Distribution and biology of the endangered kauri snail, *Paryphanta busbyi watti*

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Distribution and biology of the endangered kauri snail, *Paryphanta busbyi watti*

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ABSTRACT

The far northern kauri snail, *Paryphanta busbi watti* was restricted to three distinct locations on the end of the Aupouri Peninsula, New Zealand. The maximum areas they occupied were about 10.5 km^2 around Te Paki hill and about 5 km^2 on Kohuronaki hill, the former containing about 5500 snails, and the latter about 5000. *P. b. watti* is present in low numbers around Unuwhao but no estimate was made of the size of this population. The maximum density of snails was 600/ha. Their density was 391 ± 138 (S.E.) snails/ha in an intensively sampled area at an altitude of over 200 m on a ridge on Te Paki hill. In areas where snails occurred, live snails were significantly more likely to be encountered as altitude increased. The lowest altitude where a live snail was found was at 120 m. There was no significant association between the presence of snails and broad vegetation type although most snails were found in kanuka and broadleaf forests. Low numbers were present in low scrub and kauri forest.

178 live *P. b. watti* (including 12 that hatched from eggs) and 197 whole empty shells were found at the above sites and one live adult snail was found at Unuwhao. Minimum death rates from different causes estimated from empty shells were 7.8% from pigs, 2.1% from rodents and 0.7% from humans. Fragments of pig-damaged shell were also found in 21 of the 141 quadrats searched.

Harmonic radar transponders were attached to 114 snails, and identification numbers were engraved on them. Queen bee labels were glued to 21 small snails. Data from those with transponders indicated that adult snails died mostly between November and July. Mating occurred between April and September, with most eggs laid in August and September. The short duration of the study limited conclusions on growth and longevity, but snails initially grew rapidly and reached presumed adult size at about 3 years. Thereafter, growth rates slowed then ceased; however, 45% of snails found as adults lived at least a further 1 to 2.6 years.

Mature *P. b. watti* showed distinct site fidelity, with seven snails spending 95% of their time within areas of 160–550 m^2 over periods of up to 3 years.

Keywords: kauri snail, *Paryphanta busbi watti*, Aupouri Peninsula, New Zealand, distribution, biology, endangered species

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Plate 1. Photographs of *Paryphanta busbi watti* in the field.

A. Newly hatched snail.

B. Adult snail with harmonic radar transponder attached to its shell. The transponder was glued on with Araldite® and the diode is visible facing posteriorly. The number T7 is engraved near the shell aperture. This position was later changed to that shown in E.

C. Half grown and newly hatched snails showing queen bee labels attached to their shells. The half grown snail with queen bee label 18 also has number T18 engraved on its shell.

D. Shell of a half grown snail (number T18) showing soft periostracum projecting around the aperture.

E. Adult snail with a hardened rolled lip to the aperture of its shell and an identification number (K32) engraved in the usual position.

F. Two adults mating. When first found, the upper snail usually has the front of its body extended and bent into the shell of the lower snail. The upper snail also has a harmonic radar transponder glued on with Liquid Nails®.

G. Nest of six eggs at Site A after the top 0.5 cm of soil was removed.

(*Photographs A, E, and F by Megan McLean*.)

1. Introduction

The snail recovery group of the New Zealand Department of Conservation recognised that there was an urgent need for information about the far northern kauri snail, *Paryphanta busbyi watti* Powell (Pulmonata: Rhytitidae), because almost nothing was known about its ecology, distribution, habitat use and causes of mortality. This snail was thought to be extremely rare and to have a very limited distribution (Parrish et al. 1995). Our research was undertaken to provide preliminary information on these topics so that conservation managers could make informed decisions in relation to this species. Most of the results reported here are from research carried out between October 1994 and June 1997 at the top of the Aupouri Peninsula. We also include some additional information from samples taken up to November 1999 from marked quadrats that were established at three different sites in Te Paki Farm Park.

2. Background

Paryphanta b. watti (Plate 1) is the rarest of the two subspecies of *Paryphanta* found in New Zealand. It occurs only at the end of the Aupouri Peninsula, the northernmost part of New Zealand (Parrish et al. 1995). The other subspecies, *Paryphanta busbyi busbyi* Powell, has a scattered distribution over its natural range between Kaitaia and Warkworth. It has also been successfully introduced to small areas in the southern end of the Waitakere Ranges and in the Kaimai Ranges (Parrish et al. 1995; Montefiore, R. unpublished report 1996; O'Connell, B. unpublished report 1999; Gilchrist, A. unpublished report 2000).

Paryphanta b. watti is ranked "Category A" (Molloy et al. 1994). Only 15 live snails were found in four years prior to 1994 by Te Paki Field Centre staff during their normal duties, and during specific searches in areas of known habitat. Most evidence of their presence was empty whole shells or remains of those eaten by pigs. Prior to our study, information on *P. b. watti* was restricted to taxonomy (see references in Powell 1979) and distribution (Parrish 1992; Goulstone et al. 1993; Sherley, G.unpublished report 1993). Recent records of their distribution are also kept at the Department of Conservation in Whangarei, and at the Te Paki Field Centre. More information is available on the habitat and distribution of *P. b. busbyi* (see literature listed in Powell 1979; Ballance 1985; Montefiore, R. unpublished reports 1994, 1995, 1996), and on its anatomy, food and growth rate (Ohms 1948; Dell 1955; Coad 1998). Coad (1998) also gives details of the general biology of *P. b. busbyi*, including its movements, density, and the effects of predators at Trounsen Park, Northland. Andrew Penniket (TVNZ) has some additional unpublished information on their density at Warkworth.

The conservation status of *P. b. watti* required that special care be taken not to harm them. Live snails were only known from the vicinity of Te Paki, Kohuronaki, and Unuwhao hills before our study commenced (Parrish, R. unpublished report 1992; Sherley, G. unpublished report 1993). We therefore restricted our intensive investigation into their biology to three small areas of less than 2000 m^2 each (Fig. 1). Harmonic radar was used in these areas to find snails after we had attached transponders to them (Devine 1997; Lövei et al. 1997). The use of harmonic radar ensured that every snail tagged with a transponder was quickly located if it was in the search area. The position of each snail with a transponder could also be narrowed down to an area of leaf litter covering about 0.25 m^2 which was then searched by hand. This minimised habitat disturbance. In addition, restricting areas where repeated searches were made limited the areas where snails without transponders could be inadvertently crushed underfoot, and it limited the area subjected to trampling or other possible damage to the habitat.

