Some aspects of behaviour and ecology of the land snail *Powelliphanta traversi traversi* Powell (Rhytididae: Rhytidinae)

A Thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Zoology at Massey University

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Lake Papaitonga viewed from the southern end

Abstract:

Powelliphanta traversi traversi Powell was studied at two sites in the Horowhenua. The use of an harmonic radar allowed the snails to be relocated, and followed for 20 months in their natural habitat. Morphometrics, population sizes, diet, movement, dispersal, and predation were examined. Different formae (morphs) lived at each site but mean shell lengths (43.2 mm at Papaitonga, 42.41 mm at Makahika) did not significantly differ. Frequency histograms of shell length for live and dead *P. t. traversi* were of similar shapes and there were few small shells. This could suggest that mortality was constant regardless of age, that young grow rapidly, or they live for a long time once full sized. The mean growth of new shell to the lip of the shell was found to be 1.71 mm (range 0.11 - 6.82 mm).The densities were not significantly different at each study site at 282 snails ha^{-1} for Papaitonga and 300 snails ha^{-1} at Makahika. A significantly positive correlation was found between *P. t. traversi* presence and leaf litter depth. Karaka (*Corynocarpus laevigatus*) was the only plant that was consistently found in quadrats with high snail numbers. The number of empty shells in a quadrat was a poor predictor of the number of live snails present. *P. t. traversi* were nocturnal and moved slowly in comparison to the garden snail *H. aspersa. P. t. traversi* were not active continuously though the night, and moisture related factors were the only significant predictors of movement. The most active snail moved 152 m in 107 days. Maximum displacement from point of origin averaged 49.8% of total movement. I suggest movement could be random, but appeared to adhere to a home-range. Limited dispersal suggested that fragmented *P. t. traversi* colonies should be considered discrete populations. The primary predator of *P. t. traversi* was the ship rat *Rattus rattus*. There was no evidence of predation from the brushtail possum, *Trichosurus vulpecula*, an important *Powelliphanta* predator in other localities. Diet and water uptake of *P. t. traversi* was examined in the laboratory. *P. t. traversi* appeared not to drink, but rather obtained water via integumentary absorption. Full hydration was reached in around three hours. Earthworms were the only food items consumed in this study. The snails did not forage in dry conditions.

Prologue:

This thesis deals with several aspects of the ecology and behaviour of *Powelliphanta traversi traversi.* Each chapter is intended to encompass a subject area and stand alone. For brevity, and to reduce repetition, reference will be made to other chapters where appropriate. Because of this format, relevant literature reviews and references are included in each chapter rather than together at the end of the thesis in their own respective sections. This will enable all the information in a subject area to be presented where most appropriate.

Acknowledgments:

I always intended to do as much of this thesis as independently as possible. For this reason it is somewhat of a surprise to see how many people have aided me in the quest for the final product. I do not want to dwell too much on individuals, not because their input was not important, but because it is all too easy to leave out someone who played an important role. It is also difficult to say who helped the most, from those who spent a great deal of their own time to come into the field with me, to the people who cheered me up with a quick comment when times were difficult.

Ideas gained in 'time wasting' conversations with students in TVL and the postgrad room helped create new directions of study and improved much of the work I did. These conversations also showed me that if you desire creativity then you must nurture it by allowing freedom and time to think. In my time in the Ecology Department I have been fortunate to associate with creative people, even if they are yet to recognise this quality in themselves yet. Creativity is a rare and important trait that is not always rewarded in today's time pressured academic world, but I am sure will pay off for these people in time.

For those who are not listed below but have helped, I am truly sorry and in no way does this detract from the assistance you have given me.

On an official level I thank the Wellington Shell Club for transport and thesis production costs, the Massey Research Fund for travel costs and the Department of Ecology who funded approximately half this project from Departmental funds.

Brian Carter from the Carter Observatory and Kevin McGill of Met Service New Zealand provided Sun, Moon and Climatological data to me happily and at no cost, a wonder in today's commercial world. The aid that, Raewyn Empson, Brian Gascoigne, and the Threatened Species Unit gave in providing me with permits made the project possible.

Ian Cooksley from the Department of Conservation Waikane Field Centre helped with his knowledge of local *Powelliphanta*, gave the initial go ahead with the project and provided me with a great deal of historical information. Kath Walker, the Conservancy Advisory Scientist for the Department of Conservation Nelson / Marlborough Conservancy helped by identifying predators from damaged shells, gave me advice, and selflessly provided me with her work prior to publication. Both Ian Cooksley and Kath Walker allowed me to use numerous personal comments as did Murray Efford from Landcare in Dunedin. Murray also helped with the methodology of faecal analysis. David Havil of the Manawatu Polytechnic provided invaluable help with Rat Indexing and shell analysis. He took time out from work to help me set trap lines as well as providing the traps themselves. Gary Barker from Landcare in Hamilton helped me add the finishing touches to this thesis with the provision of species names and naming authors for several exotic molluscan species.

I thank my father Carrick for his inspiration, advice, criticism of drafts and financial support. My sister Cathy helped greatly in the field and remains one of the few social workers with snail hunting skills, although she always seems to leave this off her CV. My Grandfather Keith Flemming funded me through several of my undergraduate years, without him I wouldn't have even started this project.

An incredible number of people gave their time to help me in the lab, the bush or with ideas. Of special note were Halema Flannagan and Cathy Lake who helped with vegetation surveys and taught me a lot about things botanical. Grant Blackwell both explained how to conduct my predator density experiments, and helped me set them up. He was also invaluable in improving my understanding predator-prey interactions. Jay McCartney along with Nick Gillingham helped finish off the majority of my quadrat searching and continually provided ideas, insights and support. Anita Kauraria, Chris Currie and Kim McBreen, also ended up in the bush helping when they least expected it. Adam Broadley, Tamsin Ward-Smith and Penny Aspin helped with setting up video equipment and photography. Vaughn Keesing helped me a lot at the start, and Gavin Hunt helped at the end. Emma Baraclough helped me in so many intangible ways and I wish her the success that she so richly deserves.

Within our Department, many staff generously gave their time and advice whenever needed. They were Drs. Murray Potter, Ian Henderson, Gillian Rapson, and Russel Death. Ian Latta helped immensely early on with electronic advice, Jens Jorgenson for sorted out equipment and provided tools and Paul Barrett provided and fixed the thermohydrograph. Barbara Just was very good to me and showed that finding and acquiring equipment is best left to professionals. The secretarial staff of Petra, Erica, Kirsty, Sheila, Karen, and Jodie are friends and always did more than their jobs required. Thankyou to Liz Nicholas from the Department Plant Biology and Biotechnology who allowed me to use room A25 and a special thanks to Associate Professor David Fountain and Jenny McDonald also from Plant Biology for their support and enthusiasm at a difficult time for me.

I am indebted to Suzanne Bassett who was a mine of information in putting this thesis together. She showed me that strength must first come from within and that in the end persistence pays off.

I would particularly like to thank my supervisors, Drs Ian Stringer, Alistair Robertson and Gabor Lovei for their experience, varying specialist knowledge, advice, professional contacts, help in the field and revision of drafts. It must be hard to work with a student you see so rarely, but on the bright side we are still on talking terms!

I am grateful to Christian Cook for helping motivate me, reading drafts, for constructive criticism, and for giving me time to finish while working full-time. On that note, and finally, I would like to thank every one in the Animal Stress and Welfare Programme at M.I.R.I.N.Z. who gave me the motivation and time to finish this project at a incredibly difficult time for us all (it is not often that the person finishing a thesis is the least stressed person in a group). This of course

leads to the question, is this thesis a means to an end or a end unto itself? Well, I don't know, but at least its over.

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Chapter one

General Introduction

Powelliphanta is a terrestrial pulmonate genus that is endemic to New Zealand. Current classification has the genus placed in the family Rhytididae (Pilsbry, 1939). *Powelliphanta* was originally placed in the Streptaxacea, but is now included in the recently described Superfamily Rhytidacea (Solem, 1978). Members of *Powelliphanta* were once regarded as subgenera of *Paryphanta* Albers but they were accorded the status of a separate genus by Climo (1977a). Climo (1977a) distinguished *Powelliphanta* from *Paryphanta* anatomically. He stated that *Powelliphanta* possesses a spermatheca and a long, thin penis with a central pigmented stripe, while *Paryphanta* has a greatly reduced penis and lacks a spermatheca. Powell (1979) noted that *Powelliphanta* and *Paryphanta* also differ in that the eggs of *Powelliphanta* always have a cuticle or periostracum while *Paryphanta* eggs lack this feature. Eggs of both have a calcareous shell.

Classification within the genus *Powelliphanta* is more contentious. Powell (1979) named ten species and 37 subspecies, whereas Climo (1977b) recognised two species and five to nine subspecies (depending on his recognition of the subspecies of *P. gilliesi*). Parkinson (1979), recognised six species and 28 subspecies. Meads, Walker, and Elliot (1984), the only paper which focussed on the entire genus, followed Powell's 1979 classification but acknowledged the other classifications. This situation will probably be resolved by electrophoretic analysis being undertaken by K. J. Walker (*in prep.*).

The Rhytididae was considered by Climo (1975a) to be the oldest family of carnivorous snails. It originated in the late Palaeozoic or early Mesozoic and its members are widespread, occurring in South Africa, the Seychelles, Indonesia, Melanesia, the Caroline Islands, Samoa, Tonga and eastern parts of Australia (Climo, 1975a). Two genera of Australian snails, *Victaphanta* from Victoria and *Melavitrina* from Tasmania, are the closest relatives of *Powelliphanta* outside

New Zealand (Climo 1975a, 1977a). Climo (1975a, 1977a) considered that these two genera were the only members of a natural "*Paryphanta* - *Wainuia*" group that occurred outside New Zealand. This likely close phylogentic relationship is why *Victaphanta* was used as an outgroup for the electrophoretic testing K. J. Walker (1995, *pers comm*). I suggest that this "*Paryphanta* - *Wainuia*" group equates to a subfamily.

Knowledge of *Powelliphanta's* distribution throughout New Zealand is incomplete. Colonies of high density occur in certain areas, but their distribution on a nationwide scale is notable because of numerous disjunctions (Climo, 1975b). Climo (1975a) described their present distribution as a relict of populations from pre-Pleistocene times that had a major centre of radiation from the north of the South Island. Validated reports of *Powelliphanta* locations range from as far north as Mt. Taranaki (Parkinson, 1974) and the southern Kaimanawa ranges (Gillingham, 1994) to Resolution Island in Fiordland in the south (Climo, 1971). Other reports extend this range east to Lake Waikaremoana (Parkinson, 1979) and south-east to Lake Monowai and the Mataura range (Meads *et al.* 1984).

Powelliphanta was probably in existence before the Pleistocene but no fossils from that time, or earlier are known (Solem, 1959). Solem (1959) put this down to shell characteristics that made the mineralisation (fossilisation) process difficult. Post-Pleiestocene fossils, however, show that *Powelliphanta* occurred in the Wairarapa, parts of Hawkes Bay, Te Kuiti, and around the Wellington region (Dell, 1955). Some of these fossil shells were discovered in a peat bog less than 7000 years old (Harris, 1951, cited Dell 1955) so Dell suggested that radio carbon dating was required to determine their age. The results of this dating, if it was conducted at all, were never published.

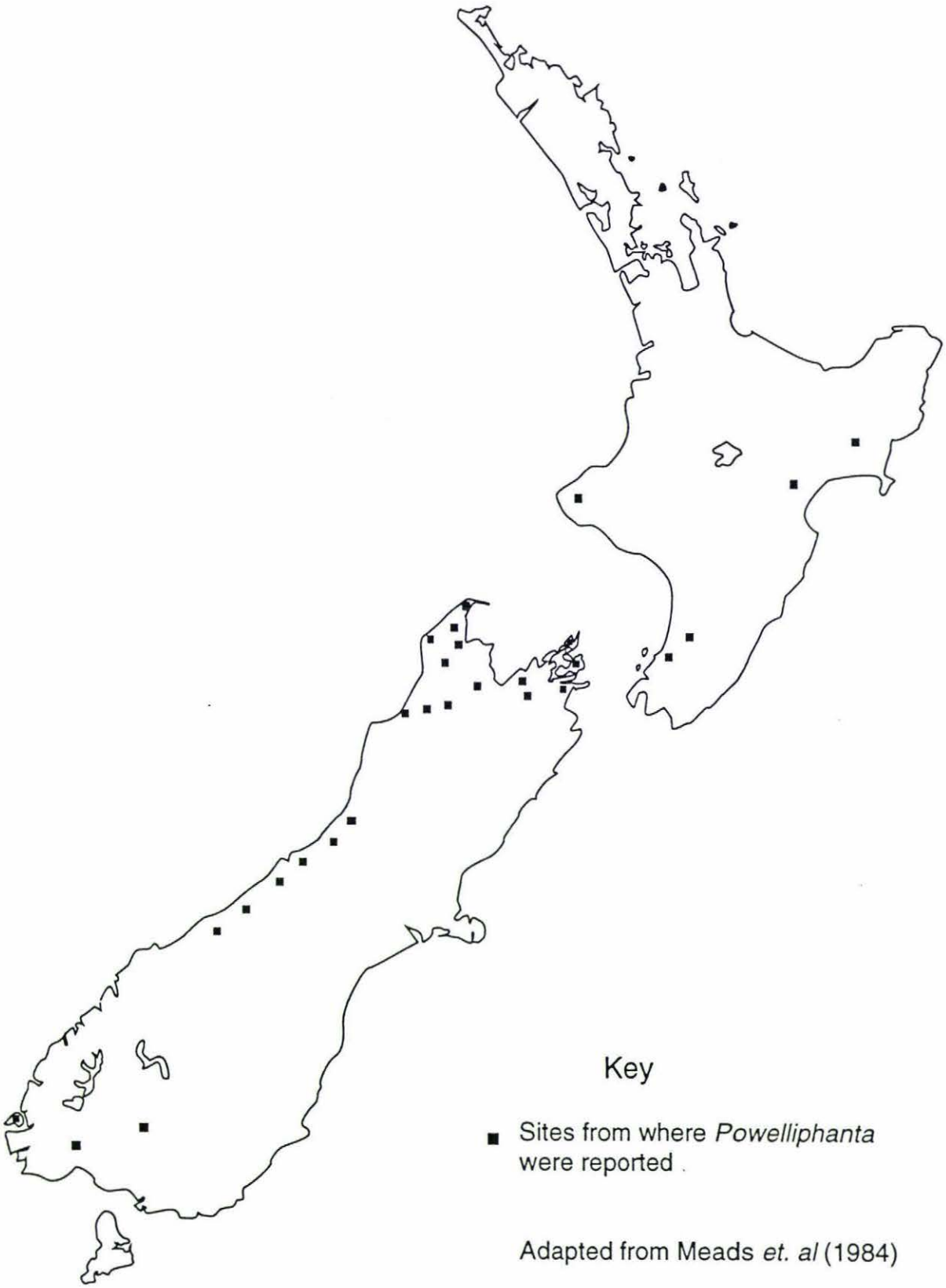

Figure 1.1: *Powelliphanta* distribution

Some aspects of the present distribution of *Powelliphanta* may be explained by former land connections. During the mid-Pleistocene and late-Pleistocene glaciations, large tongues of land joined the north western part of the South Island to Cape Egmont (Lewis and Carter, 1994) and on several occasions the Cook Strait Narrows was closed in the Wellington region (Powell, 1979). These land-bridges would have provided a route for *Powelliphanta* to disperse from the South island to its present locations in the North Island.

Powelliphanta traversi traversi Powell, the focus of this thesis, is the most common, and widely distributed of the two subspecies of *Powelliphanta traversi.* It occurs in the Horowhenua and Manawatu districts and in the Tararua ranges. The northern boundary to its distribution is probably the Manawatu Gorge because *Powelliphanta* north of this are classified as *P. marchanti* species (Powell, 1979). *Powelliphanta traversi otakia*, the other subspecies, is restricted to a few small colonies and its type locality near Otaki (Meads *et al.* 1984). *P. t. traversi* was first named *Paryphanta hochstetteri* var. *obscura* (Suter, 1913). It exists in five types which, although distinguishable, were not considered taxonomically significant by Powell (1979). These types are traversi (the original nominate subspecies), koputaroa, florida, latizona, and tararuaensis. In this thesis I use the term forma (plural formae) abbreviated to fa. for these distinguishable types. Meads *et al.* (1984) used the abbreviation fa. to distinguish types of *P. t. traversi* and forma was used in literature on land snail nomenclature. Forma, as used by Powell (1946), was defined by Pilsbry (1939) as "forms which show some differentiation, consistent in the colony, but either below the grade usually associated with subspecies, or restricted to single or a few colonies, thus having a much narrower range than is usually covered by a subspecies and without noticeable difference in the local conditions". Pilsbry (1939) suggested his definition of forma is equivalent to the 'microgeographic species of (the population geneticist) Dobzhansky'. Dobzhansky fully described his concept of the microgeographic species in Dobzhansky (1971).

P. t. traversi fa. tararuaensis, lives in the Tararua ranges at an altitude range between approximately 450m and 600m above sea level (Powell, 1938). It is and is considered by Parkinson (1979) to be the likely original type. The other formae occupy lowland habitat but are not found more than 240m above sea level (Powell, 1930, 1938, 1946, 1949). These formae were probably derived from fa. tararuaensis colonies that were washed down from the Tararua ranges during flooding (Parkinson, 1979). Each forma probably developed in geographical isolation from other colonies, but they are now sympatric in a few locations. Powell (1946), for instance, suggested that fa. traversi and fa. florida developed when they were separated several thousand years ago by the Ohau river. The two formae subsequently came into contact with one another when the river changed course. Today a fa. traversi-florida hybrid exists in Papaitonga Scenic Reserve.

P. t. traversi formae appear to be colour morphs that are distinguishable from one another by variation in banding pattern and colour. Powell (1936) justified differentiating between each type on the basis of these differences because the colour patterns are constant within the respective distributional areas of each formae, and because they were usually separated by distinct geographic boundaries. Genetic variation between the formae of *P. t. traversi* was measured by K. J. Walker (*in prep.*) who found that the differences were more significant than expected. All of the formae were classified as subspecies at one time or other but they were finally given their present status by Powell in 1979.

Little is known about the behaviour of most snails in their natural environment as they are frequently small, cryptic, and nocturnal. Those studies that exist are literally 'back yard' studies with data collected from court yards or disused gardens (eg. Potts, 1975). The notable exception to this was the study by Pollard (1975a).

Nothing was known about the movements or behavioural ecology of *P. t. traversi* prior to my study. Several works discussed the hypothetical origins and evolution of *P. t. traversi* (eg. Climo 1977b, Parkinson 1979) but only the paper

of Meads *et al.* (1984) has focussed on ecological or biological aspects of the species since original taxonomy, descriptive biology, and distribution of the species was conducted nearly 50 years ago (by Powell, 1949). Data for Meads *et al.* (1984) work was collected in 1979 and 1980 so it is possible that there were significant changes in the populations numbers and status since that time.

I studied *P. t. traversi* populations at two localities in the Horowhenua, one at Papaitonga Scenic Reserve and one at Makahika Scientific Reserve. A group of *P. t. traversi* were followed for 20 months with the aid of an harmonic radar. The radar enabled the snails to be accurately located deep within native bush without disturbing either them or their habitat. Short term, seasonal movement, and growth rates were examined. The density of live animals was able to be determined for the first time, and the morphometrics and size structure of the populations examined. Predation was re-examined and compared to previous work. In particular the affects of the brushtailed possum (*Trichosurus vulpecula* Kerr), only recently identified as a snail predator in other parts of New Zealand was examined.

P. t. traversi is now restricted to small remnants of its former habitat (Meads *et al.*, 1984). It is possible that these populations merely now survive where they do because their preferred habitat was destroyed. Vegetation within the *P. t. traversi* habitat was examined to determine if any habitat type is favoured by the snails.

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Chapter two

Study Sites and General Methods

Field work for this thesis was conducted at Papaitonga Scenic Reserve, Makahika Scientific Reserve and the Poulton block of Greenaways bush which was incorporated into Makahika Reserve near the end of the present study.

Papaitonga Scenic Reserve (114 ha.) encompasses Lake Papaitonga and is situated at the end of Buller road approximately five km south of Levin. It has a land area of 52.20 ha. including 1.3 ha. of islands. I estimate 30 percent of the land area (approximately 15.66 ha.) is either flax-koromiko shrubland, flax-raupo swamp or *Carex secta* sedgeland. The lake itself is a shallow (maximum depth 2.5 m, Archbold, 1982), naturally occurring dune lake occupying 61.80 ha. In 1973 the Horowhenua County Council designated the lake and surrounding bush a Proposed Scenic Reserve (Archbold, 1982) but at least some land surrounding the lake was put aside for the purpose of preservation in 1901. The land was finally purchased in 1980 and 1981, administration is by the Department of Conservation. The site has long been known for it's dense population of *Powelliphanta traversi traversi*, which exists in the traversi and florida forma, as well as a hybrid between the two (Powell, 1946).

Greenaways bush is a forest remnant on the Arapaepae Range situated approximately five km east of Levin near the end of Gladstone road, in the foothills of the Tararua Ranges. From 1982 the Wildlife Service recognised the importance of this area as land snail habitat (*unpubl. corres.*). The site is the type locality for *P. t. traversi* fa. latizona (Powell, 1949) and is one of the largest remaining refuges of the *P. traversi traversi* sub-species. Makahika Scientific Reserve is a 35 ha. block in the east of Greenaways bush. It has physical boundaries on three sides, farm land in the north, exotic forest in the south and Makahika stream in the east. The reserve could potentially be expanded on its western side but at present this land is privately owned. A fence was finished in August 1996 which prevented stock from entering the reserve from the north.

Makahika Scientific Reserve contains the only protected habitat for *P. t. traversi* fa. latizona.

General Methods

Data collection

All movement and predator density data were collected from Papaitonga Scenic Reserve.

Vegetation and snail number were sampled using quadrats. Serber (1982) reported that sampling by using a large number of small quadrats usually produced a smaller variance than a smaller number of large quadrats, provided that the quadrats are not so small that the majority are empty. Prior experience searching for the similarly sized land snail *Paryphanta busbyi watti* Powell (Rhytididae) indicated that a 25 m^2 or 50 m^2 quadrat would probably be to small and violate this requirement. Walker (1993) suggested that a 500 m^2 quadrat be used when surveying *Powelliphanta*. To search a quadrat of this size involved approximately a day of work by four or five people. My study was to be conducted by one worker so a quadrat size of 100 m^2 was chosen as the largest that could be practically searched in a single day.

Twenty two quadrats were examined in total. Seventeen were at Papaitonga with five located at Makahika. At Papaitonga quadrats were spaced evenly along two transects. The transects were chosen to incorporate the floral and geographical variations at the reserve (Figure 2.1). At Makahika Scientific Reserve the location of quadrats were predetermined randomly and located in the field with a global positioning compass (Silva, Sweden).

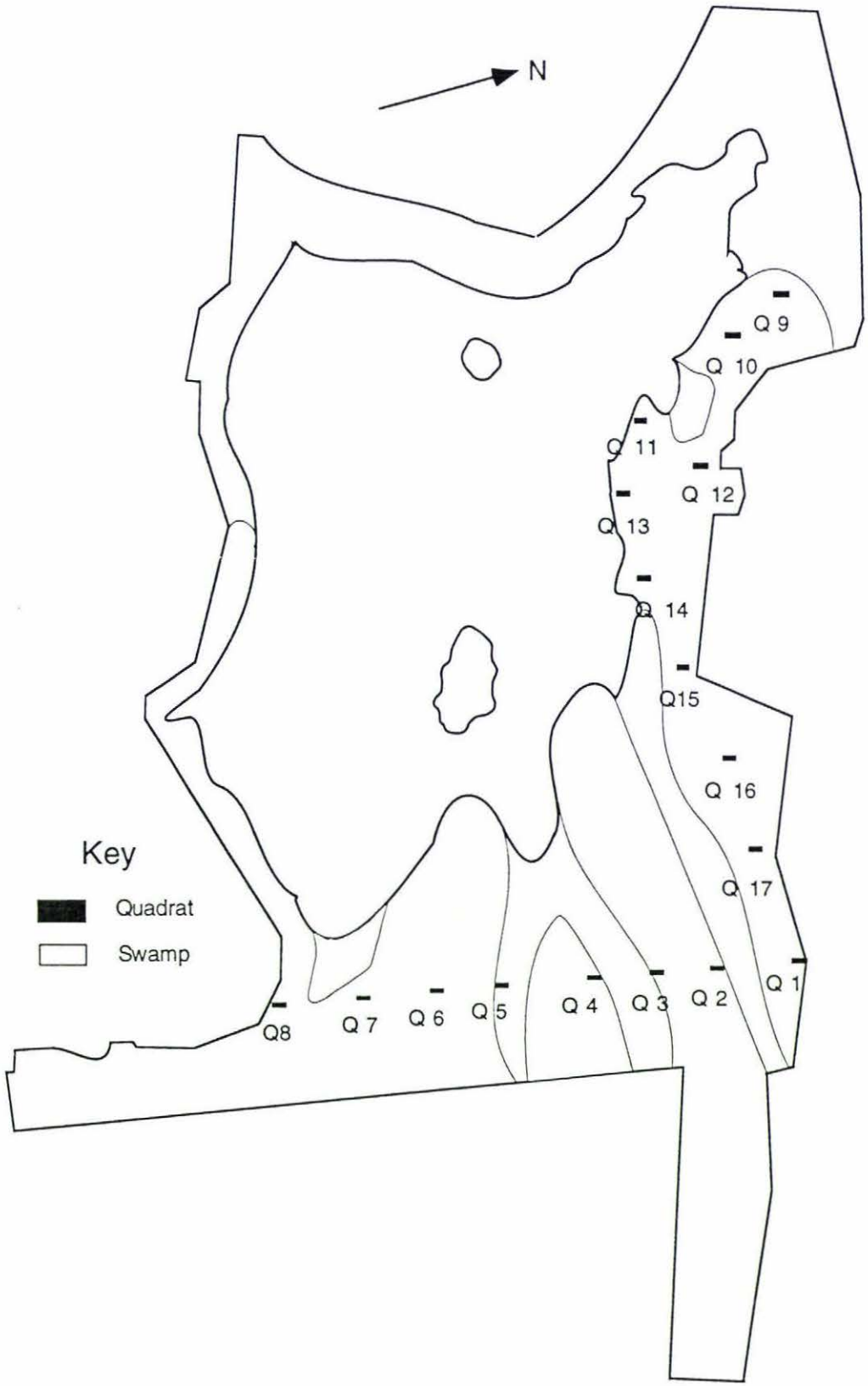

Figure 2.1: Map of Papaitonga Scenic Reserve showing quadrat locations
Scale 1.2 cm : 100 m

A plot of cumulative standard errors for the number of snails found per quadrat, versus the number of quadrats searched is shown in Figure 2.2. At Papaitonga the gradient of the cumulative standard error line levelled out after approximately 14 quadrats. This indicated that the 17 quadrats searched were probably sufficient to accurately sample snail number. The cumulative standard error curve for Makahika appeared to follow that for Papaitonga but did not level out. This suggested that at Makahika 14 rather than five quadrats would have been a more appropriate number to assess snail density. Time and access constraints precluded additional searching at Makahika.

