re-sighting data for the non-disturbed quadrats. The re-sighting data along with the temperature and relative humidity data from the non-disturbed areas were then used to explore and develop a method for including weather data into a model in a manner which could be uniformly applied across different sites despite variation in values. This was necessary because all re-sighting data were collected by a single observer to maintain integrity, which resulted in data collection stretching over a period of four months. Maximum, minimum and average relative humidity and temperature values for 12 hour periods were added to the series of control model, and then the fit of the models was compared using the quasi Akaike's Information Criterion (QAICc) which was corrected for bias (White & Burnham, 1999). This was done by employing the bootstrap GOF (goodness-of-fit) test in MARK, and estimating the over-dispersion parameter (c) of the parent model. Models were named in a compound fashion according to the variables used (for fit results for control weather models see Appendix D). The most parsimonious model (lowest QAICc) for wider application was found to be one which used the average temperature measurements, and so this method was used to create the control weather models for the three disturbed quadrats. Thus, the two control models developed which do not take

into account the effect of the disturbance were (Φ. p_t), where re-sighting probability of marked snails is different every day, and (Φ. $p_{weather}$), which took into account the effect of weather conditions for the study period on the re-sighting probability of marked snails.

These control models were then built upon to create treatment models for the re-sighting data. Three treatment models, which took into account the effect of the disturbance were tested:

- (Φ. $p_{disturb}$), where re-sighting probability was constant before the disturbance event, and then became a different constant afterwards;
- (Φ. $p_{distub+day}$), where re-sighting probability was held constant before the disturbance, and following the disturbance the probability of re-sighting a snail changed with each subsequent day;
- (Φ. $p_{weather+disturb}$) where the combination effect of the disturbance event and the weather conditions of the study locale on re-sighting probability was taken into account.

Models for each of the study quadrats were compared using the quasi Akaike's Information Criterion (QAICc) which was corrected for bias (White & Burnham, 1999). The model with the lowest QAICc was considered to be the most parsimonious, and therefore the best explanation for variability in re-sighting probabilities of marked *P. t. tararuaensis* snails.

Results

Mark-Recapture Analysis

The summary of the sighting totals for marked and unmarked snails over the survey nights is outlined below (Table 3.3). The total number of snails, as well as the number of marked snails seen, fluctuated for the first eight nights in all sites (Figure 3.3). Following the monitoring (disturbance) event, however, all three sites experienced a significant drop in sightings of marked snails (Figure 3.3; Table 3.4). The Ohau and Kahuterawa sites also had a significant decline in total snails seen after the disturbance (Table 3.4).

Most variation in the re-sighting probability was explained by the model (Φ. $p_{distub+day}$), which had the lowest QAICc for all three quadrats (Table 3.5). For this model,

re-sighting probability remains constant before the disturbance event, and gradually declines every day following the disturbance (for estimates of re-sighting parameters as predicted by the best model, see Appendix E).

Table 3.3. P. t. tararuaensis sighting data for the three disturbed treatment quadrats.

Night	Status	Ohau	Shannon	Kahuterawa
Night 1	Total # Tagged	15	12	27
Night 2	Marked	7	3	20
	Unmarked	30	4	32
Night 3	Marked	7	8	17
	Unmarked	23	11	40
Night 4	Marked	3	4	10
	Unmarked	31	5	21
Night 5	Marked	7	6	5
	Unmarked	20	15	19
Night 6	Marked	9	8	9
	Unmarked	33	22	18
Night 7	Marked	6	8	16
	Unmarked	32	18	18
Night 8	Marked	8	7	15
	Unmarked	41	20	28
Night 9	Marked	6	5	9
	Unmarked	27	12	21
Night 10	Marked	5	3	4
	Unmarked	15	10	10
Night 11	Marked	2	2	5
	Unmarked	17	24	10
Night 12	Marked	3	2	3
	Unmarked	14	13	4
Night 13	Marked	2	0	1
	Unmarked	13	13	8
Night 14	Marked	0	0	1
	Unmarked	13	11	5
Night 15	Marked	0	0	1
	Unmarked	16	15	9

Table 3.4. Mean (SD) number of marked and total snails seen each night before and after disturbance event for each site. T = T-test statistic; df = degrees of freedom; p = p-value.

Location	Status	Before	After	T	df	p
Ohau	Marked	6.71 (1.89)	2.57 (2.30)	3.68	11	0.004
Shannon	Marked	6.29 (2.06)	1.71 (1.89)	4.33	11	0.001
Kahuterawa	Marked	13.14 (5.27)	3.43 (2.94)	4.26	11	0.002
Ohau	Total	34.00 (10.30)	19.00 (6.61)	3.40	12	0.005
Shannon	Total	18.88 (8.71)	15.71 (4.92)	0.88	11	0.398
Kahuterawa	Total	36.90 (12.40)	13.00 (8.21)	4.45	12	0.001

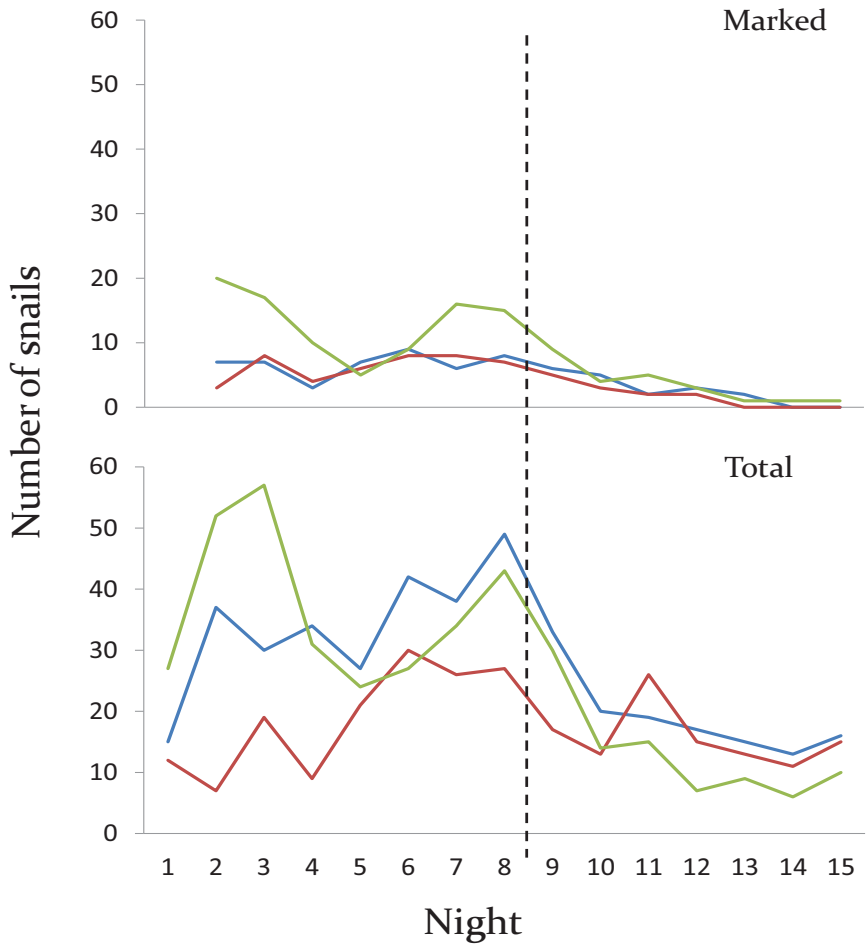

Figure 3.3. Changes in numbers of snails seen in the disturbed quadrats over the 15 nights before and after monitoring event. Night 1 was the marking event; dashed line indicates the simulated monitoring event (blue line = Ohau, red line = Shannon, green line = Kahuterawa). Total includes both marked and unmarked snails.

Table 3.5. Results summary from re-sighting probability models constructed for the treatment sites (disturbed).

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Num. Par	QDeviance
Ohau						
Phi(.) p(disturb+day)	196.8877	0	0.88004	1	2	131.7155
Phi(.) p(weather+disturb)}	200.9206	4.0329	0.11716	0.1331	2	135.7485
Phi(.) p(disturb)	208.4145	11.5268	0.00276	0.0031	2	143.2423
Phi(.) p(t)	217.9606	21.0729	0.00002	0	14	122.4827
Phi(.) p(weather)	219.2473	22.3596	0.00001	0	1	156.1797
Shannon						
Phi(.) p(disturb+day)	150.2572	0	0.99565	1	2	97.4283
Phi(.) p(weather+disturb)	162.4676	12.2104	0.00222	0.0022	2	109.6387
Phi(.) p(disturb)	162.5745	12.3173	0.00211	0.0021	2	109.7456
Phi(.) p(t)	171.905	21.6478	0.00002	0	14	87.3362
Phi(.) p(weather)	177.1483	26.8911	0	0	1	126.4434
Kahuterawa						
Phi(.) p(disturb+day)	320.8295	0	0.89679	1	2	196.8756
Phi(.) p(t)	325.2644	4.4349	0.09765	0.1089	14	174.0897
Phi(.) p(disturb)	332.3623	11.5328	0.00281	0.0031	2	208.4084
Phi(.) p(weather+disturb)	332.4019	11.5724	0.00275	0.0031	2	208.448
Phi(.) p(weather)	367.2464	46.4169	0	0	1	245.3503

Discussion

Powelliphanta snail behaviour changed after the disturbance of the quadrats. The abundance of snails decreased following the disturbance, and this was true for marked as well as unmarked snails. Published results suggest that land snail behaviour and distribution is highly dependent on temperature and humidity (Boag, 1985; Prior, 1985; Chen *et al.* 1993; Devine, 1997). However, in this study, control models constructed solely from weather data performed poorly, suggesting an additional (unknown) factor which was affecting *P. t. tararuaensis* behaviour. When the monitoring disturbance was incorporated into the models, their performance improved. Re-sighting of tagged snails was less likely following a disturbance event, and recapture probability gradually declined in the days following the monitoring simulation. The results of this study suggest that monitoring of a quadrat displaces *P. t. tararuaensis* snails from the immediate area, at least for the short-term.

Disturbance, both natural and anthropogenic, is recognised as having a crucial role in shaping the structure and function of an ecosystem (Willig & McGinley, 1999). The densities of many animal populations can be altered by a disturbance event, and this includes populations of terrestrial gastropods (Strayler *et al.* 1986). Hurricanes were found by Willig & Camilo (1991) to cause drastic short-term declines in snail densities, although the increase in litter through the action of the hurricane saw densities of some snail species reach higher levels than before the disturbance after five years. Therefore it is not only intensity, but also frequency of disturbance which directs consequences for populations (Willig & McGinley, 1999). There is very little known about the habitat requirements of *Powelliphanta,* and at present it is estimated that the acceptable period between monitoring events for the snails is one year (Walker, 1997). However, studies of disturbance on land snail populations have suggested that the effects may extend beyond a single annum. Kiss & Magnin (2006) found that Mediterranean land snails required five years between wildfires for populations to recover, and Tiny Canyon mountain snail populations may require 10-40 years between fires for population recovery (Gaines *et al.* 2011). While a monitoring disturbance is probably not comparable to the total destruction of fire, frequent monitoring of permanent quadrats may hinder *Powelliphanta* recovery, in addition to providing biased data. Without more detailed information on habitat requirements and reproduction rates, this effect cannot be accurately gauged. It is likely that, if given sufficient time to recover, *Powelliphanta*

populations will not be affected by monitoring practises, as land snails have been demonstrated to be particularly resilient to human-induced disturbance (Watters *et al.* 2005; Strom *et al.* 2009). Snails have been shown to survive adverse conditions, such as fire and forest clearance, by utilising cryptic microsites acting as refugia (Kiss & Magnin, 2003; Kiss & Magnin, 2006), or shallow hollows and crevices beside boulders and stumps (Hawkins *et al.* 1997). *Powelliphanta* may also behave in a similar manner after a disturbance event.

If *Powelliphanta* snails employ sheltering behaviour as mitigation against the effects of short-term disturbance, it may have affected the re-sighting probability. Baur & Baur (1990) suggested that sheltering behaviour in their study species of snail *Arianta arbustorum* could have affected recapture rates, as individuals may have been buried in the soil and been missed. This effect was probably unlikely to have occurred in this study, as PIT tags can be read on marked snails even while buried under soil. However, tag loss was documented for two individuals during the monitoring simulation at Shannon, and may have occurred more frequently. This was probably a result of insufficient glue setting time for the damp weather conditions, as moisture affected the set times of the Liquid Nails adhesive. Manufacturer's (Selleys®) recommendations suggest adhesive bond should be left to set until "touch-dry". If snails were held under shelter for longer periods of time during the glue setting period, recognition of the "touch-dry" state would be more accurate, and could possibly limit tag loss.

Unlike other species of snails, *Powelliphanta* cannot seal the aperture of their shell with mucous, and are therefore extremely sensitive to desiccation (Meads *et al.* 1984). Unsuitable changes in microhabitat conditions could put the snails at risk. With juvenile snails and eggs being especially susceptible to desiccation (Asami, 1993), monitoring plots may suffer lowered recruitment than the surrounding habitat, thus giving skewed population estimates (Walker, 1997). Lowered numbers of the smallest size classes of snails has already been documented in monitoring plots for the Shannon area (Chapter Two). Considering the generally low dispersal capability of land snails, short-term effects of a disturbance, for example local extinctions, may be important for the long-term survival of the species (Hylander *et al.* 2004).

It is important that the long-term effects of the current monitoring methods on populations of *Powelliphanta* snails are better understood, and the potential for alternate techniques is investigated. The implications of these findings should be considered by managers of *Powelliphanta*, as many populations are already threatened by habitat loss and exotic predators (Hitchmough *et al.* 2007). If surveys are indeed providing inaccurate information as suggested by Walker (1997), management and conservation efforts could be wrongly targeted. It may be necessary to increase the time period between bouts of *Powelliphanta* population monitoring (currently 1-2 years), or to establish temporary quadrats for each annual survey. It would also be of value to incorporate some form of mark-recapture study into the monitoring program for *Powelliphanta* snails. Rather than using the currently employed monitoring system, night searches applying mark-recapture methodology could be implemented in population surveys. If naturally occurring marks on shells of snails can be utilised, monitoring activities could be less disturbing to snails. This would allow for insight into population dynamics and life history parameters, which could be used to address the long-term effects of monitoring, as well as gleaning valuable information for the effective management of the species.

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4 Device attachment to *Powelliphanta traversi tararuaensis:* implications for depredation by ship rats (*Rattus rattus*).

Introduction

The ability to accurately identify individuals is a key aspect of many abundance estimates. Mark-recapture methods are dependent on the fact that individual organisms can be recognised consistently (Yoshizaki *et al.* 2009). Statistical models used in analysis of mark-recapture data hold certain assumptions, and the reliable identification of individuals is a required property (Henry & Jarne, 2007). Marking methods should, therefore, be selected with this in mind, ideally being long lasting, dependable and discreet (Henry & Jarne, 2007).

A commonly used system in the field of wildlife conservation biology is radio frequency identification (RFID), a method which possesses desired traits in marking techniques (Beausoleil *et al.* 2004). RFID methods involve the use of PIT (passive integrated transponder) tags. A PIT tag consists of a small microchip, an antenna and a chip-capacitor housed together within a biocompatible glass capsule. The tags are usually 2.1-3.85 mm in diameter and 11-32.5 mm in length, and each tag has a unique identification code programmed into the microchip (Boarman *et al*. 1998). These tags are typically injected either under the skin, or into the musculature of the study animals. In order to identify an individual, the tag needs to be energised by an electromagnetic field emitted by a transceiver (reader) tuned to a specific frequency (usually 125, 134.2, or 400 KHz). The tag then emits its ID code by modulating the reader's electromagnetic field. The reader detects and decodes the modulations, and by doing so, reconstructs the tag's ID (Boarman *et al.* 1998).

The use of PIT tags and RFID in studies of wildlife populations began with a study by Prentice & Park (1983), to evaluate the use of the method for measuring fish

movement (Gibbons & Andrews, 2004). The use of PIT tags in mark-recapture studies has since been applied to a range of animal groups, including mammals, birds, reptiles, and amphibians (Hill *et al.* 2006). While RFID techniques have been more popular in studies of vertebrates, there has been recently increased application of this technology in invertebrate research. The small body size of most invertebrates makes a passive reflector system particularly suitable, as it circumvents many of the problems associated with radio transmitters. Small organisms (such as snails) can only bear a small weight, and so for radio transmitters to be feasibly used with many invertebrate species, they need to be very lightweight and compact. These requirements usually make transmitters of this nature costly, indeed out of reach for many research budgets (Lovei *et al.* 1997). Additionally, radio transmitters require an energy source, thus possessing the added limitation of a specific battery life. Smaller transmitters, having smaller batteries, have very short lives. In RFID all the energy used to activate the PIT tag is sourced from the reading unit, so this method bypasses the problems associated with radio transmitters on small species (Lovei *et al.* 1997).