3. Methods

At least two trips were made to the northern end of the Aupouri Peninsula in January/February, April, June/July, August/September, October, and November/ December between August 1994 and June 1997 so that samples were taken in all seasons. Additional trips were made in July 1998, November 1998 and November 1999. Most systematic searches were done by sorting through the leaf litter and turning over all rocks and logs within measured areas of 25–400 m^2. If no live *P. b. watti* or their empty shells were found in a systematic search, a casual search was made in likely habitat nearby, such as around the bases of flax bushes and clumps of grass, or in accumulations of leaf litter. The first systematic searches were done by marking out the edges of quadrats with tape, but this was later changed to laying down a central tape measure and searching for more than 2.5 or 5 m on either side of it. The width of the area searched on each side of the tape measure depended on the number of searchers present. When three or four people were available they covered more than 2.5 m on either side of the central tape whereas 5 or more people covered more than 5 m on either side. The distance of each snail or shell found was measured from this central tape to determine if it was within 2.5 or 5 m from the tape. This proved much faster than marking out the edges of quadrats before they were searched.

Searches of measured areas were chosen in preference to doing casual searches because this provides information on the absolute density of the snails. We also believed that more of the smaller shells could be missed in casual searches and that a careful search through a measured area could provide more representative information on the size structure of the population. Results from casual searches were used only for presence–absence data.

Our initial searches were concentrated on areas where either empty or live snails had been found in the past, and on higher areas. The latter resulted from the early realisation that, if *P. b. watti* was present, its density increased with increasing altitude. We also searched in most of the bush remnants that were

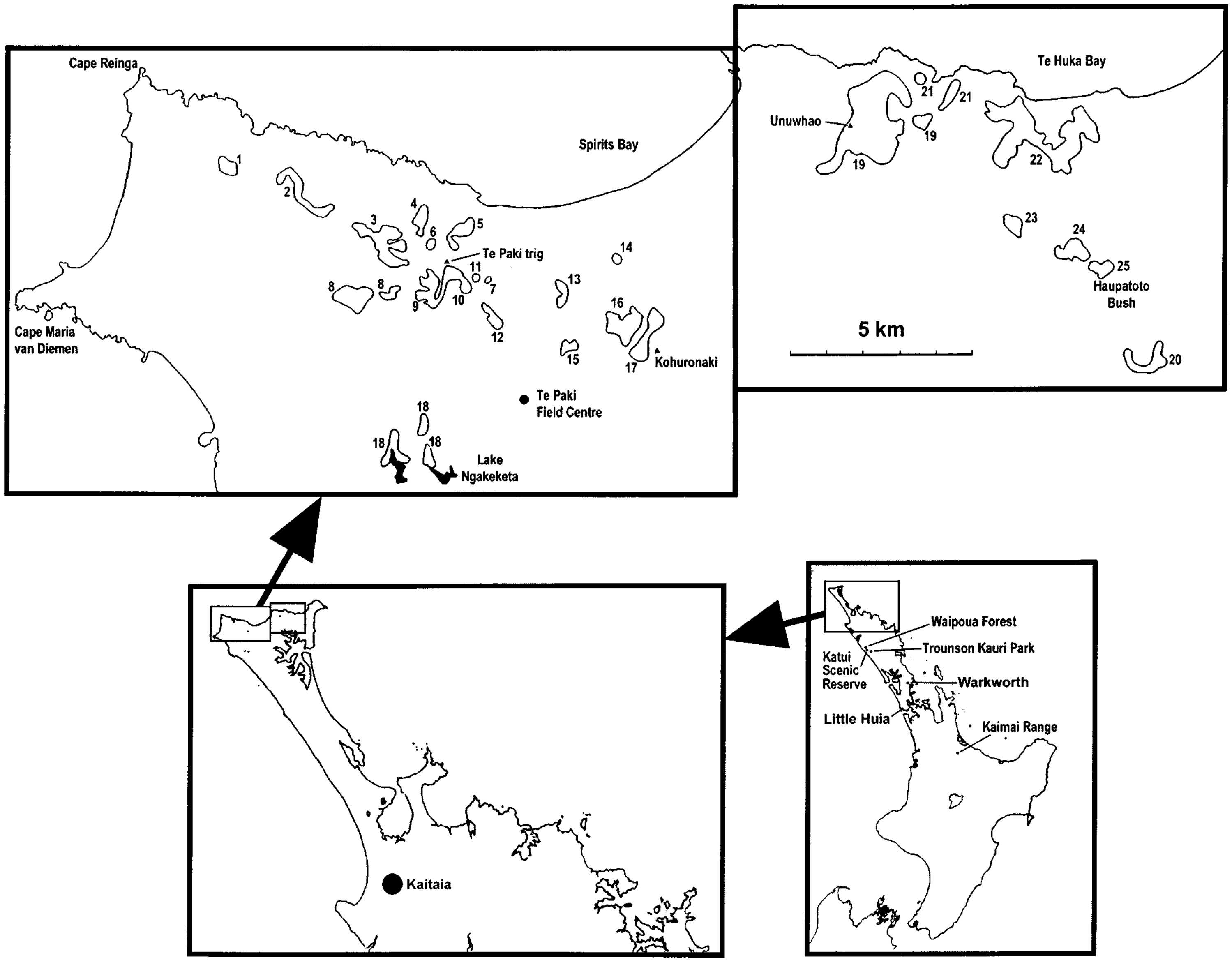


Figure 1. Map of the region at the end of the Aupouri Peninsula where searches were made for *Paryphanta busbyi watti*. Bush remnants are numbered and trig points are indicated by solid triangles.

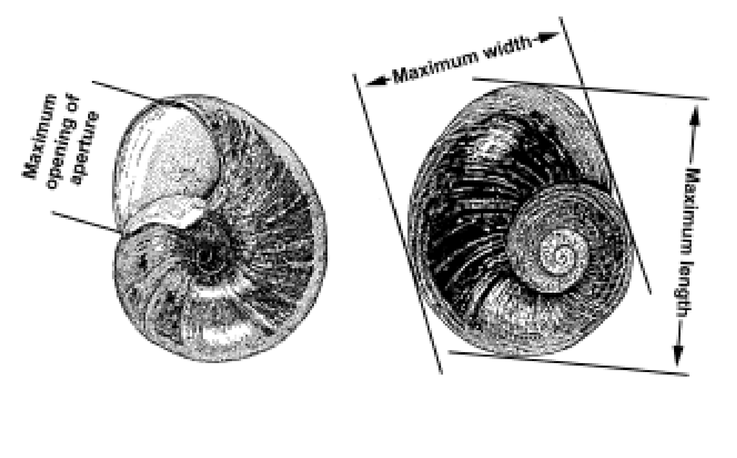


Figure 2. Measurements taken from shells of *Paryphanta busbyi watti.*

not cleared for farming early this century (Fig. 1), and we searched in any other apparently suitable areas of scrub or regenerating forest. Few systematic searches were done in low scrub because the presence of gorse (*Ulex europaeus* L.) and *Hakea* species made this difficult.