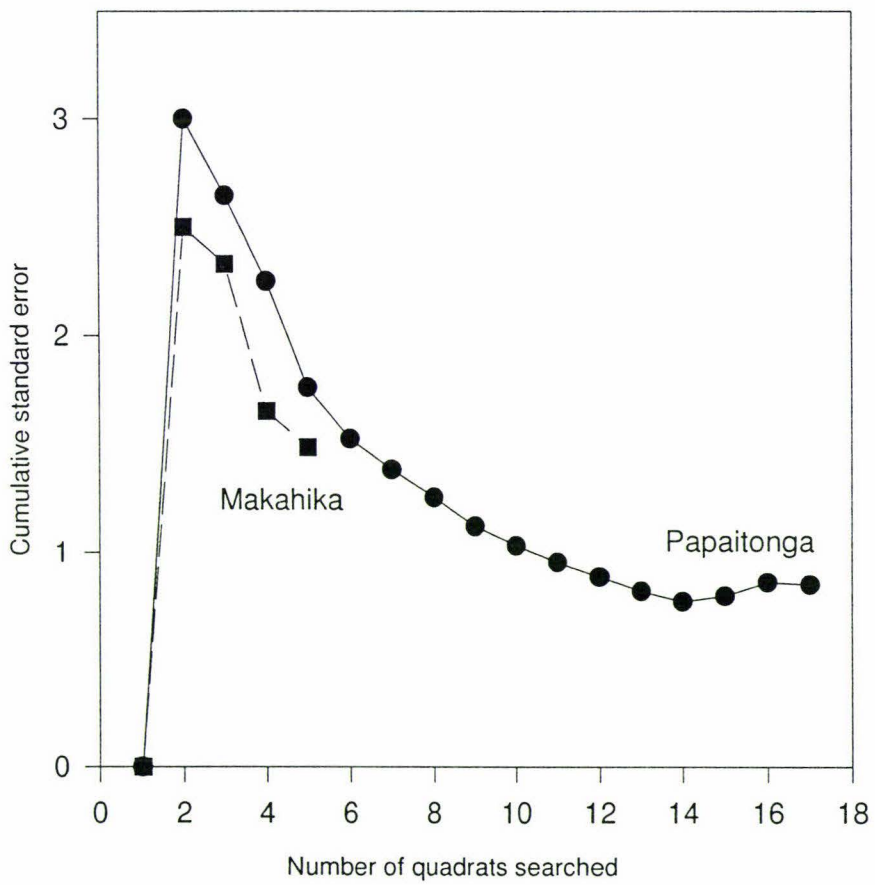

Figure 2.2: Cumulative standard errors for the number of snails found in each quadrat

Procedures to collect specimens and perform experiments:

P. t. traversi, was classed as 'Absolutely Protected Wildlife' in the 1980 amendment to the Wildlife Act 1953. It is also described as a Category C, third priority threatened species by Molloy, Davis, and Tisdall (1994). Makahika Scientific Reserve and Papaitonga Scenic Reserve are under the administration of the Department of Conservation. Permits were issued pursuant to Sections 53 and 56 of the Wildlife Act 1953 and Section 49 of the Reserves Act 1977 in order to conduct this research.

Both transponders and spool-and-thread devices were attached to *P. t. traversi* to enable relocation in the field. These devices are described in Appendix four and Chapter five respectively. The safety of the adhesives for the attachment of both the transponders and spools to *P. t. traversi* had not previously been documented. To assess acute effects of the adhesives that were to be used in this thesis tests were carried out on the common garden snail *Helix aspersa* Müller. These tests are documented in Appendix three.

All procedures were conducted with Massey University Animal Ethics Committee approval

Marking snails:

To re-identify snails each one found was assigned an individual number. This number was engraved (Easy Marker engraver) into the periostracum, on the dorsal surface one or two mm back from the shell lip. Care was taken not to engrave deep so as to penetrate the ostracum. Engraving is the usual method for applying indelible markings on *Powelliphanta* (K. J. Walker, 1995 *pers. comm.*) and other large land snails in New Zealand (I. A. N. Stringer, 1995 *pers. comm*). The technique is probably not safe for juvenile or small snails with thinner shells so these snails were marked by attaching small numbered tags embedded in epoxy resin. This method was not particularly effective in its original form but I. A. N. Stringer (1995, *pers. comm.*) subsequently improved the method so that it worked on *Paryphanta.*

Captive Observation:

Eight *P. t. traversi* captured from Papaitonga Scenic Reserve were observed in captivity between 01/12/95 and 30/01/96. The snails were kept in a laboratory and housed in a clear perspex terrarium with dimensions of 40 cm wide X 40 cm long X 40 cm high. An open skylight enabled captured snails to be exposed to the natural day-night cycle. Behaviour was monitored with an infra-red sensitive video camera (Panasonic BP 312, Japan.) using a time lapse video recorder (Panasonic AG 6040, Japan). At night the terrarium was illuminated with an infra-red lamp (Massey University design).

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Chapter three

Powelliphanta traversi traversi Powell (Mollusca: Pulmonata), its classification, morphometrics, population structure, and growth.

Abstract

The morphometrics of *P. t. traversi* were examined from snails found at Makahika Scientific Reserve and Papaitonga Scenic Reserve. There was no significant difference between shell lengths, widths, or aperture widths, within or between sites amongst either the live snails, or empty shells. The greatest maximum dimension attained by any snail was 54 mm. Mean growth from the lip of the shell was found to be 1.71 mm per year (range 0.11 - 6.82 mm), this corresponded to a mean 2.61 mm growth to the length of each shell. This growth rate was less than another larger *Powelliphanta* species. There was a significant negative correlation between initial size and growth rate. This could account for some of the negative skew from a normal distribution in the population structure (a greater number of larger snails). Few smaller sized shells of live or dead snails were found at both sites. This suggested that mortality was constant for snails of all sizes. The low number of dead snails found could suggest that few young are hatched or egg clutch size is relatively small.

Introduction

Powelliphanta land snails are endemic to New Zealand. Adult *Powelliphanta* vary in major dimension from 28mm to 90mm depending on species (Powell, 1979) and can vary greatly in shell colour and coiling (Climo 1978). Shells were popular with collectors until 1980 when the genus became 'absolutely protected wildlife' in the Amendment to the Wildlife Act 1953.

A. W. B. Powell, classified many members of the Paryphantidae in a series of papers during the 1930s and 1940s (Powell 1930, 1932, 1936, 1938, 1946, 1947, 1949). This family was later re-named Rhytididae by Climo (1977a) because of chronological precedence. At the same time Climo raised *Powelliphanta* to full generic status from it's former position as a sub-genus of *Paryphanta* (Climo, 1977a).

Ten species and 37 subspecies of *Powelliphanta* were recognised by Powell (1979). The original classification was made on the basis of physical variation. Powell typically distinguished species by differences in the size, shape and number of radula teeth (Powell, 1946) but he was not consistent. Two examples of this were documented in Powell (1946) where *P. gilliesi subfussca* Powell

and *P. s. superba* Powell were only accorded subspecies status even though they varied more in tooth number from other members of their respective species than is often found between species.
Other characteristics were used below the species level. Chief amongst these were differences in the quantity of conchin in the shell, the appearance of the parietal callus, base (underlying) shell colour, the presence of radial and spiral banding on the shell, and the shell size and shape (Powell, 1946).

Powell's 1979 revision of *Powelliphanta* reduced the six previously recognised subspecies of *Powelliphanta traversi* to two, *Powelliphanta traversi traversi* and *Powelliphanta traversi otakia*. Other *P. traversi* taxa that were formerly considered to be subspecies were relegated to 'forms without taxonomic status' (Powell, 1979). In this thesis I use the term 'forma', plural formae, abbreviation fa. for these forms (*Chapter one*). *Powelliphanta traversi traversi* now consists of the formae traversi, koputaroa, florida, latizona, and tararuaensis. *P. t. traversi* fa. traversi was the original *P. traversi* nominate subspecies prior to the revision. These formae generally occur in geographically distinct colonies in the Horowhenua plains and at lower altitudes on the Tararua ranges. The most notable exception to this is at Papaitonga Scenic Reserve where fa. traversi and fa. florida co-exist. The two formae remain pure at either end of the reserve but where their ranges over lap they have hybridised. Parkinson (1979) stated that a constant diagnostic feature for *P. traversi* is a strong colour band around the periphery of the shell. Differences between the various formae occur in the colour patterns on the dorsal and ventral surfaces of the shells.

Other terrestrial snails such as *Cepea* and *Partula* are known to exhibit a great range of colour and banding variation on their shells (Cowie, 1992). *Partula* are particularly interesting because many of our current ideas on the origin of species, partial speciation, and speciation were originated from studies on them (Murray and Clarke, 1980). The biological significance of these shell colour, and pattern differences is largely unknown. Some paler shelled *Partula* were found in sunnier, more exposed habitats. This led to the suggestion that pale shells were the result of selection for reflectance of solar radiation (Cain, 1983). Variability in shell size and shape was thought to be determined both genetically

and environmentally in some land snails, with size in particular being highly heritable (Cowie, 1992). *Partula taeniata* Morch and *P. suturalis* Pfeiffer have a complex relationship between population density, altitude and shell length (Clarke and Murray, 1971). Emberton (1982) reported that there was a higher incidence of shell colour banding, and increased shell elongation in damper, shaded valleys compared to drier, open ones.

Classification at the species level within *Powelliphanta* is contentious. One authority for instance (Climo, 1977a, 1978), classified *P. traversi* as a sub species of *Powelliphanta hochstetteri* while Parkinson (1979) retained *P. traversi* as a species that included *P. marchanti*, *P. hochstetteri obscura*, and *P. h. bicolour* as subspecies. Contemporary thought favours Powell's (1979) classification (K. Mahrfeld 1995, National Museum of New Zealand, K. J. Walker, 1996, *pers. comm*). Powell (1979), Climo (1977a, 1978), and Parkinson (1979), all agreed that the formae were not different enough to be accorded subspecies status. A recent publication (Spencer and Willan, 1995) offered a further alternative classification. This followed Climo (1978) to some extent but did not appear to be based on any additional information.

Different opinions over the classification of *P. t. traversi* also draws attention to the comments of Solem (1959) who stated that there are important conceptual differences in the methodology and systematic protocol between vertebrate and molluscan classification. This is in part because vertebrate nomenclature identifies a phyla where family and species have stabilised or are at least relatively well known, whereas molluscan nomenclature is, at present quite fluid. Murray and Clarke (1980), for example found that it was impossible to accommodate the Society Island *Partula* within a conventional Linnaean scheme. They concluded that it would be easy to argue for as little as four or as many as ten 'true' species, and that in most cases the subspecific or geographical race designation was inappropriate. A reductionist approach to land snail taxonomy would reduce the number of species and cast aside some morphological variation as superfluous. An alternative view that some 'superfluous' variation is significant and that following nomenclature as applied to vertebrates would be inappropriate.

Size and / or morphological characteristics can be used as a guide to age in many organisms (Nicol and Barry, 1980). Most gastropods for example show rapid early growth which then decelerates as size increases (Wilbur and Owen, 1964). Exceptions however do occur. Hadfield and Mountain (1980) showed that all age classes in *Achatinella mustelina* Mighels grow at the same rate.

Aspects of growth in New Zealand Rhytididae were described by Dell (1955) and Meads *et al* (1984). Dell (1955) estimated growth rates of *Paryphanta busbyi busbyi* Gray from growth rings on empty shells. Meads *et. al.* (1984) held five *Powelliphanta hochstetteri obscura* Beutler in captivity and measured their annual growth.

My study used shell morphometrics to examine *P. t. traversi* at Papaitonga Scenic Reserve and Makahika Scientific Reserve. These sites are more fully described in Chapter two. A comparison was made with Powell's records of shell sizes (Powell, 1932, 1936, 1938, 1946, 1949, 1979) to see if positive or negative factors have altered the maximum sizes that are attained. The change in the size of individuals over the course of this study will be examined to determine growth. The shell size frequency distributions of both live and dead snails, within and between study sites, will be used to compare population structures. Different formae of *P. t. traversi* live at each site. Shells from Papaitonga and Makahika will be compared to each other to see if the formae differ in shell measurements, and an attempt will be made to find the 'hybrid zone' between *P. t. traversi* fa. traversi, and *P. t. traversi* fa. florida at Papaitonga documented by Powell (1946).

Methods

Size structure of population:

Measurements were taken from the shells of all live and dead snails) found inside and outside quadrats (*Chapter two*) with a set of vernier callipers (Raco tools, accurate to ± 0.05 mm). Three measurements were taken (Figure 3.1), maximum length, width, and maximum size of shell opening (aperture size).

Measurements for some shells found outside quadrats were included in the results if they were novel by being very large or small. Because they were not found in per-unit-area searches they were not used for the size related population statistics. To use shells from outside quadrats for such statistics may have introduced a bias and may not have been representative of the population in general (large 'eye-catching' examples for instance may have been more likely to be seen and collected).

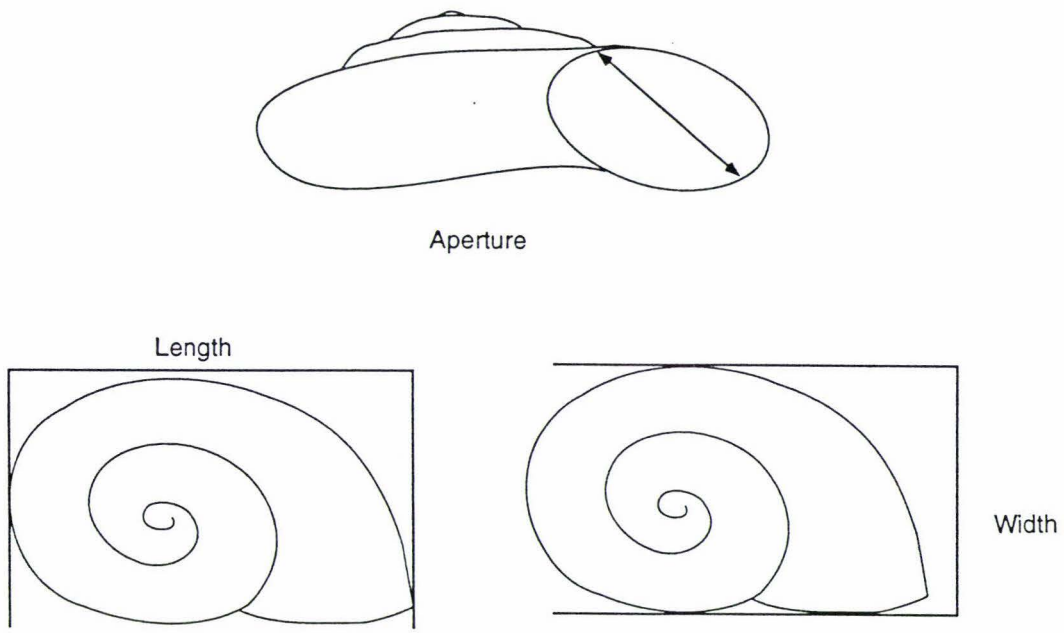

Figure 3.1: Shell measurements and dimensions used in this study

Growth rate

The growth of 13 *P. t. traversi* was measured in the field at Papaitonga Scenic Reserve. Growth was taken as the difference between two measurements in each of three dimensions (Figure 3.1). Each snail was first measured when it was found, and an harmonic radar transponder was attached to it (*Appendix four*). Every snail was then relocated with an harmonic radar at least once, and remeasured. It was possible to find and measure five of the snails for a third time on 28/09/96, 379 days after the previous measurement. In this case growth was taken as the difference between the initial measurement and third measurement. Growth rate per year was calculated with equation 3.1.

365(Actual growth/number of days between measurements)...Equation 3.1

Non-parametric tests were used to examined the relationship between shell measurements because many of the data sets collected in this study varied from a normal distribution.

Results:

Comparison between shells of live snails and empty shells

Mann-Whitney tests were used to compare the sizes of the shells of live snails and those of empty shells.

Table 3.1: Papaitonga Scenic Reserve: Size comparison between the shells of live and dead snails found in 17 quadrats, Mann-Whitney U test.

	Mean values (mm)		Difference
	Live snails	Empty shells	
Shell length	43.20 (n = 48)	41.98 (n = 46)	NS
Shell width	35.73 (n = 47)	34.56 (n = 44)	NS
Shell aperture	20.65 (n = 47)	19.68 (n = 45)	NS

NS: Not significant at $\propto$ = 0.05

Table 3.2: Makahika Scientific Reserve: Size comparison between the shells of live and dead snails found in five quadrats, Mann-Whitney U test.

	Mean values (mm)		Difference
	Live snails	Empty shells	
Shell length	42.41 (n = 15)	41.44 (n = 23)	NS
Shell width	35.15 (n = 15)	34.23 (n = 23)	NS
Shell aperture	20.65 (n = 15)	19.43 (n = 18)	NS

NS: Not significant at $\alpha = 0.05$

No significant differences were found between the sizes of shells of live snails and empty shells at Papaitonga or Makahika at the 0.05 level (Tables 3.1 and 3.2).

Size comparison: Papaitonga vs Makahika

Table 3.3: Comparison between shell lengths of all shells found at Papaitonga and all shells found at Makahika, Mann-Whitney U test.

	Mean values (mm)		Difference
	Papaitonga	Makahika	
Shell length	42.60 (n = 94)	41.78 (n = 38)	NS
Shell width	35.17 (n = 91)	35.23 (n = 38)	NS
Shell aperture	19.99 (n = 92)	19.98 (n = 33)	NS

NS: Not significant at $\alpha = 0.05$

The shells of *P. t. traversi* at Papaitonga were not significantly different ($P > 0.05$) from those at Makahika in any of the three measurements used in this study.

At each site linear regressions were conducted with data collected from all undamaged shells to examine the relationship between each of the three measured dimensions.

There was a close relationship between shell length and the other two measured dimensions. At Makahika the regression equation explained virtually all the variation between length dimension and shell width (r^2 = 99.7 %) and length dimension and shell aperture size (r^2 = 97.8 %). At Papaitonga virtually all the variation between the length dimension and shell width was explained by

the regression equation (r^2 = 97.7 %) while much of the variation between maximum dimension and shell aperture was accounted for (r^2 = 88.7 %).

Table 3.4: Dimensions of shells of *P. t. traversi* at Papaitonga Scenic Reserve

	Live snails			Empty shells		
Measurement (mm)	Length	Width	Aperture	Length	Width	Aperture
Largest	52.65	42.25	26.13	51.70	43.15	24.45
Smallest	17.63	14.95	10.00	11.15	9.15	6.60
Median	45.33	37.45	20.40	44.30	37.28	20.72
Mean	43.20	35.73	20.29	41.98	34.56	19.68
Standard deviation	6.50	5.22	2.70	9.55	8.03	3.74
Sample size	48	47	47	46	43	45
Skewness[1]	-1.77	-1.87	-1.24	-1.76	-1.79	-1.92

Table 3.5: Dimensions of shells of *P. t. traversi* at Makahika Scientific Reserve

	Live snails			Empty shells		
Measurement (mm)	Length	Width	Aperture	Length	Width	Aperture
Largest	53.35	39.75	24.40	52.00	42.93	26.35
Smallest	20.60	17.15	11.60	10.00	8.25	6.00
Median	46.15	38.00	21.45	48.45	39.35	21.98
Mean	42.41	35.15	20.65	41.44	35.29	19.43
Standard deviation	8.03	6.21	3.20	14.24	11.30	6.70
Sample size	15	15	15	24	23	18
Skewness[1]	-1.84	-2.07	-1.85	-1.60	-1.97	-1.34

1. Skewness as defined by the Microsoft 'Excel' spread sheeting software package.

At Papaitonga there was a size range of 17.63 mm to 52.65 mm for shell lengths of live snails and 11.15 mm to 51.70 mm for empty shells, while at Makahika the range of shell lengths was 20.60 mm to 53.35 mm for live snails and 10.00 mm to 52.00 mm for empty shells.

Size classes of *P. t. traversi* shells

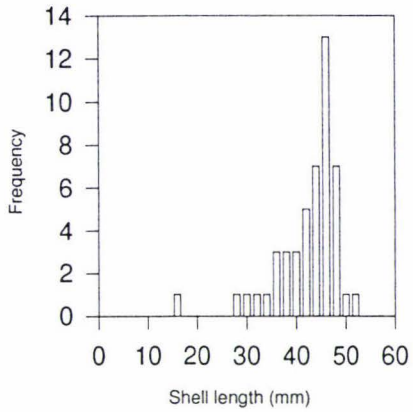

Fig 3.2a: Live snails, Papaitonga

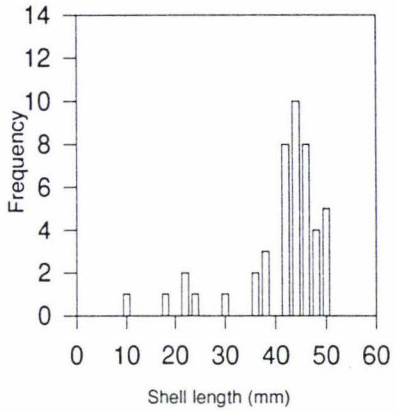

Fig 3.2b: Empty shells, Papaitonga

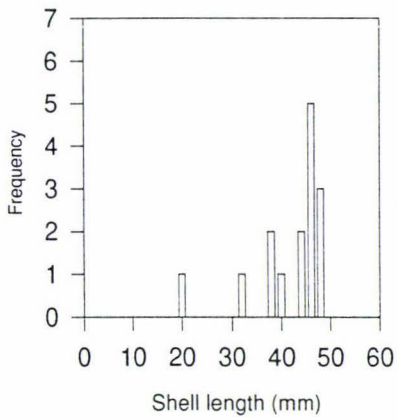

Fig 3.3a: Live snails, Makahika

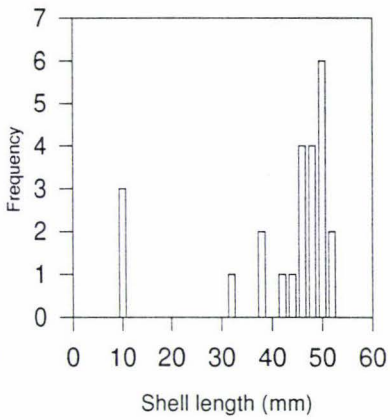

Fig 3.3b: Empty shells, Makahika

Figures 3.2a, 3.2b: Frequency histograms of the shell lengths of live (3.2a) and empty shells (3.2b) found at Papaitonga Scenic Reserve.

Figures 3.3a, 3.3b: Frequency histograms of the shell lengths of live (3.3a) and empty shells (3.3b) found at Makahika Scientific Reserve

Each shell size frequency distribution (Figures 3.2a,b and 3.3a,b) was essentially unimodal but varied from the normal by being negatively skewed, that is there were more larger shells than smaller shells. The different scale used in Figures 3.3a,b compared with 3.2a,b reflected the fact that less sampling was conducted at Makahika Scientific Reserve.

Smaller sized shells were poorly represented in each of the three shell dimensions measured for both live snails and empty shells.

Shells found outside quadrats:

Many snails were found outside quadrats at each site. One empty shell at Papaitonga Scenic Reserve had the largest length and width measurements recorded during the survey at 54.00 mm and 43.70 mm respectively.

Snails over 50mm in length were rare. At Papaitonga Scenic Reserve two live snails (4.17 %) and three empty shells (4.11 %) 50 mm in length or longer were found within quadrats. Of the empty shells found at Makahika Scientific Reserve Seven (14 %) exceeded 50 mm in length but no live animals of this size were found.

Growth

The *P. t. traversi* population was found to be dynamic, with individual snails joining and leaving throughout the study period (*Chapter five*). This resulted in each snail being followed for a different length of time.

There was a significant, positive Spearman-rank correlation of 0.65 between the number of days between measurements and growth ($P<0.05$).

Table 3.6: Growth rates of 13 *P. t. traversi* at Papaitonga Scenic Reserve expressed as changes in each of three dimensions.

Initial size (Shell length mm)	Size change per year for each dimension (mm)			
	Days of growth	Length	Width	Aperture
36.00	237	1.39	0.62	**-0.62**
37.00	629	3.22	3.25	0.95
37.20	552	2.64	4.31	1.40
40.00	115	10.7	6.82	9.13
41.35	97	3.86	1.13	1.32
41.90	552	2.39	2.18	0.91
44.00	164	2.34	**-7.7**	0.22
46.15	168	1.20	0.76	**-0.33**
47.70	636	1.54	1.24	0.29
48.00	73	0.50	0.25	7.25
48.35	177	1.13	0.26	**-1.13**
48.45	629	1.54	1.24	0.29
49.45	165	1.44	0.11	**-1.44**
Mean growth		2.61	1.11	1.40

Mean growth for both the width and aperture dimensions was affected by negative values (Table 3.6). If the negative width measurement of - 7.7 mm was excluded then mean width increase was 1.71 mm.

The identification number of one of the snails that was remeasured on 28/09/96 was approximately two cm back from the lip edge where it was engraved. The This growth was far greater than was shown by either the length, or width measurements taken at the same time.

Spearman-rank correlations were used to examine the relationship between the changes in each dimension with respect to one another (Table 3.7).

Table 3.7: Results of Spearman-rank correlations between the three measures of growth.

Dimension	Correlation	Significance
Length v width	0.702 *df.* =10	$P < 0.05$
Width v aperture	0.483 *df.* =11	NS
Length v aperture	0.528 *df.* =10	NS

NS: Not significant, P=0.05

The only significant result from the Spearman-rank correlation was that between length and width. This showed that the aperture measurement does not vary consistently with the other two measurements.

There was a significant negative Spearman-rank correlations between initial shell length and yearly growth (-0.635) (Figure 3.4). There was an overall weak positive correlation between yearly growth and percentage increase in length but this appeared to be biased by a single large snail that grew rapidly (Figure 3.5)

Evidence of shell repair after traumatic damage was seen on many shells. Three snails that I followed long term were subject to traumatic shell damage. Snail 48 was attacked by a rat and the lip of its shell gnawed (*Chapter seven* describes how to identify specific predator damage). In the 351 days that the snail lived after the attack there was 1.05 mm of growth from the lip of its shell. A second snail was attacked by a rat prior to being found. The rat had gnawed a 7.00 mm diameter hole through the peripheral shell whorl. This snail was successfully kept in captivity for two weeks but it died one month later in the field. The shell of the third live snail split explosively while awaiting engraving. This resulted in several large splits that penetrated both the periostracum and the ostracum, starting at the lip and moving back. Part of another dead *P. t. traversi* shell was glued over the broken region with epoxy resin. The snail continued to live for a period of three months but then died.

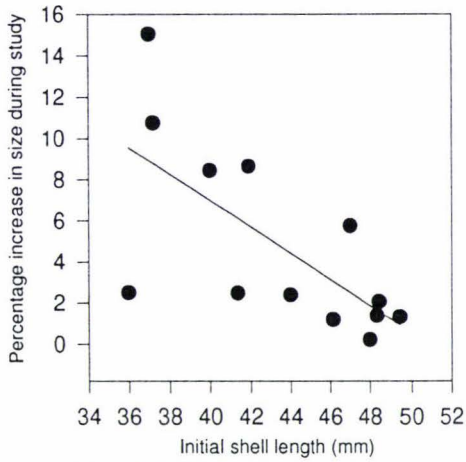

Figure 3.4: Relationship between initial shell length and % increase in shell length over time

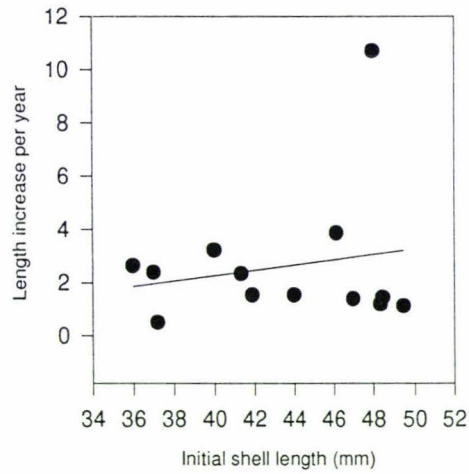

Figure 3.5: Relationship between initial size and yearly increase in shell length

Distribution of formae at Papaitonga Scenic Reserve

I estimated that the location of the overlap between the florida and traversi formae of *P. t. traversi* is near the region of quadrat two (*Figure 2.1*). Quadrat four (200 m south of quadrat two) appeared to contain pure fa. florida while those present in and around quadrat two appeared to be hybrids. The snails I classified as hybrids exhibited pale to moderately strong brown coloured spiral patterns on the dorsal surface. This banding was much less defined than in

pure fa. florida snails but is inconsistent with a fa. traversi designation. No northern boundary for the hybrid zone was decided upon because shells in quadrat 16 (220 m west-northwest of quadrat four) had the hybrid banding pattern.