Invertebrates, however, do possess a suite of traits which has made the transition of RFID from vertebrates to invertebrates not so simple. Many invertebrate species have a hardened exoskeleton; a marker would need to be internal to be useful in any long term studies, because most arthropod species moult regularly (Reichling & Tabaka, 2001). Additionally, as an animal's body size decreases, it becomes increasingly more difficult to attach tags externally, and to limit the detrimental effects of internal tags (Lauzon-Guay & Scheibling, 2008). For example, Lauzon-Guay & Scheibling (2008) found that there was no detectable effect of PIT tagging on sea urchin (*Strongylocentrotus droebachiensis)* feeding rate or survival in a 10 week laboratory experiment. However, applying a PIT tag had a detrimental effect on all measures of sea urchin performance, activity and survival in the field. Bubb *et al.* (2002) established that if PIT tags were inserted too close to the ventral nerve cord within the abdominal musculature of crayfish, the tagging process could be fatal for the animal. Purcell *et al.* (2008) concluded that PIT tagging was unsuitable for studies on tropical sea cucumbers, because the species had poor retention of the tags.

Some invertebrate species are more suited to PIT tag application, and this includes the hard-shelled gastropods. Gluing plastic identification markers to the shell is

a common practise in mark-recapture studies of snails (Henry & Jarne, 2007), and attaching diodes to the shells of *Powelliphanta* for tracking by harmonic radar has been applied in their monitoring and conservation (Lovei *et al.* 1997; Devine, 1997, Bennett, 2001). *Powelliphanta* spend the day burrowed in the leaf litter; they can only be found initially by searching with torches at night, or through a hand search of the leaf litter by day (Walker, 1997). This process is destructive to the habitat, and in addition can put the animals at risk of desiccation. However, this method has been widely used for monitoring *Powelliphanta* populations (Walker, 1997). The use of PIT tags as a research tool may allow marking, detection and identification of snails without disturbing them. It could also provide means with which to map daytime distribution of *Powelliphanta.*

Attaching external devices to snails creates an additional range of problems arising from the use of adhesives (glues). Devine (1997) evaluated a variety of adhesives and found that the four frequently used to attach transponders (non-acetic acid-based construction silicon, fast-curing epoxy resin, cyano-acrylate glue & liquid hydrocarbon based building adhesive) were all probably safe for *Powelliphanta.* However, he noticed that many snails with transponders were depredated by rats, something which was thought to be linked to the rats being particularly sensitive to the smell of the adhesives (C. Purches, pers. comm.).

New Zealand's native fauna is distinctive in its lack of most land mammals. As a result of this, many endemic species have developed a suite of traits which made them vulnerable to the exotic mammalian predators brought to New Zealand in association with its colonisation by humans (Daugherty *et al*. 1993). The ship rat (*Rattus rattus*) is a significant predator in New Zealand forests. A globally distributed species, it has capitalised on dispersal opportunities provided by humankind (Hooker & Innes, 1995). Rats are an omnivorous species, feeding largely on fruits and invertebrates, but also taking birds and lizards (Innes, 2005). In areas where rats are present, *Powelliphanta* are a frequent food source, and rat middens can contain vast quantities of *Powelliphanta* shells (Meads *et al.* 1984). Rat depredations account for a high proportion of damaged shells of *Powelliphanta traversi traversi* (Devine, 1997; Bennett *et al.* 2002), which is a taxon very closely related to *P. t. tarauaensis.* Rats have also been implicated in *P. t. tararuensis* mortality (see Chapter Two).

Understanding the consequences and risks involved with certain techniques can allow for steps to be taken to mitigate them. If RFID technology does, in fact, predispose marked individuals to predation by rats, it may be necessary to couple any monitoring/research projects using RFID methods with some form of predator control, or new methods of identifying individuals may need to be developed (Chapter Five).

In this study I presented ship rats with the scents of three adhesives used to glue PIT tags to dead *P. t. tararuaensis* shells, and measured the number and duration of any behavioural interactions associated with foraging directed towards different adhesives. I expected that if the adhesives attract rats, then the rats will spend more time interacting with shells carrying the glues than with the control. The results should give insight into whether certain glues are attractive to rats, and thus whether the use of these glues to attach tags to snails in the field may predispose marked individuals to depredation.

Methods

Maintenance of Captive Wild Rats

In order to gauge the effect of a range of adhesives on the behaviour of wild ship rats, animals captured in the wild were brought into captivity and utilised for a series of controlled trials. The experimental group consisted of eight rats, all male, which were sourced from Lake Waikaremoana by Gaylynne Carter (PhD candidate, Institute of Natural Resources - Ecology, Massey University, Palmerston North). These animals had been involved previously in an experiment examining the behavioural responses of wild rats when presented with odour cues from a range of mammalian predators. As a part of Carter's study, the rats had become accustomed to the test enclosures and acclimatised to the general experimental procedure. The trials conducted in this study were designed to be similar to those the animals had previously been exposed to. This experiment was carried out under approval from the Massey University Animal Ethics Committee (protocol # 10/113).

The research was conducted in the Small Animal Research Unit (SAPU) of Massey University, Palmerston North, in a purpose built facility. The experimental set up consisted of eight separate housing runs arranged in a stacked fashion over one another in two levels, creating four in each row (Figure 4.1). Each housing run was built to be

approximately 500mm deep x 450mm wide x 900mm high, with the back wall, floor and ceiling constructed of plywood; wire mesh and baton framed side and front walls. The housing cages were situated next to four considerably larger test enclosures, which measured approximately 1.5m deep x 2m wide x 2m high. The entire set up was contained within a steel frame with hurricane netting, with added plywood and shade cloth to shield it from harsh weather. Free-living ship rats in New Zealand forests are arboreal (Hooker & Innes, 1995), and the experimental enclosures were developed with this in mind. Environmental enrichment was supplied in the form of bamboo canes and ropes for the rats to climb on, and there were multiple platforms and plywood hides supplied within the larger experimental enclosures. This allowed for the captive animals to perform behaviours comparable to those expressed in the natural setting.

Each animal was given a weather-proof nesting box, which was customised from a trap. Rats were allowed access to nesting materials such as pieces of fabric, wood shavings and hay. The modified form of trap enabled the door of the nest box to be manipulated from the outside of both the home runs and the experimental enclosures. This, coupled with the nocturnal nature of the ship rat, meant that the animals could be moved from location to location with minimal disturbance while they rested in the nest box during the day. The animals were provided with plastic feeding dishes containing water and a variety of foods (carrot, apple, grain/seeds, rodent pellets and peanut butter). These resources were available *ad lib*.

Experimental design

Three commonly used adhesives were tested, all of which have been shown by Devine (1997) to be safe for snails:

- Liquid hydrocarbon-based building adhesive (Selleys Liquid Nails®)
- Fast-curing epoxy resin (Selleys Five Minute Araldite®)
- Cyano-acrylate glue (Loctite®)

Each glue was used to attach a PIT tag (Trovan® ID 100A) to the dorsal surface of eight empty snail shells. The dead snails were sourced from the Kahuterawa Recreational Reserve (see Chapter Three). Shells of snails assumed to have recently died of natural causes (see Chapter Two) were collected. A control group of eight shells was also included, giving a total number of 32 shells tested. The shells were each filled with a

piece of fabric which had been in contact with a live *Powelliphanta* snail for approximately 30 minutes, to provide the shells with the smell of live snails. Four rats were tested at once, each in its own enclosure. The other four rats (inactive test subjects) were left in the home runs, and were trialled the following night. This meant that the testing period was spread over two nights.

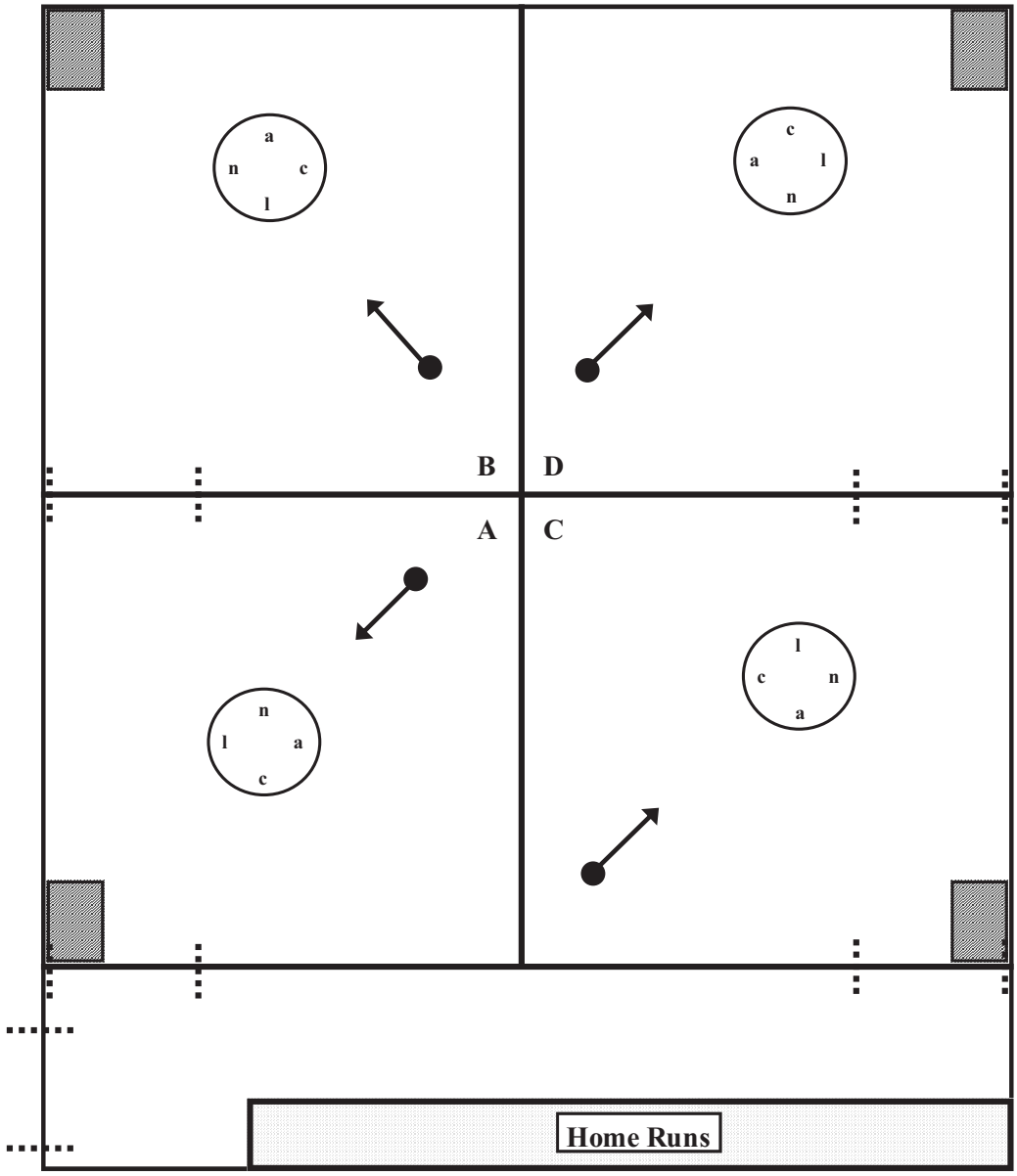

Figure 4.1. The enclosure setup. The home runs were located in one end of the steel frame/hurricane netting pen. Rats which were not being tested that night were allowed to roam their assigned home run while the four tested rats were released in the corresponding test enclosures (A, B, C & D). The two groups were alternated, so each rat had a night in the home run, and a night in the test enclosure. Camera locations are indicated by black dots and camera orientations by arrows. Access points are indicated by the dashed lines. The location of the platform on which the nest box was placed and thus the rat released is indicated by the area containing diagonal lines. The test arenas are depicted as circles showing the treatment array: n = Selleys Liquid Nails®, a = Selleys Five Minute Araldite®, l = Loctite® and c = the control shell.

Each rat was tested against a set of four treatments (Selleys Liquid Nails®, Selleys Five Minute Araldite®, Loctite® & control), such that each individual rat acted as a replicate. The shells were presented in a circular test arena situated in a relatively central location within the test enclosure. Within the test arena, the four different treatments were arranged so that each of the four rats within the test enclosures (A, B, C & D) was given a different spatial arrangement of shells (Figure 3.1). The two night trial system meant that two rats tested within the same test enclosure experienced the same shell arrangement. A camera (Sony Camcorder™ DCR SR42 in test enclosure A, and Sony Camcorder™ DCR SR45 in B, C & D) was mounted in a location such that the field of view was centred on the test arena, and the greatest available outlook of the entire enclosure was obtained. The cameras were fixed in "night-mode", and coupled with infra-red lamps (IRLamp 6, Bat Conservation and Management Inc., Pennsylvania, USA) powered by 12V sealed rechargeable batteries to illuminate the field of view without disturbing the nocturnal rats with white light. The rats were released from their enclosures at 21:00 when filming began. Filming finished at 05:00 the following day. The timing was chosen to include the hours of the night when *Powelliphanta* snails were usually active (pers. obs.), and when wild rats were likely to encounter free-living *Powelliphanta*.

Each of the eight rats, therefore, were video recorded for eight hours (64 hours of footage in total). The videos were watched in real time and the time each rat spent in the test arena (as opposed to anywhere else within the enclosure) was recorded, as well as three types of interactions with the shells classified as being related to foraging: "investigating", "manipulation with mouth" and "manipulation with mouth and forepaws" (Figures 4.2, 4.3 & 4.4).

Figure 4.2. Rat portraying behaviour classified as "investigating". This behaviour involves no direct physical manipulation of the shell. Photo from author's video.

Figure 4.3. Rat portraying behaviour classified as "manipulation with mouth". Photo from author's video.

Figure 4.4. Rat portraying behaviour classified as "manipulation with mouth and forepaws". Notice the distinction between this behaviour, which involves the rat sitting up in a hunched position with hind limbs supporting the body weight, and "manipulation with mouth", where the body weight is supported by all four paws. Photo from author's video.

Statistical Analysis

A Friedman's test, with length/number of interactions as the response variable and the type of adhesive as the treatment factor blocked by individual rat, was used to examine the effect of glue on the rats' behaviour. The analysis was done using the statistical software package SPSS (version 17.0.1, Dec. 1, 2008). Where the overall Friedman's test was significant, the pairwise means comparisons for each of the glues against the control were performed using Mann-Whitney tests in Minitab (Version 14). Minitab (Version 14) was also used to graph the descriptive statistics for the duration and number of behavioural interactions for each of the four treatments.

Results

Rats were found to spend significantly more time interacting with snail shells bearing Loctite and Araldite compared with Liquid Nails and the control (Tables 4.1, 4.2; Figure 4.5).The animals spent on average more time (seconds) performing the "mouth and forepaws" behaviour on the shells with Araldite (median = 43, range 0 - 211) and Loctite (median = 34, range = 0 - 120) when compared with the control (median = 0, range = 0 - 24) and Liquid Nails (median = 0, range = 0 - 0) ($S = 14$, $df = 3$, $p = 0.003$).

Rats also performed a significantly greater number of interactions with the Loctite and Araldite glued shells (Tables 4.1, 4.2; Figure 4.6). The treatment effect was found to be significant for the counts of both the "investigate" and "mouth and forepaws" behaviours ($S = 10.06$, $df = 3$, $p = 0.018$; $S = 14$, $df = 3$, $p = 0.003$ respectively). On average, the Loctite (median = 2.5, range = 0 - 8) and the Araldite (median = 2, range = 0 - 3) shells were investigated most when compared with the control (median = 0.5, range = 0 - 2) and Liquid Nails (median = 0, range = 0 - 3) shells. Similarly, the median number of "mouth and forepaws" behaviours was higher with Araldite (median = 2, range = 0 - 6) and Loctite (median = 1.5, range = 0 - 7) than with the control (median = 0, range = 0 - 1) and Liquid Nails (median = 0, range = 0 - 0) shells.

Table 4.1. Summary of Friedman's tests for the hypothesis of no effect of adhesives used on Powelliphanta PIT tags on rat foraging behaviour (treatment factor = type of adhesive, block = rat, df = 3). S = Friedman's statistic; p = p-value.