The presence or absence of live and dead snails was recorded together with the maximum diameter, diameter at the aperture, and the maximum internal length of the aperture opening of each shell (Fig. 2), the weight of live snails, and the probable cause of mortality. We also recorded whether each shell was juvenile or adult, using an operational definition following Johnson & Black (1991). The shell of an adult snail has the edge of its aperture rolled inward to form a hard rounded ridge (Plate 1e) whereas the shell of a juvenile snail has a soft lip where the periostracum projects past the ostracum (Plate 1d). Care was taken not to distort this flexible lip when juvenile snails were being measured. Empty shells were collected and later cleaned and measured. They were subsequently replaced on later trips. When nests of eggs were found, the eggs were very carefully removed and cleaned with tissue paper to remove as much soil as possible, then their maximum lengths and widths, and their weights were taken. Particular care was taken not to damage the fine membrane surrounding newly laid eggs. The eggs were then carefully replaced in the holes they were found in, and the holes were covered over again gently with loose soil before the area was sprayed lightly with water. Half the nests were subsequently left alone and half were revisited and checked again each time the areas were revisited until the snails hatched and left.

Records were made of the vegetation present, the altitude, and any evidence of pig foraging for each systematic search. Map references, where we can provide these, are all from NZMS 260 sheet MO2, NO2.

Any live *P. b. watti* that were found in a locality that was likely to be revisited were individually marked so that they could be identified if they were recaptured. Identification numbers were engraved on those with a maximum diameter of greater than about 20 mm. This was done by carefully grinding through the periostracum with a 12 V battery-operated engraver (“Arlec”, Dick Smith Electronics). These numbers were usually positioned on the under side of large shells about 1 cm from the opening (Plate 1e), and on the upper surface of small shells near the opening and close to the junction with the next inner whorl (Plate 1c, d) where the number would not get overgrown as the shell enlarged. Small tags used for marking queen bees were embedded within drops of “5 minute Araldite” (Selleys) on the top of the protoconchs of snails smaller than about 20 mm (Plate 1c, d). The shells were first dried with tissue paper then lightly buffed with fine carborundum paper to ensure good adhesion. Numbered markers placed in the ground were used to ensure that all live snails were replaced exactly where they were found after being handled.

Harmonic radar transponders were attached to snails that were used to investigate movement and growth, and to obtain general biological information.

Each transponder consisted of a semi-circular aerial of thin copper with the ends connected through a Z 3040 diode (Dick Smith Electronics) (Plate 1b). The copper aerial was first heat-annealed before being pressed to the shape of a shell. Transponders were fixed to the shells with either "5 minute Araldite" or "Liquid Nails" (Selleys) (Plate 1f). The shells were first cleaned and dried with tissue paper, then lightly buffed with fine carborundum paper.

Harmonic radar searches were made each time the Aupouri Peninsula was visited. These searches were restricted to three localities where marked quadrats were established in Te Paki Farm Park. All three sites were above an altitude of 200 m. Two of the sites were on the ridge where the Te Paki trig is situated and the other was on Kohuronaki hill (Fig. 1). Two marked quadrats were established at site A on the Te Paki ridge, an east quadrat of 150 m^2 and a west quadrat of 75 m^2. These were 9.1 m apart (Fig. 3). Site B was about 600 m to the Northeast of Site A and consisted of a single quadrat covering 225 m^2 (Fig. 4). Site C was on Kohuronaki hill and consisted of one northern quadrat of 150 m^2 and one southern quadrat of 225 m^2 (Fig. 5). All marked quadrats were searched by hand once a year. The southern quadrat at site C was used as a control for the effects of trampling in the other marked quadrats. It was never searched using harmonic radar but it was searched by systematically sorting through the leaf litter once a year, except for an interval of 25 months between 1996 and 1998.

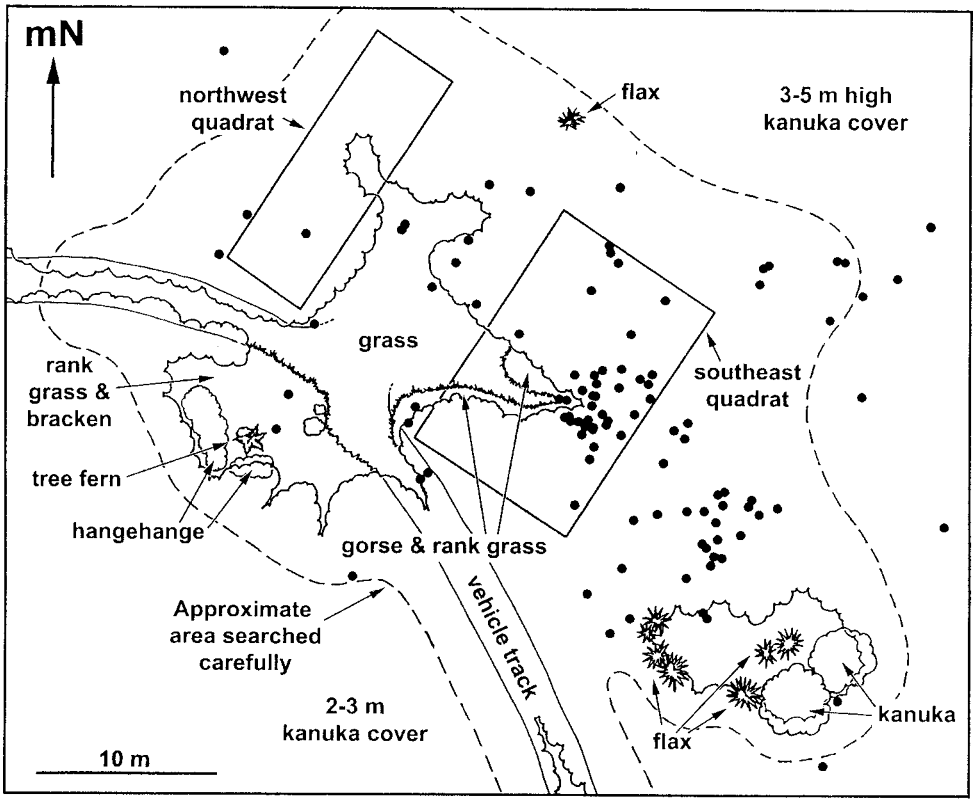


Figure 3. Map of the area surrounding the marked quadrats at site A on Te Paki Hill ridge. Dots indicate where *Paryphanta busbyi watti* equipped with harmonic radar transponders were recaptured.