Discussion:

Large size is one of *Powelliphanta's* most obvious characteristics and it is frequently quoted (eg. Powell, 1979). The largest empty *P. t. traversi* shell that I found had a shell length of 54 mm. This was the same size as the largest *P. t. traversi* documented by Powell and was larger than the holotypes of each individual *P. t. traversi* forma (Powell, 1930, 1938, 1949). This suggested that any habitat degradation or predation pressure since Powell's investigations has not suppressed the maximum size attained by the subspecies. This is relevant because there is circumstantial evidence that rats had not reached substantial numbers in the Horowhenua until approximately 1946 (*Chapter seven*). The size ranges published by Powell are however difficult to interpret. He stated a size range between 40 mm and 53.5 mm for *P. t. traversi* (Powell, 1979). This range was clearly not for the whole species because *P. t. traversi* hatches from an egg with a maximum dimension of 11 mm (Powell, 1979). It would be reasonable to assume that Powell was referring to adult sizes, but I could not differentiate between juveniles, and adults except on size. Powell (1946) identified adult lips on mature shells in *Paryphanta busbyi busbyi* Gray and *P. b. watti* Powell, but never referred to this feature for *Powelliphanta.* Dr. Ian Stringer (1996, *pers. comm*) who worked with both *P. b. busbyi* and *P. b. watti* had never noted an adult lip on either of these species.

I found a strong relationship between the length, width and aperture measurements of shells collected at both Papaitonga and Makahika. This suggested that any of the three dimensions could be used to describe the 'size' of a *P. t. traversi.* To simplify descriptions of size in subsequent chapters I used shell length to describe the size of a *P. t. traversi.*

Shell dimensions were not significantly different between Papaitonga and Makahika. This was despite different formae living at each site (latizona at

Makahika, and florida, traversi, and a florida-traversi hybrid at Papaitonga). The different formae described by Powell (1979) were readily distinguishable but it was difficult to discriminate between pure formae and hybrids. Snails in quadrats 1, 2, 16, and 17 (*Figure 2.1*) all appeared to be a florida-traversi hybrid but the hybrid zone may extend further into the north western reaches of the reserve.

Powell (1936, 1946) noted that other authors might consider his naming of forms on the basis of subtle colour differences as 'species splitting' and of no taxonomic value. He disagreed with this and stated that the differences he documented could not be likened to variants that may occur in a breeding colony irrespective of location (Powell, 1938). Simpson (1929) suggested that although many different land snail forms would 'doubtless' be fertile hybrids, they were still important in reconstructing the story of past evolution, migration and distribution. Powell (1946) considered that accepted designations of species and subspecies were too rigid to be applied to races of land snails which are not wholly rigid or stable in their make up. This view was shared by Murray and Clarke (1980).

A clear trend can be seen in the changing classification of *Powelliphanta*. The original descriptive literature focussed on minute detail (Powell 1930, 1932, 1936, 1938, 1946, 1947, 1949). This resulted in the recognition of many species, subspecies and other forms, and was essentially a recognition of diversity. The contemporary tendency is toward broader groupings (eg. Climo 1977b, 1978). It is likely that neither approach is entirely correct. A recent paper by Martin (1996) stated that adoption of the phylogenetic species concept will lead to the inevitable loss of the subspecies. Many subspecies will be combined into new species or conversely elevated to that of a species in their own right. A logical outcome of this is that recognition of diversity of form in a species like *P. t. traversi* will be lost, as they are combined into larger groupings, while there could be recognition of genetic diversity between individuals of identical phenotypic form.

Allozyme analysis by gel electrophoresis was conducted on several *Powelliphanta* including *P. t. traversi* by Kath Walker (1996, *pers. comm.*). This

will provide a genetic basis of classification that may overcome many problems relating to the classification of *P. t. traversi* when she releases this information as part of her revision of *Powelliphanta's* taxonomy. Early indications are that, rather than absorbing all *P. t. traversi* into *P. hochsteteri* as suggested by Climo (1978), *Powelliphanta* in Papaitonga Scenic Reserve will continue to be classified as *Powelliphanta traversi traversi.* The Makahika *P. t. traversi* fa. latizona and *P. t. traversi* fa. tararuaensis colonies may have more complex affinities with *P. marchanti* (K. J. Walker, 1996, *pers. comm*).

Most pulmonate shells grow in a logarithmic spiral (Pomeroy, 1969). In *Powelliphanta* new growth is added to the shell from the growing edge on the outermost whorl (Figure 3.6). Pomeroy (1969) noted that spiral growth would be better described by angular measurements rather than linear ones. In hindsight such a measure would have been valuable in my study, but it was difficult to measure in the field and was not recorded. Length required only that a shell be orientated so that the vernier callipers were maximally separated. This resulted in length being both the simplest and most reproducible the three dimensions I used in this study. In contrast to my use of shell length to describe a *P. t. traversi's* size, I suggest that short term growth is better expressed by the width measurement. This is because one side of the calliper is placed directly against the growing surface (Figure 3.4). When the time between measurements increases, angular growth tends toward infinity (Figure 3.4) and the width measurement becomes less representative of true movement. I believe that this was the case with the growth of the five snails that were measured on 28/09/96 more than 500 days after their original measurement. The identification number of one of these snails was two cm back from the lip edge where I normally engraved it suggesting this was close to the true amount of angular growth.

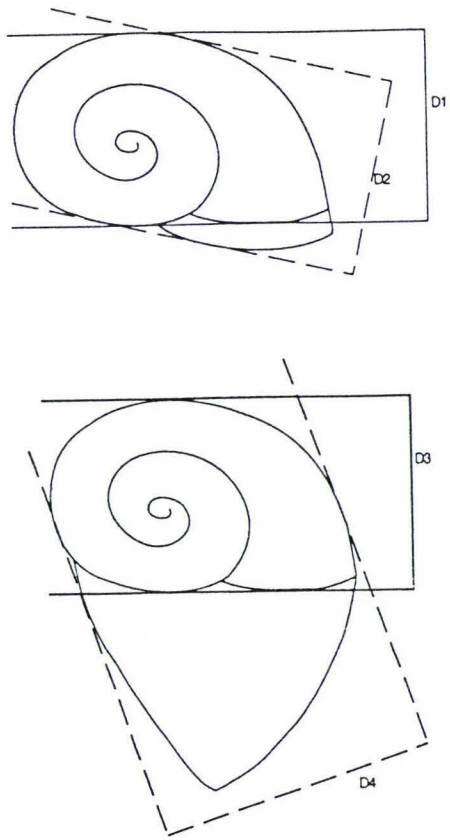

Figure 3.6: Growth as expressed by the difference in two width measurements. In the first instance D2 - D1 approximates true growth from the shell lip. In the second exaggerated case D4 - D3 is less representative. When time between measures is relatively short, as in the present study, the first case is more likely. For longer term studies the method used here may not be appropriate.

The most variable measurement of the three dimensions recorded was aperture size. Aperture size is strongly correlated with the other two dimensions when one-off measurements are taken. When shells were remeasured at end of the growth study, four of 13 snails aperture widths had reduced. There were two likely reasons for this. The method used to measure aperture was somewhat inexact and difficult to reproduce. Sometimes the shell lip was soft and flexible or the exact place of previous measure could not be located. The other reason could be due to a morphological characteristic that I originally called 'shell drooping' that altered the shape of the aperture. In this growth type, the shell grows a new portion with the growth directed downward, rather than continuing as a perfect spiral. This orientation change is called an acceleration of the final whorl (Cooksley, 1996, *pers. comm.*) and was frequently mentioned by Powell.

This characteristic is typical of *Powelliphanta traversi* (I. Cooksley, 1996 *pers. comm.*), but was more noticeable in larger shells, or where a shell had previously earlier suffered damage.

The significant positive correlation between growth, and the number of days between measurements clearly showed that *P. t. traversi* increased in size with time, and therefore with age. The significant negative correlations between initial size and both percentage increase in size and yearly increase in size suggested that growth rate decreases with age. A mean measure of 1.11 mm per year was added to the lip of the average *P. t. traversi* shell but, a more representative measure is probably the mean of 1.71 mm calculated discounting one large negative value (Table 3.6). This corresponded to a mean 2.61 mm increase in shell length. This was much less than the mean of five mm added to the lip of the five 'adult' *P. hochstetteri obscura* held in captivity by Mike Meads (Meads *et. al.* 1984). The study by Meads *et. al.* (1984) directly measured lip growth over three years. *P. h. obscura* grows much larger than *P. t. traversi* (up to 70mm maximum dimension, Powell, 1930) and this may be a reason for a higher growth rate. In addition Meads *et. al.* (1984) kept his snails in captivity. Captive snails have shown elevated growth rates in some species (I. A. N. Stringer and E. A. Grant, 1996 *pers. comm.*). Meads *et. al.* (1984) also noted that growth did not occur at a constant rate, instead new shell was laid down in increments. Seasonal growth patterns were not addressed in my study. Sample size was low and the growth of a given snail at different stages of the year could have been as much a result of individual, as seasonal variation.

My observations indicate that *P. t. traversi* can repair damage from the lip of their shells but it is not known if damage on other parts of the shell can be repaired, or what affect damage may have on life expectancy. Three snails with shell damage followed in this study died (one snail had damage to the shell lip, the other two with holes through other parts of the shell). This may indicate that snails with damaged shells are more likely to die prematurely. A possible reason for this is that physiological / energetic investment in shell growth may lower energy reserves, leaving the snail more susceptible to disease or habitat stressors.

Several species of snail are known to change the shape of their shells as they mature according to Cain (1977a). He also suggested that different shell shapes might be more advantageous for feeding on surfaces of different orientations (vertical or horizontal). The accelerated whorl characteristic in *P. t. traversi* may improve the ability of a snail to survive dry conditions by increasing the capability of the animal to apply its aperture to the ground.

The shape of the shell length frequency histograms were similar for live and dead snails at both study sites. In additions smaller size classes of both live snails and empty shells were poorly represented at each site. These results suggested several possibilities. Mortality may be similar for all sizes of *P. t. traversi.* That there are few small shells suggested that only a few eggs are laid, eggs are laid infrequently, or relatively few eggs survive until hatching. In addition smaller *P. t. traversi* may grow rapidly relative to large snails so they may not remain small for long. A confounding variable was that smaller snails were less likely to be found than larger ones. This was discussed in detail by Philbert, Wobeser, and Clarke (1993) and in Chapter four.

Many factors may affect the size and shape of *P. t. traversi* in the Horowhenua. Solem (1959) suggested that much variation in land snail morphology is the result of differences in precipitation, altitude, or ecological stratification. He also indicated that frequent geographic changes caused by earthquakes or orogenous processes can also result in localised variation. Dispersal in a slow moving organism like *P. t. traversi* (*Chapter five*) is limited. Certainly many colonies of *P. t. traversi* are geographically separated from one another today mainly due to human influences (*Chapter four*). The potential for genetic drift or for the environment to provide selection pressure that alters the frequency of alleles in isolated colonies may well be high. The subtle variations in colour in different formae are particularly interesting in this respect. Whether or not these changes in colour are locally adaptive or selectively neutral and due to a 'founder affect' on a small initial population may well be worth addressing. A comparison between gene frequencies of present day Makahika *P. t. traversi*, and the colony of 40 individuals translocated from there to Kandahala

approximately 50 years ago by O'Connor (Powell, 1949) could be of considerable interest. Solem (1959) also noted that many land snails are very sensitive to a reduced moisture supply and that dwarf individuals in particular can occur in areas where rainfall is reduced. It is generally accepted that *P. t. traversi* is descended from snails that radiated from the top of the South Island (Climo, 1977b). Many *Powelliphanta* in that region exceed size dimensions measured in this study. *P. t. traversi* may be descended from genotypically smaller individuals or conversely, its phenotype may be constrained by environmental variables. The former would seem more likely, as all North Island *Powelliphanta* are in a broadly similar size range and cover a large geographic (and presumably environmental) range.

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Chapter four

The distribution, and relationship between habitat and density of *Powelliphanta traversi traversi* Powell (Mollusca: Pulmonata).

Abstract:

Density of the endemic land snail *P. t. traversi* was estimated at the sites of its two largest lowland populations. At Papaitonga Scenic Reserve there were 282 snails ha^{-1} and at Makahika Scientific Reserve there were 300 snails ha^{-1}. These densities were not significantly different (α = 0.05). There was no significant relationship between number of live snails and the number of empty shells within each quadrat. A positive association was found between snail abundance and the plant karaka (*Corynocarpus laevigatus*). There was a significant correlation between the number of snails present in a quadrat and leaf litter depth.

Introduction:

Powelliphanta is a genus of large, leaf litter dwelling land snail that is endemic to New Zealand. It lives solely in native tussock, forest, or exotic forest when it is associated with remnants of native forest (I. Cooksley, 1994 *pers comm*). Factors or agents that negatively effect these habitats are therefore deleterious to *Powelliphanta*. Over New Zealand as a whole, forest clearance resulted in a reduction in area of native forest and light woodland to 29 percent of the original (King, 1990). The costal plains of the Manawatu and Horowhenua, the habitat of four of the five formae of *P. t. traversi*, were almost completely deforested (Molloy, 1984).

The biota of New Zealand developed without selection pressure from mammals. Human settlers introduced many mammalian species and these exotic animals exacted a grazing pressure that native flora never evolved to tolerate. The result of this was that the smaller area of forest that remained was further degraded. Examples of such damage caused by Red deer (*Cervus elaphus scoticus* Lonnberg) goats (*Capra hircus* L.) and cattle (*Bos taurus* L.) were well documented (Cockayne, 1928, McKelvey, 1959). Without exception all the introduced herbivores which became established in the wild have had a deleterious effect on their new habitat (King 1990).

All species of *Powelliphanta* have to some degree, been subject to habitat loss, or modification (Meads, Walker, and Elliot 1984). Meads *et al.* (1984) found that the habitats of 60 percent of *Powelliphanta* taxa were modified due to a reduction in understorey or litter. The same percentage had habitats of 'moderate distribution' while in 71 percent of cases all colonies of a form, subspecies or species were found within eight kilometres of one another.

The suitability of a habitat for an organism could be an important factor in determining the size and health of a population. Moisture, shelter, and the availability of calcium were considered important in determining land snail distribution by Boycott (1934). Lundgren (1954) suggested that vegetation patterns defined good land snail habitats but Solem (1959a) disagreed with this and believed that the type of plant cover in a habitat was in itself immaterial, and that only the physical nature of the habitat that they provide is important.

Most of the literature about *Powelliphanta* was written in the 1930s, and 1940s, by A. W. B. Powell. Powell focussed his research on morphological variation and macro-distribution of species. He did not address density or population sizes so the size of past populations will never be known. Recently, Walker (1993) established a quantitative protocol for monitoring *Powelliphanta* populations but to date only qualitative estimates of density exist (eg. Walker, 1982, Meads *et al.*, 1984).

My study examined *P. t. traversi* at two sites in the Horowhenua, Papaitonga Scenic Reserve and Makahika Scientific Reserve. The first quantitative density survey was conducted for *P. t. traversi*, and the suitability of empty shell presence as an indicator of live population size was tested. Snail number was related to the vegetation present to investigate possible habitat preferences.

Methods:

Quadrats were searched at Papaitonga Scenic Reserve and Makahika Scientific Reserve as described in Chapter two. The number of live *P. t. traversi*, and the number of empty shells was recorded.

At Papaitonga a vegetation survey was conducted in each quadrat searched for snails. Vegetation was divided into five height categories (Table 4.1). Within each category the proportional area covered by each species present was recorded. In addition litter depth was recorded for each quadrat.

Table 4.1: Height categories of flora for vegetation survey

Category	Definition
Canopy	flora above 5 m in height
Sub canopy	between 2 m and 5 m in height
Shrub	between 0.3 and 5 m in height
Ground	below 0.3 m
Litter composition	dead or fallen flora

In some cases the intra-quadrat variation was too great for the whole quadrat to be described by one description. In these cases the quadrat was divided into sections that were individually described. This resulted in data for 26 discrete areas from 17 quadrats.

The grouping of quadrats with floral similarities was examined by using the MVSP statistical package (Kovach Computing Services). A detrended correspondence analysis (Hill and Gauch, 1980) was conducted on vegetation data from each category and combinations of categories. The analysis generated a series of axes that summarised variation in descending order of importance. Two or three dimensional ordination diagrams were constructed from these axes. Axis one and two were always plotted but axis three was only plotted if it described a similar proportion of the variation as axis one or two. The number of live snails per unit area were superimposed over the quadrat ordination diagrams to determine if any quadrat groups corresponded

with high or low snail densities. The proportion of habitat that was very wet, and therefore likely to be poor land snail habitat, was estimated from an aerial photograph.

Results:

P. t. traversi density

Table 4.2: Quadrat search summary, Papaitonga Scenic Reserve

Category	Type of snail / shell			
	Live snails	Empty shells		
		Total empty shells	Empty no predation	Empty with predation
Mean number snails / 100m^2 quadrat	2.82	4.35	3.35	1.00
Standard deviation	3.50	5.59	4.93	1.99
Highest number found in 1 quadrat	10	21	20	8
Lowest number found in 1 quadrat	0	0	0	0
Quadrats with no snails	7(41%)	4(23.5%)	4(23.5%)	13(76.5%)

The mean number of live snails found in each quadrat was 2.82 with a range between 0 and 10 (Table 4.2).

This equated to 282 ± 17 snails ha^{-1}. The 95 % confidence interval for the *P. t. traversi* population at Papaitonga Scenic Reserve (50.9 ha. not including islands) is between 13488 and 15219 snails (α=0.05). I estimated that 30 % ($\approx$ 15 ha.) of the land area (not including islands) was either wet flax-koromiko-shrub tussockland, Flax-raupo swamp, or *Carex secta* sedgeland. If very wet regions were poor land snail habitat then the effective habitat would be 35.9 ha. A 95 % confidence population estimate for the reserve would then be between 9513 and 10734 snails.

Table 4.3: Quadrat search summary, Makahika Scientific Reserve

Category	Type of snail / shell			
	Live snails	Empty shells		
		Total empty shells	Empty no predation	Empty with predation
Mean number snails/100 m^2 quadrat	3	10	6	4
Standard deviation	3.50	3.31	2.92	3.54
Highest number found in 1 quadrat	8	17	10	10
Lowest number found in 1 quadrat	0	5	2	1
Quadrats with no snails	2 (40%)	0	0	0

The mean number of live snails found in each quadrat was 3.00 with a range between 0 and 8 (Table 4.3). This is a density of 300 ± 31 snails ha^{-1}. The 95% confidence interval for the *P. t. traversi* population at Makahika Scientific Reserve is between 9415 and 11585 snails.

Intra-site comparison between live snail, and empty shell number:

A summary of the numbers of live snails and empty shells found within quadrats at Papaitonga and Makahika are shown in Tables 4.2 and 4.3 respectively. Table 4.4 shows a comparison between the numbers of live snails and categories of empty shells.

Table 4.4: Spearman-rank correlation between numbers of live snails and empty shells in each quadrat

Interaction	Rank correlation	Significance
Papaitonga (n = 17)		
Live v all empty shells	0.296	NS
Live v empty with predation	0.083	NS
Live v empty undamaged	0.296	NS
Makahika (n = 5)		
Live v all empty shells	0.158	NS
Live v empty with predation	0.564	$P < 0.05$
Live v empty undamaged	-0.051	NS

NS: Not significant at $\alpha = 0.05$

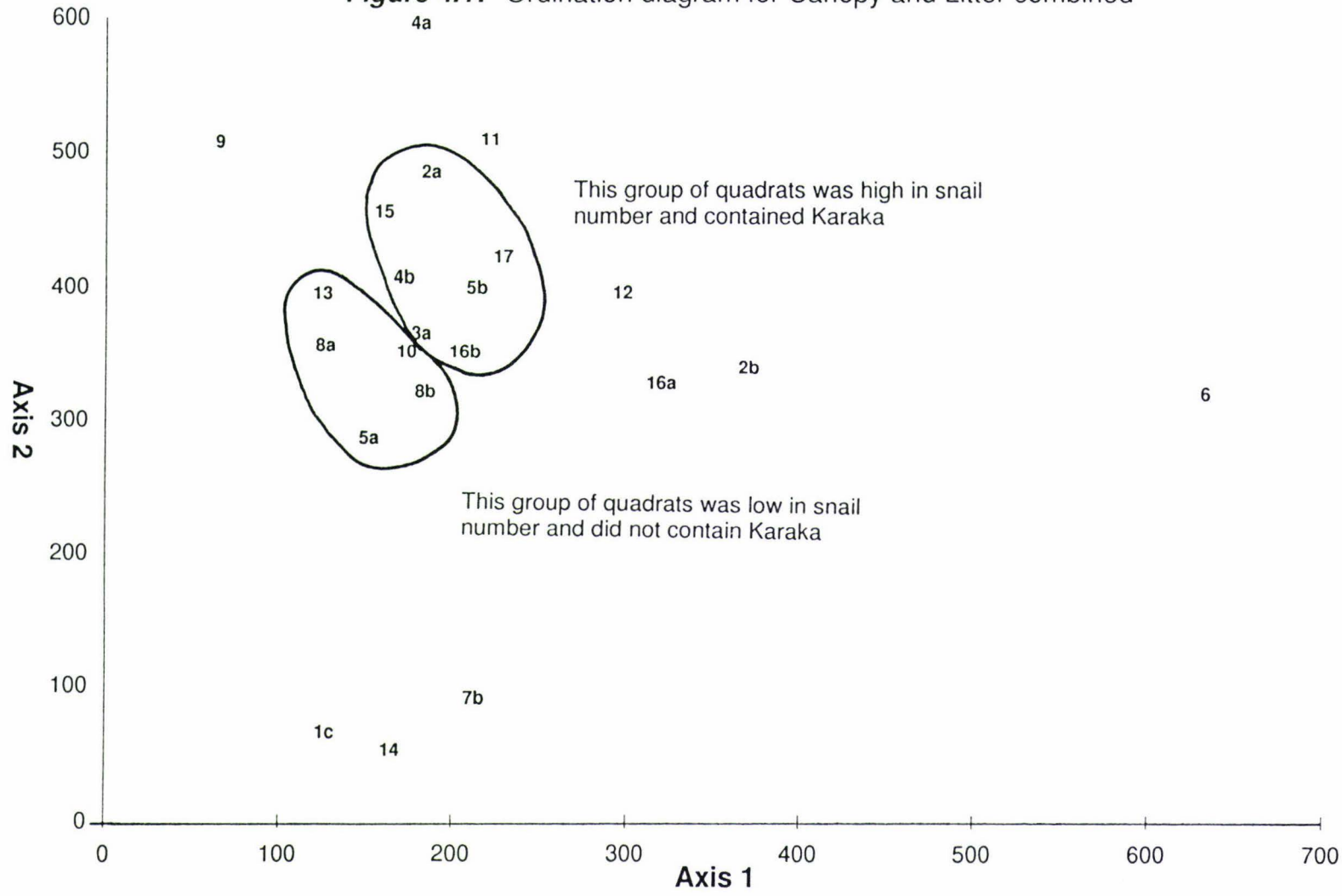
Papaitonga:

The number of live snails showed a significant correlation ($P < 0.05$) with the number of predator damaged empty shells in each quadrat. There was no significant correlation between live snail number and all empty shells or undamaged empty shells within a quadrat.

Makahika:

No significant correlation was found between the number of live shells and any category of empty shells at Makahika Scientific Reserve at the 0.05 level of significance.

Figure 4.1: Ordination diagram for Canopy and Litter combined



Between site comparison of live snails, empty shells, and categories of empty shells:

Table 4.5: Between site comparison for number of snails and or shells per quadrat, Mann-Whitney U test.

	Mean number of snails / 100 m^2		Significance level of difference
	Papaitonga	Makahika	
Live snails	2.82	3.00	NS
Total empty shells	4.35	10.00	$P< 0.05$
Empty, no predation	3.35	6.00	NS
Empty with predation	1.00	4.00	$P< 0.05$

NS: Not significant at $\alpha = 0.05$

The number of live snails per quadrat did not vary significantly between sites (see Table 4.5 for a summary of each test). There were significantly more empty shells ($P< 0.05$) per quadrat at Makahika than at Papaitonga. The number of empty shells were categorised into those with predator damage and those without. Shells in both of these categories were in higher number at Makahika, but this difference was only significant for shells with predation ($P< 0.05$).

Relationship between habitat and snail number at Papaitonga Scenic Reserve.

The ordination of individual categories showed no obvious quadrat groupings that were high, or low in snail number. The analysis for canopy and litter categories combined (Figure 4.1) showed a cluster of quadrats, half of which were relatively high in snail number, the other half low. Karaka (*Corynocarpus laevigatus* J. R. et G. Forst.) was common to the quadrats that had a high of density of snails for individual, and combined categories.

There was a significant Spearman-rank correlation of 0.44 between the number of snails present and litter depth (P=0.035, *df*=22) but no significant correlation (0.35) between the number of snails and the proportion of the quadrat that was covered with litter (P=0.078, *df*=25).

Discussion

The relatively large size of Papaitonga Scenic Reserve and Makahika Scientific Reserve make them two of the most important remaining habitats for *P. t. traversi.* The status and continued health of the snail populations that live there are vital to the conservation of the species.

Stabilisation of the cumulative standard error curve for the number of snails found per quadrat (*Figure 2.2*) indicated no more information would be obtained by searching more quadrats at Papaitonga. The Makahika cumulative standard error curve clearly followed that for Papaitonga but did not stabilise because of the number of quadrats examined. This trend suggested that it would have been preferable to search more quadrats to effectively sample Makahika, but also that the data collected was still likely to be of use.

Serber (1982) suggested that quadrats should be as small as possible with the premise that they are not so small that the majority are found to be empty. He also stated that searching many smaller quadrats will usually reduce variance compared with searching a lesser number of large quadrats. The majority of quadrats sampled did contain snails (59% at Papaitonga, 60 % at Makahika) and if the area was reduced there was likely to be a greater proportion that were empty. This suggested that the 100 m^2 quadrat area used in my study was probably close to optimal size for *P. t. traversi.*

Densities at both sites were similar and the population of each was estimated to be over 9000 individuals. Certainly the snails appeared to be quite numerous subjectively. No comment can yet be made on the respective state of each population based on these numbers for several reasons. There was

no quantitative estimate of density prior to my study, reproductive rate is unknown and there is a dearth of literature on the densities or carrying capacities of various habitats for other carnivorous landsnails. *P. t. traversi* is a hermaphrodite so the minimum viable population size is likely to be much smaller than that required for slow moving animals with separate sexes.

There will always be some error associated with searching for small cryptic animals like land snails. Searching quadrats is more accurate than per-unit-time searches and can give meaningful density and population size estimates. Quadrat searches are less reliant on the previous experience and ability of the searcher, and smaller individuals are more likely to be detected. Subjectively, I believe less care is taken when 'hen peck' searching an area for snails. In addition because the areas searched are not randomly chosen and are of unknown size their results are of limited value.

The number of empty shells was a poor indicator of the number of live snails present and so it should not be used to estimate population size. It is unlikely that this method will be of more use when information on the rate of shell break-down is known (R. Montifiore, 1994, *pers. comm.* is presently working on this topic). This is because it is likely that decay rates differ between sites in relation to moisture, soil pH, and could be influenced by the way the snail died (eg. crushing damage).

Rats (*Rattus* sp.) often cache empty shells when eating their contents (*Chapter seven*), and this was expected to result in a poor relationship between live snails and predator damaged empty shells. This was not always the case. At Makahika the number of live snails was significantly correlated with the number of empty shells that showed predator damage. In spite of this result care should be taken when assessing predation from the remains of dead snails. Empty shells could be removed from a quadrat by a predator or the presence of a cache in a quadrat could greatly elevate the number of shells above the true habitat density.

The use of empty shells for purposes other than density assessment does still have some validity. Walker (1993) for instance noted that it can give an indication of the extent of predation and show which predator is responsible. It can also indicate intra-population morphology differences and is a useful tool in determining range of a forma, subspecies and species.