Behaviour	Response	S	p
Investigate	Duration	6.79	0.079
Investigate	Number of Interactions	10.06	0.018
Mouth	Duration	7.6	0.055
Mouth	Number of Interactions	7.71	0.052
Mouth & Forepaws	Duration	14	0.003
Mouth & Forepaws	Number of Interactions	14	0.003

Table 4.2. Summary of Mann-Whitney tests for pairwise means comparisons of different glues against the control. W = Mann Whitney statistic; p = p-value.

Treatment	Rat behaviour	Response	W	p
Araldite	Investigate	Number of Interactions	52.2	0.0924
Araldite	Mouth and Forepaws	Number of Interactions	52.5	0.0908
Araldite	Mouth and Forepaws	Duration	52.5	0.0924
Loctite	Investigate	Number of Interactions	49.5	0.0483
Loctite	Mouth and Forepaws	Number of Interactions	50.0	0.0510
Loctite	Mouth and Forepaws	Duration	49.5	0.0483
Liquid Nails	Investigate	Number of Interactions	80.0	0.0764
Liquid Nails	Mouth and Forepaws	Number of Interactions	77.5	0.2120
Liquid Nails	Mouth and Forepaws	Duration	80.0	0.0764

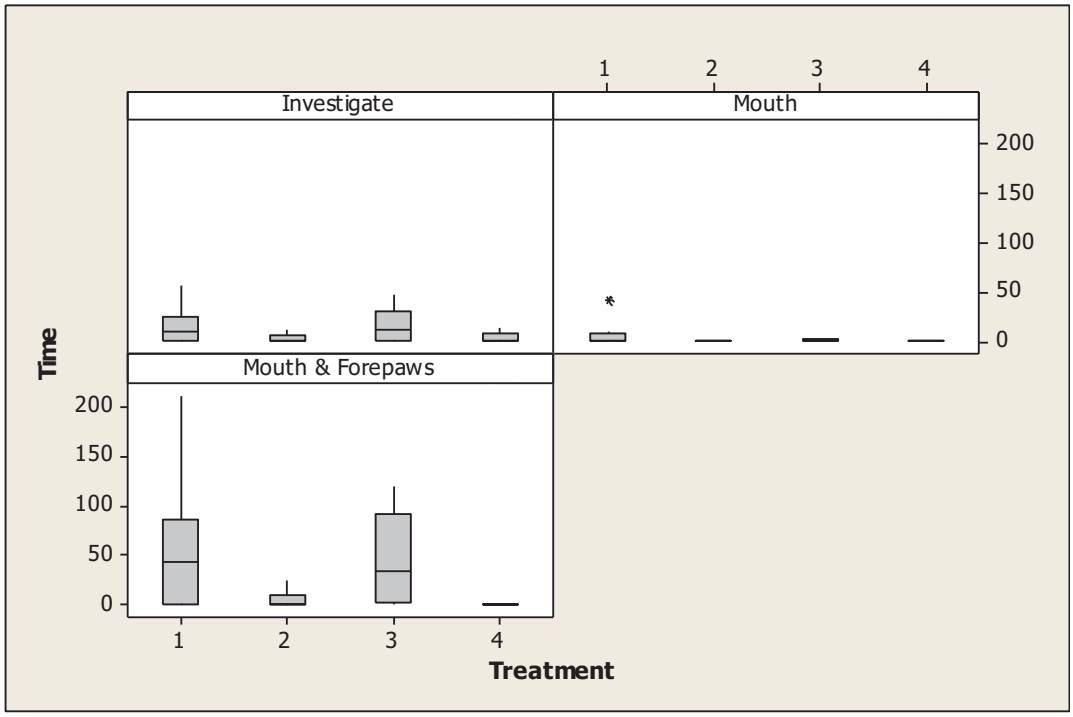

Figure 4.5. Time (seconds) spent interacting with each glue treatment (1 = Araldite, 2 = Control, 3 = Loctite, 4 = Liquid Nails) for the three types of foraging behaviour in captive rats. Whiskers represent range of data (min, max), asterisk signifies an outlier value.

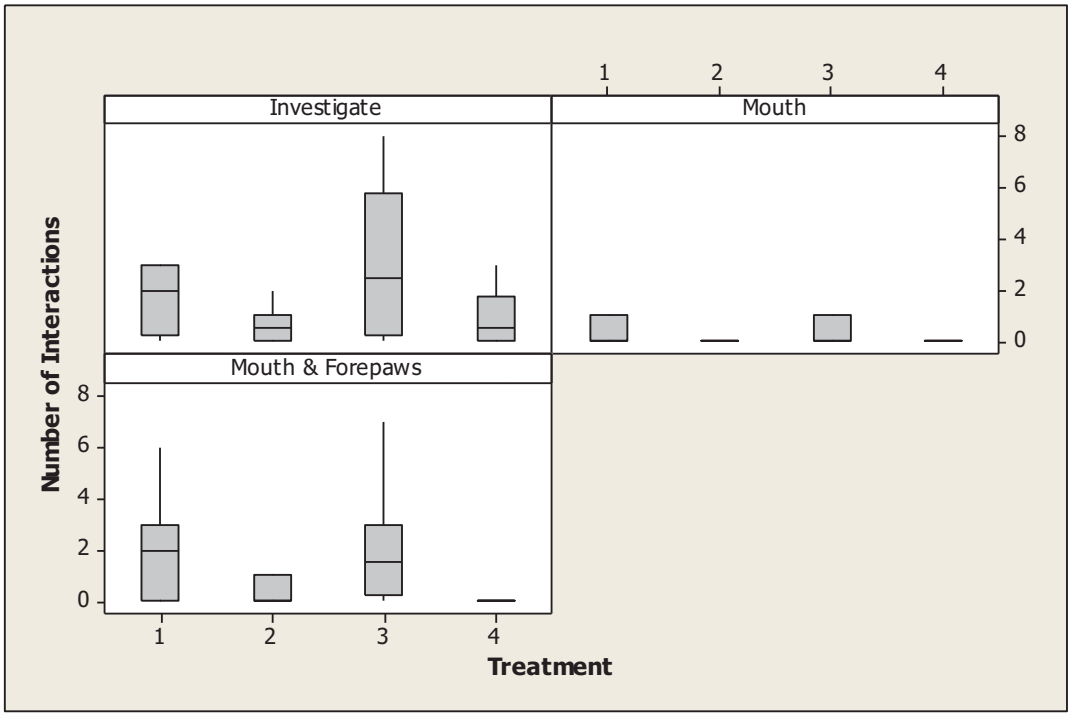

Figure 4.6. Number of interactions with each treatment (1 = Araldite, 2 = Control, 3 = Loctite, 4 = Liquid Nails) for the three types of foraging behaviour in captive rats. Whiskers represent range of data (min, max).

Discussion

The main finding of this study is that rats were significantly more attracted to snails tagged using Loctite and Araldite glues. Rats seemed to react to the snails tagged using Liquid Nails in a manner akin to the control, with these two shell types having a similar spread of results. This indicates that perhaps there is a low level of attractiveness of the Liquid Nails adhesive, so much so that the scent could be masked by that of the snail itself. Therefore, if an adhesive is to be used in the field for marking *Powelliphanta* snails where rats are known to be present, the results of this study indicate that the best choice of glue is Liquid Nails. The findings indicate that Araldite and Loctite should both be avoided, as they may boost the potential for marked snails to be located by foraging rats.

While these results are significant, it should be noted that two of the test rats (25%) did not venture onto the test arena at all, and had no interactions with the *P. t. tararuensis* shells. Because all animals used in this trial were familiar with the captive

situation and testing procedure, it is likely that the rats experienced minimal stress. Therefore, such behaviour could be viewed as a neophobic response, which is defined as the avoidance of an unfamiliar object in a familiar place (Barnett, 1958; Clapperton, 2006). The rats were from a region where *Powelliphanta* snails do not occur, and so the shells (and potentially the scent of adhesive) may be novel to them. On the other hand, this response may signify that the rats were not interested at all in the snails and the glues, and for this reason they did not come to examine them. In contrast, another individual spent significantly more of his time in the test arena when compared with the other rats. This level of difference in response within such a small sample could indicate that the true breadth of responses in wild populations of ship rats may be vast. Also, only male rats were available for this study. If there is a level of variation in behaviour between sexes, the variation in behavioural responses could be even broader. It would be of value that the variability of responses is investigated further with greater sample sizes, as well as with female rats. Overall, however, 75% of the tested rats interacted with the shells, showing that any neophobia existing in the population may be low. The animals that interacted with the shells displayed a preference for particular glues, suggesting that *Powelliphanta* will probably be at risk of depredation if certain adhesives are used, despite the response variation in individual rats.

It has been suggested that certain synthetic additives to foodstuffs elicit the curiosity of rodents, and when applied to a food item (as opposed to being added into it), make an item more attractive (Smythe, 1976; Clapperton, 2006). This appeared to be the case for the more volatile adhesives (Araldite and Loctite), with rats interacting more frequently and for longer periods with snails shells bearing these glues. This could have severe implications for mark-recapture studies of *Powelliphanta* employing these adhesives. If rats are attracted to the scents of these glues, rates of depredation of marked snails may be increased, threatening the results of any study, but more significantly, the *Powelliphanta* populations themselves. Even though the degree of heterogeneity seen in this study indicates that a percentage of rats may not respond in this manner, studies in social facilitation of feeding in rats suggest there is potential for spread of the phenomenon. Naive rats will eat an unfamiliar food item if they observe another rat feeding on that food (Posadas-Andrews & Roper 1983; Galef *et al*. 1984; Strupp & Levitsky, 1984; Galef & Whiskin, 2000; Galef & Whiskin, 2001; Clapperton, 2006), suggesting that a rat which may typically display neophobic behaviour could learn

to take marked snails. Female Norway rats may also transmit cues to her nursing pups, which determines the dietary preferences of the young at weaning (Galef & Clark 1972; Valsecchi *et al.* 1993; Clapperton, 2006), and if a female takes marked snails this inclination may be passed to her offspring.

Further exploration of the response of rats to adhesives used to mark *Powelliphanta* is vital, especially to establish the length of time for which glues will elicit a response in free-living rats. For further studies of *Powelliphanta* requiring the use of adhesives, such information would provide guidelines to protect tagged snails. For example, a time frame for which tagged snails could be held before release to avoid rodent predation; or the need for rodent control around the periphery of study sites. Longer testing periods could allow the responses of rats to repeated contact with marked snails to also be investigated. Assessing the behavioural responses of other known *Powelliphanta* predators (other rodents and possums) towards marked snails would also be of value. It would be interesting to explore the implications documented by this study for other species. Vulnerable and endangered birds in New Zealand have radio transmitters attached using glue (hihi, *Notiomystis cincta,* Armstrong *et al.* 1999*;* saddleback, *Philesturnus carunculatus rufusater,* Sullivan, 2006) and this may place the birds at risk of predation by rats.

Rats are effective predators, capable of taking large numbers of snails (Meads *et al.* 1984). Therefore any research tool which only slightly increases the successful location of land snails by rats could be damaging to a population in decline. The results of this study imply that adhesives should be used with caution when researching land snails and other species, especially when concerning populations which are threatened.

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5 Photographic identification of *Powelliphanta traversi tararuaensis:* a novel method for monitoring terrestrial gastropods.

Introduction

Being able to accurately recognise individuals within a population allows for the production of realistic estimates of population size, and the detailed study of survival (Gilkinson *et al.* 2007). Individual recognition can also be an effective tool in understanding life history parameters, movement patterns, reproduction and foraging (Gilkinson *et al.* 2007).

The most common vehicle for the recognition of individual animals is the application of an artificial mark, and the suite of techniques available is formidable. Marks vary in their structure, permanence, and in the level of invasiveness of the marking procedure. These differences, in part, determine their applicability to particular research questions. Applying any artificial mark, by either the marking process or the mark itself, may affect the animals involved through the alteration of behaviours, intra- & inter-specific interactions, survival, reproduction and/or other aspects of population dynamics (Beausoleil *et al.* 2004).

Techniques such as branding, ear/flipper tagging, tattooing, ear notching, toe clipping, or PIT (Passive Integrated Transponder) tagging are all associated with a high degree of permanence, a desirable trait for long term population studies. On the other hand, some of the aforementioned also involve tissue damage, thereby causing pain and posing the potential to further threaten the welfare of the organism (Mellor *et al.* 2004). They also require physical capture of the individual, a stressful process (Mellor *et al.* 2004). Other, more temporary solutions such as paints, dyes and fur/hair removal, can be less intrusive. While the risk associated with these less invasive procedures is not as significant, in many cases the need to capture and restrain the animal cannot be skirted.

An additional factor with any project that adopts artificial marking is the logistics behind tagging a representative sample. Difficulties and challenges in the marking process itself can constrain sample size or introduce bias, upsetting the accuracy of any predictions drawn from such data (Mackey *et al.* 2008). It is thus essential that when selecting a suitable marking option, biologists must put serious thought to the implications for ecological balance and the welfare of the study species (Mellor *et al.* 2004), in addition to the considerations of research aims, budget, time and field restraints.

Comparatively, there have been fewer mark-recapture based studies in invertebrates than vertebrates (Henry & Jarne, 2007). It is interesting to note that land snails are among the mark-recapture destitute, which is especially intriguing given that many species are important vectors of human parasites or are of significant economic value (Henry & Jarne, 2007). The possession of a hard shell also makes applying an artificial mark relatively simple. Nevertheless, land snails are no exception to the widely recognised complications of artificial marking. The gastropod shell is a structure specialised to shield the animal from mechanical damage and to regulate moisture loss. Commonly applied marking techniques such as shell engraving and drilling are considered invasive (Severns, 2009), and can affect the functioning of the shell. Attaching plastic discs or tags using adhesive or applying paints or nail varnishes directly to the shell can avoid this dilemma, but is prone to the issues surrounding mark loss. Bulky tags can also impede the animals' daily motions; and the porous nature of many species' shells raises the question of chemical compounds diffusing through to the animal (Henry & Jarne, 2007). Henry & Jarne (2007) noted that, while evaluating impacts of marking on an individual prior to tagging is a common practice in mark-recapture studies of vertebrates, it is rarely considered and almost never tested in comparable studies of gastropods. Not considering the impact of marks has the potential to narrow the body of accurate mark-recapture based studies on hard-shelled gastropods.

Another possible way to identify individual animals is by using unique physical characteristics which make them different from conspecifics. The use of natural markings for individual recognition circumvents many of the problems attributed to artificial marks. It offers the benefits of long-term artificial marks, as well as a significant reduction in the level of stress and trauma induced by the marking process. In many

cases the necessary data is obtained using methods such that the target individual is not disturbed or altered in any way, virtually eliminating any degree of invasion. This is of immense benefit when working with sensitive or threatened species. The use of natural marks is also inexpensive, and recent advances in pattern-matching software mean that large databases of individuals can be created and searched with relative ease and efficiency (Kelly, 2001; Arzoumanian *et al.* 2005; Van Tienhoven *et al.* 2007; Gamble *et al.* 2008).

Photographic identification based on natural markings is a craft reserved for "charismatic" vertebrates. It has been applied to a wide number of groups falling within this definition, most commonly the cetaceans (Karczmarski & Cockcroft, 1998; Friday *et al.* 2000; Gowans & Whitehead, 2001; Harlin *et al.* 2003; Coakes *et al.* 2005; Calambokidis *et al.* 2009; Falcone *et al.* 2009), but also pinnipeds (Forcada & Aguilar, 2000; Mellor *et al.* 2004; Gerondeau *et al.* 2007; Mackey *et al.* 2008; Thompson & Wheeler, 2008), elasmobranches (Arzoumanian *et al.* 2005; Castro & Rosa, 2005; Van Tienhoven *et al.* 2007; Gubili *et al.* 2009), felids (Kelly, 2001; Jackson *et al.* 2006; McCarthy *et al.* 2008), amphibians (Holzapfel *et al.* 2005; Smale *et al.* 2005; Gamble *et al.* 2008), horses (*Equus caballus*; Dawson & Miller, 2008; Vernes *et al.* 2009), elephants (*Elephas maximus*; Goswami *et al.* 2007), polar bears (*Ursus maritimus*; Anderson *et al.* 2007), hyenas (*Hyaena hyaena*; Harihar *et al.* 2010), sea otters (*Enhydra lutris*; Gilkinson *et al.* 2007), turtles (*Caretta caretta;* Schofield *et al.* 2008), and anemone fish (*Amphiprion ocellaris;* Nelson *et al.* 1994).