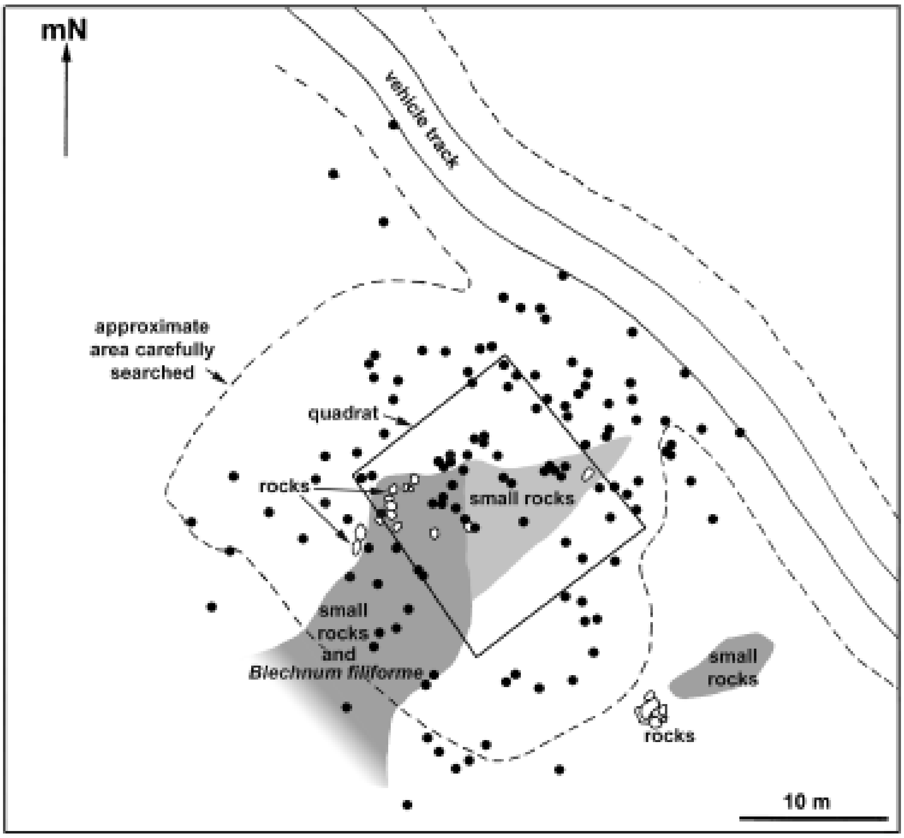


Figure 4. Map of the area surrounding the marked quadrats at site B on Te Paki Hill ridge. Dots indicate where *Paryphanta busbyi watti* equipped with harmonic radar transponders were recaptured.

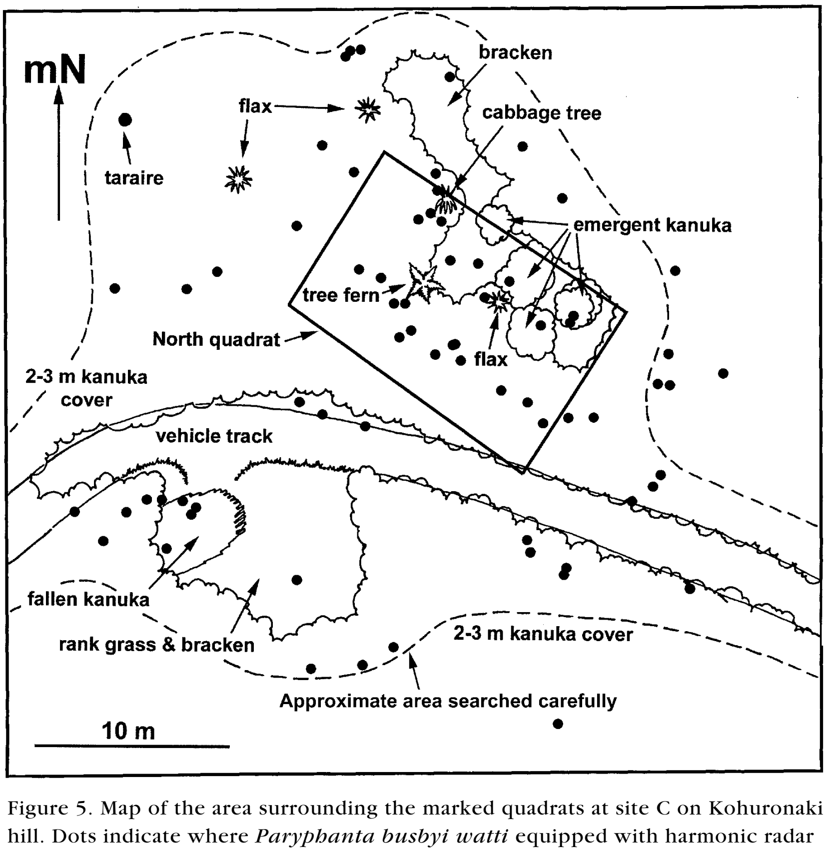


Figure 5. Map of the area surrounding the marked quadrats at site C on Kohuronaki hill. Dots indicate where *Paryphanta busbyi watti* equipped with harmonic radar transponders were recaptured.

Harmonic radar searches were restricted to within 10 m of the quadrats and along the tracks leading to them. Every new snail found in the marked quadrat sites was marked, and a transponder was fitted if the shell was larger than about 26 mm in maximum length. All empty and broken shells found within the quadrats during the hand searches were recorded and placed outside the quadrats so that the number of snails that died within the quadrats each year could be recorded.

Home range analysis was done with the Calhome programme (Kie et al. 1994) using the adaptive kernel method of Worton (1989). Statistical analyses were done using SAS version 6.12.