Habitat preference:

Graham (1957) stated that molluscs are not genuinely terrestrial in the way that arthropods or vertebrates are, but they survive by avoiding truly dry terrestrial conditions and restrict themselves to habitats of high humidity. *P. t. traversi* were found in most parts of Papaitonga Scenic Reserve including those that were very dry. There were no snails in the one quadrat I searched that consisted of flax raupo swamp but this was a particularly difficult habitat to accurately sample because of the densely packed vegetation. It is likely, however that such habitat is unsuitable for snails for two reasons. Land snails prefer a moist environment but they are not suited to life in water because it diffuses passively into their bodies and can condense in their mantle cavities. In addition, terrestrial earthworms which form an important component of the *P. t. traversi* diet (*Chapter six*) do not live in water.

Snail density was positively, and significantly, correlated with litter depth. This result was expected because *P. t. traversi* live and forage in leaf litter. Penniket (1981) found a similar result with *Placostylus*, a genera of large herbivorous land snails that live in the far north of New Zealand.

The only plant that *P. t. traversi* was positively associated with was karaka (*Corynocarpus laevigatus*). *Placostylus* was also frequently found under karaka by Penniket (1981) but this relationship was probably influenced by karaka being one of its food species. Karaka aside, there was no other noticeable relationship between snail number and plant species. There was no obvious association with species common in regenerating forest as suggested by Richard Parrish who surveyed *P. t. traversi* at Makahika in 1982 (*pers. comm.* 1994). There is some evidence to suggest that karaka either introduced to New Zealand or was distributed far beyond its natural range by

Polynesian immigrants who valued it as a food item (Salmon 1980, P. Van Essen 1997 *pers. comm.*). My results could therefore suggest that karaka provided or reflected the physical or chemical variables that comprise good *Powelliphanta* habitat but the plant species itself is not important. This conclusion is in agreement with Solem's general theory of snail habitat requirement (Solem, 1959) and is consistent with the high densities of *P. t. traversi* under the introduced ground cover plant *Tradescantia fluminensis* (I. Cooksley, 1994 *pers comm*). The relationship between *P. t. traversi* and *T. fluminensis* was not examined in my study because there was only one small patch of this plant at Papaitonga and none was found at Makahika. Time constraints precluded the search of areas that were not part of the population survey.

The detrended correspondence analysis showed that quadrats with snails and without them were frequently grouped together. This suggested that either the presence of snails was determined by factors other than flora or that these molluscs used a microhabitat that was not detected at the level I measured. It is also possible that the sample size in my study was too small to detect subtle relationships. Further work would certainly be warranted to examine the relationship between snail presence and soil moisture, calcium concentration, pH, and in relation to available food such as worms. Moisture, particularly would be likely to vary at different times of the year. It is likely that any change in ground moisture would be very important in determining snail presence because of the role it plays in determining movement and feeding (*Chapter five* and *Chapter six* respectively).

Habitat area requirements:

Most *P. t. traversi* populations now survive in relatively small pockets of native bush surrounded by farmland. The dispersion ability of *P. t. traversi* discussed in Chapter five indicated that in most cases these small stands of bush are functionally isolated from other populations. The small, persistent, resident snail populations are likely to have survived as isolated pockets since forest clearance, perhaps as long as 100 years. Such small habitats have both

advantages and disadvantages. Large predators such as feral pigs will not persist in a small isolated tracts of bush (Turner and Corlett, 1996). Small habitats may be fenced to keep out farm animals that can cause habitat damage, and there is a higher chance of successful rodent and possum removal. Conversely, there is a higher probability of deleterious stochiastic events contributing to the extinction of these small populations. Ian Cooksley (1994, *pers. comm.*) believed rats follow human scent to bush isolates and juvenile possum disperse up to 40 km. to find a place to settle (Wright, 1995). A single rat probably has the ability to kill several *P. t. traversi* a night. At a snail density of around 0.03 snails m^{-2} a single rat would be able to eat every snail in a 100 or 200 m^2 habitat in a single night.

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Chapter five

Seasonal, short term, and nightly movement of *Powelliphanta traversi traversi* (Mollusca: Pulmonata).

Abstract

Harmonic radar was used to follow *P. t. traversi* in native forest over a year. *P. t. traversi* was essentially nocturnal. Most activity was at night but on 20 % of days in captivity there was at least one incident where a snail moved during daylight hours. The snails were not active continuously though the night, but no particular activity peaks were found. Moisture related factors were the only significant variables affecting movement. The most active snail moved 152 m in 107 days. Maximum dispersal from point of origin averaged 46 % of the total movement during intensive study. Dispersal was remeasured 260 days after the intensive study had concluded. Six of the seven snails found on the previous trip were located. Four of the six snails were closer to their point of origin than on the previous trip, the other two had dispersed less than 2.0 m further. This indicated that *P. t. traversi* adhered to a home-range. Limited dispersal suggested that small fragmented *P. t. traversi* colonies are functionally isolated as opposed to part of a metapopulation. This means each *P. t. traversi* colony should be considered a discrete population.

Introduction

Powelliphanta (Pulmonata: Rhytididae) is a genus of large terrestrial snail that is endemic to New Zealand. Adults grow to a maximum shell dimension of between 28 and 90 mm depending on the species (Powell, 1979). Nothing has been published on the dispersal of *Powelliphanta*, but permanent quadrats were established in several localities (including Papaitonga Scenic Reserve, I. Cooksley, 1994 *pers. comm.*) and these are likely to produce information on immigration and emigration rates. There are some reports on the movement of *Paryphanta*, another large endemic land snail which is in the same family. On one occasion a *Paryphanta busbyi busbyi* Gray was found 21.5 m away from its point of origin after two weeks (Pennekit, 1981) while Ogle (1982) reported that *Paryphanta* can disperse up to 800 m in 15 -18 years.

Dispersal of an animal can be difficult to follow through a landscape, especially when the species is cryptic. It is also difficult to quantify when the animal disperses slowly (Sarre, 1995). Measuring variation of mitochondrial DNA is a recent technique for the measurement of dispersal at the population level (Sarre, 1995). This allows the spatial radiation of genetic material to be

estimated, but it is less relevant for measuring real-time movement because it requires mating events to have occurred. Both *Powelliphanta* and *Paryphanta* are cryptic. Without the use of some form of device to find individuals from one day to the next, the direct measurement of movement and dispersal would be logistically difficult.

The vast majority of behavioural and physiological properties of any organism vary in a rhythmic daily pattern (Hamner and Enright, 1967). Rhythmic activity in animals may be controlled endogenously by a form of innate 'biological clock' or exogenously by environmental cues. In some cases exogenous cues are used to keep the animals behaviour in phase with its habitat even when the behaviour pattern is primarily controlled endogenously.

Avoiding desiccation is of particular significance to terrestrial pulmonates (Ford and Cook, 1987) because water evaporates freely from their soft, moist bodies. The generally lower humidities and higher temperatures during daytime make this a particularly hazardous period for terrestrial slugs, so they typically avoid activity at this time. A shell affords a land snail a greater degree of protection from desiccation. Variation in shell characteristics give snails from different habitats different abilities to tolerate arid environments (Machin, 1967). A land snail may 'escape in time' from adverse conditions when it retreats inside its shell, unlike a terrestrial slug. Snails can wait for several weeks for optimal conditions (Lewis, 1969b) but any advantage gained by waiting would be lost if they did not possess two other capabilities. A terrestrial snail must, firstly, be able to accurately monitor it's environment in order to detect the optimal condition. Secondly, the snail must be able to rapidly exploit advantageous conditions when they occur (Bailey, 1975).

Several authors suggested snails can monitor the temperature of their environment, however opinions vary on whether changes in temperature actually affect activity. Dainton (1954) and Dainton and Wright (1985) found that the slug *Agriolimax reticulatus* Müller detected temperature changes as little as 0.1°C while Cameron (1970b) noted that three species of helicid snails increased their activity most between 0°C and 8°C. Counter to this observation

were Lewis (1969a) who found no relationship with temperature and range, and Rollo (1991) who suggested that some conclusions about molluscan activity and temperature were made with little evidence.

Other factors that affect the onset of activity in pulmonates were well studied by several authors. Wind, other air currents, and humidity, affect movement (Dainton 1943, Lewis 1969b). Lewis (1969a) suggested that *Arion ater* L. could detect small changes in light intensity and this may enable it to find cover after an active period. In addition he showed that the endogenous activity patterns of *A. ater* were lost or reduced after several weeks of constant temperature and darkness.

Slugs and snails that are normally nocturnal may become active in daylight in damp conditions, or after a shower of rain (Lewis 1969a, Bailey 1975, Climo, 1975). Bailey (1975) also reported a significantly positive relationship between soil moisture and activity. He considered that soil moisture was a residual measure of earlier precipitation.

The object of my study was to establish when and how far *Powelliphanta traversi traversi* Powell moved in native forest, its natural habitat. The snails were followed intensively for 12 months to determine general movement patterns. Nightly movement was measured and this was related to several environmental variables that could potentially effect movement. This information was supplemented with data obtained from captive observation. The distance from where each snail was initially found to its last known position was recorded. This served as a measure of dispersal.

Methods:

Data collection:

Laboratory data collection

Two groups, each of four *P. t. traversi* were captured from Papaitonga Scenic Reserve and housed as detailed in Chapter two. Each group was observed for

two weeks and then released to comply with permit requirements. By using the two groups sequentially the study was able to be continued for a total of four weeks.

Field data collection

A 100 m^2 quadrat at Papaitonga Scenic Reserve known from an earlier density survey (*Chapter three*) to contain a high number of *P. t. traversi* was searched. Each snail found in the quadrat was numbered, and a small transponder of relatively low mass (0.7 g to 1.25 g) was attached. The transponders were specifically developed for this study and they enabled the snails to be found again with an harmonic radar unit (*Appendix six*). The harmonic radar unit was a transceiver that produced a directional, audible tone when its microwave beam reflected from a transponder.

Additional study animals:
Some snails were lost and new ones were found, both inside and outside the original quadrat, as the study progressed. Transponders were attached to these new snails and their movement followed.

Recording movements

Long term movement:
A numbered metal peg marked the last known position of each snail. Each time a snail was found using the harmonic radar, the direction and distance it had moved from the peg was recorded. I termed this measurement 'displacement'. The time intervals between visits to Papaitonga to search for snails varied considerably from two days to 260 days. The last interval of 260 days was only used to assess maximum dispersal.

Short term movement:
To determine the effect of environmental variables on movement measurements were taken on consecutive days on 43 dates spread throughout the study period. In addition, the path the snail had taken to reach its resting place was estimated with an adaptation of the spool-and-thread method of Dole

(1965). Each snail had a spool attached (Loctite 401 adhesive, Australia) by a loop of cotton to the trailing end of its shell (Figure 5.1). The spool, a plastic sewing machine bobbin (21 mm maximum dimension) had up to eight metres of cotton wound around it (mass ≈ 1.3 g with cotton wound on). The free end of the cotton was pegged to the ground allowing additional cotton to unravel from the bobbin as the snail moved.

Environmental data

Climate:

Precipitation was measured with a rain gauge (Nylex 600, Australia) set up under the canopy in the middle of the quadrat. Temperatures were measured at ground level with a thermohydrograph (Toyo Industries, Japan) that ran continuously on a weekly cycle. The thermohydrograph was housed in a Stevenson's screen. The humidity meter on the thermohydrograph repeatedly failed and as a consequence few readings were obtained.

Data approximation:

Continuous climate data was required to relate to *P. t. traversi* movement. Where Papaitonga data was discontinuous, missing values were estimated using data from the Levin Research Centre Automatic Weather Station. The latter was approximately three km east of Papaitonga Scenic Reserve. A linear regression between Papaitonga and Levin data generated equations (*Appendix two*) that estimated the missing values.

Humidity data was taken directly from Levin rather than being estimated.

Sun and moon data:

Astronomical twilight (morning and evening) was taken as the time of sunrise and sunset. This is the time when there is no illumination from the rising or setting sun and it is regarded as being dark (B. Carter, Carter Observatory 1995 *pers. comm*). Illumination by the moon was expressed by using the phase of the moon and the length of time when the moon was above the horizon while the sun had set. Moon phase was the proportion of the full moon potentially

visible at midnight. All raw sun and moon data was provided by the Carter Observatory calculated using the latitude and longitude for Levin.

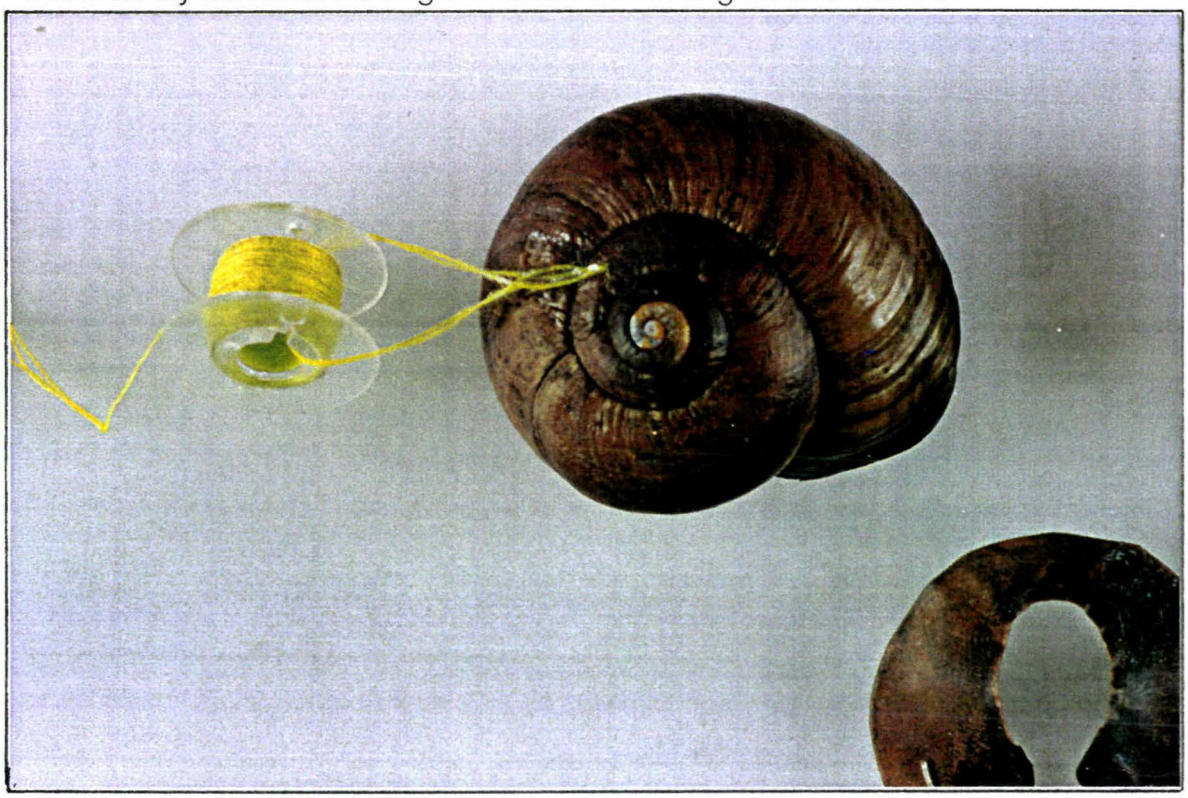

Figure 5.1: Snail with bobbin attached.

Movement data analysis:

The variables I examined are shown in Table 5.1. To determine if movement varied with date or between individual snails, analysis was conducted with a general linear model (GLM) (SAS Institute, 1990). The data was normalised with a $\log_{10}$ transformation.

The GLM calculated a least squares mean of movement which took into account the days in which each individual snail's movement was recorded, this was the dependant variable for the analysis. The relationship between environmental factors and variation in movement was examined with a stepwise multiple regression procedure (SAS Institute, 1990). The dependant variable for the stepwise procedure was the least squares mean of movement generated by the GLM.

Table 5.1: Factors that were related to variation in movement.

Variable Measured
Dawn temperature
Mid-dark period temp
Dusk temperature
Maximum humidity
Minimum humidity
Rainfall, sum previous 24h
Rainfall, sum previous 48 h
Rainfall, sum previous 72h
Rainfall, sum previous 96h
Night length
Length of time moon up while sun was down
Moon phase

About the Stepwise Procedure:

To be included in the final model a variable had to significantly improve the variation the model described. It is important to note that this procedure inserts variables into the model in descending order of the additional variation that each variable accounts for. This means that for instance Σ 72 hours rain may not necessarily be unimportant in describing snail movement but that rather it did not describe any additional movement not accounted for by Σ 96 hours rain.

Territoriality and home range.

Data input requirements for current computer software packages that estimate homerange sizes require that an animal move around in its habitat to a reasonable extent. Confidence intervals are then calculated estimating the likelihood of the organism being in an area at a given time, this becomes the organisms homerange. Many of the study animals in my study covered a large area but did not use this area rigorously enough for the data to be analysed by a homerange programme.

Results

Active period

Laboratory results:

Six days and nights of behaviour were recorded using infra-red video recording equipment from the four snails in captivity.

Table 5.2: Summary of activity onset and termination in captive *P. t. traversi* [1]

Date (morning)	1st move	Sunset	Last move	Sunrise
1/11/95	20 00	18 58	04 55	05 07
5/12/95	20 00	19 37	03 30	04 42
6/12/95	19 49	19 38	**05 41**	04 42
19/1/96	**17 00**	19 49	04 42	05 10
20/1/96	23 55	19 48	00 30	05 11
22/1/96	**08 06**	19 48	**09 00**	05 13

1. 1st movement refers to the earliest time any snail in the terrarium moved on a given date, last move refers to the latest any captive snail moved. In general movement is during darkness and thus usually spanned two dates. The 1st movement for an active period is on the date recorded, the last movement for an active period will normally be on the date which followed the first although this need not be the case.

The numbers in bold type indicate daytime movements

Activity was mostly nocturnal. Movement commenced before sunset and stopped before sunrise in three of the five nights that at least one snail moved (Table 5.2). Snails did not generally move at the same time but on 50 % of occasions more than one of the four were active. *P. t. traversi* regularly encountered each other during nightly activity. When snails met, one often crawled over the other even when the other snail was inactive.

There were only two movements during daylight hours, each involved a single snail. Both the commencement and termination of the 54 minute daytime movement on 22/01/96 appeared on Table 5.1. This was because it was the only movement by any snail in that 24 hour period. The snail had rested exposed on the litter surface overnight and a few hours after the sun came up the snail became active, moved under a large leaf, and stopped. The other

daytime movement was on 19/01/96, the date that the snails were first placed in the terrarium. It was not a particularly dull day, nor had the sun passed behind a cloud.

Once movement began no clear activity pattern emerged. On some nights snails moved for a short period after sunset then stopped and resumed for a period before sunrise, on other occasions the snails moved all night, then did not move at all, or moved only after the sun had already come up.

Movement in captivity was constrained by the terrarium walls. In the majority of cases the snail did not re-cross its own path but on occasions this did occur. In no cases did the snails progress up the side of the terrarium, this resulted in turning when a wall was encountered or the snail moving along parallel to the wall.

Activity data was also collected during the dehydration and water-uptake experiment documented in Chapter six. There was no movement the night after regular moisture application with an atomiser ceased. Movement was not observed on any of the following nights but resumed within ten minutes during daylight hours when the snails were placed in a container that allowed free access to standing water.

Field data:
Nine or ten snails were followed at any given time but when losses and additions to the study group were taken into account, twenty snails were followed in total.

Undisturbed *P. t. traversi* were never observed moving during daytime even at dusk or when it was raining. *P. t. traversi* were never found attached to any plants standing above ground but they were frequently found amongst the root masses of live and dead trees and within litter. Thread trails from bobbins attached to snails unravelled over low fallen logs and up relatively steep soil

banks and cuttings. There was no evidence that trees and shrubs were climbed by *P. t. traversi*.

Speed of *P. t. traversi*

Table 5.3: Speed of four timed locomotory movements in captive *P. t. traversi*

Distance (cm)	Duration (min)	Velocity (cm min^{-1})
20	6	3.33
40	17	2.35
31	14	2.21
20	10	2.00
Total 111	47	2.36

Snails did not usually move at a constant speed for long periods. Activity normally involved progression of a few cm followed by stopping and head waving. There were four occasions where snails moved continuously for sufficient distance that velocity could be estimated from video tape recordings (Table 5.3). The fastest of the four movements was 3.33 cm min^{-1} and the slowest 2.00 cm min^{-1}. The mean of the four velocities was 2.36 cm min^{-1}

Tracking methods

Snail movement was recorded by two methods, thread trails and displacement. In the thread trail method, thread could potentially snag on incidental projections from the ground as a snail moved and record changes in its direction. This meant that a change in direction was only shown if a projection was present. Such projections were numerous because in practice, slight undulations of the ground, small leaves, or twigs proved sufficient to snag the thread. Spool and thread attachments were not suited to measure long term movements because they regularly tangled, which prevented further movement, and could only measure distances up to the end of the thread.

Transponder displacement measurements could not show the path followed. Spool and thread measurements regularly recorded such occurrences. A

comparison was made between the length of unravelled thread, and the displacement from a snails earlier position.

Point-to-point = 15.4 + 0.554(thread length)....Equation 5.1.

Equation 1. was calculated by a linear regression using 93 paired observations. It accounted for r^2 (adj) = 67.3 % of the variation between the two measurement techniques. The positive y intercept indicated that the thread trail method detected movement that the simple displacement did not. This included movements where the snail doubled back over its own trail or moved in a circle.

The effect that transponders had on snail movement was not tested because the devices were essential in re-finding the snails and once attached were impossible to remove. When a spool unravelled freely it always required less than 0.005 N and generally did not register on a hand-held force meter (Prazisionswaagen precision scales, Switzerland, ± 0.3 % accuracy at maximum load). In cases where the device snagged or became tangled the snail became constrained up to the breaking strain of the thread. No *P. t. traversi* ever broke the thread.

Long-term movement

Intensive study:

Movement trails for each snail were constructed by adding successive displacement measurements end to end. Figure 5.1 shows the movement trails of five of the 20 snails followed. The length and date of relatively long movements is noted. Movement is shown relative to a central quadrat where 10 of the 20 study animals were originally located. The movement of the 15 other snails is included in Appendix two.

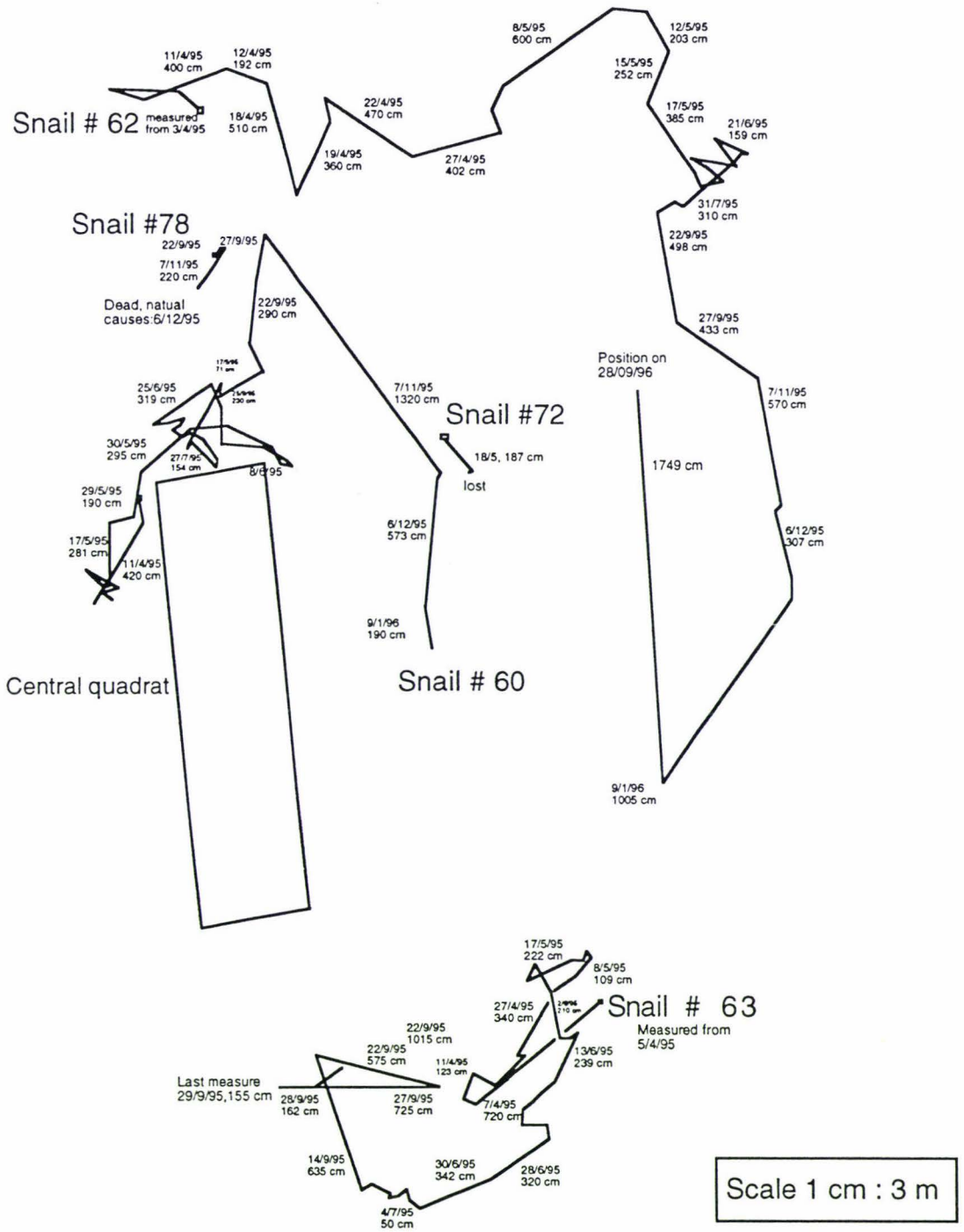

Figure 5.2: Long term movement for snails 60, 62, 63, 72 and 78

Snails numbered 63 and 62 travelled similar mean distances per day (Table 5.3 for summary of movements). At the end of the intensive study the distance snail 62 had moved from the position where it was initially found was 17 % of the total distance it actually moved. The distance snail 63 was found from its point of origin was 47 % of its actual movement. Snail 60 is intermediate between the two. Snails 78 and 72 were both followed for short periods, 78 died and 72 disappeared.

Table 5.4: Summary of intensive long-term movement study of *P. t. traversi* followed with the harmonic radar[1].

Snail #	7	48	49	51	52	53	54	55	56	57	58	59	60	61	62	63	72	76	78
Days followed	299	354	3	15	321	354	75	196	354	95	107	295	281	279	281	178	12	89	83
Distance travelled $(m)^2$	131	54.4	0.04	1.72	92.5	49.8	3.01	101	44.3	39.5	152	91.9	85.9	68.7	94.1	68.4	2.0	14.6	2.7
Distance travelled / day followed	0.43	0.15	0.01	0.11	0.29	0.14	0.04	0.52	0.13	0.42	1.42	0.31	0.31	0.25	0.34	0.38	0.17	0.12	0.03
Maximum distance/ 24 hrs^3	2.93	2.40	0.02	0.36	1.63	2.05	0.58	2.93	1.05	2.30	2.80	5.58	2.10	2.85	4.70	3.60	1.72	1.55	0.05
Total dispersal on 9/1/96[4]	51.9	3.72	0.04	1.68	23.9	29.8	8.38	49.1	17.5	13.9	31.5	33.1	13.6	12.5	36.5	11.9	1.75	11.1	1.82
% total movement represented by displacement	39.6	7	100	98	26	59.8	92	49	39.5	35	21	36	15.8	18.2	38.8	17	87	76	67

1. All snails except snail 50 which was followed for one night, carried 3.40 m by a rat and killed.

2. Sum of long term displacement measurements.

3. Maximum distance moved per day between samples.

4. Dispersal is the point-to-point measure from where the snail was discovered to its final position, as opposed to the sum of individual movements.

The greatest distance covered during the intensive study period by any snail (snail 58) was 152 m in 107 days, a mean distance of 1.42 m day $^{-1}$. The time between sampling was frequently longer than 24 hours. The greatest mean nightly movement between measurements was 5.58 m night^{-1} by snail 59.

Total displacement from where a snail was initially found was generally much less than the total distance it travelled (46 % of total movement). The greatest displacement from point of origin for any snail was 51.91 m. The snail made movements which added up to 131 m in order to disperse that far. Actual distance travelled was closest to displacement for snails that were followed for the shortest time (Table 5.4).