Despite the fact that the invertebrates compose over 95% of all described animal life (Wilson, 1987), there have been relatively few projects employing photographic identification in the group. Most research into the application of photo ID techniques for invertebrate study focuses on the decapod Crustacea. MacDiarmid *et al.* (2005) were able to recognise rock lobsters (*Jasus edwardsii*) using markings on the pedate processes, the epistoma and the antennular plate; and a similar study by Frisch & Hobbs (2007) successfully used colour patterns (via photo ID) to distinguish individuals of the painted crayfish (*Panulirus versicolor*). Photographic identification using natural markings has also been applied in research on snow crabs (*Chionoecetes opilio;* Gosselin *et al.* 2007), and rock shrimp (*Rhynchocinetes typus*; Gallardo-Escarate *et al.* 2007). Considering many

invertebrate species possess high levels of patterning and colouration, it is an enigma why the method is not more popular in invertebrate research.

Powelliphanta traversi tararuaensis is a handsome species of carnivorous land snail belonging to an endemic New Zealand group (Meads *et al.* 1984). Despite the genus being found throughout the lower North Island and the South Island, the *Powelliphanta* land snails generally remain cryptic to the public as many species are restricted to small, localised patches (Walker, 2003). Current conservation efforts include the monitoring of extant populations by regular surveys of established quadrats to assess changes in the numbers of snails over time through changes in their density (Walker, 1997). However, while this monitoring system provides a general indication of population trends, it does not account for snail life expectancy, individual movements, and territoriality. Recent documentation of a newly discovered species of *Powelliphanta* being pushed to the edge of extinction in the quest for economic gain (Trewick *et al.* 2008; Walker *et al.* 2008) highlights the desperate need for knowledge surrounding aspects of population dynamics for these animals.

To address some of the questions surrounding the ecology and behaviour of *Powelliphanta*, shell engraving and attaching relatively large, conspicuous devices to the animals is frequently employed in research and monitoring (Devine, 1997; Lovei *et al.* 1997; Bennett *et al.* 2002; Standish *et al.* 2002). Despite these techniques being applied, there is still a distinct scarcity of knowledge surrounding basic life history traits within the genus. One method to combat this information paucity is to incorporate a simple system of individual recognition into a monitoring program. This would allow for the establishment of a mark-recapture study for gaining sorely needed population data.

Powelliphanta naturally possess a strikingly coloured shell, the beauty of which has captivated people for generations. In fact, the collection of shells was a major threat to the genus up until 1982, when the activity was declared illegal (Walker, 2003). The distinct banding and colouration patterns, ridges and dents in their shells (Figures 5.1 & 5.2) suggest that there is potential for the application of photographic identification techniques. Being able to identify individual *Powelliphanta* without having to apply expensive or potentially dangerous marks would be important both to improve our knowledge of their biology, and to establish the effectiveness of conservation

management. This Chapter determines if natural markings could be used for individual identification of *Powelliphanta,* and then tests whether this technique could be applied to management of the species.

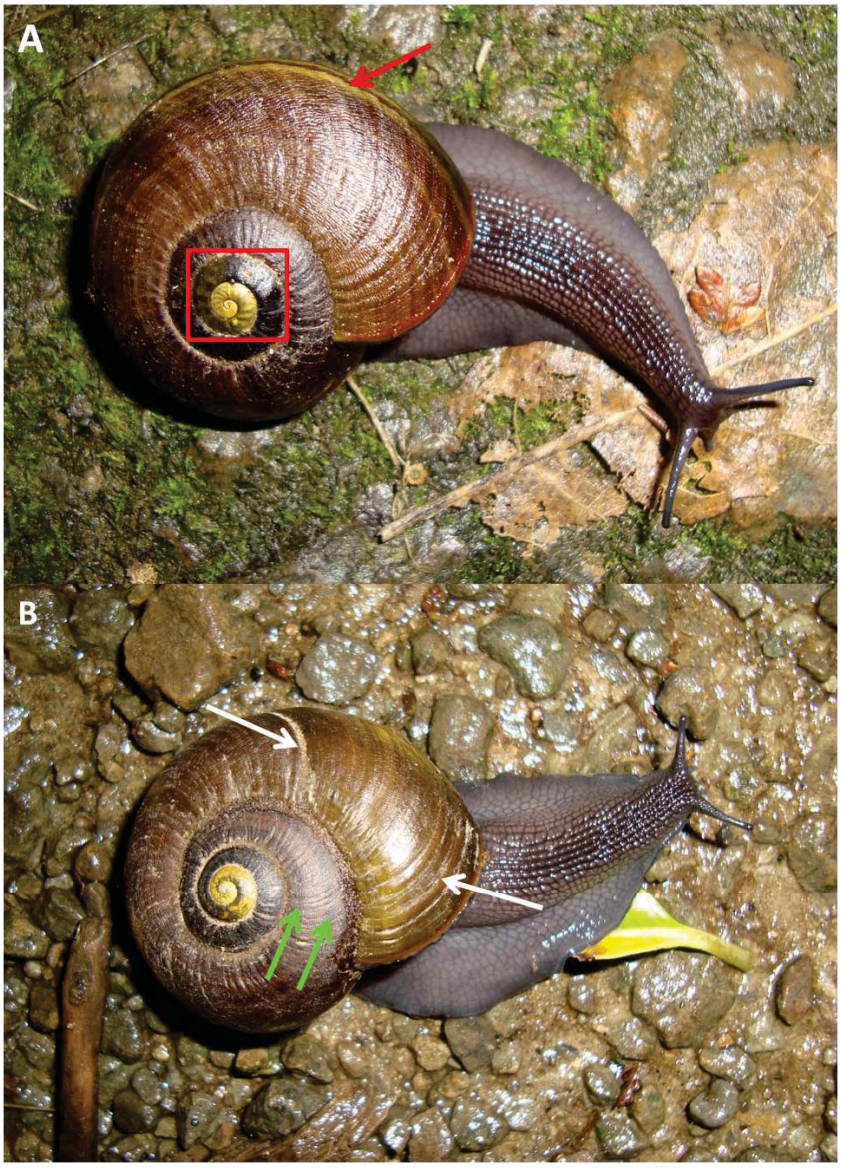

Figure 5.1. Two individuals of Powelliphanta traversi tararuaensis. A =The area encompassed by the red rectangle is the protoconch – the larval shell; the red arrow indicates a distinctive yellow colour band. B = White arrows indicate distinctive dents and ridges in the shell; green arrows point to a section of the banding pattern on the shell. Photo by the author.

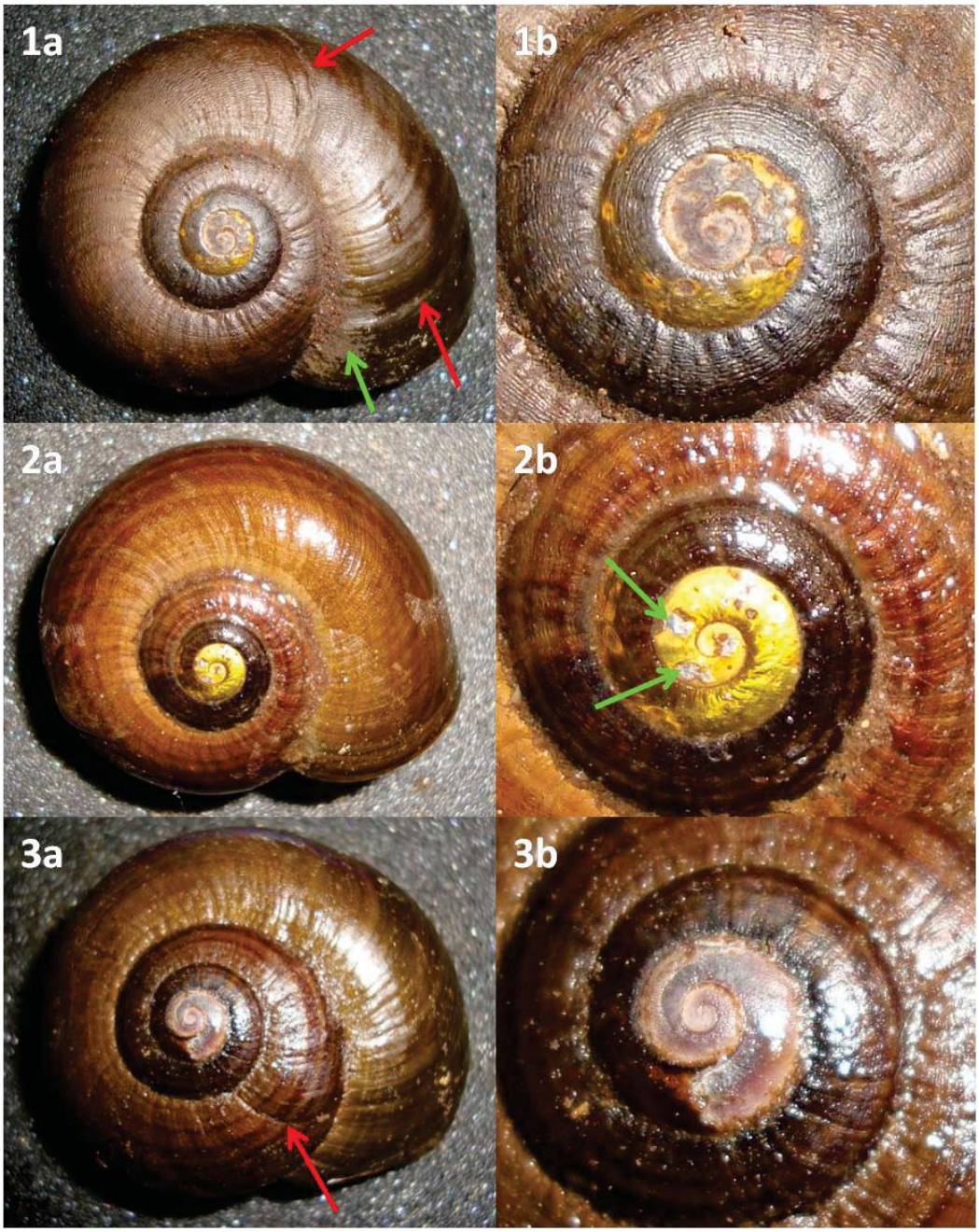

Figure 5.2. Variations in natural markings of individual snails. Numbers 1-3 correspond to individual snails, a =image of the full shell; b = close-up image of the protoconch. Individuals were found to differ significantly in the presence of dents and ridges (red arrows), colouration (entire shell between individuals 1 and 2; protoconch in all three animals) and marks on the shell (green arrows). Photo by the author.

Methods

Data Collection

Snails from an area of the Kahuterawa Recreational Reserve were used to build a photographic database consisting of 55 recognisable individuals (for a description of the site, see Chapter Three).

During the months of August 2009 to March 2010, an approximately 200m section of the Back Track was patrolled during the snails' nocturnal active period. Every time an individual was encountered, photographs were taken of the dorsal side of its shell using a digital camera (Sony Cyber-shot™). Prior to being photographed, snails were gently touched on the shell to encourage them to withdraw. This prevented any stress or injury to the animals which could be caused by the camera flash. If a low quality image was obtained, repeat pictures were taken. Each new individual encountered was issued with a unique identification number, corresponding to the date the animal was first catalogued. This was written on the ventral side of the animals shell, using a metallic ink marker, as recommended by Severns (2009). These photographs were used to then build a database of known animals.

On subsequent nights, reencounters with marked individuals were recorded and then animals were again photographed. These recaptures were added to the initial entry of that individual in the database.

Photograph Matching – Initial Evaluation

I initially evaluated the snail photos myself to ensure that *Powelliphanta* could be identified by their natural markings. This was possible as upon initial "capture" each snail was given a number-coded mark, and photographs of the individual were assigned to this number code. As a result I was able to browse the photographic database after it had been created, and visually assess whether photographs of snails on subsequent nights were "recaptures" without referring to the identification code of that individual. This posed a means for validating my ability to correctly match individuals, and assess accuracy by confirming the true match using the number codes of the individual snails. The computer-stored database allowed me to focus on certain areas of the shell when matching photographs, as I was able to zoom in on particular marks and patterns. *Powelliphanta* monitoring and conservation work is generally carried out by managers

and volunteers, however, and thus, I wanted to test the accuracy of photographic matching on a body of subjects who were consistent with this set of people.

Photograph Matching – Naive Subject Evaluation

To assess the accuracy of photographic identification by volunteers and managers involved in *P.t.tararuaensis* monitoring, a test was created and presented to a group of people. The test subjects were a mix of final year high school science students, given the task by their teacher as part of their biology curriculum. Test participants were given no training or tips, with the exception of basic directions on what was required of them for the test. There were four variations of this test created. Each person was given one of the four tests:

- Test set SD: participants were asked to match different photographs of the same individual snail taken on the same day.
- Test set SM: asked participants to match photographs of the same individual snail, but the time lapse between the two photographs was over six months.
- Test set PD was the same as test set SD, but the photographs given were images of the protoconch only (the first whorl of the snails shell – see Figure 5.1).
- Test set PM was the same as test set SM, but the photographs were images of the protoconch only.

There were 16 participants for each test. Each test consisted of five trials; a single trial is described below:

A picture of a known individual snail was given, along with a spread of 20 other photographs for comparison. 19 of these were negative matches, one photograph, depending on the test, was either a positive match taken on the same day of the given individual, or was a positive match of the given individual taken over six months later. The 19 incorrect profiles were selected at random from the database of snails, with the one correct profile inserted into the display spread in a random position among them. Test subjects were then required to match the photograph of the given animal with the corresponding positive profile in the 20 picture spread, and had the option of also declaring no match (new capture). Each trial was recorded as either a correct or incorrect match, and the time taken (minutes) to complete the full test (five trials) was also noted. The five trials were given in a random order within each subject's test.

Statistical Analysis

Data were analysed with the aid of SPSS (version 17.0.1, Dec. 1, 2008). A one-way ANOVA was performed to compare time taken (minutes) to complete the test as well as the total number of correct matches, with test type as a covariant. Where the overall one-way ANOVA was significant, pairwise means comparisons were performed using a Tukey's post hoc test.

Results

Photograph Matching – Initial Evaluation

My personal ability to match individuals of *P. t. tararuaensis* using photographs validated by unique number codes was very accurate (100%), regardless of the time lapse between photographs. The time taken to assess a single photograph was not recorded, although nearing the end of data collection, when the database approached n=50 individuals, it took approximately three hours per photograph. There was some evidence of change in marks on individuals after six months (Figure 5.5). Mark loss and gain also seemed to be heterogeneous, with some individuals appearing to gain new marks more rapidly than others (Figures 5.3, 5.4 & 5.5).

Photograph Matching – Naive Subject Evaluation

Participants took a significantly shorter time (minutes) on average to match photographs if the two images were collected on the same day ($F = 16.147$, $df = 3$, $p = 0.000$; Tables 5.1 & 5.2), and were quickest to complete the PD (mean = 14.625, SD = 3.263) and SD (mean = 16.063, SD = 3.586) tests.

People also scored significantly higher in total if they were asked to match a pair of photographs taken on the same day ($F = 10.024$, $df = 3$, $p = 0.000$; Tables 5.1 & 5.2), and the highest scores were gained for the PD (median = 5, range = 5-5) and SD (median = 5, range = 4-5) tests.

Table 5.1. Average (mean, standard deviation) time taken (minutes) to complete the snail photo ID tests, and average (median, minimum, maximum) scores for the four types of test. There were 16 test subjects and five trials per subject for each test type.

Test Type	Average Time Taken	SD	Average Number Correct	Minimum	Maximum
SD	16.063	3.586	5	4	5
SM	21.250	2.671	4	1	5
PD	14.625	3.263	5	5	5
PM	19.000	2.066	4	1	5

Table 5.2. Summary of Tukey's post hoc tests for pairwise means comparisons. p = p-value; SD, SM, PD, PM = the four test types.