4. Results

Twenty four field trips were made to the Te Aupouri Peninsula involving 123 days of field work relating to *P. b. watti*. A total of 141 temporary quadrats covering an area of 13 954 m^2 were hand searched between August 1994 and June 1997. The regions in which these quadrats were searched are given in Fig.6. Forty four live *P. b. watti* were found, including two that hatched from eggs. A further three eggs were found which did not hatch. The temporary quadrats also contained 126 empty intact shells together with 15 shells that had evidence of mammalian damage (Table 1).

TABLE 1. NUMBERS OF *Paryphanta busbyi watti* SHELLS FOUND IN TEMPORARY QUADRATS TOGETHER WITH THOSE DAMAGED BY MAMMALS.

	NO. FOUND	NO. OF QUADRATS WHERE FOUND
Empty intact juveniles	76	25
Empty intact adults	50	24
Pieces of shell	31	18
Rat-damaged juvenile shells	1	1
Rat-damaged adult shells	2	2
Pig-damaged juvenile shells	1	1
Pig-damaged adult shells	10	4
Human-damaged adult shells	1	1

The marked quadrats were repeatedly searched from August 1994 until December 1999. A total of 71 live adult and 61 live juvenile *P. b. watti* were found (Appendix 1). Identification numbers were engraved on to all adults and on to 43 large juveniles. Labels used for identifying queen bees were glued to the other 18 small juveniles and to a further 13 juveniles that hatched from eggs. Harmonic radar transponders were attached to 50 of the adult snail shells and to 19 large juveniles. We also found 27 eggs, 20 empty adults and 51 empty juveniles. These empty shells included 12 adult shells and three juvenile shells that had died with harmonic radar transponders attached to them.

There were no significant differences between the numbers of live shells or whole empty shells of *P. b. watti* found by hand searching the experimental and control marked quadrats (Table 2).

TABLE 2. MEAN NUMBERS OF LIVE AND EMPTY *Paryphanta busbyi watti* FOUND IN MARKED QUADRATS.

The control quadrat was visited once a year and the experimental quadrats (n = 4) were frequently visited. Area searched in m^2, rates of accumulation given per m^2 per month. Standard errors given in brackets.

	Total area searched per year	Live juveniles	Live adults	Rate of accumul. of whole empty juveniles	Rate of accumul. of whole empty adults	Empty damaged shells
Control plot (all years)	225	44.4 (25.7)	74.1 (39.2)	66.156 (3.319)	0 (0)	0.590 (0.590)
Expt plots (all years)	600	74.1 (25.3)	122.2 (27.1)	10.272 (3.310)	1.039 (0.552)	1.329 (1.039)

There was a considerable reduction in the density of live adult snails and an increase in the density of live juvenile snails in the experimental quadrats once they were repeatedly visited (Table 3). This suggests that frequent visits to the quadrats benefits young snails and disadvantages older snails.

TABLE 3. MEAN DENSITY (number/ha) OF LIVE AND EMPTY *Paryphanta busbyi watti* FOUND IN 3 AREAS WHERE EXPERIMENTAL MARKED QUADRATS WERE ESTABLISHED.

Standard errors given in brackets.

	Live juveniles	Live adults	Whole empty juveniles	Whole empty adults
1994	11.11 (11.11)	300 (33)	50 (50)	33 (33)
1995	73.1 (53.4)	59.3 (14.8)	0	0
1996	44.4 (44.4)	88.9 (25.7)	177.8 (88.9)	29.6 (14.8)
1998	74.1 (74.1)	133.3 (67.9)	266.7 (179.6)	44.4 (44.4)
1999	88.9 (51.3)	103.7 (29.6)	148.1 (106.8)	0

In addition to *P. b. watti* snails, we found 41 live snails and 63 empty shells of *Placostylus ambagiosus* Suter (Pulmonata: Bulimulidae) in the quadrats and 29 live snails and 118 empty shells of *Rhytida duplicata* Suter (Pulmonata: Rhytitidae) (Table 4).

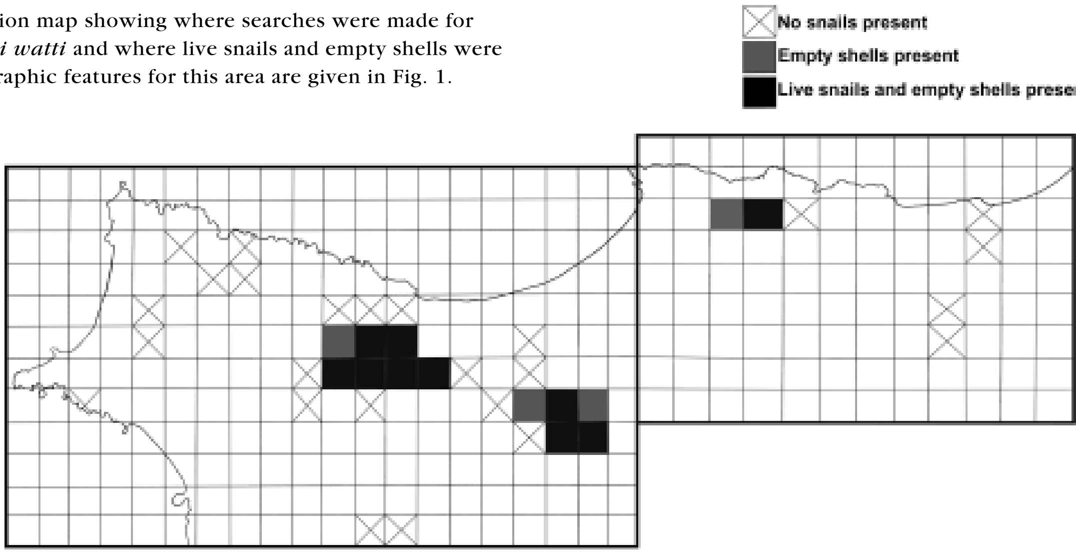
TABLE 4. NUMBERS OF OTHER SPECIES OF LARGE SNAILS FOUND WITH *Paryphanta busbyi watti* IN TEMPORARY QUADRATS.

SPECIES	MARKED QUADRATS		TEMPORARY QUADRATS	
	Alive	Empty	Alive	Empty
Adult *Placostylus*	7	4	20	35
Juvenile *Placostylus*	3	4	9	20
Rhytida duplicata	2	1	27	117

4.1 DISTRIBUTION

The areas where live and recently dead *P. b. watti* were found are shown in Fig. 6. They clustered into three localities centred around Te Paki, Kohuronaki and Unuwhao hills (Fig. 6). Empty *P. b. watti* shells were found over a much wider area than live snails but some of the empty shells may have rolled down steep slopes or been carried downhill in streams. Despite this, it is possible that live snails do occur, albeit in low densities, where most empty shells were found.