Subsequent dispersal measurement:

One additional trip (28/09/96) was made to assess dispersal 260 days after the intensive study had concluded. Six of the seven snails found on the previous trip (09/01/96) were located, one was dead. Dispersal for each snail found on 28/09/96 was recalculated and compared to its dispersal on 09/01/96 (Table 5.5).

Table 5.5: Dispersal from where each snail was initially found on 09/01/96 and 28/09/96

Snail	7	53	56	60	61	62
Dispersal distance on 9/1/96	51.91	29.75	17.49	13.58	12.54	36.52
Dispersal distance on 28/9/96	50.13	26.30	16.26	14.29	14.34	23.40*

* Dead when found

Four of the six snails found on 28/09/96 were closer to where they were found at the beginning of the study than they were on 09/01/96 (Table 5.5). Of the two snails that were further away, one had dispersed an additional 1.80 m, the other 0.71 m.

Factors effecting movement

General Linear Model Procedure result for data collected at 24 hour intervals:

Table 5.6: GLM ANOVA Table for variables effecting log_{10} movement.

Source	*d.f*	MS	F	Significance
Snail	19	10.3539	3.45	P< 0.001
Day	42	12.8597	4.29	P<0.001
Error	285	2.997		

P. t. traversi moved an average 57 cm per 24 hour period. There were significant differences in how far each snail moved and movement varied significantly with date (Table 5.6).

Stepwise procedure result:

Table 5.7: Stepwise procedure result for variables effecting movement.

Source	*d.f*	MS	F	Significance
Intercept	1	4.77	6.68	P<0.05
Previous 96 hours rainfall	1	29.52	41.34	P<0.01
Maximum humidity	1	5.41	7.57	P<0.01
Error	33	0.714		

Three variables were entered into the model. The sum of rainfall for four days preceding a movement was highly significant and accounted for 54.30 % of variation in movement (refer to Table 5.7 for significant variables). Maximum humidity the night of a movement was also accounting for 8.53 % of variation in movement. There was a significant, positive y intercept which showed there was residual movement not accounted for by any of the environmental predictors. The sum of rain 24 hours before a movement was entered into the model initially but did not significantly improve the model. The overall model therefore accounted for 62.83 % of variation in movement.

Discussion

P. t. traversi is generally nocturnal. Diurnal movements occurred but these were usually on occasions where the snail was handled or placed in direct sunlight.

Water availability is a necessity for movement in all snails because they rely on the continuous production of pedal mucus, and this consists of up to 97 % water (DeMont, 1992). Moisture related factors appeared to have a major effect on determining activity in *P. t. traversi* and, as such, had a great bearing on the timing, frequency and duration of activity. *P. t. traversi* will cease activity in a terrarium within one day if regular moisture application with an atomiser is withheld (*Chapter six*). After two weeks of inactivity they will resume movement within ten minutes when placed near a pool of water. In the field the only significant environmental variables to affect snail movement were the maximum humidity on the night of the movement and the total rainfall during the previous 96 hours. To delay activity until after a few days rain would appear a logical response to avoid moving inappropriately after only a light shower during drought. The significance of a few days rain and high humidity to movement may suggest that an important factor for activity is the moisture of the leaf litter that the snails live in. Evaporative water loss from the litter and the snail itself would be lower when humidity is high.

I suggested the advantages of waiting for optimal conditions would be negated if a snail could not accurately monitor its environment. Chapter three clearly showed that *P. t. traversi* can detect water and reacts quickly to take advantage of its presence. No significant relationship was found between temperature and movement. This runs counter to the findings of Cameron 1970b with *Cepaea nemoralis* L., *C. hortensis* Müller, and *Arianta arbustorum* L., and Dainton 1954a with the slug *Agriolimax reticulatus* Müller, but is in concurrence with Rollo (1991) who studied *Deroceras reticulatum* Müller (*A. reticulatus* and *D. reticulatum* are the same animal, *D. reticulatum* has chronological precedence).

A truly nocturnal animal has several hours more of darkness in which it can move in winter than in summer and so it could potentially move further in this

extra time. Field data showed that this was not the case. An explanation could be that *P. t. traversi* is not active continuously throughout the night, but rather centres activity around a specific time or times. Single and dual activity peaks were well documented in slugs and other families of snails (Baily and Lazaridou-Dimitriadou, 1986, Flari and Lazaridou-Dimitriadou, 1995, Beetson and Morgan, 1979). My results with captive snails were however at odds with this and showed that *P. t. traversi* was not active in any particular part of the night, and that not all snails were active at the same time. This finding was in concurrence with many other authors (eg. Runham and Hunter 1970, with slugs).

Richard Montifiore (1994, *pers. comm.*) noted that *P. busbyi busbyi* responded slightly to red filtered light at night but this light did not inhibit activity. On one occasion in the laboratory, a snail crawled under cover during the day after a night without moving. This could suggest that *P. t. traversi* is more sensitive to changes in light intensity around dawn. Elevated sensitivity at this time would be beneficial in entraining activity patterns or allow a snail to make use of a particularly damp overcast morning where high humidity and low light effectively continue night conditions into the day. *Powelliphanta* are sometimes active on darker wet mornings (Climo, 1975a). In such cases it would seem logical that early daylight movement is a continuation of a late dark period activity rather than an additional period of activity. This would be consistent with my field movement measurements and help explain increased movement on wet days but does not agree with my laboratory results. This discrepancy could be explained by the regular and consistent moisture application to the terrarium the laboratory snails were housed in.

Mary McIntyre (1995, *pers. comm.*) found that Mercury Islands tusked weta (*Hemideina* sp.) avoided activity on moonlit nights (independent of cloud cover). She suggested that this was to avoid predation by tuatara (*Sphenadon punctata* Gray) which are nocturnal visual predators. Skutelsky (1996) came to a similar conclusion about reduced activity in the in the scorpion *Buthus occitanus* Shulov stating that it too avoided well lit nights. *P. t. traversi* did not appear to avoid periods when the moon was visible or especially bright. The principle

predator of *Powelliphanta* prior to mammalian introductions was the weka *Gallirallus australis greyi* Buller (Climo, 1975a). This bird is a visual predator but frequently forages during daylight and at dusk (Bramley, 1994). Avoiding moon illumination would not be an important advantage in protecting *Powelliphanta* from weka.

Simple displacement from where any given snail was initially found was an underestimate. Cotton trails indicated that relatively long distances were sometimes covered over the course of several nights. In some cases snails returned to near where they started. The distance between start and end point was only a fraction of the true distance moved in these instances. Thread trail length despite this was not a good method to measure the movement of snails in comparison to displacement. This was because bobbins tangled too readily. A comparison between daily displacement and thread trail length where the bobbins did not tangle showed over two thirds of movement was described. As the interval increased this accuracy probably reduced but the data collected with long intervals between was still useful in estimating dispersal.

When measuring dispersal, the route a snail takes is not as important as where it ends up. After one year the greatest distance dispersed by any *P. t. traversi* was 51.91 m. Fifty five percent of snails were within 15 m of where they were originally found. Two hundred and sixty days later, the snails that still could be found were in much the same area.

Dispersal results suggested several possibilities. A proportion of the *P. t. traversi* population may tend to disperse, and were lost from the study group. Any analysis on the remaining snails could therefore be criticised as being biased toward snails that don't disperse. It is speculative to theorise on what happened to the seven snails that were lost from the study. The general linear model clearly showed that there is individual variation in snail movement, and some snails do move more than others. The movement and dispersal results from the snails that were followed for the whole study or died after being followed for a substantial period suggested that *P. t. traversi* adheres to a home

range or territory. This does not preclude the possibility that movement may be random within the home range.

The fastest velocity a *P. t. traversi* achieved was 3.33 cm min^{-1}. This is relatively slow compared to *H. aspersa* which can move up to 12 cm min^{-1} and a Puerto Rican snail which can move as fast as 45 cm min^{-1} (species not stated, Judd 1990) but is still sufficient to travel greater distances, and thus disperse much further than they in fact did. In captivity *P. t. traversi* was shown to have two distinct patterns of locomotion. Most common were short disjunct movements punctuated with head waving when the snail stopped. Continuous movement was rare. The first pattern of movement suggested that snails spend much of their active period examining their environment or foraging. This may suggest that movement is physiologically expensive (eg. because of water loss) and that typically *P. t. traversi* only moved to forage. In a homogenous habitat a deterministic approach to movement may not convey an advantage. However, if some parts of a habitat became poorer it would be an advantage to be able to move on. Without a detailed knowledge of the factors which comprise an ideal *P. t. traversi* habitat, it may be premature to dismiss movement patterns as random when they may in fact be related to an unknown factor (*Chapter four*).

P. t. traversi is found only patchily distributed in discrete pockets. The dispersal rates of *P. t. traversi* calculated from movement in this study indicate that there is probably little chance that most fragmented colonies in the Horowhenua could be considered part of a metapopulation (a population of interacting populations, Burgmann, Ferson and Akucakaya 1993, cited Sarre, 1995). This is probably one reason why so many different forma have developed (*Chapter three*). Isolation would be further imposed by major vehicle routes which criss-cross the country side in the Horowhenua, considering the findings of Baur and Baur (1990) who suggested that populations of the snail *Arianta arbustorum* L. separated by roads with a high traffic density may effectively be isolated from one another.

The experimental methods that were used to follow *P. t. traversi* may affect movement. Snails with transponders attached would require additional energy to move. It was not considered that this was significant on larger or intermediate sized snails but may have been a factor on smaller ones. Transponders were individually sculptured to fit each snail and so varied in mass. Lighter transponders were attached to smaller individuals. A typical transponder ranged from seven to nine percent of a snails mass. In comparison, on a weekly basis an individual *P. t. traversi* may vary in mass by three to five percent (*unpubl. data*). The addition of weights to snails was shown not to affect the linear relationship between the frequency of pedal waves or speed of locomotion (Croizer and Federighi, 1925b cited Jones, 1975) while Taylor (1914, cited Jones, 1975) showed *H. aspersa* can drag 50 times its own mass horizontally and up to nine times its own mass vertically. The effort of unravelling thread from a spool was negligible but on the smallest snails the combination of a transponder, and a spool could add up to 25 percent of the animals mass.

Continually disturbing a snail in order to identify it upon re-location could illicit an increase or decrease in locomotion. Both of these responses were noticed in other New Zealand Rhytididae, with Judd (1990) noting disturbance caused *Powelliphanta* to stay in it's shell for several hours while photographers waited, while I. A. N. Stringer (1995, *pers. comm.*) noticed increased movement in *Paryphanta busby watti* Powell during the night following a disturbance. In the present study it was not possible to reliably differentiate between snails that had been disturbed and those that had not.

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Chapter six

Diet and water uptake of the native Land Snail *Powelliphanta traversi traversi* (Mollusca: Pulmonata)

Abstract

Diet and water uptake of wild captured *P. t. traversi* was examined in the laboratory. *P. t. traversi* appeared not to drink, but rather obtained water via integumentary absorption, reaching full hydration (an increase in mass of approximately 20 %), from a dehydrated state, in around three hours. Exotic and native earthworms were the only food items consumed in this study, foraging did not occur when the snails were dehydrated.

Introduction

The consumption of green leaf material by common molluscan agricultural pests such as *Achatina fulica* Bowdich and *Helix aspersa* Müller is not the usual land snail diet. Cain (1983) considered land snails to be more generalist, while Solem (1959) observed dead plant material, fungi, or meat were more likely to be food items. Eight carnivorous families are present in the land snail super-order Stylommataphora (Solem, 1974). World-wide the carnivorous habit is quite well documented with a review article by Mead (1979) listing 19 species of snail that were introduced to Hawaii as potential biological controls for the giant African snail *A. fulica*. The New Zealand land snail fauna is known to have several carnivorous examples most notably in the Rhytididae, one of which (*Rhytida urnula* Pfeiffer) was videoed capturing and eating amphipods (M. Efford, 1996, *pers. comm.*).

There are no specific studies published on the diet of *Powelliphanta* but there is considerable anecdotal evidence that they are carnivorous. Many workers including Powell (1930) reported predation upon annelids. One author, (Judd, 1992) recently published photographs to support this. Other sources stated that slugs, snails, fleshy fungi, and millipedes are also consumed (Powell, 1979, Climo 1975b, and Meads, Walker, and Elliot, 1984).

It is not known if terrestrial pulmonates drink. Riddle (1983) stated that drinking has yet to be established, but Pusswald (1948, cited Riddle 1983) believed that

it does occur. Water may be obtained from ingested food (Machin, 1975) but in at least one species of slug this proved insufficient to maintain full hydration (Hunter, 1968). Terrestrial pulmonates are known to re-hydrate through their integument when exposed to rain, dew, or tap water, aided by the hydrophilic nature of superficial mucus (Machin, 1965).

Mucus is required by all land snails for locomotion (DeMont, 1992), it also keeps their integument, and respiratory membranes moist. Water is a major constituent of mucus and as such mucus production is responsible for the majority of water loss in terrestrial molluscs (Machin, 1975). Most species conserve water by behavioural means. In *H. aspersa* pulling back into the shell, and reducing mucus production during aestivation, can reduce water loss to as little as three percent of that of an active animal (Cameron, 1970a). Many snails manufacture an epiphragm of dried mucus that (apart from an air hole) blocks the shell aperture which is the major site of water loss in an aestavating snail (Machin, 1975).

During my study I offered potential food items to captive *P. t. traversi* and examined faecal samples produced by wild snails. In addition to this, the method and quantity of water uptake in dehydrated *P. t. traversi* was observed.

Methods

Faecal samples

Seven *P. t. traversi* were captured from Papaitonga Scenic Reserve, each was placed in a one litre plastic container. It was intended to hold the snails until faecal pellets were produced but within a few days a strong odour indicative of nitrogenous waste was evident. To avoid possible injury the snails were returned to the wild.

Faecal samples were preserved in 70% ethanol and examined under a dissection microscope.

Observational data

For the observational study four large (between 47 and 49 mm in shell length) and one juvenile (shell length 12 mm) *P. t. traversi* were collected from Papaitonga Scenic Reserve. The snails were housed and video taped as described in Chapter two. Distilled water was applied inside the terrarium daily with an atomiser.

Formal experiment:

The *P. t. traversi* were not fed for two weeks prior to the experiment. Each potential food item was tested by placing it on the floor of the terrarium that housed the snails. A different potential food item was offered every second night for a single night in the following order: Lettuce leaves, commercially grown mushrooms, grass grubs, thin slivers of lamb kidney and beef, live *H. aspersa*, live exotic earthworms and live native earthworms.

The video tape record showed if a *P. t. traversi* moved toward or touched the potential food item but the video camera did not have sufficient resolution for actual ingestion to be observed. A food item was considered 'consumed' if it was missing from the terrarium, was present but had marks consistent with radula abrasion, or was found projecting from a *P. t. traversi* shell.

Miscellaneous observation:

After the conclusion of the formal experiment natural leaf litter was placed on the floor of the terrarium. The litter contained a variety of naturally occurring invertebrates including unidentified coleopterans, amphipods, isopods, and native earthworms. The interaction between the seven captive *P. t. traversi* and the invertebrates and litter was recorded on video tape for one week.

At the end of the experiment all the *P. t. traversi* were returned to Papaitonga Scenic Reserve .

Water uptake and loss

Four *P. t. traversi* (not used in the feeding experiment) were obtained from Papaitonga Scenic Reserve were housed in the same terrarium used for the feeding experiment. The base of the terrarium was covered with natural leaf litter and the snails were provided with a regular supply of exotic earthworms. No water was added to the container for two weeks.

For rehydration the snails were placed in another container without potential food sources. This container was a flat-bottomed 4 L plastic container tilted approximately 3° and filled with distilled water until approximately one third of the base of the container was immersed. Each snail was weighed (Mettler ± 0.0005 g electronic balance) prior to placement in the 4 L container and then reweighed each hour for six hours. When mass stabilised the snails were placed back in the original terrarium.

Results

Faecal analysis

The only identified items found in faecal samples were radula teeth.

Video analysis, response to potential food items

Table 6.1: Response to potential food items offered to *P. t. traversi*

Potential food item	Response
Lettuce leaves	Not Consumed
Commercially grown mushroom	Not Consumed
Grass grub	Not Consumed
Lamb kidney strips	Not Consumed
Beef flesh strips	Not Consumed
H. aspersa	Not Consumed[1]
Exotic earthworm sp.	Consumed
Native earthworm sp.	Consumed

1. *Helix aspersa* and *P. t. traversi* did not interact because *H. aspersa* moved to the lid of the terrarium, while *P. t. traversi* remained on the base.

P. t. traversi ate exotic and native earthworms. Neither the kidney, muscle tissue, grass grubs, *H. aspersa*, lettuce or commercially grown mushroom were touched (Table 6.1).

Food capture was never actually recorded but behaviour shortly after capture was clearly observed. Shortly after capture snails engulfed prey with their foot and pulled back into their shells. Video resolution was to poor to see if the snails consumed any insects or constituents of the litter.

P. t. traversi did not eat every night even when food is present. The juvenile *P. t. traversi* was never observed to consume anything and it died during the trial. Two other *P. t. traversi* died during the experiment. The other snails gathered around the dead animals, but it was not possible to see if cannibalism occurred.

No damage consistent with cannibalism was found on the dead snails the next morning.

Water balance and uptake

Activity ceased the first night water was not applied to the terrarium. On the fourth night one snail moved for ten minutes. No other snail moved at all for the entire two week dehydration period.

The *P. t. traversi* were placed in the 4L container at 10.00 am, during daylight hours. Each snail became active within ten minutes and moved to the wet end of the container. All four snails entered the water until they were submerged almost to the level of their pneumostomes, extending fully from their shells. No movements in the pharyngeal region were observed that would indicate oral water uptake.

Table 6.2: Summary of water uptake in four captive *P. t. traversi*

	Snail a[1]	Snail 79[1]	Snail 83[1]	Snail 84[1]
Initial mass (g)	14.4468	15.3185	15.8873	18.5512
Max. mass (g)	17.7193	18.7300	18.7000	20.6377
Water uptake (g)	3.2725	3.4115	2.8127	2.0865
% increase	22.65	22.27	17.70	11.25

1. All snails found in the field were marked with an identification number (*Chapter two*).

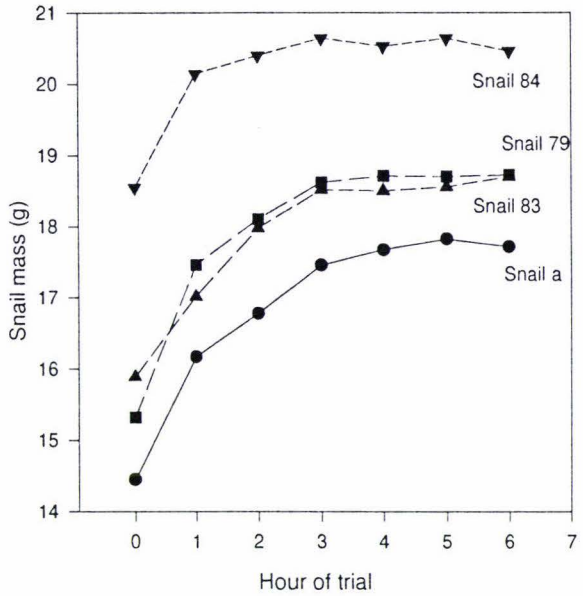

Figure 6.1: Mass versus time; dehydrated snails exposed to water

The water uptake of each snail as expressed by change in mass is shown in Table 6.2. The lightest snails increased their mass the most, both in total mass gained and as a percentage of original body mass.

The rate of increase in mass was most rapid in the first hour and decreased progressively thereafter (Figure 6.1). Snails 'a' and '84' reached their maximum masses after five hours, decreasing slightly at the final reading (hour six). Snails 79 and 83 were still increasing in mass at the final reading.

Discussion

The availability of water appeared to be an important constraint of activity in *P. t. traversi.* Activity ceased immediately when regular moisture application was halted, but resumed within ten minutes when the snails were exposed to free standing water. The direction of movement was toward and into the water which suggested that activity was not triggered to escape a potential localised flood or similar which could occur in the field. All snails must produce pedal mucus in order to move (DeMont, 1992). Mucus production requires a lot of water so a reduction in movement when the environment was dry was expected.

In addition to not moving when it is dry, *P. t. traversi* cannot seal the aperture of its shell to a surface (*pers. obs.*) and cannot produce an epiphigram (Meads, *et*

al. 1984). In dry conditions it must therefore tolerate water loss. Many terrestrial pulmonates can tolerate a high level of desiccation. Runham and Hunter (1970) stated that the ability to lose 50 % of their body mass in water is common. My study showed that *P. t. traversi* can tolerate a loss of at least 20 % of its body mass in water with no ill effects. There were no indications that *P. t. traversi* rehydrated by drinking. When dehydrated *P. t. traversi* were given the opportunity they crawled into water and extended fully from their shells. This behaviour was consistent with attempting to rehydrate by integumentary absorbtion, the method used by the slug *Limax maximus* L. (Dainton, 1954a).

A consequence of not moving when it was dry in the terrarium was that the snails also did not feed during this period. During the dehydration part of the study *P. t. traversi* did not eat or drink for two weeks.

P. t. traversi are clearly not generalist feeders and there was no evidence that dead animal tissue is eaten. The only items confirmed as food in this study were exotic and native earthworms. It is possible that worms are the sole constituent of the *P. t. traversi* diet but the limited nature of my feeding study precluded making such a conclusion.

Earthworms burrow deeply in to the soil when conditions are dry. If *P. t. traversi* only eat worms would have to fast during dry periods because they do not burrow (*Chapter five*). It is possible therefore that inactivity in dry conditions is also an adaptation to avoiding situations when food is scarce.

Other native snails in the Rhytididae are known to eat non-annelid items. Murray Efford (1996, *pers. comm.*) observed predation by *Delos* on *W. urnula urnula* Pfeiffer eggs, *Rhytida partula* Hutton predation on *P. lignaria* Hutton eggs and the consumption of amphipods by *W. urnula*. Ian Stringer recently reported cannibalism of dead *P. busby watti* conspecifics (1995, *pers. comm.*) and I have observed that species scraping the ostracum of an empty *Placostylus* shell with its radula.

The behaviour of the juvenile *P. t. traversi* was of particular interest during my study. This snail was active initially but was never observed to feed and died in captivity. If young *P. t. traversi* require a different diet to adults it is possible that the juvenile died of malnutrition. Diet change with age in snails was shown for *Helix pomatia* L. by Pollard (1975). *H. pomatia*, is herbivorous as an adult but young snails will eat unhatched eggs from their own clutch. Runham (1975) stated the number and shape of teeth of *H. pomatia* can vary over the life of the animal. A gross difference between the radulae of juvenile and adult *P. t. traversi* could reveal differences in diet.

Faecal analysis revealed nothing of the *P. t. traversi* diet and video resolution was too poor to record the interaction between *P. t. traversi* and native invertebrates or litter. Murray Efford (1995, *pers. comm.*) recently reported success in the identification of dietary components of South Island *Powelliphanta* from faecal samples so despite lack of success in my study I believe that faecal analysis and video taped observation will, with further refinement prove useful in revealing the *Powelliphanta* diet. Testing the response of *P. t. traversi* to a wider variety native invertebrates, plants and fungi would be warranted. It is possible that failure to consume the items offered in this study was due to a lack of familiarity with the feeds I tested.

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Chapter seven

Predators and predation of *Powelliphanta traversi traversi* Powell (Mollusca: Pulmonata)

Abstract

Predation upon the N. Z endemic land snail *Powelliphanta traversi traversi* was examined at two sites in the Horowhenua. The primary predator, that I identify here as the ship rat *Rattus rattus*, was present in higher numbers than in other lowland North Island native forests. Empty *P. t. traversi* shells with rodent damage were not significantly different in size from the shells of live snails. This indicated that rats did not prefer a certain size of snail. There was no evidence of predation from brushtail possum, *Trichosurus vulpecula* which was present in high numbers. The potential predation of native invertebrates and introduced *Vespula* sp. is discussed.

Introduction

Competitive interactions between snails and other invertebrates was well studied in marine systems (eg. Paine, 1966), but predation is the only aspect that is well studied influence with respect to terrestrial molluscs (Cain, 1983, Pollard 1975). The best examples are provided by accounts of the effects of introduced predators. One well documented example is that of the predacious snail *Euglandia rosea* Ferussac. *E. rosea* was introduced to Moorea in French Polynesia around 1967, as a biological control for the introduced African giant snail *Achatina fulica* Bowdich (Clarke, Murray, and Johnston, 1984). The subsequent spread of *E. rosea* and its lack of specificity for *A. fulica*, resulted in the complete eradication of all species of *Partula*, an endemic tree snail that was the subject of influential evolutionary studies prior to its extinction (Murray, Murray, Johnston, and Clarke, 1988).

Several species of potential *Powelliphanta* predators have been introduced to New Zealand. Of these, mice (*Mus musculus,* L.) rats (*Rattus* sp.), possum (*Trichosurus vulpecula,* Kerr), pigs (*Sus scrofa,* L.), rabbits (*Oryctolagus cuniculus cuniculus,* L.), and hedgehogs (*Erinaceus europaeus occidentalis,* Barret-Hamilton) were shown to consume either native or exotic land snails (Meads, Walker, and Elliot, 1984, Walker and Elliott *in prep*) or are known to consume pulmonates overseas (Cain 1983, Pollard 1975). A good example of the effects that the ship rat (*Rattus rattus,* L.) can have in New Zealand

occurred at Waiapehu Reserve, the type locality for *P. t. traversi* fa. traversi. At one stage prior to rat-trapping, all the empty *Powelliphanta* shells found and the remaining living snails had damage consistent with rat attack (I. Cooksley, 1994 *pers comm*).

Powelliphanta evolved in the absence of mammalian predators, except for the greater short tailed bat *Mystacina robusta* Dwyer and lesser short tailed bat *M. tuberculata* Gray. *M. tuberculata* spends up to 80 % of its time foraging on the forest floor and consumes non-arthropod invertebrates (McCartney, 1994) but *M. robusta* is now extinct and its diet is unknown. Weka (*Gallirallus australis greyi* Buller) was thought by Climo (1975a, b) to be the only important predator of *Powelliphanta* prior to the introduction of exotic mammals. Mammalian predators, including the possum, exert a heavier predation pressure than was ever delivered by weka (Climo 1975a, b). Possum were originally thought to be solely herbivorous but are now recognised as predators of native bird eggs (Atkinson and Cameron 1993) and are confirmed predators of *Powelliphanta* in many parts of the country (Walker and Elliott *in prep*). Nick Gillingham (1994), for example, found very few live *Powelliphanta marchanti* Powell in the Otemateanui stream catchment of the southern Kaimanawa ranges, but 82 % of empty shells had damage consistent with possum attack.

Native predators of *Powelliphanta* have lived along side these snails for relatively long periods of time, so it is reasonable to suppose that the life history and morphology of *Powelliphanta* evolved to cope with this. In contrast the first two introduced mammals, the Polynesian rat (*Rattus exulans* Peale) and the Norway rat (*R. norvegicus* Berkenhout) were probably introduced around AD 800 (Atkinson and Moller, 1990) and 1772 (Moors, 1990) respectively. This is only 80 and 15 *Powelliphanta* generations respectively, using the age to reproductive maturity quoted by Meads *et al* (1984). It is not known exactly how long rats have been established in the Horowhenua, but the spread of *R. rattus* was more or less coincidental with the decline of the New Zealand robin (*Petroica australis*) (Atkinson, 1973a). The robin became extinct in the Tararua range in approximately 1946 (I. Cooksley, 1996, *pers. comm.*).

The object of the present study was to survey predators and predation rates upon *P. t. traversi* at, Papaitonga Scenic Reserve and Makahika Scientific Reserve in the Horowhenua. In addition, predation and attempted predation was recorded upon a group of live snails with transponders attached (*chapter five*).