Test A	Test B	Factor	Mean Difference	p
SD	SM	Time	-5.188	0.000
SD	PD	Time	1.438	0.519
SD	PM	Time	-2.938	0.033
SM	PD	Time	6.625	0.000
SM	PM	Time	2.250	0.148
PD	PM	Time	-4.375	0.001
SD	SM	Total Correct	1.500	0.001
SD	PD	Total Correct	-0.125	0.986
SD	PM	Total Correct	1.188	0.011
SM	PD	Total Correct	-1.625	0.000
SM	PM	Total Correct	-0.313	0.830
PD	PM	Total Correct	1.313	0.004

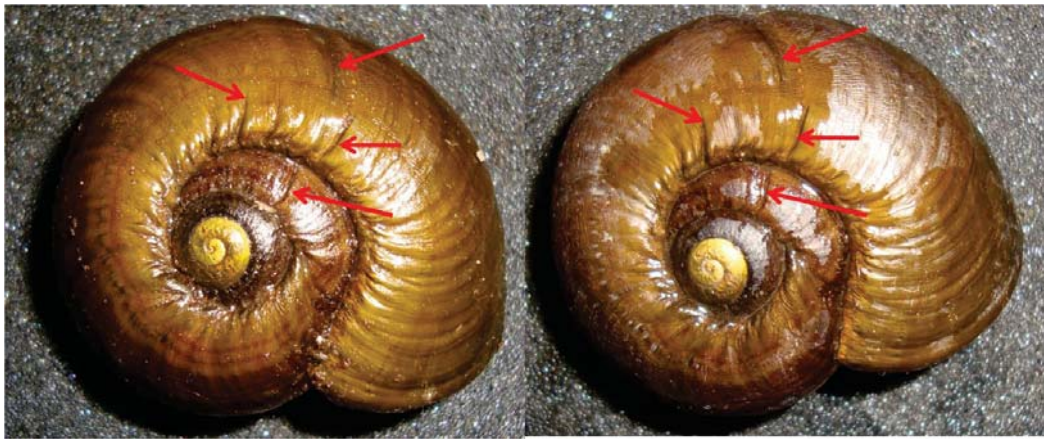

Figure 5.3. Full shell of the same snail at the first encounter with the individual (left) and six months later (right). Note the constant nature of the distinctive ridges (red arrows). Photo by the author.

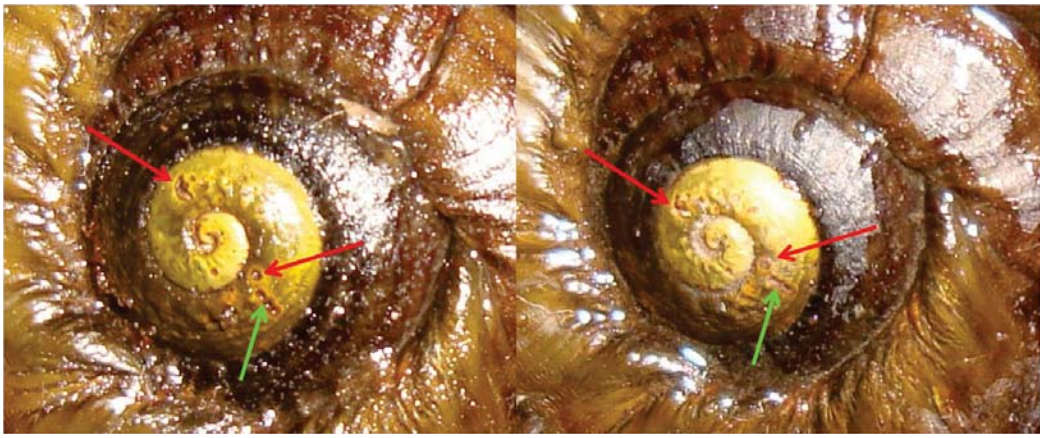

Figure 5.4. Protoconch of the same snail at the first encounter with the individual (left) and six months later (right), depicting the constant nature of marks on some animals (red arrows). Notice the striking degree of similarity, despite the fact mud has filled some dents of the shell (green arrows). Photo by the author.

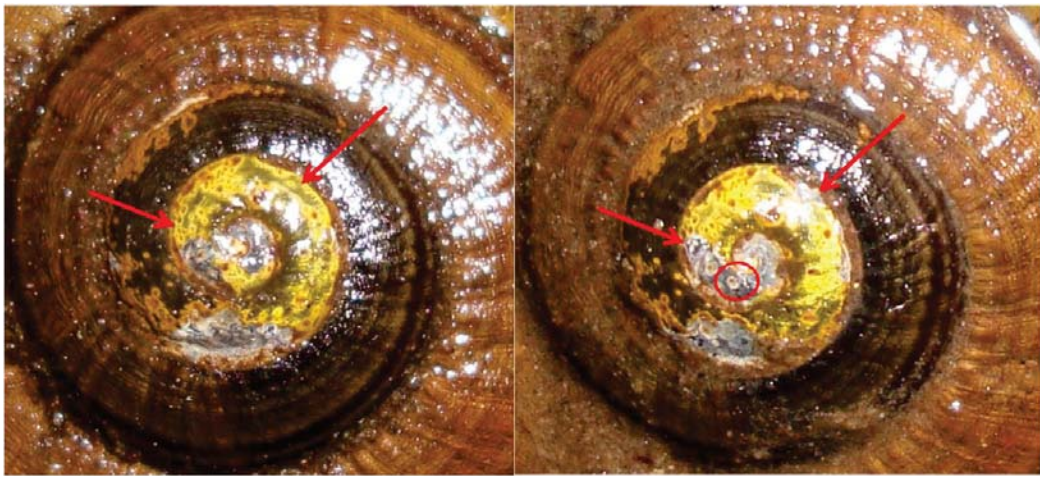

Figure 5.5. Protoconch of the same snail at the first encounter with the individual (left) and six months later (right), depicting natural mark change. Note the subtle differences between the two images (red arrows), especially the large gain of silver colouration highlighted by the red circle. Photo by the author.

Discussion

The paramount finding of this research is that *Powelliphanta* snails can be individually identified by the unique patterns and marks (dents and ridges) of their shells. These individual differences can be detected by humans, but the reliability of the identification can be affected by the natural changes that occur in shells over time.

Walker (2003) pointed out that in the areas where animals suffer a summer drought, growth periods can be seen in the shell of mature animals as thickened axial ridges. As all snails in a population probably experience these seasonal adverse effects on growth, there may be a number of animals sharing a similar pattern of ridges, which can make individual identification difficult. I found that in these cases the characteristics of the protoconch can act as a "fingerprint" for each individual, aiding identification. Whilst in this investigation there was no difference in the number of correct matches whether the whole shell or just the protoconch was available, the information held within the protoconch may prove to be invaluable for individual identification as image databases grow. It may be necessary to subject the database to a constant evolutionary process and continually update photographs of known individuals, as it is recognised that the

difficulty of re-identifying an individual using natural markings increases with time (Gubili *et al.* 2009). This was reflected in the naïve participants' drop in accuracy when matching photographs separated by a six month time lapse.

Poor photograph quality and observer/user inexperience frequently plague mark-recapture studies using natural markings (Forcada & Aguilar, 2000; Friday *et al.* 2000; Kelly, 2001; Jackson *et al.* 2006; Anderson, *et al.* 2007; Dawson & Miller, 2008; Schofield *et al.* 2008; Gubili *et al.* 2009; Harihar *et al.* 2010). Resulting mismatches can seriously bias population parameter estimates (Yoshizaki *et al.* 2009), and thus it is important to either correct for any error, or strive to improve photo quality and worker experience. Unlike more elusive or challenging photograph subjects such as hyenas and whales, the issue of photo quality in *Powelliphanta* can be sidestepped with ease. Repeat photographs can be readily gained as the animals are slow moving. Photographs can, thus, be conveniently added to the standard list of measurements currently performed as part of *Powelliphanta* monitoring.

The results of this investigation suggest that untrained people can reliably match individuals from very recent photographs, but over longer time lapses the accuracy decreases. The high degree of correct identifications I achieved with my own level of experience extending only through the time of this investigation, suggests that to improve photograph-matching accuracy people may not necessarily require explicit training. This is a particularly appealing trait of the technique, as it heightens the promise of a wide range of users being able to reliably use such a database. Experienced workers are more accurate, and can speed up the matching process (Kelly, 2001). A level of training may boost the chances of positively identifying individuals which have not been encountered for longer periods, although this may require further investigation. It may also be worth considering computer-aided photograph matching for *Powelliphanta* photo ID. While this study demonstrates that it is possible to match small numbers of photographs by eye with little formal training, the task could rapidly grow to mammoth proportions as databases expand. Semi-automated computer matching programs have been developed for a number of species; including sharks (Arzoumanian *et al.* 2005; Van Tienhoven *et al.* 2007), cheetahs (Kelly, 2001) and salamanders (Gamble *et al.* 2008). Such programs can help with the inefficiency and unreliability headaches associated with

scouring large databases by eye (Arzoumanian *et al.* 2005), and could potentially assist with the hitch of user errors.

It would also be of value to further scrutinise the applicability of the photo ID technique to juvenile snails, as this investigation had a limited number of young *Powelliphanta* within the database (only a single animal with a maximum length less than 20mm), and thus gives little insight into this demographic group. This scarcity of juveniles is probably due to the difficulty of locating smaller individuals with the night spotlighting method, and possibly created a source of bias in the photographic database. Smaller animals are less likely to be seen in comparison to the more striking mature individuals, and thus the database could contain levels of juveniles not representative of the true population.

An often overlooked facet of using artificial marks to identify wildlife is the public perception of the chosen method. Public support is an integral ingredient in research, especially within the realms of government funded studies (Mellor *et al.* 2004). With the push towards considering the intrinsic value of wildlife, and the recent boost in community involvement in conservation, it is essential that researchers display both the suitability and humane nature of any chosen marking techniques (Mellor *et al.* 2004). Methods which appear to hinder, harm or grossly modify the appearance of the animal are likely to dissolve positive attitudes towards wildlife research (Mellor *et al.* 2004). In areas where there could be high level of public/wildlife contact, instilling an aura of humaneness about the marking method should be paramount. Kahuterawa Recreational Reserve is a heavily promoted outdoor leisure zone, and therefore such considerations are particularly applicable. Individuals of *P. t. tararuaensis* regularly venture onto the walking and mountain biking tracks in the reserve. It is likely that people in the area will see a live animal, and almost certain they will notice a remnant shell or two. While it could be argued that in general the level of consideration given by the public to our native snail fauna is relatively meagre, the recent plight faced by *P. augustus* over its loss of habitat to coal mining operations (Trewick *et al.* 2008; Walker *et al.* 2008) was highly publicised. This has raised awareness and concern for the genus. In places like Kahuterawa, where large numbers of shells readily accumulate in close proximity to the view of the public, discovery of a conspicuously tagged deceased snail could fuel suspicious about the humanity of such a marking method. In such areas photographic

identification could be a worthwhile endeavour, allowing for estimates of population parameters while avoiding many of the negative facets of marking wildlife.

Incorporation of photo ID into plot monitoring could be a valuable development in the quest to better understand the environmental requirements and population dynamics of the *Powelliphanta* land snails, something which is recognised as a key conservation goal (Walker, 2003). It would also offer a less invasive monitoring option than the current methodology (see Chapter Four). The consistency of the proposed photo ID method, applied over a range of *Powelliphanta* groups, would also allow for direct comparisons across populations and species – an exciting possibility for unlocking some of the mysteries surrounding relationships between taxa.

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6 Summary and Recommendations

The Current State of Powelliphanta traversi tararuaensis Populations

Monitoring populations of conservation concern is extremely important, because it warns of declines, as well as the effectiveness of management to mitigate them (Campbell *et al.* 2002). Powell, as early as in 1930's, noticed declines in populations of *P. traversi* as a result of predation and habitat destruction. He commented that the chances of survival for the *P. t. tararuaensis* subspecies were "*slender*" (Powell, 1946). Mercifully the subspecies persists, although at greatly reduced densities than those Powell (1946) voiced concern over (Walker, 2003). Predation, primarily by rodents, but also to a lesser degree by possums and pigs, is still a cause of snail declines (Chapter Two). The remaining habitat suitable for *P. t. tararuaensis* is fragmented, and is frequently degraded by the action of stock (Walker, 2003). In addition, the Shannon Forest stronghold for *P. t. tararuaensis* populations appears to be suffering a lack of recruitment (Chapter Two). It is unclear at this stage whether *P. t. tararuaensis* populations can continue to persist at lowered densities, and this is a common theme within the *Powelliphanta* genus (Walker, 2003). The current monitoring program for the snails lacks the means to achieve the answer to this uncertainty.

Limitations of the Current Monitoring Program

I believe management of a species should be a dynamic process, with information gleaned from monitoring programs feeding back into the system and contributing to the development of more effective and targeted management processes. Adaptive monitoring strategies have been identified as a method to achieve such objectives (Smit, 2003). In comparison to traditional monitoring methodologies, an adaptive approach is more fluid, actively incorporating new information to direct response where needed (Smit, 2003). As remarked by Ringold *et al.* (1999), adaptive monitoring "*overcomes barriers to monitoring design by adaptively implementing monitoring rather than waiting for new information or designing a system that does not anticipate new information*". The

current monitoring program for *P. t. tararuaensis* holds a degree of stagnancy, with abundance data gleaned presenting little in depth knowledge past the stamp of "decline" or "increase" (Chapter Two). Estimating demographic parameters is an important aspect of adaptive management (Smit, 2003), and could aid with achieving targeted conservation goals for *Powelliphanta* snails (Walker, 2003). Currently we estimate *Powelliphanta* densities to establish a base line "population" on which to rest management decisions (Walker, 1997). However, examining population size alone may not give enough information about the dynamics of the population for effective management (Chapter Two). To improve our chances to successfully and effectively manage *Powelliphanta* populations, it is necessary to investigate local demographic parameters, immigration and emigration (Walker, 2003). In the absence of this information many problems in the populations may be overlooked (Chapter Two). These observations are also true of both *Wainuia* and *Rhytida.* Their populations seem to be at even lower levels than *Powelliphanta* in the sites investigated (Chapter Two). However there is currently little knowledge surrounding natural abundance levels for *Wainuia* and *Rhytida,* and a monitoring program designed specifically for these genera would be of benefit. The current management regime for *Wainuia* and *Rhytida* is little more than an umbrella-like inclusion in the *Powelliphanta* management plan, but it is possible that the source of declines for these genera is completely different to that of *Powelliphanta.* Without a monitoring program focused on these taxa independently, factors causing population declines may be overlooked.

It is clear the current monitoring system holds other failings (Chapter Three). There appears to be a significant short-term effect on the behaviour of *P. t. tararuaensis*, whether this extends into the long-term or has population level effects remains unclear (Chapter Three). Although restricted by the limited time of Masterate research, findings of this study should be carefully considered as short-term effects may hold significance for the long-term, especially for threatened populations (Hylander *et al.* 2004). To indulge in a speculation, consider the case of *Powelliphanta augusta.* A recent study stemmed from the need for almost every individual in the species to be brought into captivity, as a result of the near complete destruction of its natural habitat by an opencast coal mine (Allan, 2010). The sliver of remaining habitat is now being used for translocations, and has been deemed to be "*at best sub-optimal*" (Trewick *et al.* 2008). The potential for success of such translocations has been questioned (Trewick *et al.*

2008), and I am prompted to contemplate it in regard to this study's findings (Chapter Three). If the snails are released into the sub-optimal habitat, and that habitat is then monitored for assessment of translocation success, to what extent will the monitoring disturbance put the population at risk? Coupled with a below par habitat, would the monitoring disturbance alter the release site enough to push it beyond tolerable status for *P. augusta*? Such questions incite the need for further research into aspects of the current monitoring program, as well highlighting the important findings of this study regarding new monitoring strategies for *Powelliphanta* snails.

The Application of New Monitoring Techniques

There is a desperate need for information on *Powelliphanta* life history traits and population dynamics (Walker, 2003). Monitoring programs, as of now, have neglected to explore mark-recapture methods for studying *Powelliphanta* populations; a surprising matter considering the hard shell of snails offers a convenient surface for applying marks, and has a degree of natural variation (Chapter Five). Methodologies for individual recognition of *Powelliphanta* snails (RFID and photographic identification) as described in this study (Chapters Four and Five) offer novel pathways to exploring uncertainties surrounding population dynamics and life history parameters. Photo ID, especially, is an exciting possibility for the monitoring and management of *Powelliphanta* snails. The unobtrusive nature of the technique, combined with habitat-friendly night searches of *Powelliphanta* survey quadrats, offers an answer to many of the problems with the current monitoring system identified by this study. The findings of this study should be considered when designing monitoring programs for invertebrates, as they may assist in mitigating behavioural effects of research and the gleaning of valuable data for assessing management and conservation progress.

Recommendations

- Continue predator control in all major strongholds of *P. t. tararuaensis*, especially rodent targeted schemes. Numbers of small *P. t. tararuaensis* are declining in Shannon (Chapter Two), and predation is still a major cause of death for snails.

- Investigate the long-term effects of the monitoring process (disturbances) on the movements and life history parameters of *P. t. tararuaensis.* The results of this study (Chapter Three) indicate that there are effects of the monitoring scheme

on the short-term behaviour of *Powelliphanta* snails. Whether these effects have long-term implications for monitored populations needs to be determined.

- Incorporate a mark-recapture based study into the monitoring program for acquisition of life history parameters and information on population dynamics of *Powelliphanta* land snails. The results of Chapter Four and Five imply this could be done using RFID or photographic identification.