Figure 6. Distribution map showing where searches were made for *Paryphanta busbyi watti* and where live snails and empty shells were found. Some geographic features for this area are given in Fig. 1.



No live *P. b. watti* were found in the 8 temporary quadrats (total 650 m^2) we searched on Unuwhao and only one live snail and three empty shells were found in casual searches there. An harmonic radar transponder was attached to the live snail and this was located again only once 97 days later. We were also unable to find any trace of *P. b. watti* where we had previously found them close to Unuwhao (Sherley, G. unpublished report 1993). Pigs had extensively damaged much of the ground in the area we visited on the slopes and top of Unuwhao, and our subjective impression is that *P. b. watti* is probably very rare there.

Isolated shells of *P. b. watti* had previously been reported from near the quarry (921443), in bush remnants at Tapotupotu Bay, in Haupatoto Bush (064494) and some distance down two of the valleys from Kohuronaki (956462 and 452956) but we found no trace of them in any of these locations. Elsewhere, with one exception, neither live *P. b. watti* nor their empty shells were found where pigs had dug up the ground although they were found where pigs had disturbed the leaf litter. The exception was in bush remnant 8 (Fig. 1) at an altitude of 180 m, and here we found two fragments of *P. b. watti* shell.

4.2 DENSITY AND HABITAT

The numbers of live snails and empty shells of *P. b. watti* that were found during searches of temporary quadrats are given in relation to the main vegetation types and altitudinal ranges in Table 5. The highest density of live snails found in any quadrat was 600 snails/ha. This quadrat was in tall kanuka adjacent to mixed broadleaf forest at an elevation of 200 m a.s.l. on Kohuronaki. The location where we sampled most extensively was an area of about 4 ha situated above 200 m a.s.l. on Te Paki trig ridge. We searched seven quadrats and found that the density of live snails there was 391 ± 138 (S.E.) snails/ha. No accurate estimate could be made of the population of snails over the entire area where they occurred because our samples were not designed to do this.

TABLE 5. NUMBERS OF *Paryphanta busbyi watti* FOUND IN TEMPORARY QUADRATS IN RELATION TO MAIN VEGETATION TYPE AND ALTITUDE.

Main vegetation type	Altitude (m)	Area (m^2)	No. of quadrats searched	Alive, juvenile	Alive, adult	Empty shells, juvenile	Empty shells, adult	No. of nests	Total no. of eggs	No. of juveniles in nests
kanuka	0-90	375	13	0	0	0	0	0	0	0
kanuka	100-200	425	6	0	0	0	0	0	0	0
kanuka	>200	1275	15	2	4	1	8	0	0	0
kanuka/ broadleaf	0-90	1122	6	0	0	0	0	0	0	0
kanuka/ broadleaf	100-200	1450	14	4	10	8	9	0	0	0
kanuka/ broadleaf	>200	775	6	3	4	37	12	0	0	0
kanuka/ low scrub	>200	450	3	5	2	4	0	2	3	2
kanuka/ podocarp	100-200	150	1	0	0	0	0	0	0	0
kauri	100-200	750	6	0	0	0	0	0	0	0
low scrub	0-90	25	1	0	0	0	0	0	0	0
low scrub	100-200	175	2	0	0	0	0	0	0	0
low scrub/ broadleaf	>200	75	1	0	0	0	1	0	0	0
broadleaf	0-90	978	12	0	0	1	1	0	0	0
broadleaf	100-200	4474	44	3	2	12	8	0	0	0
broadleaf	>200	1455	11	1	2	13	11	0	0	0
Total		13954	141	18	24	76	50	2	3	2

Broad vegetation type did not appear to give a good indication of whether *P. b. watti* was likely to be present or not (Table 6). There was no significant association between the presence of these snails and the three main vegetation types (kanuka, broadleaf, and mixed kanuka/broadleaf; Fisher's exact test, $p = 0.457$) when only those 99 quadrats were considered that were located within 1 km of where *P. b. watti* were found. However, only a few quadrats were searched in kauri forest, low scrub, or mixtures of low scrub and other vegetation (Table 6) so these vegetation types were poorly represented in our samples. All of the latter quadrats were situated as near as possible to sites where other people had previously observed *P. b. watti*, but no trace of these snails was found.

P. b. watti does occur in low scrub, because two live snails and a nest containing two recently laid eggs were found under a hangehange bush in very low scrub on the north side of Te Paki trig hill. In addition, several snails and empty shells were found in casual searches along a vehicle track through low scrub near the top of the hill immediately to the west of Te Paki trig hill. *P. b. watti* also occurs in kauri forest because one empty juvenile shell was found during a casual search in this habitat.

There was a highly significant positive relationship between the presence of *P. b. watti* and increasing altitude (Fisher's exact test $p > 0.0001$) when the 99 quadrats located within 1 km of where *P. b. watti* were found are considered. Both the number of snails found per area searched and their presence in quadrats increased with increasing altitude (Table 5). This occurred in both broadleaf and kanuka forest. No live snails and few empty shells were found below an altitude of 100 m.

TABLE 6. NUMBERS OF QUADRATS CONTAINING LARGE SNAILS IN RELATION TO THE MAIN VEGETATION TYPE.

	Kanuka	Broadleaf	Kauri	Kanuka/ broadleaf	Kanuka/ low scrub	Low scrub	Low scrub/ broadleaf
Paryphanta	2	3	0	19	0	0	1
Rhytida	3	2	0	5	0	0	0
Placostylus	1	4	0	4	0	0	0
Paryphanta & *Rhytida*	1	4	0	1	0	0	0
Paryphanta & *Placostylus*	2	3	0	2	1	0	0
Rhytida & *Placostylus*	1	0	0	3	0	0	0
Paryphanta, Rhytida & *Placostylus*	0	0	0	0	1	0	0
Snails absent	25	10	6	33	1	3	0

There was no apparent relationship between the occurrence of *P. b. watti* and the presence of either *R. duplicata* or *P. ambagiosus* (Fisher exact test $p=0.283$) when all quadrats were considered (Table 7).

TABLE 7. OCCURRENCE OF *Paryphanta* IN RELATION TO OTHER LARGE SNAILS IN ALL TEMPORARY QUADRATS.