Methods

Predation level:

Predation level was estimated from damaged empty shells found in 22 (100 m^2) quadrats (quadrat locations and selection is described in Chapter two). Predator damage was determined by comparing damaged shells to descriptions of damage given by Meads *et al.* (1984) and Walker and Elliot (*in prep.*) or from expert opinion offered by Kath Walker. Many shells I found were old and in such an advanced state of decay that it was impossible to distinguish whether damage was due to a predator or caused by natural decay. These shells were classed as 'not predator damaged'. A predator was considered to be the cause of death of a snail if the shell had any evidence of gouges, stab holes, gnawing, or scrapes, or if toothmarks were present on them. It was not possible to tell if damage occurred pre or post-mortem.

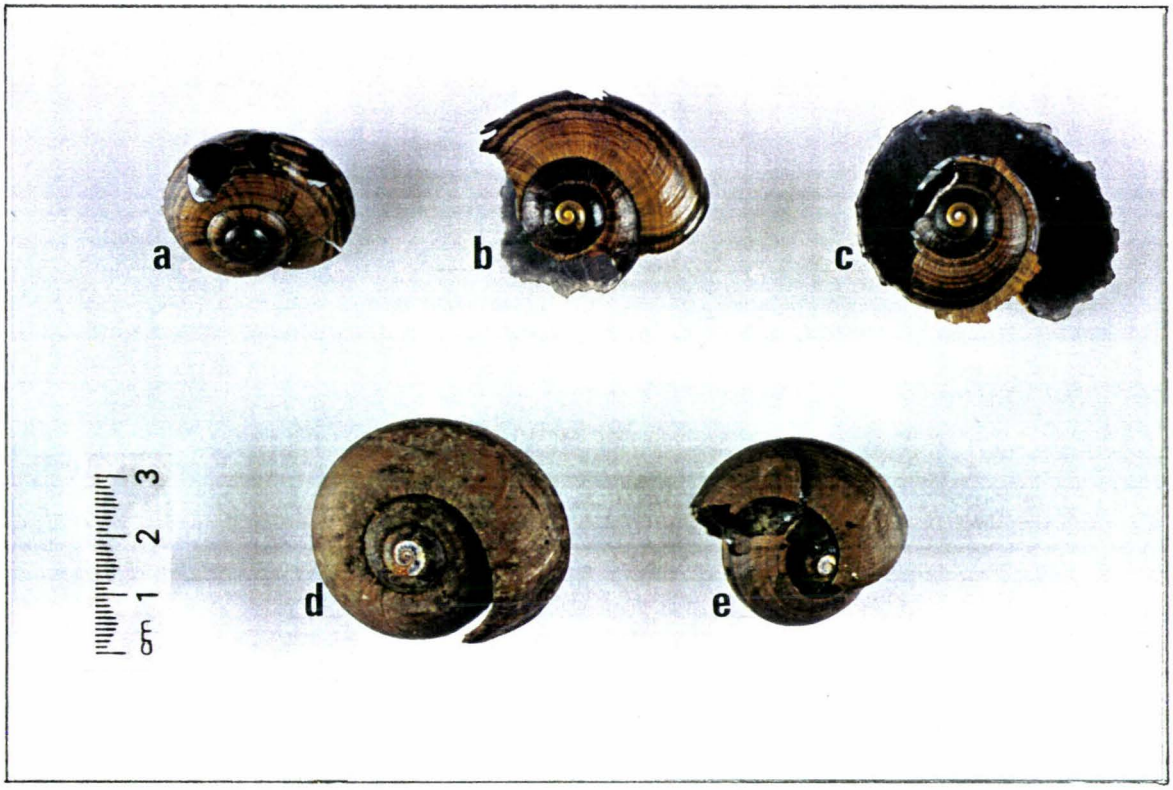

Figure 7.1: Empty *P. t. traversi* shells

a. Non rat predator damage.
b. Ship rat type damage.
c. Norway rat type damage.
d. and e. Old degraded shells where cause of death was difficult to determine in many cases.

The size of snails attacked by predators

The shell lengths of empty shells with predator damage were compared to those of both live snail shells and undamaged empty ones. Where shell length could not be measured due to damage it was estimated from either shell aperture or width from linear regression equations.

Estimating predator abundance

Rats:

The relative abundance of rats at Papaitonga Scenic Reserve was estimated during the period between 7/4/95 and 13/4/95. Two sites separated by a swampy gully (sites A and B in Figure 7.2) were sampled by snap-trapping without prior baiting. The standardised method used by the former Department of Scientific and Industrial Research (Innes 1990) was employed with two exceptions. Mouse traps were not used in tandem with rat traps and the traps were baited with crunchy peanut butter, rather than a peanut butter and rolled oats mixture.

A trap night is equal to one trap set for one night. One hundred trap nights is the minimum number that should be used for comparative purposes. In this study twenty traps were set at each site every night for five nights. On the sixth night sufficient traps were set bring the total number of trap nights corrected for sprung traps to 100 at each site. Trap success calculations were corrected using the method of Nelson and Clarke (1973). Rats were identified according to Table 34 of King (1990).

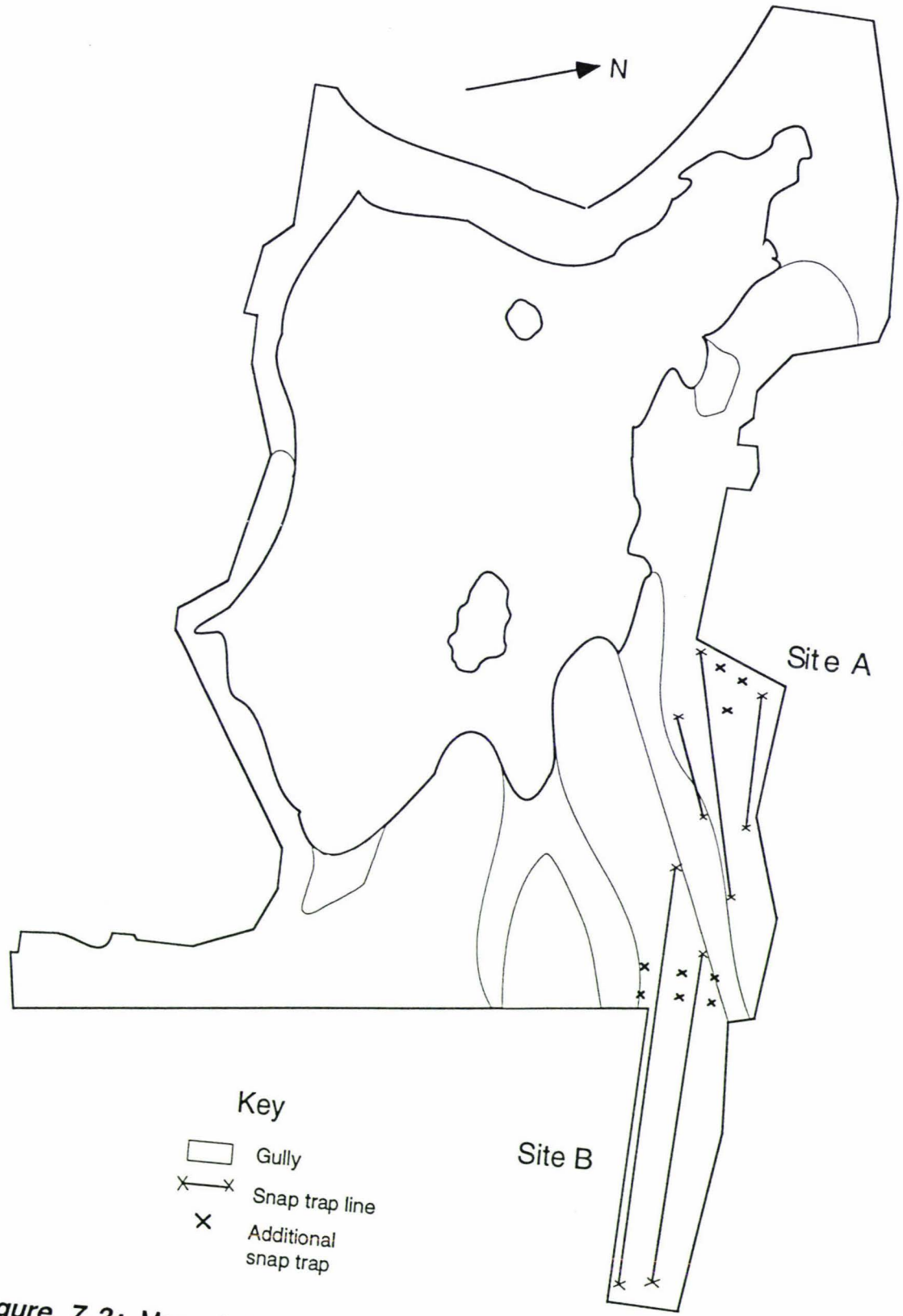

Figure 7.2: Map of Papaitonga Scenic Reserve showing location of rat traps and trap lines. Scale 1.2 cm : 100 m.

Each trap was placed on the ground under an aluminium cover with a semi-circular cross section. Each cover was approximately 120 cm long by 15 cm high (Figure 7.2). One end was closed off with chicken wire so that rats could only approach the traps from the direction that would ensure a kill. The open end was also partially blocked off with sticks pushed into the ground to prevent the entry of possums. Bait was replaced every second day or when it disappeared.

Figure 7.3: Snap trap and Aluminium cover.

Estimate of possum number:

There is no published index derived from trapping possum although it is likely that experienced trappers could make a subjective comparison between sites. My study coincided with the Department of Conservation (Waikanae Field Centre) starting to possum trap at Papaitonga Scenic Reserve so it was possible to calculate the number of possums captured per 100 trap-nights, and calculate a minimum density using their raw data.

Presence of snail radulae in rat guts.

The stomach and intestinal contents of ten ship rats were examined for radulae or radula teeth, and a cursory examination of the other dietary components was made. Gut contents were first washed through a 45μm grid sieve with water. The stomach and intestinal contents were then boiled for a few minutes in 10% KOH following the method of Millar (1978) to dissolve most of the softer dietary components. The remaining material was then studied using a dissection microscope (Zeiss, W.Germany).

Protection of study snails from predators

Live *P. t. traversi* that were followed with an harmonic radar at Papaitonga Scenic Reserve were sometimes later found to have been attacked by rats. A narrow strip of annealed copper was attached to the lip of ten snail shells with a cyanoacrylate adhesive (Loctite 401, Australia) to protect them. This hindered rats from gnawing back more than one or two mm of shell (Figure 7.2).

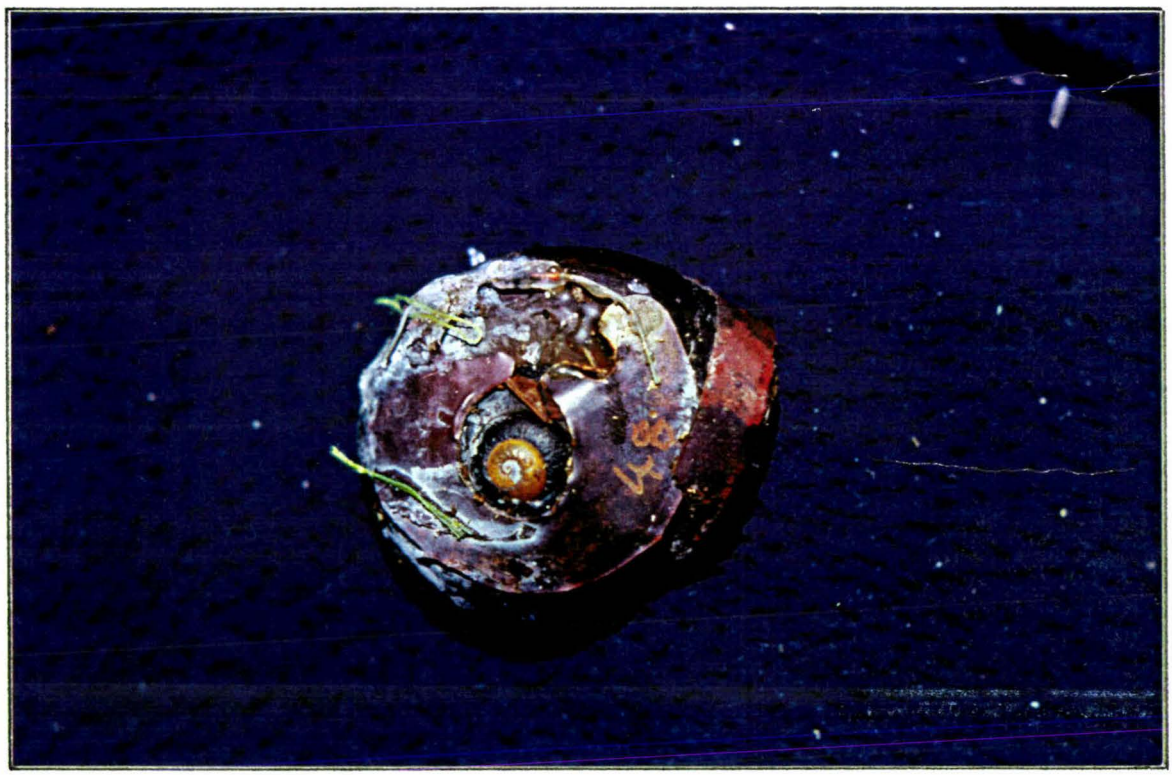

Figure 7.4: *P. t. traversi* with copper strip protecting the lip of its shell.

Results

Live *P. t. traversi* population followed at Papaitonga Scenic Reserve.

Table 7.1: Mortality and incidence of predation in 20 live *P. t. traversi* monitored at Papaitonga Scenic Reserve

Snails	Number
Total followed	20
Number known to survive study	11
Died without signs of predation	4
Killed by rat[1]	3
Attacked by rat but survived[2]	2
Disapeared[3]	2

1. All snails classed as killed by rats showed Norway rat (*Rattus norvegicus*) type damage (Meads *et al*, 1984) to their shells. 'Norway rat' damage is regarded as taking place where the rat extracts (or attempts to extract) the snail from its shell by nibbling back from the shell lip.

2. One of the snails that survived a rat attack died eleven months later, however, this could not be attributed to the attack.

3. Disappeared during a period when all snails were essentially not moving. These two snails would have had to move further than recorded for any snail in the movement study (Chapter five) to have left the range of the harmonic radar by its own means.

The three snails killed by rats and the two which survived rat attacks (Table 7.1) had recently either had epoxy resin or cyano-acrylate adhesives applied to their shells to attach transponders, spool and thread tracking devices (*Chapter five*), or both. Fumes released during the curing process were easily detectable by humans so they were also likely to be detected by rats. The cotton thread which unwound from spools was highly visible.

Two live snails being followed with the harmonic radar disappeared on days that all other snails exhibited little movement. On 11/08/95 the cotton from a spool attached to a snail was followed up a slanting tree trunk approximately four metres into the canopy. The thread snagged at this point and the snail fell back down to the forest floor, showing no ill effects.

Protection from predation:

Only one of the ten snails with copper strips glued around their shell lips was attacked. This snail was killed after the copper was pulled off. Several scratches were obvious on the copper indicating some effort was required to remove it. Experimentation with stronger glues was not pursued because ship rat type damage, that would not be prevented by the copper strip, was discovered and predation became less common with only one case in five months following three in the first week.

Table 7.2: Empty shells found within quadrats at Papaitonga Scenic Reserve

Type of shell	Number found
Total	70
Not damaged	53
Damaged by rat	11 (64 % of predation)
Unknown predator	6 (36 % of predation)

Table 7.3: Shells found within quadrats at Makahika Scientific Reserve

Type of shell	Number found
Total	50
Not damaged	30
Damaged by rat	16 (80 % of predation)
Unknown predator	4 (20 % of predation)

24.35 % of the 70 empty shells found within quadrats at Papaitonga Scenic Reserve showed signs of predation (Table 7.2), 64 % of this predation was directly attributable to rats. In contrast 40 % of empty shells found within quadrats at Makahika Scientific Reserve (Table 7.3) had predator damage, 80 % of this was attributed to rats. At both sites empty shells with rat predation were found littering the forest floor outside quadrats. Shell caches were found at both Papaitonga and Makahika in hollows under the roots of trees and on branches several metres above the ground. Shells with damage consistent with both ship rat type and Norway rat type predation were found at both Papaitonga and Makahika but the two types of damage never occurred within one cache.

The size of snails attacked by predators

There was no significant difference in shell length between predator damaged, and both live snails and empty undamaged shells (Mann-Whitney U test, $P < 0.05$).

Attacks upon live snails occurred on both the second smallest and on one of the largest individuals (24.05 mm and 49.2 mm in shell length respectively). *Rattus* sp. were clearly responsible for each of these attacks.

The three smallest empty shells found had no predator damage. These snails were 10.00, 10.20, and 11.05 mm in maximum dimension respectively.

Table 7.4: Comparison between shell lengths: Predator damaged shells versus other *P. t. traversi* shells Mann-Whitney U test.

Comparison	Means of compared values (mm)		Difference
Papaitonga:			
Live v. empty predator damaged	42.77	41.06	NS
Empty not damaged v. predator damaged	42.39	41.06	NS
Makahika:			
Live v. empty predator damaged	42.41	39.43	NS
Empty not damaged v. predator damaged	41.66	39.45	NS

NS: not significant $\alpha = 0.05$

Estimating predator abundance

Rats:

Table 7.5: Summary of rats trapped at Papaitonga Scenic Reserve

	Number caught per 100 trap nights
Site A:	10
Site B:	7
Combined mean of A and B	8.5

Ten rats were caught at site A and seven at site B. The mean of site A and B was 8.5 rats per 100 trap nights (Table 7.5). All rats caught were ship rats (*R. rattus*).

Possum:

Table 7.6: Possum trapped at Papaitonga Scenic Reserve in 1994

Variable	Number
Total trap nights	1696
Possum caught	205
Total sprung traps (including captures)	205 (estimate, data not supplied)
Possums / 100 trap nights[1]	12.9

1. Corrected trap nights using equation of Nelson and Clarke (1973)

Table 7.7: Possum trapped at Papaitonga Scenic Reserve in 1995

Variable	Number
Total trap nights	1411
Possum caught	237
Total sprung traps (including captures)	311
Possums / 100 trap nights[1]	18.9

1. Corrected trap nights using equation of Nelson and Clarke (1973)

Possum browse damage was most noticeable on kohekohe (*Dysoxylum spectabile*). Many shrubs of this species less than 1 m in height were stripped of leaves. Some large trees were totally defoliated.

Papaitonga Scenic Reserve has a land area of 50.9 Ha. not including islands (Chapter two). From the number of possum trapped (Tables 7.6 and 7.7) I calculate that there was a possum density of at least 4.03 possum Ha^{-1} in 1994 and 4.65 possum Ha^{-1} in 1995.

Possum faecal pellets were regularly found on the ground at Makahika indicating their presence.

Other potential predators and causes of snail death

Shells with bird damage consistent with the Meads *et al* (1984) weka, blackbird or thrush predation category were occasionally found in farmland immediately adjacent to Makahika, but never within a quadrat. Cattle had churned up sections of the forest floor and degraded parts of the reserve at Makahika, and one shell with crush damage due to direct downward pressure was found on a walking track was found at Papaitonga Scenic Reserve. Possum traps at Papaitonga captured one ferret and a cat. Rabbit droppings were also seen within the forest at Papaitonga. Feral pigs were not seen at either site nor were there signs of rooting, or the characteristic shell damage that Meads *et al.* (1984) reported that pigs cause.

Rat diet.

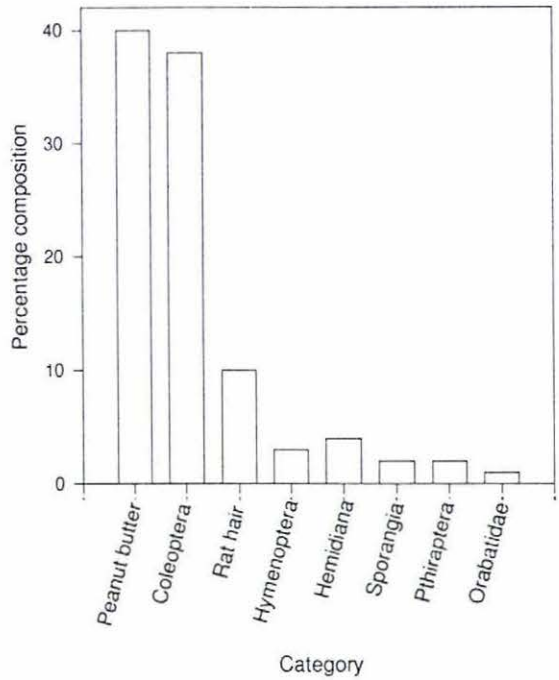

Figure 7.5: Histogram of the gut contents of ten *R.rattus*

No snail radulae were found in the gut contents of any of the rats. The most common item found was the peanut butter that I used as bait. Other readily identifiable items were pieces of Tenbrionidae, weta, coleoptera exoskeleton and wing, nematodes and hymenopteran larvae. Entire lice (Pthiraptera), orabatid mites, and sporangia (asexual fern buds) were found. Tape worms were present in the stomachs of four of the ten rats.

Discussion

Vertebrate predation

Rats were the chief predators at both Papaitonga Scenic Reserve and Makahika Scientific Reserve. The distribution of empty shells that showed rat predation indicated that rat predation occurs over most of Papaitonga Scenic Reserve. I believe that the three *P. t. traversi* killed in my long term study group of 20 individuals followed for one year (15% predation per annum) is dangerously high for an organism reputed to live for up to forty years (Meads *et al.* 1984). This is especially so because circumstantial evidence strongly

suggested two additional snails were also taken by predators (bringing the total to 25% predation per annum) and because such mortality is presumably in addition to natural mortality. Damaged empty shells, where the type of predator could not be determined, accounted for 36 % and 20 % of predation at Papaitonga and Makahika respectively. It is important to note that the level of predation measured may be unnaturally high. Experimental manipulations in my study such as transponder attachment with aromatic glues could have attracted rats and increased the chance of attack. I suggest that snails should be protected in a container or in captivity until glues have dried and the smell dissipated. It may be prudent for workers to wear gloves or consider the application of anti-rodent or aversion forming compounds to the snail's shell when handling *Powelliphanta* from small colonies with a high predation pressure.

Rats did not appear to show a preference for snails of any particular size. This was in contrast to the work by Hadfield, Miller and Carwile (1993) who found size selection by rats on the Hawaiian land snail *Achatinella mustelina* Mighels. In that particular study, rats did not consume individuals smaller than 15 mm in maximum dimension. I found that there were too few empty small shells to conclude that rats avoid smaller snails. *P. t. traversi* do not form a major part of rat diet which appeared to be arthropod based. The snails are relatively scarce (*Chapter four*) and small individuals were poorly represented in the populations I sampled (*Chapter three*). For these reasons it would seem reasonable to suggest that rats do not have to make an energetic decision when taking *P. t. traversi* and would not deliberately select snails of a particular size. Snails have no defence against rats except by retreating into their shells. Some *P. t. traversi* do survive rat attacks but I believe this is due to good fortune rather than any other factor.

Results of snap-trapping (8.5 rats/100 trap nights) indicated that the rat population was higher than other similar tracts of bush. Brockie (1992) reported that Keebles bush had a trap index of 2.8 and both the Tiritea forest and Orongorongo Valley had 3.9 rats / 100 trap nights. A higher rate of capture was previously recorded at Papaitonga by David Havill (1994, *pers. comm.*) who

captured 12 rats in one night with 12 traps. This Figure cannot be directly compared with a per-hundred-trap-night index as it was much less than the minimum of one hundred trap nights, but it showed that high rat numbers were also present in the past.

Taylor (1975a, 1978a, 1984) reported that there is strong competitive exclusion between the four established rodent species in New Zealand. All the rats I captured were ship rats (*R. rattus*) which suggested that this species was the only one present at Papaitonga Scenic Reserve. Meads *et al* (1984), however, suggested that *R. norvegicus* was present there over a decade ago. They distinguished two distinct types of shell damage caused by rats on *Powelliphanta* shells (Figure 7.1). The first was where gnawing occurred through the side of the shell, this was considered typical of ship rat damage, while gnawing back from the lip of the shell was regarded as typical Norway rat damage. The occurrence of a given damage type was not necessarily diagnostic of the respective species presence because on occasion either species could cause both types of damage (Meads *et al*, 1984). I found both methods of predation in my study, but never in the same cache. This leaves open the possibility that *R. rattus* and *R. norvegicus* co-exist at the two study sites.

The attempt to protect the study animals from rodent predation with copper strips glued around the shell lip met with some success. The only snail with the copper strip attached that was attacked was killed, but only after the rat had obviously taken some considerable effort to remove the strip. If epoxy resin was used rather than cyano-acrylate adhesive, copper strips may reduce gnawing-from-the-lip type predation but would not prevent through-the-side-type predation.

Attacks on the study population generally occurred the night after the handling process that was required to glue transponders and spools for tracking purposes (*Chapter five*). The smell of curing glue was obvious to humans It is possible that this or the scent left by the handler may have attracted rats. If this

was the case then such attacks could be minimised in the future by using gloves or taking the snail into captivity overnight while the glue cured.

The snail who's thread trail was followed up into the canopy was almost certainly carried by a rat. I base this on my observations that *Powelliphanta* do not climb (*Chapter five*) and that the way the thread unwound for a substantial distance along the ground before moving up the tree. This would make it unlikely that the snail was carried by a bird in flight. The presence of shell caches both in chambers under trees, and in forks between branches in trees indicated that rats take the snails both to retreats on the ground and up in trees. The three snails that were eaten, and the two that survived attacks were either carried to a safe place such as the crook of a tree to be consumed, or the cotton trail they unravelled tangled while they were heading directly toward one. This suggested that these sites were habitually used.

Possum which are known to be the main predators of *Powelliphanta* in some areas of New Zealand (Walker and Elliott *in prep*, Gillingham, 1994) and they live in all North Island *Powelliphanta* habitats except for the upper slopes of Mt. Taranaki (Cowan, 1990) . My study showed no evidence of predation by this species despite reasonably high numbers at both study sites. This finding is in agreement with Walker and Elliot (*in prep.*) who noted that possum do not eat *Powelliphanta* in some regions including the Horowhenua.

It is not known why some possum eat snails whereas others do not, but the habit has developed separately in both the North and South Islands (Walker and Elliott *in prep*). Further investigation would be required to determine if *Powelliphanta* eating behaviour is conditional on factors such as food availability. Kath Walker (1995, *pers. comm.*) suggested that snail consumption may be a learned behaviour. If this is true then the behaviour may not occur in the Horowhenua because it has yet to be culturally transmitted there, or that snail eating is not locally adaptive. This would preclude its development, or introduction from an outside source according to Galef (1995). The former

would seem more likely if recent evidence of possum predation on *P. t. traversi* fa. tararuarensis can be confirmed (I. Cooksley, 1995, *pers. comm.*).

The importance of bird predation upon *P. t. traversi* remains unknown. Birds certainly eat *P. t. traversi* at Makahika, but bird damaged shells were only found outside the reserve. It is possible that some more mobile predator species, such as some birds, are not permanently resident in *P. t. traversi's* habitat but move into it from outside. In such cases the ratio between the physical area of a reserve and its boundary length may be an important factor in the level of predation (an increased 'edge effect'). Snails that live in relatively small bush areas that have long boundaries would thus be more vulnerable to predation from predators that only move short distances into the forest. Feral pigs, known to consume both South Island *Powelliphanta* (Meads *et al*, 1984) and North Island *Paryphanta* (Parish, Sherley, and Aviss 1995), were not observed at either site but they were reported in the exotic plantation adjacent Makahika Scientific Reserve (J. Townsend, 1994, *pers. comm.*). I believe that Makahika is close enough to Tararua Forest Park for feral pigs to gain access occasionally

Farm animals can kill snails both indirectly and directly. Parish *et al* (1995) noted that domestic and feral cattle (*Bos taurus*, L.), sheep (*Ovis aries*, L.), horses (*Equis caballus*, L.) and goats (*Capra hircus*, L.) can cause habitat destruction and degradation and that this lead to the decline of snails. In addition, a farm animal may crush snails by standing on them. This kind of damage was not observed but was possible at Makahika during research for this thesis because cattle had access from an adjoining farm. Makahika Scientific Reserve was recently fenced to rectify this problem.