- Further explore the response of rats to marked *Powelliphanta,* incorporating a lengthier testing period to assess the potential for learning in predators which have previously encountered marked individuals. Assess the behavioural responses of other known *Powelliphanta* predators towards marked snails (other rodents and possums especially).

- Develop computer-aided photograph matching software for use with photographic identification databases, allowing for conceivable application to the management of *Powelliphanta* snails. The findings of this study (Chapter Five) suggest that people can match photographs of individual snails, but accuracy decreases over time. Computer software could be developed to limit human error, especially for photographs separated by large time frames.

- Initiate a monitoring program for *Wainuia* and *Rhytida.* This could be done by establishing important habitat for both genera, and instigating a mark-recapture based study.

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Appendix A

Generalized Linear Model: Ohau Powelliphanta

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* Generalized Linear Models.

GENLIN Powelliphanta BY Area (ORDER=ASCENDING)

  /MODEL Area INTERCEPT=YES

 DISTRIBUTION=POISSON LINK=LOG

  /CRITERIA METHOD=FISHER(1) SCALE=1 COVB=MODEL MAXITERATIONS=100
MAXSTEPHALVING=5 PCONVERGE=1E-006(ABSOLUTE) SINGULAR=1E-012
ANALYSISTYPE=3(WALD) CILEVEL=95 CITYPE=WALD LIKELIHOOD=FULL