	No. of other large snails	*Rhytida*	*Placostylus*	*Rhytida* & *Placostylus*
Paryphanta present	25	7	9	1
Paryphanta absent	100	13	12	3

4.3 LIFESPAN AND GROWTH

Full details of the growth rates and lifespans of snails will be published elsewhere, but some preliminary information is included here on the lengths of time we followed juvenile and adult snails, and on changes in shape of the shells that occur during development.

TABLE 8. CHANGE IN MAXIMUM SHELL DIAMETER OF *Paryphanta busbyi watti* WITH ADULT SHELLS THAT WERE MEASURED ON MORE THAN ONE OCCASION.

Snails marked with an asterisk were first found as juveniles but the initial size is given when first found as adult. Growth of juveniles is given in Fig. 7. Data for snails that grew again (developed a soft aperture lip) after forming an adult shell are given in Table 9.

SNAIL NUMBER	INITIAL SIZE (mm)	FINAL SIZE (mm)	TIME INTERVAL (DAYS)	SNAIL NUMBER	INITIAL SIZE (mm)	FINAL SIZE (mm)	TIME INTERVAL (DAYS)
2*	52.70	53.38	483	K18A	50.44	50.44	41
5	47.42	56.90	922	K33	55.56	54.72	142
6*	57.61	57.41	1007	T2	54.35	54.23	166
11*	62.00	60.20	439	T4*	59.00	59.14	280
12*	54.75	54.92	420	T5*	56.60	56.60	855
17	55.70	55.80	92	T7	52.00	56.48	913
20	59.70	60.18	149	T8	57.20	57.17	126
23	58.50	58.76	171	T9	54.14	54.20	362
K3	61.78	61.82	117	T11	53.18	53.12	437
K4	54.18	53.84	544	T15	53.10	53.10	708
K6	57.08	56.96	117	T19	58.00	58.04	632
K7	56.16	56.10	683	T25	56.82	55.60	518
K13	56.08	56.36	582	T28	59.32	59.22	153
K15A	56.80	56.68	551	T31	58.49	58.76	179
K24	57.45	58.40	364	T32	59.84	59.76	127
K20A	56.76	56.38	287				

Most snails did not grow appreciably once the edges of the apertures of their shells had rolled inward to form hard rounded ridges (Table 8). Four snails, however, did continue to grow again after this and they subsequently developed new hard aperture edges (Table 9). The shell of each of these snails had a deformity that followed the original line of the aperture lip when it was hard. This deformity appeared as a slight ridge on the shell. Up to 6 similar deformities were visible on some other shells from all localities (Table 10). Most snails that had recently hatched from their eggs also had a slight constriction on their shell that marked the position of the edge of the protoconch when the snail hatched (Fig. 12a). The shell gets largely overgrown by subsequent whorls as the snail grows and this mostly obscures the first growth deformity.

The growth patterns for all snails are shown in Fig. 7. No snail was followed from hatching until its shell stopped growing. Seven newly hatched snails were

TABLE 9. DETAILS OF SNAILS THAT GREW AFTER THEY HAD DEVELOPED AN ADULT SHELL.

SNAIL ID NUMBER	MAX. LENGTH, FIRST HARD APERTURE LIP	MAX. LENGTH, SECOND HARD APERTURE LIP	MAXIMUM NO. OF DAYS OF GROWTH
3	53.88	57.62	329
22	55.2	58.7	235
T3	51.7	55.6	504
T14	55.72	55.73	140

TABLE 10. RELATIONSHIP BETWEEN THE NUMBER OF GROWTH DEFORMITIES IN SHELLS AND THE SIZE AND DEVELOPMENTAL STATE OF THE SHELLS (N = 171).

SIZE	NUMBER OF GROWTH DEFORMITIES 0	1	2	3	4	5	6
Adult	13	18	13	12	5	2	4
Juvenile > 40 mm	3	3	8	4	3	0	1
Juvenile 27.1–40 mm	3	3	3	0	0	0	0
Juvenile < 27 mm	23	46	11	3	0	0	0

tagged with queen bee labels when they were found in nests underground and these were found again in their original nests when these were dug up again on the next field trip. Some clearly grew while they were underground, but the shells were so delicate that it was not possible to take exact measurements (Fig. 7). None of the snails that hatched were caught again after they emerged from the ground and only 6 snails with shells smaller than 40 mm in maximum length when first caught above ground were recaptured (Fig. 7). A further 21 snails with shells greater than 40 mm in maximum length when first caught were recaptured and 12 of these were followed until they became adult. Juvenile snails showed a wide variation in growth rate, but in general their growth slowed markedly some months before the hard aperture lip developed. In some cases there was a slight reduction in the maximum length of the shell when the periostracum rolled inward to form the hard lip (Fig. 7).