Measures of predation are likely to be inaccurate for a variety of reasons. For example, not all shells of snails taken and consumed in trees fall to the ground to be counted. Some predators may be able to extract a snail from its shell without causing shell damage, or may consume small shells entirely (Schifferli 1977, cited Cain 1983). The existence of caches of shells show that remains of snails killed by predators are not always randomly distributed. A combination of these factors could explain the discrepancy between predation on the snails

followed with the harmonic radar (43 % of snails which died during the study were killed by a predator) and empty shells damaged by a predator at Papaitonga (where 24.3% of empty shells had some form of predator damage).

In other parts of the world, many invertebrates are known snail predators. These include several species of coleoptera, centipedes, diptera, platyhelminthes, hymenoptera, and other snails (see review by Mead 1979). My study found no evidence of such predation but native Rhytidids such as *Wainuia* Powell and *Rhytida* Martens that were present at each study site both eat snails (see Chapter six for comment on the diets of some New Zealand snails). Barker (1989) recorded the native flatworm *Geoplana ventrilineata* Dendy attacking, and eating both introduced and endemic slugs. Introduced *Vespula* species were observed attacking and killing weta (*Hemidiena*) for food in South Island beech forests (Harris, 1991). The sting of *Vespula* could potentially kill a snail and would leave no obvious shell damage.

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Chapter Eight

Summary and Recommendations

Powelliphanta traversi traversi remains threatened, but the Department of Conservation (Waikane Field Centre) is proactive in its conservation. At least one *P. t. traversi* fa. koputaroa colony has had poison bait regularly laid in it to reduce rodent numbers. Makahika Scientific Reserve was obtained by the Department of Conservation for snail conservation purposes and was recently fenced to protect the reserve from farm animals and poisoning programme directed toward reducing possum number implemented. Possum trapping, and bait stations at Papaitonga Scenic Reserve are specifically for snail preservation, and a permanent *P. t. traversi* quadrat was established there. Ian Cooksley (DOC Waikane field centre) has finished an in-depth study on the status of all *P. t. traversi* colonies recorded in historical literature, but has not had the resources to produce a report on the subject.

Knowledge about the basic biology and population dynamics of *Powelliphanta* is still lacking. This thesis highlighted that the lack of such information prevents an accurate assessment of the health of populations and their ability to sustain various levels of predation. Frequency of egg laying, clutch size, and hatching success could be examined in captivity. Any programme that held *Powelliphanta* in captivity would be enhanced by a better knowledge of diet, especially interesting would be that of juveniles and possible consumption of fungal and plant material.

It must be stressed that rats were by far the major cause of *P. t. traversi* predation in my study. There was no evidence that possum ate *P. t. traversi.* Removal of possum will undoubtably be beneficial to the *P. t. traversi* habitat at both Papaitonga Scenic Reserve and Makahika Scientific Reserve but at this stage will not reduce the high levels of predation on *P. t. traversi.* Rats have a shorter life cycle than *Powelliphanta* and as a consequence reproduce at a younger age, probably at a much higher rate. There is evidence to suggest that

rats killed up to 25% of my study population in one year. Ideally rats should be eliminated from sites known to contain major *P. t. traversi* colonies. Recent advances in pest control that help attract target animals and eliminate bait shyness (as I presented to the National Possum Control Agencies Conference, November 14th 1996) should make such goals a reality. Until these products become available I strongly recommend that rat numbers be monitored at both Papaitonga and Makahika. If or when the rat population rises above 'normal' levels for these types of forest a poisoning programme should be implemented to reduce their numbers. There is evidence to suggest that at Papaitonga 'normal' levels are regularly exceeded (*Chapter seven*, D. Havill, 1995 *pers. comm.*). Monitoring of rat number at both Papaitonga and Makahika, could be conducted in conjunction with the Manawatu Polytechnics (Levin) conservation course.

The genetic analysis conducted by Kath Walker will rectify many of the problems of *Powelliphanta* nomenclature. Depending on the results of Walker's work a closer analysis of the relationship between various *P. t. traversi* formae may be warranted. A comparison could be made between *P. t. traversi* at Makahika Scientific Reserve and those translocated to Kandahala in Wellington 50 years ago could be of considerable interest.

Recommendations:

- Current rodent control at Koputaroa should continue and be expanded to include Papaitonga Scenic Reserve and Makahika Scientific Reserve.
- Rat number should be monitored regularly (perhaps bi-monthly) with three day snap-trap indexing at the site of major *P. t. traversi* colonies. When rat numbers exceed normal levels they should be controlled.
- Possum management should continue but not at the expense of rat control. Unless possum predation is shown to occur in the Horowhenua I would favour rat control in preference to possum control.
- Ian Cooksley should be provided with the resources to complete his report on the status of *P. t. traversi* colonies.

- Formal protection of properties containing *P. t. traversi* fa. tararuaensis colonies should be investigated.
- K. J. Walker should be consulted on the need for more work on the molecular ecology of *P. t. traversi*. Such work could easily be conducted at Massey University.
- Frequency of egg laying, clutch size, and hatching success should examined in captivity if reasonable estimates cannot be obtained elsewhere from unpublished work on other members of the genus.

Appendices

Appendix one

Classification:

The classification of *Powelliphanta* is contentious. The research undertaken for this thesis falls after the death of A. W. B. Powell and before publication of both the results of electrophoretic tests conducted by K. Walker, and the long awaited Monograph by F. M. Climo. The following classification is derived from the literature and is likely to reflect current thought but has not been assembled in this form previously.

Table a1.1: Classification of *Powelliphanta traversi traversi*

Class: Gastropoda

Subclass: Pulmonata

Superorder: Stylommatophora

Order: Stigmurethra

Superfamily: Rhytidacea

Family: Rhytididae (Pilsbry, 1893)

Subfamily: Rhytidinae (Pilsbry, 1893)

Genus: *Powelliphanta* (O'Connor, 1945)

Species: *traversi* (Powell, 1930)

Subspecies: *traversi* (Powell, 1930)

Forma: traversi (Powell, 1930), koputaroa (Powell, 1946), florida (Powell, 1946), latizona (Powell, 1949), and tararuaensis (Powell, 1938), The above classification is based on that by Solem (1978) down to family level, Climo (1977a) for genus and species, and includes work by Powell (1979) to recognise different forma.

Appendix two

Regression equations for climatological data approximation and long term movement diagrams

Climate data approximation

Equations generated by linear regressions on paired data collected concurrently at Papaitonga Scenic Reserve and the Levin Research Centre Automatic Weather Station.

Temperature:

Papaitonga dawn temperature = 2.51+ 0.846(Levin dawn temperature)

R^2 (adj) = 91.4%

Middle of dark period Papaitonga temp. = 2.41 + 0.859(Levin mid-dark temp.)

R^2 (adj) = 91.0%

Dusk temp. Papaitonga = 0.792 + 0.913(Levin dusk temp.)

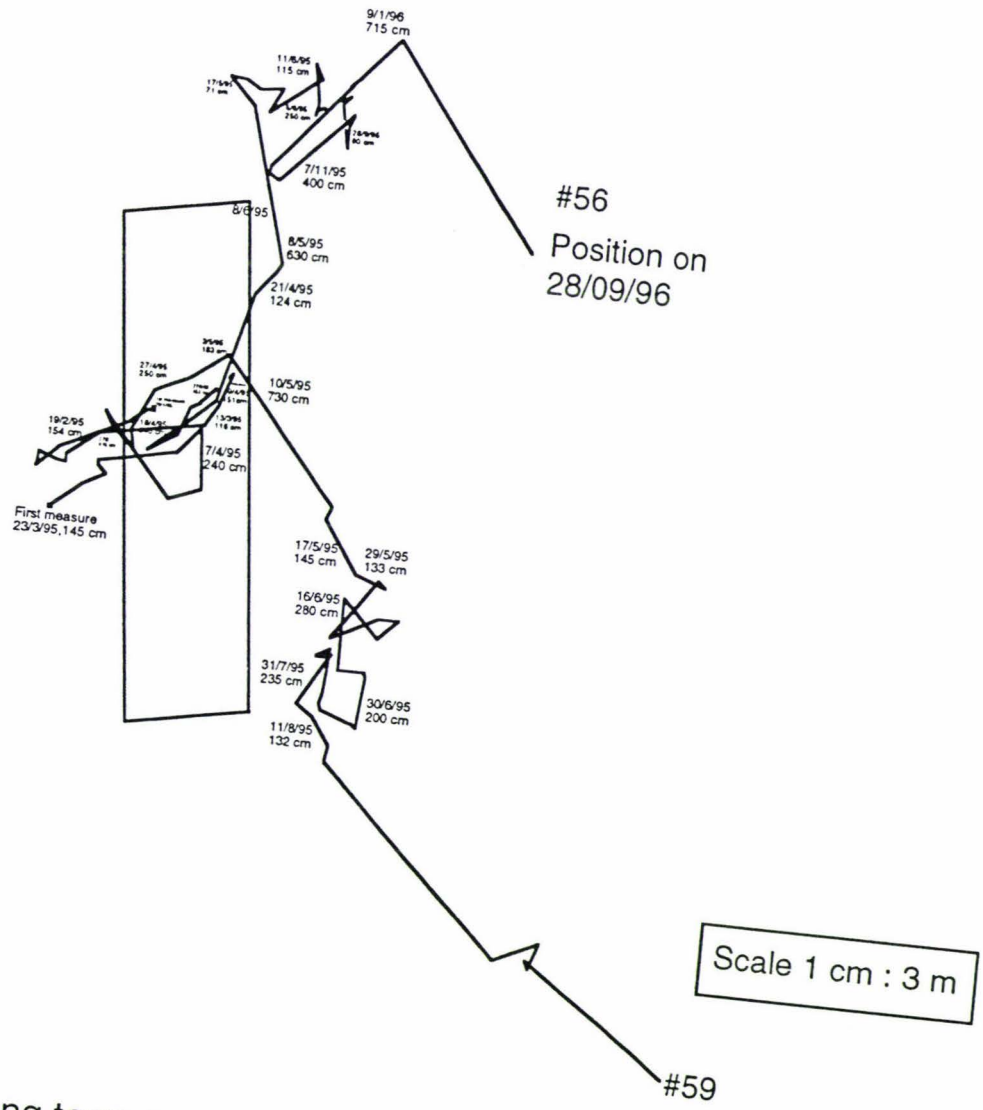
R^2 (adj) = 89.0%

Rainfall:

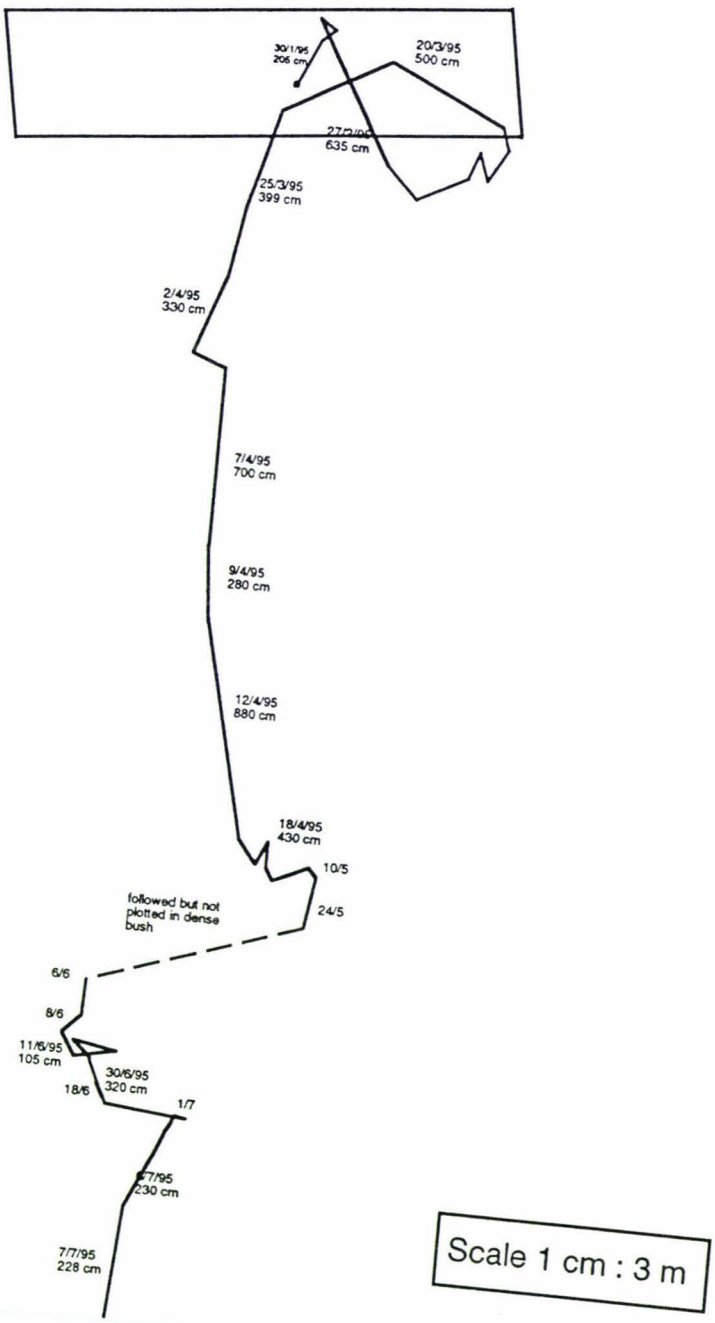
Rain Papaitonga = 0.24 + 0.783(Levin rain)

R^2 (adj) = 49.1%

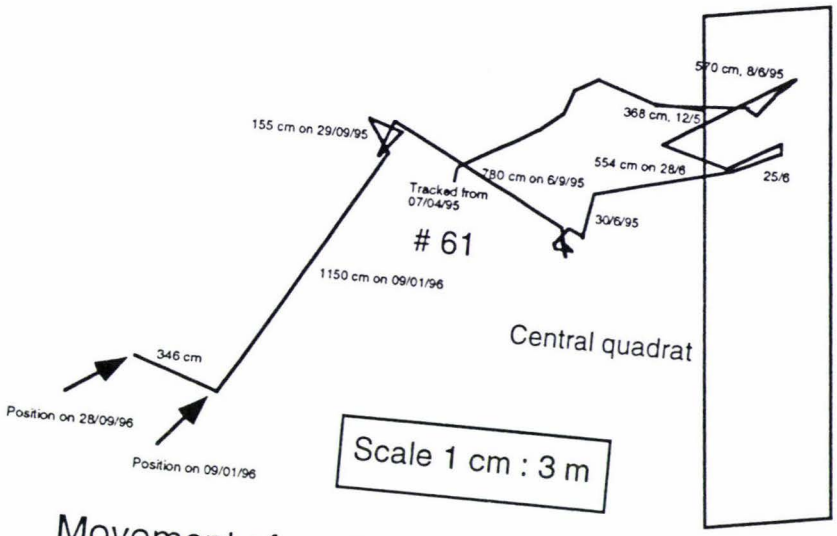
Long term movement of all snails followed with the harmonic radar



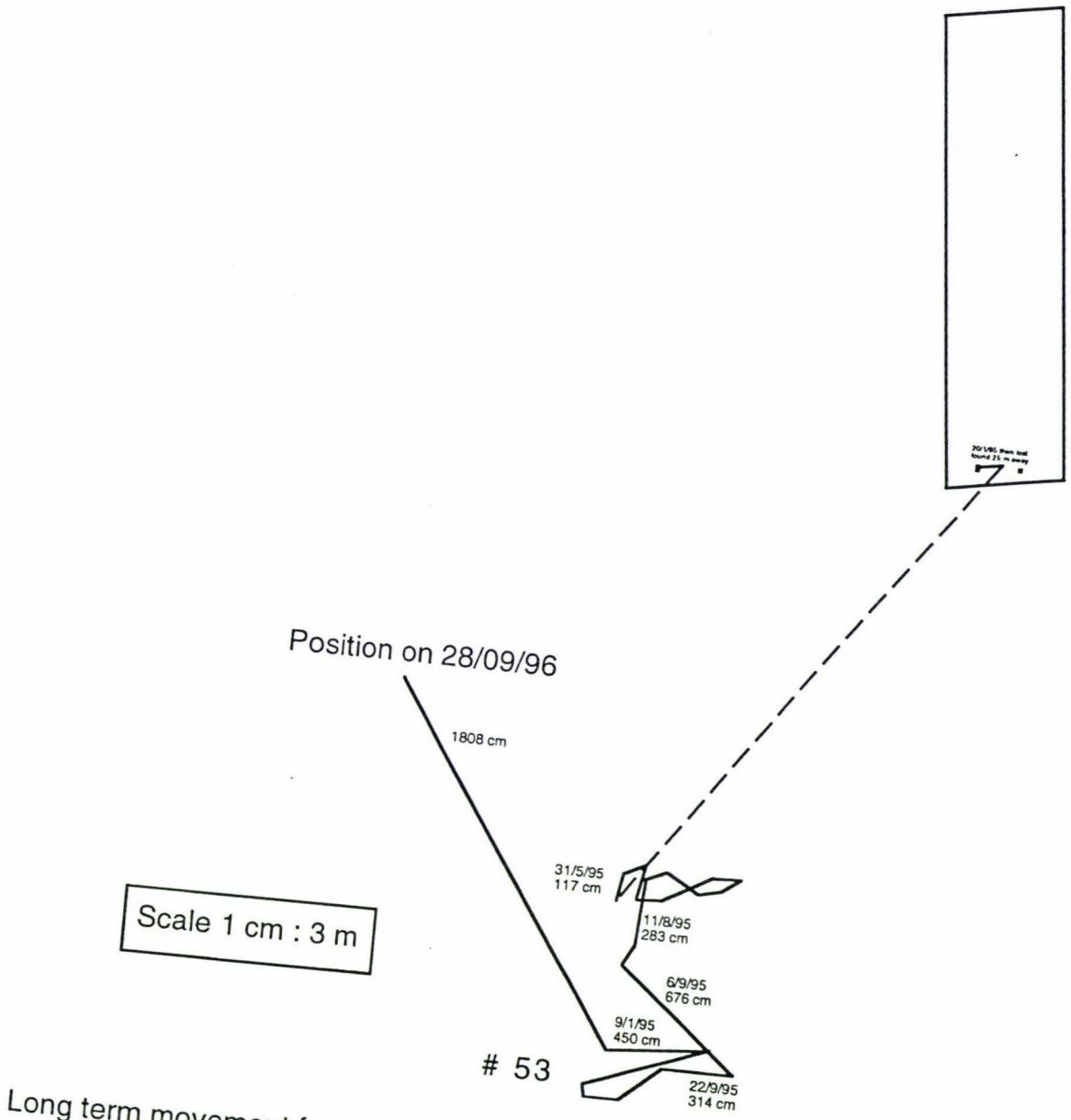
Long term movement for snails 56,59,



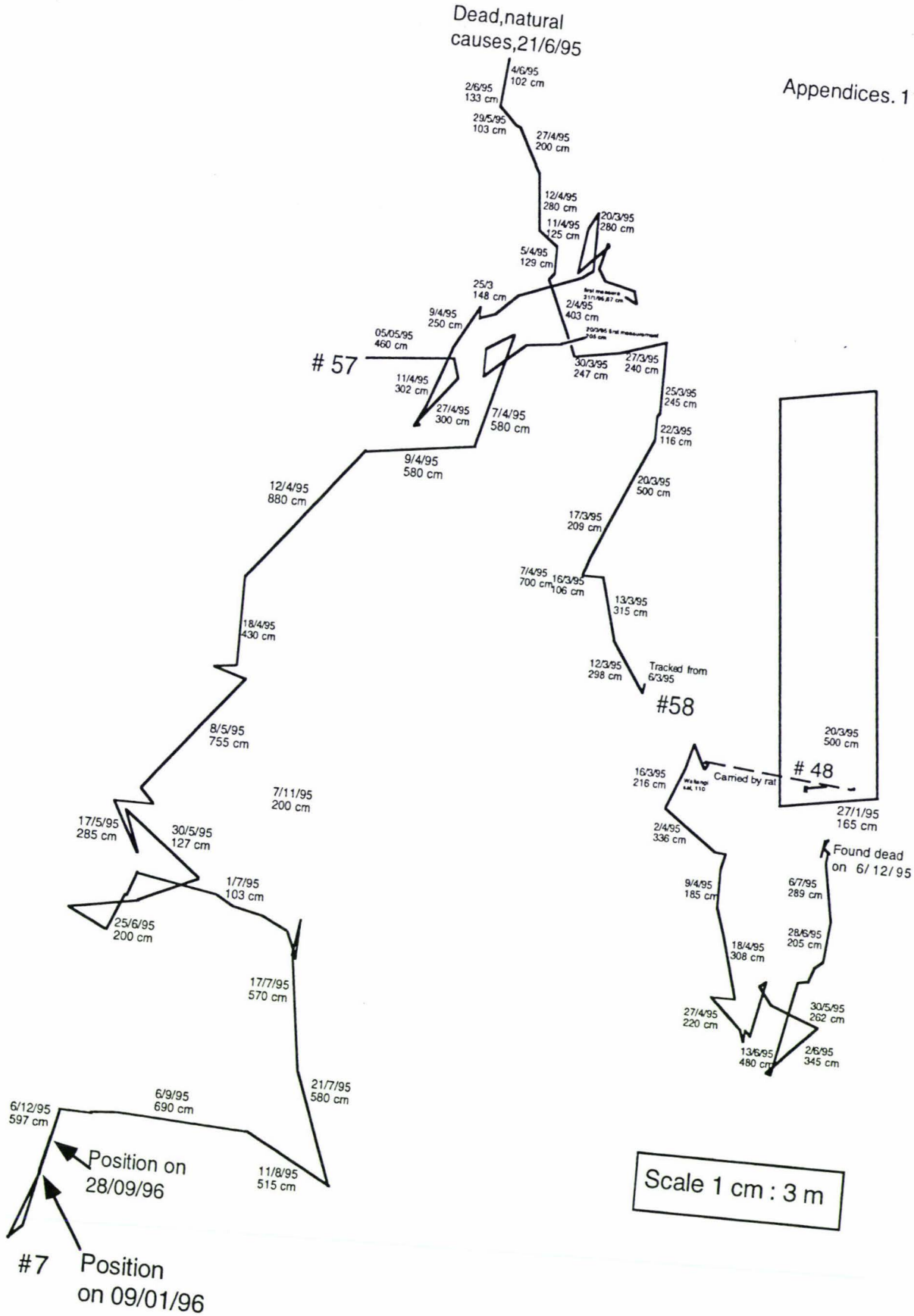
Long term movement of snail # 55



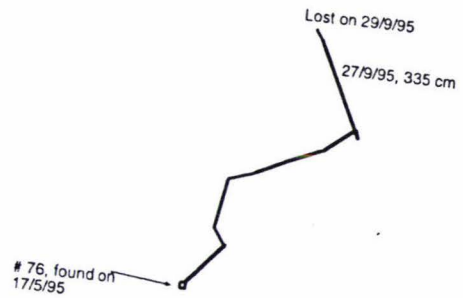
Movement of snail # 61 for entire trial

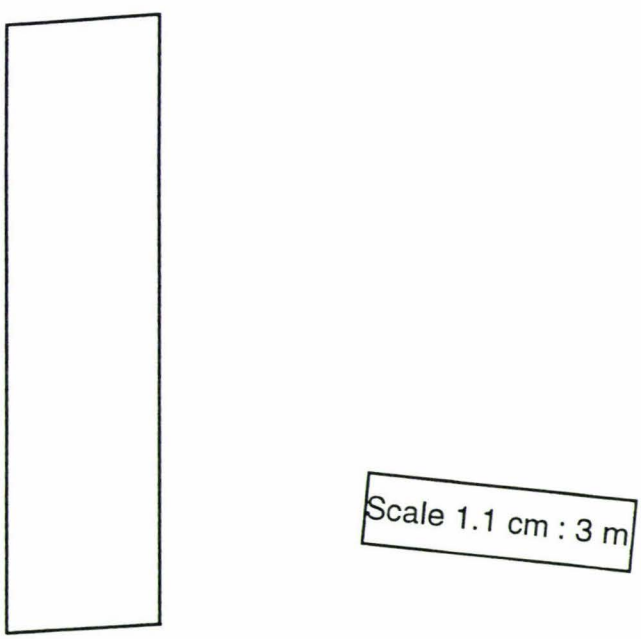


Long term movement for Snail # 53

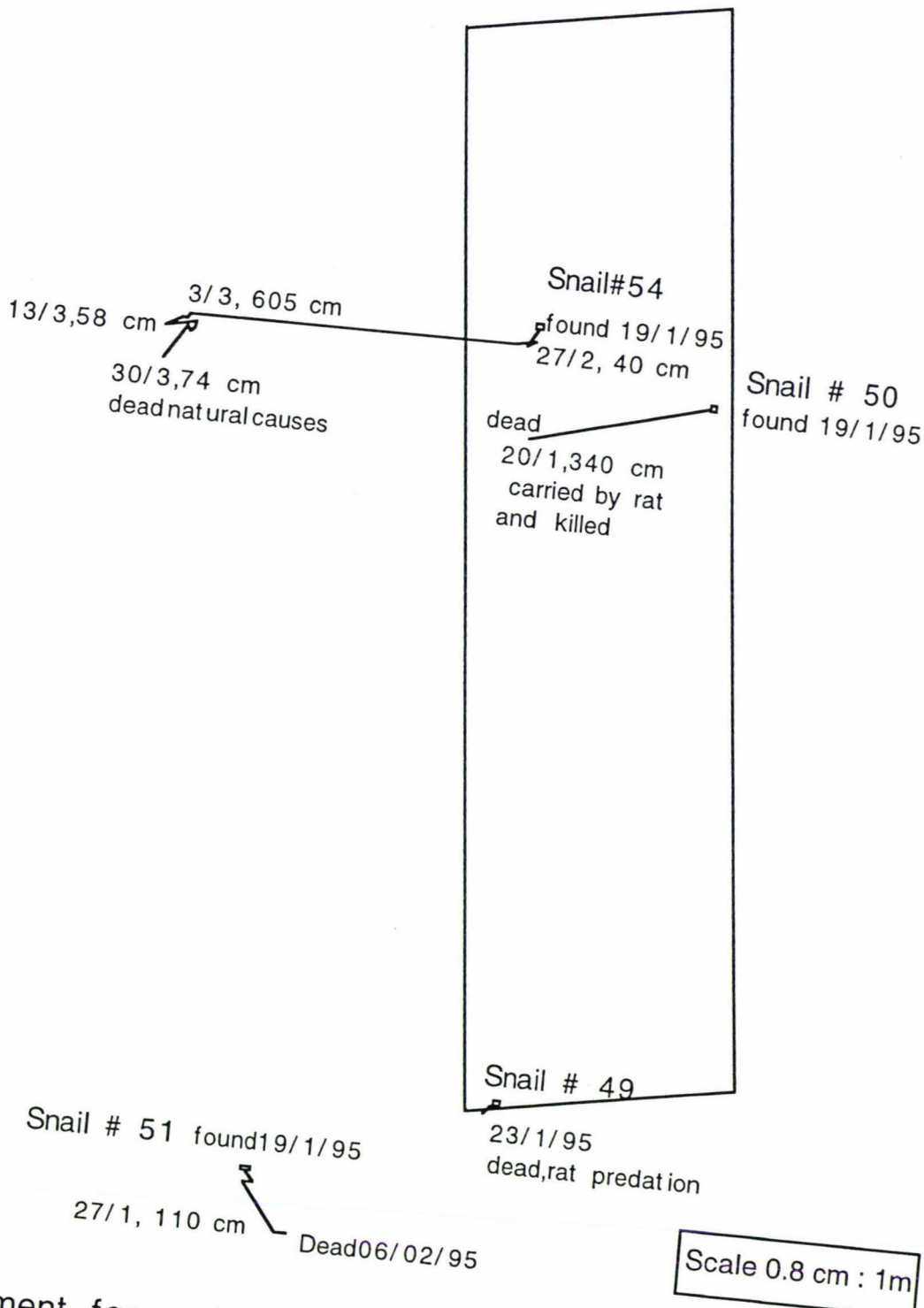


Long term movement for snails 7, 48, 57, and 58





Long term movement of snail # 76 for entire trial



Movement for entire trial for the snails that exhibited the least movement

Appendix three

The acute effects of adhesive application to the shell of *Helix aspersa* Müller (Mollusca: Pulmonata)

Abstract

Four common adhesives were applied to the periostracums of *H. aspersa* land snails in the laboratory to determine their toxicity and suitability for attaching tracking devices to protected land snails. No acute effects were observed but adhesive was not applied to the body of the snails. Chronic effects were not assessed.