  /EMMEANS TABLES=Area SCALE=ORIGINAL COMPARE=Area CONTRAST=PAIRWISE
PADJUST=LSD

  /MISSING CLASSMISSING=EXCLUDE

  /PRINT CPS DESCRIPTIVES MODELINFO FIT SUMMARY SOLUTION.
```

Categorical Variable Information

			N	Percent
Factor	Area	1	4	20.0%
		2	8	40.0%
		3	4	20.0%
		4	4	20.0%
		Total	20	100.0%

Continuous Variable Information

		N	Minimum	Maximum	Mean	Std. Deviation
Dependent Variable	Powelliphanta	20	.00	36.00	10.3000	13.05898

Goodness of Fit[b]

	Value	df	Value/df
Deviance	22.369	16	1.398
Scaled Deviance	22.369	16	
Pearson Chi-Square	22.316	16	1.395
Scaled Pearson Chi-Square	22.316	16	
Log Likelihood[a]	-35.644		
Akaike's Information Criterion (AIC)	79.288		
Finite Sample Corrected AIC (AICC)	81.954		
Bayesian Information Criterion (BIC)	83.270		
Consistent AIC (CAIC)	87.270		

Dependent Variable: Powelliphanta

Model: (Intercept), Area

a. The full log likelihood function is displayed and used in computing information criteria.

b. Information criteria are in small-is-better form.

Omnibus Test[a]

Likelihood Ratio Chi-Square	df	Sig.
327.673	3	.000

Dependent Variable: Powelliphanta

Model: (Intercept), Area

a. Compares the fitted model against the intercept-only model.

Tests of Model Effects

Source	Type III		
	Wald Chi-Square	df	Sig.
(Intercept)	14.996	1	.000
Area	81.552	3	.000

Dependent Variable: Powelliphanta

Model: (Intercept), Area

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
(Intercept)	-1.386	1.0000	-3.346	.574
[Area=1.00]	4.673	1.0047	2.704	6.642
[Area=2.00]	.693	1.1180	-1.498	2.884
[Area=3.00]	4.543	1.0053	2.573	6.514
[Area=4.00]	0[a]	.	.	.
(Scale)	1[b]			

Dependent Variable: Powelliphanta

Model: (Intercept), Area

a. Set to zero because this parameter is redundant.

b. Fixed at the displayed value.

Parameter Estimates

Parameter	Hypothesis Test		
	Wald Chi-Square	df	Sig.
(Intercept)	1.922	1	.166
[Area=1.00]	21.633	1	.000
[Area=2.00]	.384	1	.535
[Area=3.00]	20.424	1	.000
[Area=4.00]	.	.	.
(Scale)			

Dependent Variable: Powelliphanta

Model: (Intercept), Area

Estimated Marginal Means: Area

Estimates

Area	Mean	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
1	26.7500	2.58602	21.6815	31.8185
2	.5000	.25000	.0100	.9900
3	23.5000	2.42384	18.7494	28.2506
4	.2500	.25000	-.2400	.7400

Pairwise Comparisons

(I) Area	(J) Area	Mean Difference (I-J)	Std. Error	df	Sig.
1	2	26.2500[a]	2.59808	1	.000
	3	3.2500	3.54436	1	.359
	4	26.5000[a]	2.59808	1	.000
2	1	-26.2500[a]	2.59808	1	.000
	3	-23.0000[a]	2.43670	1	.000
	4	.2500	.35355	1	.480
3	1	-3.2500	3.54436	1	.359
	2	23.0000[a]	2.43670	1	.000
	4	23.2500[a]	2.43670	1	.000
4	1	-26.5000[a]	2.59808	1	.000
	2	-.2500	.35355	1	.480
	3	-23.2500[a]	2.43670	1	.000

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable Powelliphanta

a. The mean difference is significant at the .05 level.

Pairwise Comparisons

(I) Area	(J) Area	95% Wald Confidence Interval for Difference	
		Lower	Upper
1	2	21.1579	31.3421
	3	-3.6968	10.1968
	4	21.4079	31.5921
2	1	-31.3421	-21.1579
	3	-27.7758	-18.2242
	4	-.4430	.9430
3	1	-10.1968	3.6968
	2	18.2242	27.7758
	4	18.4742	28.0258
4	1	-31.5921	-21.4079
	2	-.9430	.4430
	3	-28.0258	-18.4742

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable Powelliphanta

Overall Test Results

Wald Chi-Square	df	Sig.
193.624	3	.000

The Wald chi-square tests the effect of Area. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

Generalized Linear Model: Shannon Powelliphanta

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* Generalized Linear Models.

GENLIN Powelliphanta BY Year Quadrat (ORDER=ASCENDING)

  /MODEL Year Quadrat INTERCEPT=YES

 DISTRIBUTION=POISSON LINK=LOG

  /CRITERIA METHOD=FISHER(1) SCALE=1 COVB=MODEL MAXITERATIONS=100
MAXSTEPHALVING=5 PCONVERGE=1E-006(ABSOLUTE) SINGULAR=1E-012
ANALYSISTYPE=3(WALD) CILEVEL=95 CITYPE=WALD LIKELIHOOD=FULL

  /EMMEANS TABLES=Year SCALE=ORIGINAL COMPARE=Year CONTRAST=PAIRWISE
PADJUST=SEQSIDAK

  /EMMEANS TABLES=Quadrat SCALE=ORIGINAL COMPARE=Quadrat CONTRAST=PAIRWISE
PADJUST=SEQSIDAK

  /MISSING CLASSMISSING=EXCLUDE

  /PRINT CPS DESCRIPTIVES MODELINFO FIT SUMMARY SOLUTION

  /SAVE XBPRED STDDEVIANCERESID.
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Categorical Variable Information

			N	Percent
Factor	Year	2007	12	50.0%
		2009	12	50.0%
		Total	24	100.0%
	Quadrat	1	2	8.3%
		2	2	8.3%
		3	2	8.3%
		4	2	8.3%
		5	2	8.3%
		6	2	8.3%
		7	2	8.3%
		8	2	8.3%
		9	2	8.3%
		10	2	8.3%
		11	2	8.3%
		12	2	8.3%
		Total	24	100.0%

Continuous Variable Information

		N	Minimum	Maximum	Mean	Std. Deviation
Dependent Variable	Powelliphanta	24	1.00	15.00	5.0000	4.10726

Goodness of Fit[b]

	Value	df	Value/df
Deviance	12.760	11	1.160
Scaled Deviance	12.760	11	
Pearson Chi-Square	12.201	11	1.109
Scaled Pearson Chi-Square	12.201	11	
Log Likelihood[a]	-44.477		
Akaike's Information Criterion (AIC)	114.954		
Finite Sample Corrected AIC (AICC)	151.354		
Bayesian Information Criterion (BIC)	130.268		
Consistent AIC (CAIC)	143.268		

Dependent Variable: Powelliphanta

Model: (Intercept), Year, Quadrat

a. The full log likelihood function is displayed and used in computing information criteria.

b. Information criteria are in small-is-better form.

Omnibus Test[a]

Likelihood Ratio Chi-Square	df	Sig.
58.777	12	.000

Dependent Variable: Powelliphanta

Model: (Intercept), Year, Quadrat

a. Compares the fitted model against the intercept-only model.

Tests of Model Effects

Source	Type III		
	Wald Chi-Square	df	Sig.
(Intercept)	113.816	1	.000
Year	5.543	1	.019
Quadrat	42.341	11	.000

Dependent Variable: Powelliphanta

Model: (Intercept), Year, Quadrat

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
(Intercept)	.854	.4238	.024	1.685
[Year=1.00]	.440	.1870	.074	.807
[Year=2.00]	0[a]	.	.	.
[Quadrat=1.00]	1.253	.4629	.345	2.160
[Quadrat=2.00]	1.041	.4749	.111	1.972
[Quadrat=3.00]	1.099	.4714	.175	2.023
[Quadrat=4.00]	-.182	.6055	-1.369	1.004
[Quadrat=5.00]	1.153	.4683	.235	2.071
[Quadrat=6.00]	-.182	.6055	-1.369	1.004
[Quadrat=7.00]	-1.099	.8165	-2.699	.502
[Quadrat=8.00]	.154	.5563	-.936	1.245
[Quadrat=9.00]	.405	.5270	-.628	1.438
[Quadrat=10.00]	.405	.5270	-.628	1.438
[Quadrat=11.00]	-1.099	.8165	-2.699	.502
[Quadrat=12.00]	0[a]	.	.	.
(Scale)	1[b]			

Dependent Variable: Powelliphanta

Model: (Intercept), Year, Quadrat

a. Set to zero because this parameter is redundant.

b. Fixed at the displayed value.

Parameter Estimates

Parameter	Hypothesis Test		
	Wald Chi-Square	df	Sig.
(Intercept)	4.065	1	.044
[Year=1.00]	5.543	1	.019
[Year=2.00]	.	.	.
[Quadrat=1.00]	7.324	1	.007
[Quadrat=2.00]	4.810	1	.028
[Quadrat=3.00]	5.431	1	.020
[Quadrat=4.00]	.091	1	.763
[Quadrat=5.00]	6.059	1	.014
[Quadrat=6.00]	.091	1	.763
[Quadrat=7.00]	1.810	1	.178
[Quadrat=8.00]	.077	1	.782
[Quadrat=9.00]	.592	1	.442
[Quadrat=10.00]	.592	1	.442
[Quadrat=11.00]	1.810	1	.178
[Quadrat=12.00]	.	.	.
(Scale)			

Dependent Variable: Powelliphanta

Model: (Intercept), Year, Quadrat

Estimated Marginal Means 1: Year

Estimates

Year	Mean	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
2007	4.6667	.66442	3.3645	5.9690
2009	3.0046	.50140	2.0219	3.9873

Pairwise Comparisons

(I) Year	(J) Year	Mean Difference (I-J)	Std. Error	df	Sequential Sidak Sig.
2007	2009	1.6621[a]	.71314	1	.020
2009	2007	-1.6621[a]	.71314	1	.020

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable Powelliphanta

a. The mean difference is significant at the .05 level.

Pairwise Comparisons

(I) Year	(J) Year	95% Wald Confidence Interval for Difference	
		Lower	Upper
2007	2009	.2644	3.0598
2009	2007	-3.0598	-.2644

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable Powelliphanta

Pairwise Comparisons

(I) Year	(J) Year	95% Wald Confidence Interval for Difference	
		Lower	Upper
2007	2009	.2644	3.0598
2009	2007	-3.0598	-.2644

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable Powelliphanta

Overall Test Results

Wald Chi-Square	df	Sig.
5.432	1	.020

The Wald chi-square tests the effect of Year. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

Estimated Marginal Means 2: Quadrat

Estimates

Quadrat	Mean	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
1	10.2506	2.24648	5.8476	14.6536
2	8.2981	2.01959	4.3398	12.2564
3	8.7862	2.07857	4.7123	12.8601
4	2.4406	1.09260	.2992	4.5821
5	9.2743	2.13596	5.0879	13.4607
6	2.4406	1.09260	.2992	4.5821
7	.9762	.69059	-.3773	2.3298
8	3.4169	1.29331	.8820	5.9517
9	4.3931	1.46707	1.5177	7.2685
10	4.3931	1.46707	1.5177	7.2685
11	.9762	.69059	-.3773	2.3298
12	2.9287	1.19712	.5824	5.2751

Pairwise Comparisons

(I) Quadrat	(J) Quadrat	Mean Difference (I-J)	Std. Error	df	Sequential Sidak Sig.	95% Wald Confidence Interval for Difference	
						Lower	Upper
1	2	1.9525	3.00925	1	1.000	-6.9181	10.8231
	3	1.4644	3.04847	1	1.000	-7.3247	10.2534

	4	7.8100	2.49397	1	.096	-.4827	16.1026
	5	.9762	3.08722	1	1.000	-7.6668	9.6193
	6	7.8100	2.49397	1	.096	-.4827	16.1026
	7	9.2743[a]	2.34848	1	.005	1.3813	17.1674
	8	6.8337	2.58661	1	.344	-1.6738	15.3412
	9	5.8575	2.67619	1	.713	-2.8154	14.5303
	10	5.8575	2.67619	1	.713	-2.8154	14.5303
	11	9.2743[a]	2.34848	1	.005	1.3813	17.1674
	12	7.3218	2.54069	1	.199	-1.1013	15.7449
2	1	-1.9525	3.00925	1	1.000	-10.8231	6.9181
	3	-.4881	2.88779	1	1.000	-8.5729	7.5966
	4	5.8575	2.29257	1	.407	-1.6571	13.3720
	5	-.9762	2.92880	1	1.000	-9.1758	7.2233
	6	5.8575	2.29257	1	.407	-1.6571	13.3720
	7	7.3218[a]	2.13284	1	.035	.2099	14.4338
	8	4.8812	2.39335	1	.791	-2.7719	12.5344
	9	3.9050	2.49020	1	.976	-3.9062	11.7161