Introduction

This study was undertaken to determine whether certain adhesives kill or have harmful acute effects on snails when applied to their shells. The adhesives were intended to attach small diode transponders and labelling tags to the shells of land snails of the genus *Powelliphanta* (Pulmonata: Rhytididae). Transponders allow snails to be found using an harmonic radar detector (Mascanzoni and Wallin 1986). All species of *Powelliphanta* are protected under the Wildlife Amendment Act 1980, so it is essential that any adhesive used should not harm them. All trials were performed on *Helix aspersa* Müller to see if the adhesives had any acute effects before their application to the protected species.

The gastropod shell is protective, reducing the effects of predation as well as shielding the animal from the environment. A typical gastropod shell consists of two layers, a calcium carbonate ostracum overlaid with a proteinaceous periostracum. The ostracum defines the size and shape of the shell and provides much of its strength, but it can be porous. The periostracum is waterproof and prevents desiccation. Anything that damages the periostracum may leave the animal susceptible to potentially hazardous chemicals that could diffuse through the ostracum.

Each adhesive tested has a different mechanisms of adhesion and different properties that could be useful for various applications. The non-acetic silicon compound tested was designed for the manufacture of fish aquaria or to seal iron where conventional silicon with acetic acid would contaminate the water or cause corrosion. The fast curing epoxy resin used is a two part product which requires the accurate combination of a resin and hardener. Cyano-acrylate adhesives (commonly called 'super glues') work by a polymerisation process

(Adam 1995, Barraclough 1995). When a thin film is applied the glue sets in a matter of seconds and becomes chemically inert. The hydrocarbon based building adhesive tested was a solute/liquid hydrocarbon (35 % w/w) solvent combination. The solvent evaporates after application allowing the adhesive solute to set.

Methods

Adhesives used:
Non acetic acid based construction silicon (Bostik brand)
Fast curing epoxy resin (Selleys 'five minute Araldite')
Cyano-acrylate glue (Loctite type 401)
Liquid Hydrocarbon based building adhesive (Fullers 'Max bond')

Study animals:
120 wild captured *H. aspersa.* These ranged from 0.7 cm to 2.5 cm in maximum shell dimension.

Housing and care:
The snails were kept in three glass terrariums (dimensions 40 X 40 X 40 cm) with paper lined bases (one for snails with each type of adhesive applied and their respective controls). Humidity was maintained by applying distilled water with an atomiser. Fresh lettuce was provided daily as food.

Duration of study: Fifteen days

Experimental animals were treated in two ways. Half had their shells cleaned with a soft cloth and the other half had the periostracum lightly buffed with fine grain sandpaper. The latter was done to investigate if such abrasion was required for the adhesives to bond securely. Adhesive was then applied to each experimental animal. Application was conducted during daylight when the snails are normally inactive. Snails were checked every hour for the first three hours following glue application and twice daily thereafter. The treatment method changed slightly during the trial. The silicon was applied 12 hours before the other adhesives because of its long curing time. While this was happening it became apparent that the buffing these snails received was too severe. Thereafter all subsequent buffing consisted of just roughening the periostracum with the abrasive paper.

The fast curing epoxy resin required the combination of equal amounts of resin and hardener. The quantity of adhesive required necessitated that two batched be prepared. Proportionally less hardener was added in the second preparation. Initially this was thought to be within tolerable limits but the glue did not cure properly. The two preparations did not affect the integrity of the experiment as each batch was applied to snails in both the buffed and cleaned groups.

Table a3.1: Treatment of study animals

Adhesive	Number of snails		
	Experiment		Control
	Cleaned	Buffed	
Silicon	10	10	10
Epoxy	10	10	10
Cyano - acrylate	10	10	10
Hydrocarbon based	10	10	10

Results

No experimental animals died during the 15 days of the study. All of the snails retreated into their shells when handled and while adhesive was being applied to them. When re-placed in the terrarium each snail was briefly inactive, reattached to its container, and spent approximately 20 minutes moving about. Following this the snails became inactive until after night fall. All of the experimental animals were active during the night following adhesive application.

There was only one incident where an adhesive touched the foot of a snail. This occurred when one snail crawled over another which had un-cured silicon on its shell. The affected snail retracted into its shell and produced copious mucus but began moving again one hour later. No ill effects were noted. A confounding variable was introduced when cleaning solvent was left in the terrarium containing snails with silicon adhesive attached. All snails including controls appeared stressed. The terrarium was re-cleaned and all except one control snail fully recovered.

Those snails that were excessively abraided prior to application of silicon extended fully from their shells and appeared distressed. All of these snails recovered within two days. To avoid distress to the other buffed treatment snails their periostracums were only roughened with the sandpaper.

Bond strength:
The cyano-acrylate adhesive, building adhesive, and epoxy resin bonded securely to both buffed and cleaned shells but the incorrectly mixed epoxy and the silicon did not. The silicon compound required the shell to be buffed in order for a strong bond to form. The cyano-acrylate based glue took a long time to set when it was applied thickly.

Table a3.2: Response *H. aspersa* to experimental manipulations

Treatment	Response to treatment			
	Non-acetic silicon	Fast curing epoxy	Cyano-acrylate	Hydrocarbon based
Cleaned	None	None	None	None
Buffed	Some[1]	None	None	None
Control	None	None	None	None
Conclusion	Safe	Safe	Safe	Safe

1. Appeared distressed due to excessive shell abrasion but recovered.

Discussion

Silicon, previously used to safely secure 'beta light' transmitters to the thoraxes of the Mahoenui giant weta, *Deinacrida* nov. sp. (Richards, 1994) is confirmed as safe to *H. aspersa* when applied to its shell. Light buffing of the periostracum, is however necessary to ensure a good bond. Heavier buffing caused short term distress to snails so care should be taken when sanding the shell. In practice the heavy buffing some of the study animals were subject to was much more than is needed to prepare a shell for glue application. In the field the slow curing nature of silicon is a disadvantage but it may be useful when an adhesive is required that can be removed after an experiment.

Epoxy resin is safe for application to *H. aspersa* shells. The product takes approximately five minutes to 'touch dry' but must be mixed in the correct proportions for a strong bond to form.

The use of cyano-acrylate adhesives in surgery on vertebrates is common (eg. Cook *et al.* 1991) which suggests that that it has low toxicity to many animals. It was also used to attach tracking devices to carabid beetles without adverse effects (Mascanzoni and Wallin 1986). I noted no ill effects when this glue was used on *H. aspersa*. Of particular interest for future use is the ability of cyano-acrylate glue to adhere well to damp surfaces and in humid conditions. This is because polymerisation of cyano-acrylate adhesives is enhanced by water or other hydrogen-bearing compounds (Goodliffe, 1995). In the field this provides the advantage that a surface need not be perfectly clean and dry.

The hydrocarbon based adhesive has the advantage that it requires no mixing, and it becomes 'touch dry' quickly while still remaining viscous long enough to re-orientate the objects to be bonded for a short period after application. It appeared safe for application to *H. aspersa.*

Attaching tracking devices to land snails requires that the adhesive has good adhesion to the shell and that it can also cover the device. The fast curing epoxy resin and hydrocarbon based adhesive are therefore more suitable than the silicon (which cures slowly) and the cyano-acrylate adhesive.

In conclusion, all four adhesives appear to cause no ill effects when applied to *H. aspersa* shells, and they are therefore likely to be safe for application to *Powelliphanta*, and other land snails. This seems especially so if they have thicker shells than *H. aspersa*. The instructions for all adhesives tested specified that they have a clean surface in order to bond. In most cases this can be achieved by cleaning and drying the shell surface with a soft cloth. If the shell has difficult to move dirt, or is particularly glossy, then light buffing can clean and roughen the surface safely.

Despite my results there are still potential dangers involved in using the adhesives tested. The sample size used to test each adhesive was relatively small and only the silicon adhesive touched the body of any snail. In addition, this experiment only tested short term affects.

Several of the tested adhesives were subsequently used on native land snails in the field. Epoxy resin, and the general purpose building adhesive with liquid hydrocarbon solvent were applied to *Paryphanta busbyi watti* while epoxy resin and cyano-acrylate based adhesive were applied to *P. t. traversi.* Field tests

have revealed that as long as the shell is reasonably clean and dry (with the exception of cyano-acrylate which binds better when the surface is damp) a slight roughening of the periostracum is all that is required to ensure a good bond. Many snails with these adhesives on their shells have been part of ecological studies for over two years. It is not possible to make any conclusions of the chronic affects of the adhesives but acute affects appear negligible.

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Appendix four

The development of Harmonic Radar transponders for use on native New Zealand land snails.

Abstract

A selection of diodes and antennae were tested to determine the best configuration for making passive tracking transponders for native land snails. The Z 30 40 diode was found to be best although several diodes successfully used overseas were not available. Long wire antennae were much less detectable perpendicular to the microwave beam than when parallel. A flat, circular, transponder, was developed. This transponder, with a mass of approximately 1.25 g, was equally detectable from all directions. The circular transponder was well suited for attachment to a snail shell, the rounded shape of the antenna reducing the likelihood of the transponder catching on objects and impeding the snail.

Introduction

The harmonic radar was designed to find avalanche victims under the snow (Fuks 1981, cited Mascanzoni and Wallin, 1986) but was first used for scientific purposes to track Carabid beetles in cereal fields (Mascanzoni and Wallin, 1986). The Harmonic Radar Unit used here is a hand held transceiver attached to a back-pack housed battery. A low power (1.7 W) continuous microwave (917 Mhz) signal is produced which energises a transponder made from a Schottky diode and aerial. The transponder then emits a signal at an harmonic (1834 Mhz) of the initial microwave signal which minimises false reflections and spurious background noise (Mascanzoni and Wallin 1986). The transponder signal is then detected by the receiver unit which produces a directional, audible tone.

Harmonic radar transponders have advantages over more commonly used active radio transmitters in some circumstances. The transponders are passive, and require no attached power source so they can be effective indefinitely. In addition, they can be made much smaller and lighter than active transmitters despite recent advances in transmitter technology. Where the study animal is very small, or when it is to be followed for long periods without an opportunity to

change a battery the harmonic radar can be a useful experimental tool. The range of detection is however typically shorter than active transmitters.
A relatively high initial purchase price (approximately $NZ 14000) is offset by the small cost of transponders (less than one dollar) and the lack of maintenance costs.

Harmonic radar transponder design is constrained by the size and behaviour of the experimental subject. Transponders supplied by Recco Rescue Systems® (the radar's manufacturer) were designed to be used in ski clothing and were not necessarily optimal for attachment to any particular study animal. They were also in limited supply. *Powelliphanta* and *Paryphanta* are relatively large (adults are between 28 mm and 90 mm in maximum dimension, Powell 1979), endemic land snails that live in native forest leaf litter. My intention was to track these snails long term with harmonic radar and that the transponders would not be removed at the end of the experiment. An important consideration therefore was that the transponders did not inhibit the snail in any way.

The aim of this experiment was to compare locally available diodes to the ones supplied by the manufacturer and to find both an acceptable or superior alternative, and to develop a suitable aerial configurations.

Methods:

Diode testing

The following diodes were tested:

Recco® S2
HI 48
HP 280C3C1 (5082-2800)
HP 2835
Z 3040
Z 3232
1N 34 and 1N 60, which are equivalents
BAT 85

Transponders were made by soldering an aerial of copper wire (0.5 mm diameter to a diode to form a closed loop.

The length of the wire was then varied between six cm (the shortest length that could be easily made into a loop) and 20 cm, in 1 cm increments.
Each transponder was tested with the wire loop in two configurations, a circle and a flattened loop that formed a long narrow oval (see Figure a4.1). Flattened readings were taken with the Harmonic radar when the long axis of the loop was either parallel or perpendicular to the microwave beam.

Following the closed-loop test, each diode was coupled with the rectangular Recco® (Figure a4.1) antenna and measured parallel and perpendicular to the microwave beam.

The four diodes which performed best were tested again with a single length of wire attached to the cathode end of each diode (see Figure a4.1 f). This was approximately the same design as the transponders used successfully by Mascanzoni and Wallin (1986). The copper wire was varied between 0 cm and 20 cm. Parallel and perpendicular readings were made.

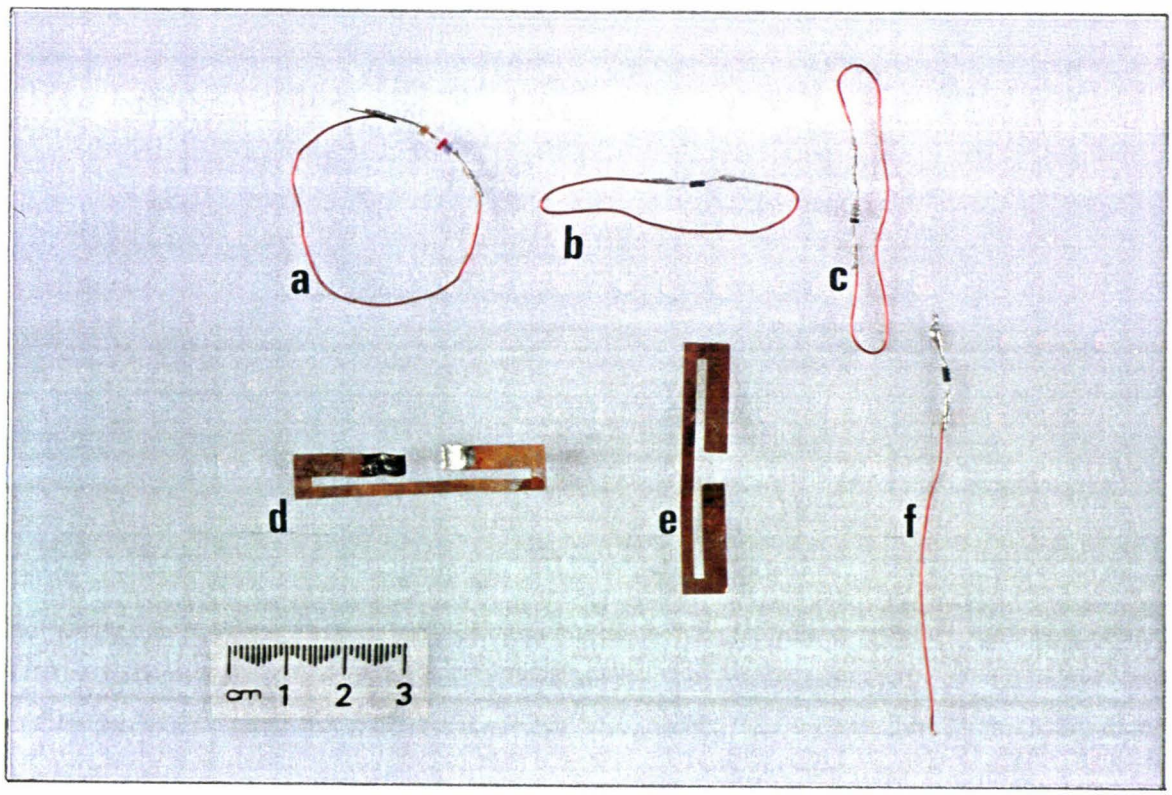

Figure a4.1: Transponders and orientations used for part A.
a. Circular configuration.
b. Flattened perp. (perpendicular to beam if beam aimed from bottom of page to top).
c. Flattened par. (parallel to beam).
d. Recco perp. Recco corporation antenna orientated perpendicular to the beam.
e. Recco par. Recco corporation antenna orientated parallel to the beam.
f. Test 2. configuration in the parallel orientation, this was repeated in the perpendicular orientation.

Tests were conducted in an open field. Each transponder was placed on a plastic plate to isolate it from the ground to control for environmental factors such as damp grass that alter detectable range. Readings were taken with the radar held 1.2m above the ground. This is the normal operating height for field work. Care was taken to keep the polarity of the diodes the same relative to the direction of the beam.

Transponder testing

The diode that proved most effective in the first part of the experiment was used to test different antenna arrangements. Maximum detectable distance was an important attribute but the transponder also had to fit without projections onto the

shells of *P. t. traversi*. Trailing wire antennae as used by Mascanzoni and Wallin (1986) and Roland, McKinnon, Backhouse, and Taylor (1996) were therefore not considered suitable. The transponders (see Figure a4.2) were made from thin copper sheeting coupled with the chosen diode and attached to an empty *Powelliphanta* shell. Tests were conducted with the snail shell placed directly on the ground to simulate field conditions. Records were made of the maximum detectable distance when the shell was uncovered, when covered with a five cm thick layer of dry leaf litter and when it was placed behind a tree with trunk diameter of 30.0cm.

Results:

Diode testing

Table a4.1: Maximum detectable distance for all diodes tested.

	Detectable distance for each diode (m)							
Antenna Config.	Recco S2	HI 48	HP 280C 3C1	Z 30 40	Z 32 32	1N 34 / 60	HP 2835	BAT 85$^{\psi}$
Elongated parallel$^{\delta}$	5.30	2.20	2.70	6.60	5.30	5.70	4.10	not tested
Elongated perp.$^{\delta}$	2.40	0.50	1.40	3.10	2.50	2.80	1.90	not tested
Circular$^{\delta}$	2.20	0.60	1.40	2.60	1.90	2.80	2.10	not tested
Recco parallel	13.20	7.70	3.80	8.00	8.00	7.00	10.30	1.20
Recco perp.	3.60	3.00	1.40	3.40	3.40	2.90	6.00	0.00

δ. Mean result of detectable distance for loop wire transponders with wire varied between 6 and 20 cm, in 1 cm increments.
ψ. The BAT 85 diode responded poorly in initial tests so was not tested in all combinations.

A strong directional effect was evident with transponders always detected from further away when in the parallel orientation.

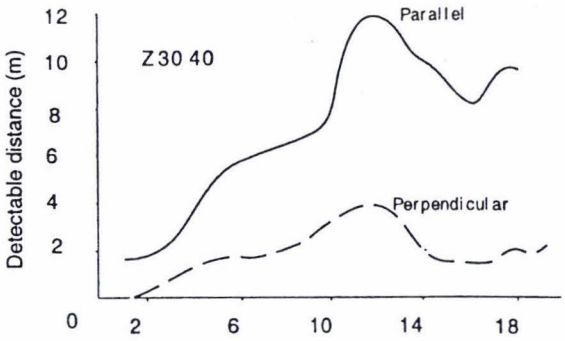

Figure a4.2:

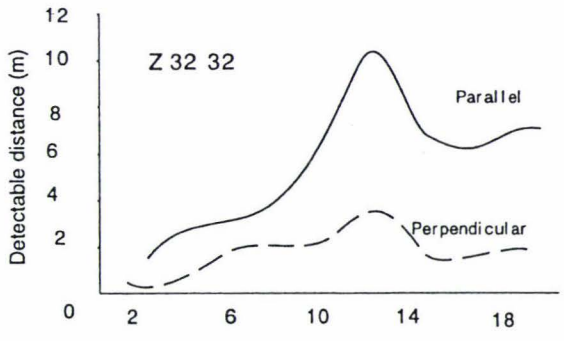

Figure a4.3:

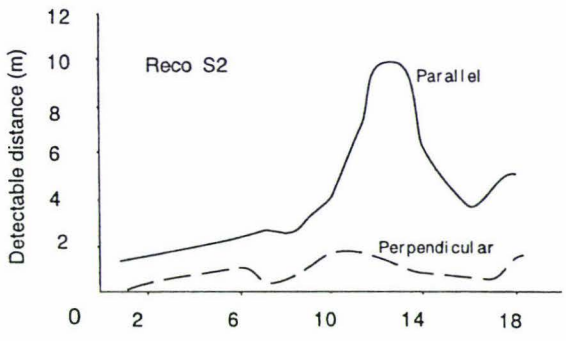

Figure a4.4:

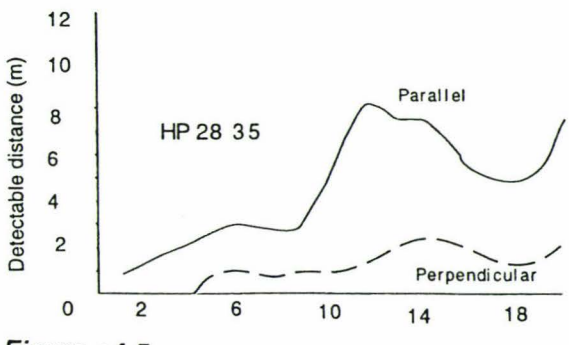

Figure a4.5:

Figures a4.2-a4.5: Relationship between single wire antenna length and detectable distance. The wire was always attached to the cathode end of the diode.

Detectable distance varied with antenna length. The maximum detectable distance for each diode occurred when the antenna was about 12 cm long. This maximum occurred when the transponders were both parallel and perpendicular to the microwave beam. The parallel orientation was always detected from further than the perpendicular.

Seven distances were measured for each diode (Table a 2.2, Figure a4.1). The Z 30 40 was the best diode for four measurements, second best for one, and third equal in the final two.

Transponder testing:

Table a4.2: Relationship between detectable distance for transponders manufactured from Z 30 40 diode - copper sheeting combinations

	Detectable distance for each transponder				
Orientation / location	Narrow rectangular	Wide rectangular	Continuous circular/ diode across	Large circular	Small circular
Parallel	5.50	10.70	1.50	7.60	6.10
Perpendicular	5.50	10.60	1.50	7.40	6.20
Behind tree	1.70	3.80	0.00	3.10	1.90
Under litter	5.50	10.90	1.50	7.50	4.60

The directional effect was less pronounced for the copper sheeting transponders in comparison with the wire antenna transponders in the diode testing section. The best response was obtained for the copper-sheet transponders was from the wide rectangular transponder followed in order of effectiveness by the large loop transponder, the small circular transponder, the small rectangular transponder and the continuous circular transponder. Transponders with a larger surface area were detectable from greater distances than transponders of lesser surface area, although this effect could not be fully isolated from the overall size of the

transponder (regardless of surface area). Performance was superior when the diode is part of, rather than short circuiting a circular antenna.

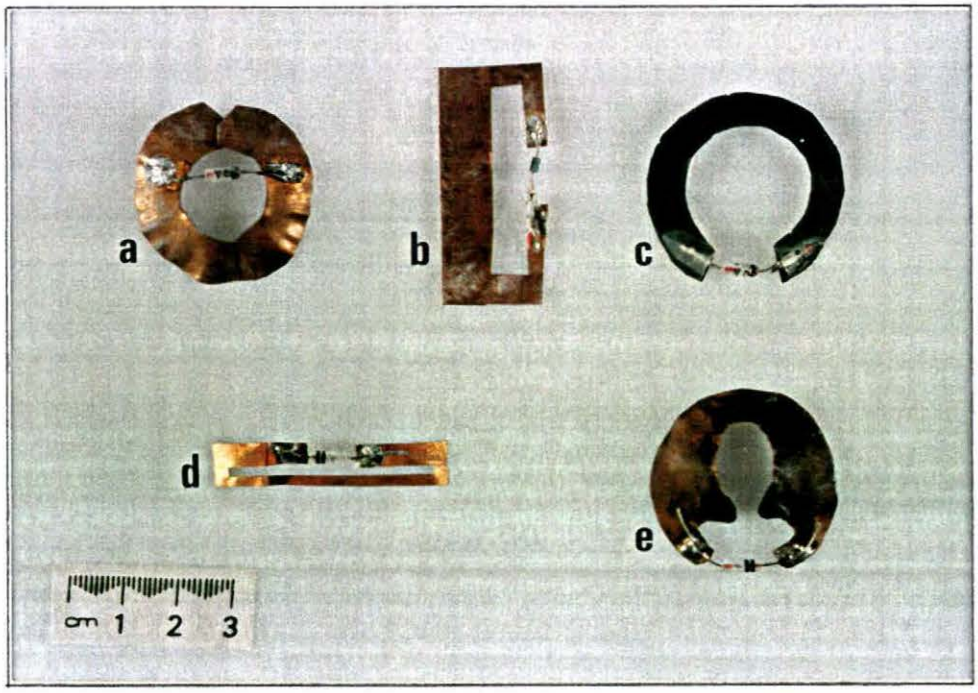

Figure a4.6: Various antenna shapes and sizes combined with the Z 30 40 diode

a. Continuous loop / diode across. The diode may have higher resistance than the antenna which would mean there is low or no electron flow through the diode.
b. Wide rectangular transponder, shown in parallel configuration (if beam aimed from the bottom of the page).
c. Large loop. A scaled down version was also tested (Small loop)
d. Narrow rectangular, shown in the perpendicular configuration. As with b. this transponder was tested in both parallel and perpendicular orientation.
e. Final transponder constructed. Has large surface area relative to size, but still has the diode as part of the loop, mass approx. 1.25 g.

Discussion:

The diode with the best all round performance was the Z 30 40. This is a Dick Smith Electronics® component number, which corresponds to the 1N 60 international specification but offered better performance than 1N 60 diodes of other manufacturers. Diodes that were successfully used by other authors are the HP 5082-2837 (Roland *et al* 1996), the Phillips AA 119 and Toshiba 1SS242 (Greg Sherley, 1994 *pers. comm.*). It was not possible to obtain these diodes in New Zealand.

The Recco antenna was superior to the simple wire loop antennae. It is possible that this was due to the larger surface area of the Recco design. Certainly the large surface area copper sheet antennae were always superior to the wire loop antennae of similar loop size and were sometimes better than wire loop antennae regardless of loop size (*unpubl. data*). The pioneering work using harmonic radar with Carabidae by Mascanzoni and Wallin (1986) appeared to use diodes with an antenna attached to one end of the diode. This is an open circuit and differs from the transponders supplied by Recco®, but appeared to give better results, especially when parallel to the microwave beam.

Mascanzoni and Wallin (1986) found that virtually no spurious signals were generated by the harmonic radar. In contrast, my study was affected by a great deal of background noise that was sometimes louder than that generated by a transponder. It was often caused by incidental metal objects such as refuse, metal fences or rubbish tins. Operator experience helped significantly role in distinguishing background noise from the transponder signal at extreme range.

One clear result comes from this experiment. The orientation of a transponder with respect to the microwave beam can have a marked affect on the maximum detectable distance. If the long axis of the transponder lies perpendicular to the beam, the detectable distance is much smaller. Mascanzoni and Wallin (1986) probably made their measurements with the transponder in the parallel position because their results for the only diode common to the present study (the HP28 35) gave similar readings in this position. The reduced signal when in the perpendicular orientation is so noticeable that it could not be missed.

A circular transponder was chosen for attachment to *P. t. traversi* to avoid the low perpendicular detection distance. This circular design was not as good as long rectangular transponders measured parallel but was consistently good from all directions.

Copper sheet antennae have the advantages of being robust tracking devices which offer good detection distances when compared with thin wire transponders. They have a much reduced directional affect and they do not project from the shell or trail behind. *P. t. traversi* has a relatively flat, circular shell. A circular transponder enables the largest area antenna to be attached, although in this experiment the large rectangular transponder offered the best response. An antenna with a large surface area has the disadvantage of being heavier than a thin wire transponder of similar size. Terrestrial snails were shown to be able to carry up to 50 times their body weight by Croizer and Federighi (1925b cited Jones 1975) so I concluded the 0.7 to 1.25 g transponder finally attached to *P. t. traversi* was probably acceptably light (≈10 % of body weight).

Two recent studies used harmonic radar to track flying insects, Riley, Smith, Reynolds, Edwards, Osborne, Williams, Carreck, and Poppy (1996) and Roland *et al.* 1996. Transponders in these studies were developed with different constraints to those in my study with respect to shape and robustness, but offered better detection ranges and weighed much less (0.4 mg for Roland *et al.* 1996).

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Roland, J., McKinnon, G., Backhouse, C., and Taylor, P. D. (1996). Even smaller radar tags on insects, *Nature* **381,** pg. 120.