	10	3.9050	2.49020	1	.976	-3.9062	11.7161
	11	7.3218[a]	2.13284	1	.035	.2099	14.4338
	12	5.3694	2.34348	1	.632	-2.2556	12.9943
3	1	-1.4644	3.04847	1	1.000	-10.2534	7.3247
	2	.4881	2.88779	1	1.000	-7.5966	8.5729
	4	6.3456	2.34448	1	.303	-1.3909	14.0821
	5	-.4881	2.96915	1	1.000	-8.8006	7.8244

	6	6.3456	2.34448	1	.303	-1.3909	14.0821
	7	7.8100[a]	2.18868	1	.022	.4919	15.1280
	8	5.3694	2.44304	1	.713	-2.5639	13.3026
	9	4.3931	2.53792	1	.948	-3.6603	12.4465
	10	4.3931	2.53792	1	.948	-3.6603	12.4465
	11	7.8100[a]	2.18868	1	.022	.4919	15.1280
	12	5.8575	2.39425	1	.495	-1.9622	13.6771
4	1	-7.8100	2.49397	1	.096	-16.1026	.4827
	2	-5.8575	2.29257	1	.407	-13.3720	1.6571
	3	-6.3456	2.34448	1	.303	-14.0821	1.3909
	5	-6.8337	2.39531	1	.212	-14.7628	1.0953
	6	.0000	1.54358	1	1.000	-3.6857	3.6857
	7	1.4644	1.29179	1	1.000	-2.5332	5.4619
	8	-.9762	1.69102	1	1.000	-5.9272	3.9747
	9	-1.9525	1.82682	1	1.000	-7.6057	3.7008
	10	-1.9525	1.82682	1	1.000	-7.6057	3.7008
	11	1.4644	1.29179	1	1.000	-2.5332	5.4619
	12	-.4881	1.61895	1	1.000	-5.0206	4.0443
5	1	-.9762	3.08722	1	1.000	-9.6193	7.6668
	2	.9762	2.92880	1	1.000	-7.2233	9.1758
	3	.4881	2.96915	1	1.000	-7.8244	8.8006
	4	6.8337	2.39531	1	.212	-1.0953	14.7628
	6	6.8337	2.39531	1	.212	-1.0953	14.7628
	7	8.2981[a]	2.24317	1	.014	.7781	15.8181

	8	5.8575	2.49178	1	.581	-2.2655	13.9805
	9	4.8812	2.58480	1	.888	-3.3637	13.1262
	10	4.8812	2.58480	1	.888	-3.3637	13.1262
	11	8.2981[a]	2.24317	1	.014	.7781	15.8181
	12	6.3456	2.44400	1	.377	-1.6792	14.3704
6	1	-7.8100	2.49397	1	.096	-16.1026	.4827
	2	-5.8575	2.29257	1	.407	-13.3720	1.6571
	3	-6.3456	2.34448	1	.303	-14.0821	1.3909
	4	.0000	1.54358	1	1.000	-3.6857	3.6857
	5	-6.8337	2.39531	1	.212	-14.7628	1.0953
	7	1.4644	1.29179	1	1.000	-2.5332	5.4619
	8	-.9762	1.69102	1	1.000	-5.9272	3.9747
	9	-1.9525	1.82682	1	1.000	-7.6057	3.7008
	10	-1.9525	1.82682	1	1.000	-7.6057	3.7008
	11	1.4644	1.29179	1	1.000	-2.5332	5.4619
	12	-.4881	1.61895	1	1.000	-5.0206	4.0443
7	1	-9.2743[a]	2.34848	1	.005	-17.1674	-1.3813
	2	-7.3218[a]	2.13284	1	.035	-14.4338	-.2099
	3	-7.8100[a]	2.18868	1	.022	-15.1280	-.4919
	4	-1.4644	1.29179	1	1.000	-5.4619	2.5332
	5	-8.2981[a]	2.24317	1	.014	-15.8181	-.7781
	6	-1.4644	1.29179	1	1.000	-5.4619	2.5332
	8	-2.4406	1.46520	1	.960	-7.0642	2.1830
	9	-3.4169	1.62040	1	.768	-8.6461	1.8124

	10	-3.4169	1.62040	1	.768	-8.6461	1.8124
	11	.0000	.97625	1	1.000	-2.3310	2.3310
	12	-1.9525	1.38119	1	.992	-6.2569	2.3520
8	1	-6.8337	2.58661	1	.344	-15.3412	1.6738
	2	-4.8812	2.39335	1	.791	-12.5344	2.7719
	3	-5.3694	2.44304	1	.713	-13.3026	2.5639
	4	.9762	1.69102	1	1.000	-3.9747	5.9272
	5	-5.8575	2.49178	1	.581	-13.9805	2.2655
	6	.9762	1.69102	1	1.000	-3.9747	5.9272
	7	2.4406	1.46520	1	.960	-2.1830	7.0642
	9	-.9762	1.95259	1	1.000	-6.6058	4.6533
	10	-.9762	1.95259	1	1.000	-6.6058	4.6533
	11	2.4406	1.46520	1	.960	-2.1830	7.0642
	12	.4881	1.75998	1	1.000	-4.4392	5.4154
9	1	-5.8575	2.67619	1	.713	-14.5303	2.8154
	2	-3.9050	2.49020	1	.976	-11.7161	3.9062
	3	-4.3931	2.53792	1	.948	-12.4465	3.6603
	4	1.9525	1.82682	1	1.000	-3.7008	7.6057
	5	-4.8812	2.58480	1	.888	-13.1262	3.3637
	6	1.9525	1.82682	1	1.000	-3.7008	7.6057
	7	3.4169	1.62040	1	.768	-1.8124	8.6461
	8	.9762	1.95259	1	1.000	-4.6533	6.6058
	10	.0000	2.07093	1	1.000	-4.9448	4.9448
	11	3.4169	1.62040	1	.768	-1.8124	8.6461

	12	1.4644	1.89072	1	1.000	-4.1775	7.1062
10	1	-5.8575	2.67619	1	.713	-14.5303	2.8154
	2	-3.9050	2.49020	1	.976	-11.7161	3.9062
	3	-4.3931	2.53792	1	.948	-12.4465	3.6603
	4	1.9525	1.82682	1	1.000	-3.7008	7.6057
	5	-4.8812	2.58480	1	.888	-13.1262	3.3637
	6	1.9525	1.82682	1	1.000	-3.7008	7.6057
	7	3.4169	1.62040	1	.768	-1.8124	8.6461
	8	.9762	1.95259	1	1.000	-4.6533	6.6058
	9	.0000	2.07093	1	1.000	-4.9448	4.9448
	11	3.4169	1.62040	1	.768	-1.8124	8.6461
	12	1.4644	1.89072	1	1.000	-4.1775	7.1062
11	1	-9.2743[a]	2.34848	1	.005	-17.1674	-1.3813
	2	-7.3218[a]	2.13284	1	.035	-14.4338	-.2099
	3	-7.8100[a]	2.18868	1	.022	-15.1280	-.4919
	4	-1.4644	1.29179	1	1.000	-5.4619	2.5332
	5	-8.2981[a]	2.24317	1	.014	-15.8181	-.7781
	6	-1.4644	1.29179	1	1.000	-5.4619	2.5332
	7	.0000	.97625	1	1.000	-2.3310	2.3310
	8	-2.4406	1.46520	1	.960	-7.0642	2.1830
	9	-3.4169	1.62040	1	.768	-8.6461	1.8124
	10	-3.4169	1.62040	1	.768	-8.6461	1.8124
	12	-1.9525	1.38119	1	.992	-6.2569	2.3520
12	1	-7.3218	2.54069	1	.199	-15.7449	1.1013

2	-5.3694	2.34348	1	.632	-12.9943	2.2556
3	-5.8575	2.39425	1	.495	-13.6771	1.9622
4	.4881	1.61895	1	1.000	-4.0443	5.0206
5	-6.3456	2.44400	1	.377	-14.3704	1.6792
6	.4881	1.61895	1	1.000	-4.0443	5.0206
7	1.9525	1.38119	1	.992	-2.3520	6.2569
8	-.4881	1.75998	1	1.000	-5.4154	4.4392
9	-1.4644	1.89072	1	1.000	-7.1062	4.1775
10	-1.4644	1.89072	1	1.000	-7.1062	4.1775
11	1.9525	1.38119	1	.992	-2.3520	6.2569

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable Powelliphanta

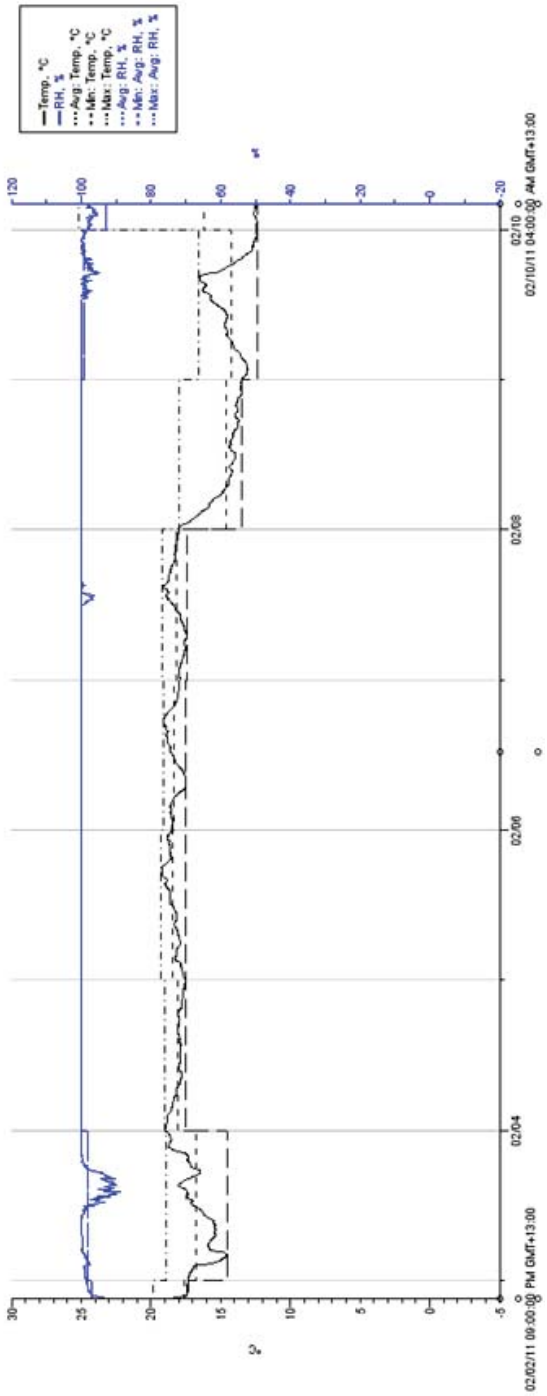
a. The mean difference is significant at the .05 level.

Overall Test Results

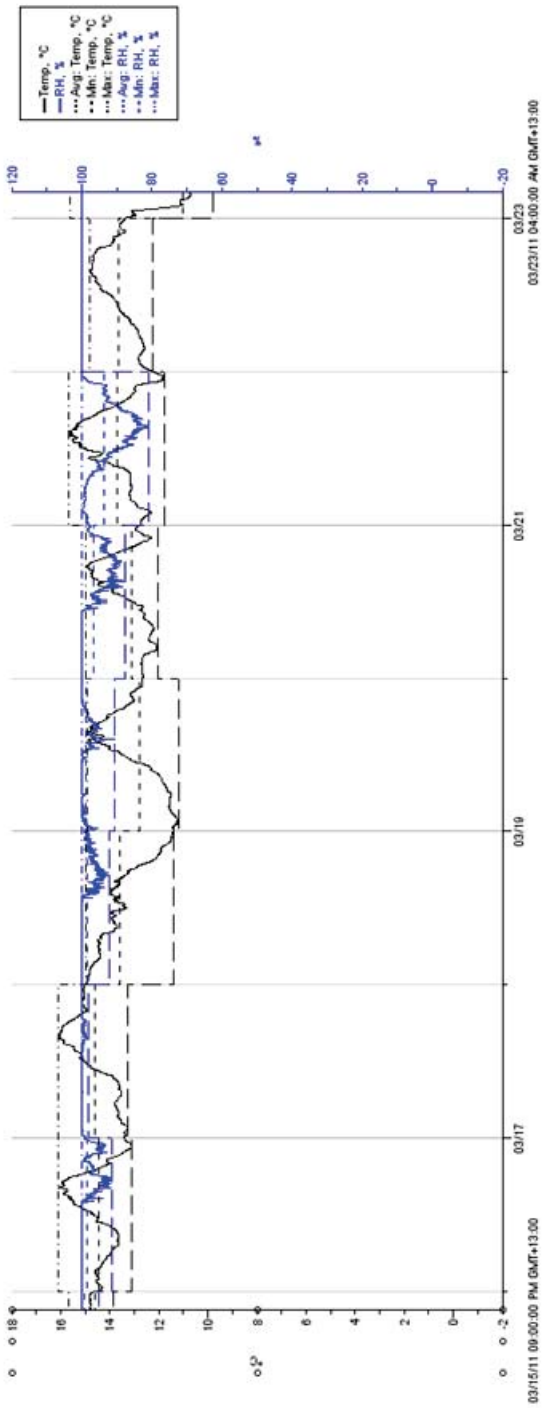
Wald Chi-Square	df	Sig.
51.785	11	.000

The Wald chi-square tests the effect of Quadrat. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

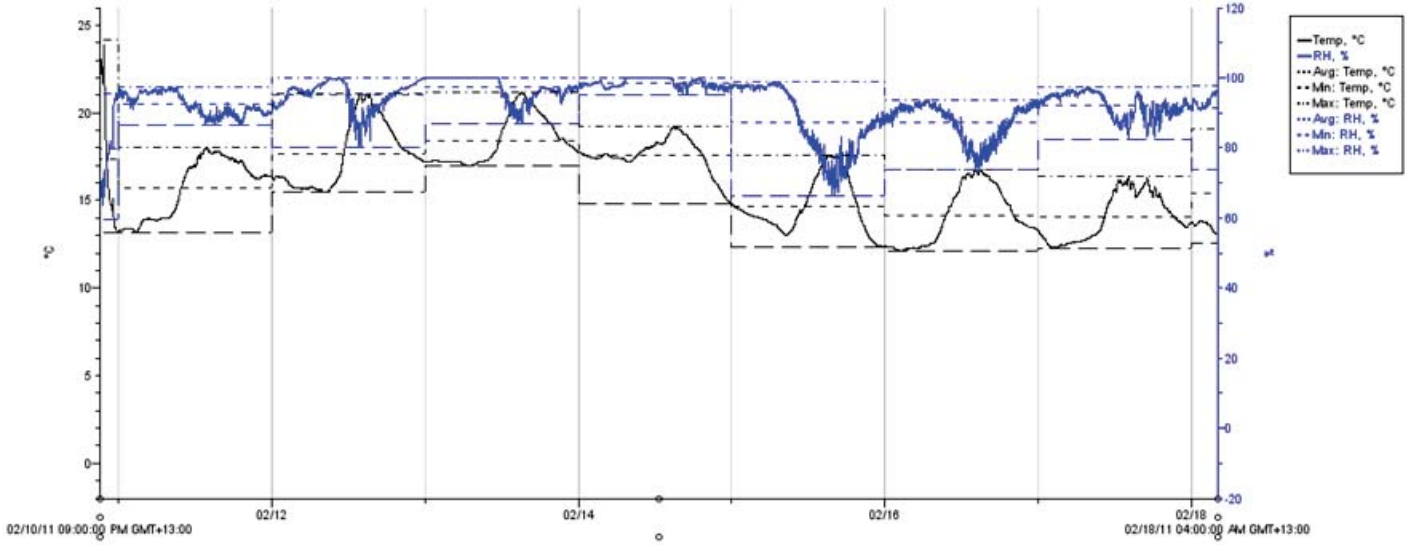
Appendix B



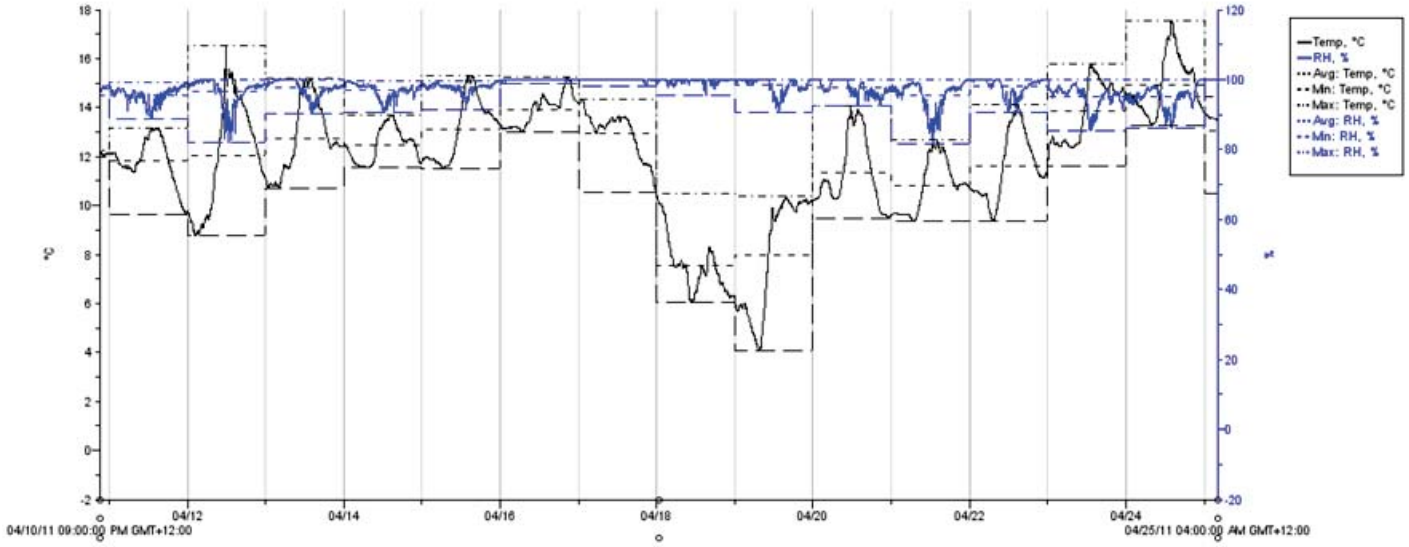
Weather data for Ohau non-disturbed site.



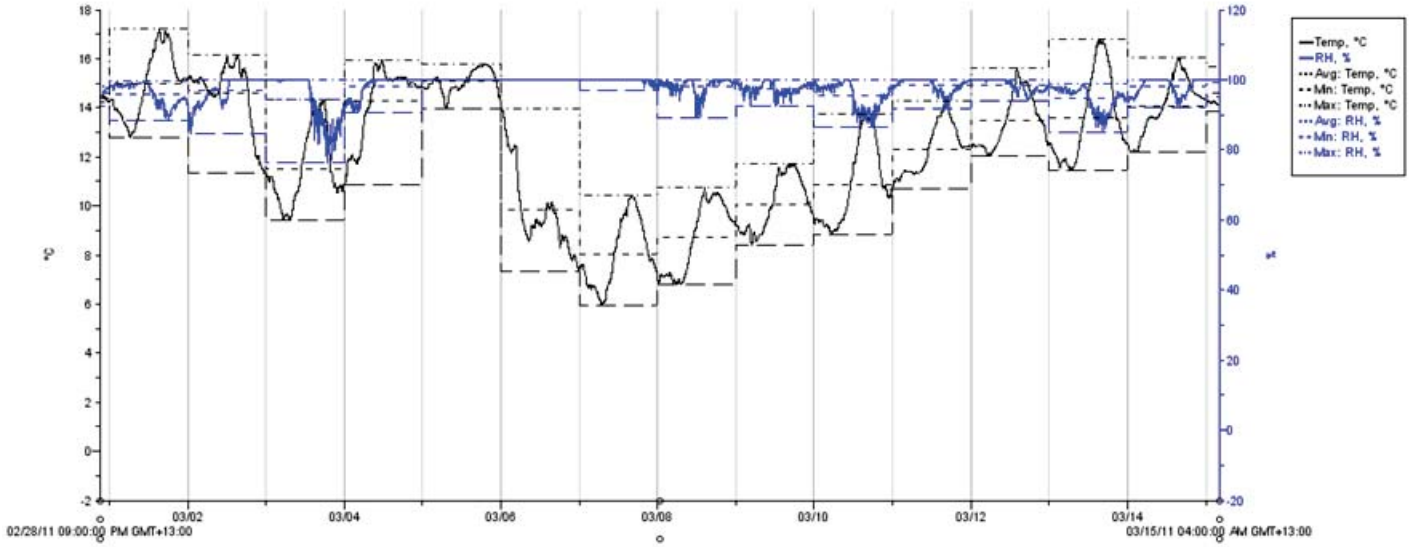
Weather data for Shannon non-disturbed site.



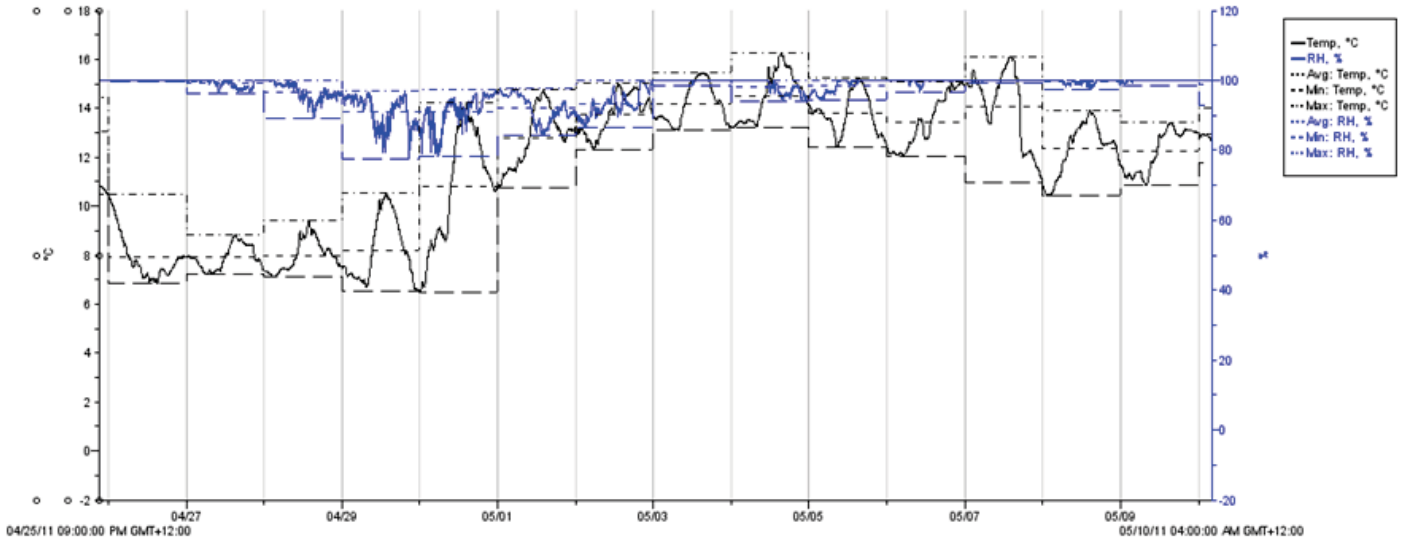
Weather data for Kahuterawa non-disturbed site.



Weather data for Ohau disturbed site.

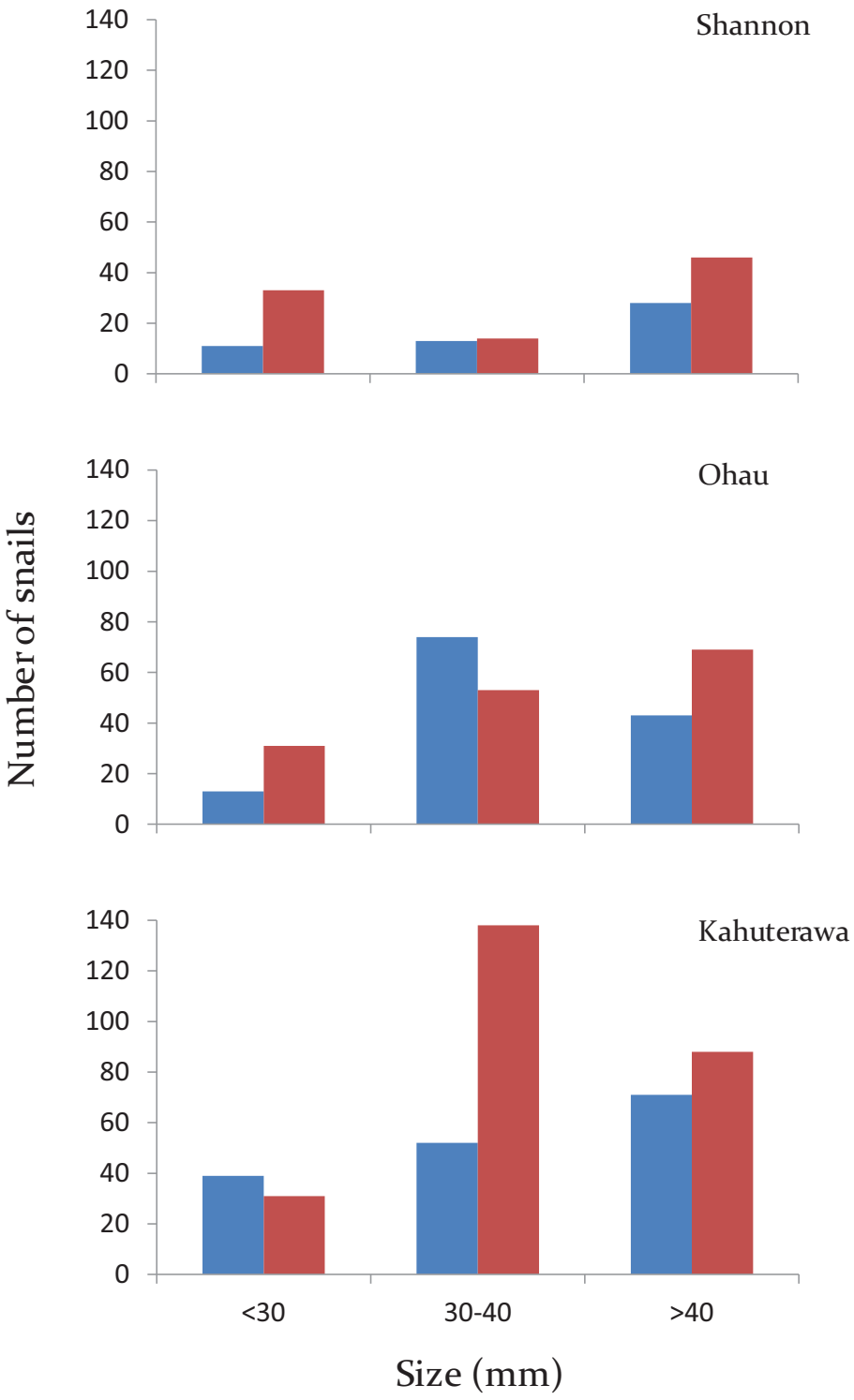


Weather data for Shannon disturbed site.

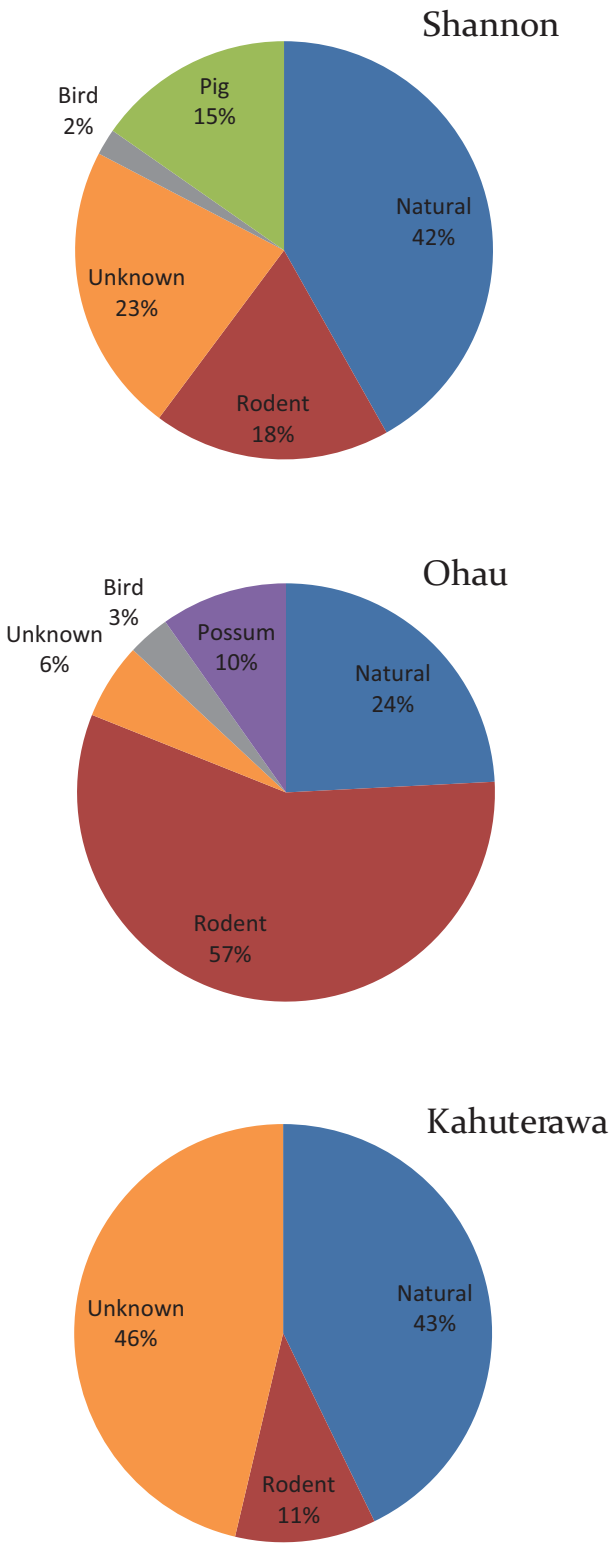


Weather data for Kahuterawa disturbed site.

Appendix C



Numbers of live (blue) and dead (red) snails found in each size class for the three sites.



Causes of death for snails found in the monitoring simulations at the three sites.

Appendix D

Results from construction of control models.

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Num. Par	QDeviance
Ohau						
Phi(.) p(avg temp)	96.6807	0	0.40098	1	1	50.9169
Phi(.) p(RH & max temp)	97.2085	0.5278	0.30797	0.7681	1	51.4447
Phi(.) p(min temp)	97.3308	0.6501	0.2897	0.7225	1	51.5669
Phi(.) p(t)	108.0625	11.3818	0.00135	0.0034	7	48.1301
Shannon						
Phi(.) p(RH & min temp & avg temp)	74.816	0	0.56772	1	1	41.705
Phi(.) p(max temp)	75.3654	0.5494	0.43136	0.7598	1	42.2545
Phi(.) p(t)	87.6612	12.8452	0.00092	0.0016	7	39.5344
Kahuterawa						
Phi(.) p(min temp)	145.1447	0	0.25573	1	1	70.2651
Phi(.) p(avg temp)	145.5589	0.4142	0.20789	0.8129	1	70.6793
Phi(.) p(max RH & max temp)	145.6909	0.5462	0.19461	0.761	1	70.8113
Phi(.) p(avg RH)	145.8394	0.6947	0.18069	0.7066	1	70.9598
Phi(.) p(min RH)	146.1176	0.9729	0.15722	0.6148	1	71.238
Phi(.) p(t)	153.5324	8.3877	0.00386	0.0151	7	65.3161

Appendix E

Real function parameters of Phi(.) p(disturb+day) for the Ohau disturbed quadrat. 95% confidence interval, with standard error and confidence intervals corrected for c-hat = 1.1780000.

Parameter	Estimate	Standard Error	Lower	Upper
1:Phi	1.0000000	0.0000000	1.0000000	1.0000000
2:p	0.4620317	0.0497103	0.3672214	0.5596701
3:p	0.4620317	0.0497103	0.3672214	0.5596701
4:p	0.4620317	0.0497103	0.3672214	0.5596701
5:p	0.4620317	0.0497103	0.3672214	0.5596701
6:p	0.4620317	0.0497103	0.3672214	0.5596701
7:p	0.4620317	0.0497103	0.3672214	0.5596701
8:p	0.4620317	0.0497103	0.3672214	0.5596701
9:p	0.3545021	0.0399060	0.2806753	0.4359781
10:p	0.2599075	0.0395683	0.1900586	0.3445078
11:p	0.1833834	0.0412037	0.1157947	0.2780188
12:p	0.1255675	0.0396773	0.0660510	0.2257496
13:p	0.0841021	0.0350413	0.0362812	0.1829858
14:p	0.0554611	0.0289210	0.0195105	0.1476778
15:p	0.0361884	0.0227151	0.0103678	0.1186067

Real function parameters of Phi(.) p(disturb+day) for the Shannon disturbed quadrat. 95% confidence interval, with standard error and confidence intervals corrected for c-hat = 1.1690000.

Parameter	Estimate	Standard Error	Lower	Upper
1:Phi	1.0000000	0.0000000	1.0000000	1.0000000
2:p	0.5341220	0.0558796	0.4247154	0.6403414
3:p	0.5341220	0.0558796	0.4247154	0.6403414
4:p	0.5341220	0.0558796	0.4247154	0.6403414
5:p	0.5341220	0.0558796	0.4247154	0.6403414
6:p	0.5341220	0.0558796	0.4247154	0.6403414
7:p	0.5341220	0.0558796	0.4247154	0.6403414
8:p	0.5341220	0.0558796	0.4247154	0.6403414
9:p	0.3771076	0.0480145	0.2885412	0.4747198
10:p	0.2422494	0.0503641	0.1573412	0.3537428
11:p	0.1444353	0.0480056	0.0730777	0.2655119
12:p	0.0818499	0.0389549	0.0312661	0.1975795
13:p	0.0449584	0.0281105	0.0128788	0.1451914
14:p	0.0242554	0.0187953	0.0052144	0.1054561
15:p	0.0129567	0.0119621	0.0020944	0.0758720

Real function Parameters of Phi(.) p(disturb+day) for the Kahuterawa disturbed quadrat. 95% confidence interval, with standard error and confidence intervals corrected for c-hat = 1.2360000.

Parameter	Estimate	Standard Error	Lower	Upper
1:Phi	1.0000000	0.0000000	1.0000000	1.0000000
2:p	0.4787296	0.0382731	0.4047437	0.5536605
3:p	0.4787296	0.0382731	0.4047437	0.5536605
4:p	0.4787296	0.0382731	0.4047437	0.5536605
5:p	0.4787296	0.0382731	0.4047437	0.5536605
6:p	0.4787296	0.0382731	0.4047437	0.5536605
7:p	0.4787296	0.0382731	0.4047437	0.5536605
8:p	0.4787296	0.0382731	0.4047437	0.5536605
9:p	0.3481331	0.0311856	0.2897499	0.4114651
10:p	0.2369674	0.0317672	0.1803866	0.3046979
11:p	0.1529691	0.0315975	0.1006994	0.2255651
12:p	0.0950374	0.0278282	0.0527595	0.1652825
13:p	0.0575545	0.0221357	0.0267110	0.1196356
14:p	0.0342947	0.0163929	0.0132814	0.0856682
15:p	0.0202332	0.0115607	0.0065416	0.0608266