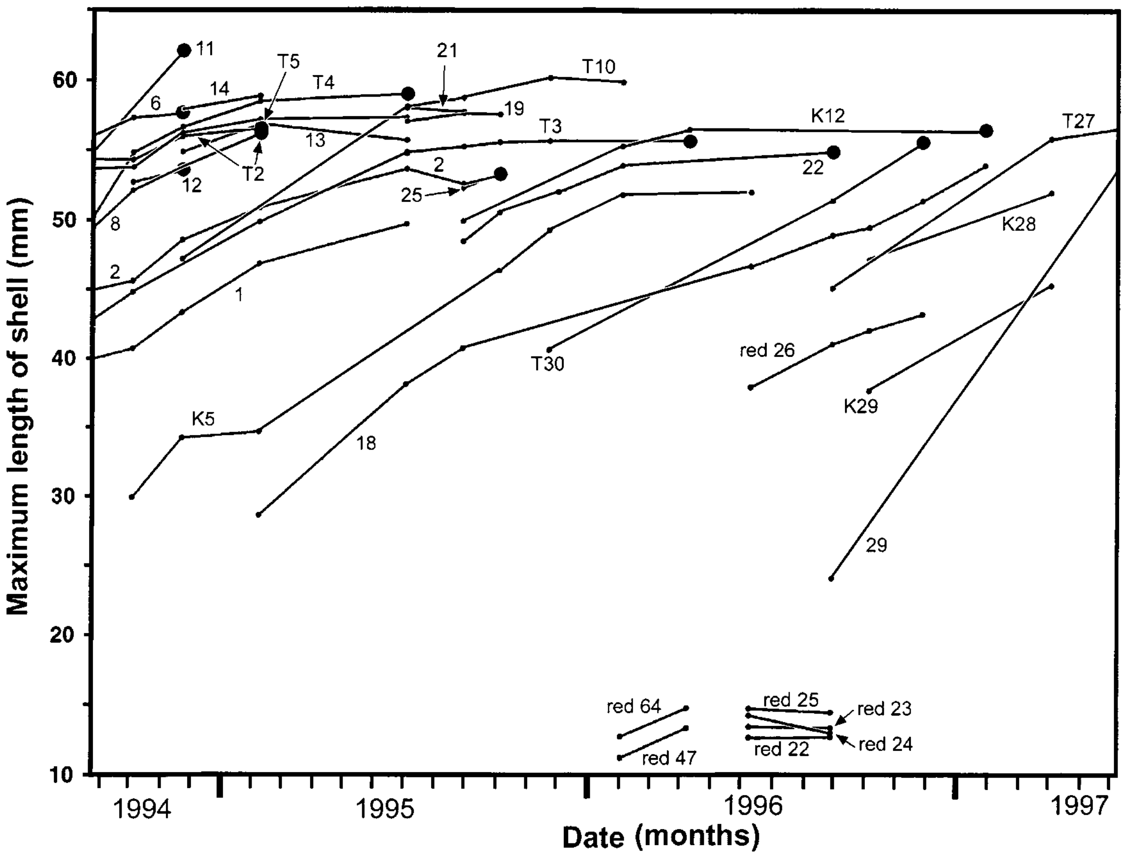


Figure 7. Growth patterns of snails. Only the first measurement for each adult shell is shown as a large dot. Lifespans of adults are given in Figs 8 and 9, and in Tables 8 and 9.

We have accurate data on the adult period for only three snails. These were the only snails that were followed from juveniles until they died as adults. Their minimum adult lifespans were 0.32 to 1.42 years (time from first found as adult to last found alive) (Fig. 8). Five other snails that were first found as adults and were followed until they died had lifespans of 0.99 to 2.18 years (Fig. 8). A further 12 snails that were either known to be still alive at the end of the study or that had moved out of the search area, were known to be alive from 1.0 to 2.69 years after they were first found (Fig. 9). Seven adult snails that were found in marked quadrats were never recaptured.

The shell of *P. b. watti* changes shape as the snail grows. Initially, there is a linear relationship between maximum length of shell and either the width of the shell or the maximum opening of the aperture. This continues until the shell

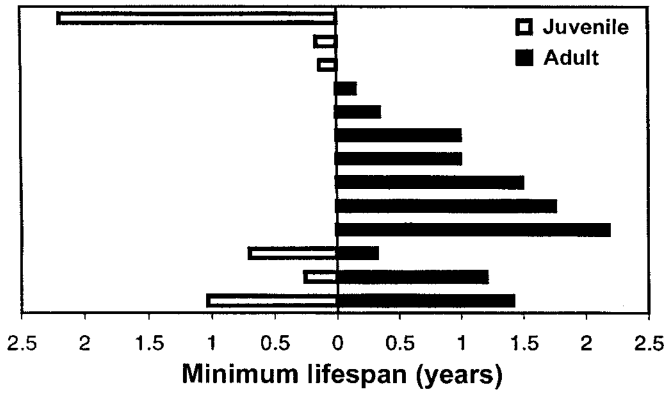


Figure 8. Minimum periods lived by *Paryphanta busbyi watti* that died. The time is given to last time they were found alive.

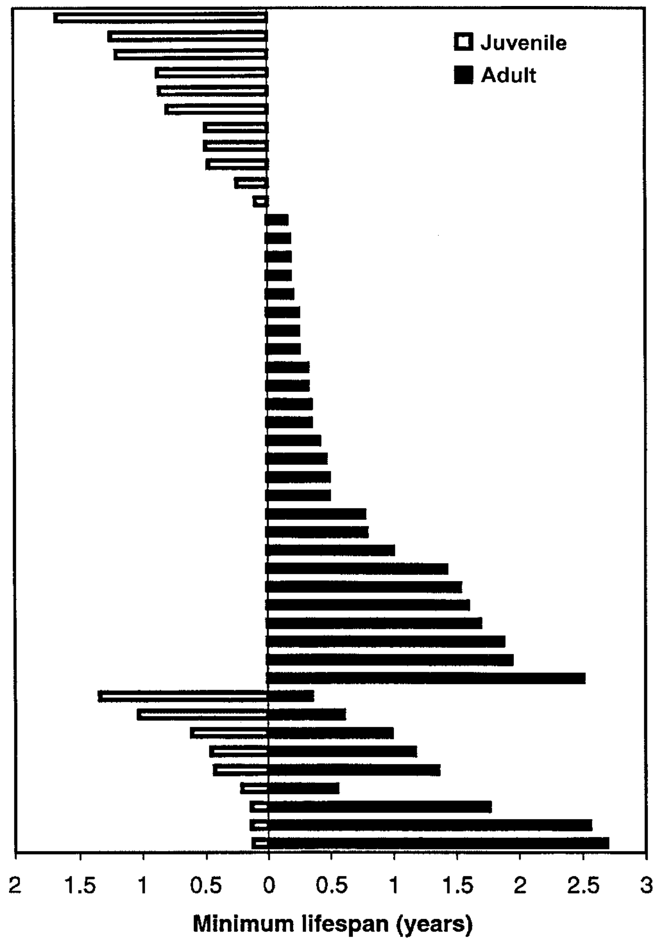


Figure 9. Minimum periods lived by *Paryphanta busbyi watti* that were either still alive or had moved out of the search area.

reaches about 40 mm in maximum length (Figs 10, 11). The rate of increase in both the width and the aperture then slows down in relation to the maximum length of the shell indicating that the shape of the shell changes at this point. The relationship between these dimensions and maximum length still remains linear although the relative rate of increase with respect to maximum length is slower. During this latter growth period, the body whorl of the shell forms a widening spiral (Fig. 12b, c). An axis that passes through the maximum opening of the aperture also changes during growth. Initially this makes an angle of about 25–30° to the axis through the column in young snails (Fig. 12a) but this angle subsequently changes until it makes an angle of about 70–80° to the column axis (Fig. 12b, c). As the snail reaches maturity, the upper surface of the end of the body whorl starts moving down relative to the previous whorl and the aperture starts becoming directed more ventrally. Part of the anterior dorsal surface behind the aperture often forms a slightly downward-directed flap in front of the aperture (Fig. 12c). Finally, the edge of the opening becomes rolled inward and hardens as described above. The weights of both the shell and the entire snail show approximately allomorphic relationships with shell length (linear when plotted as logarithm of both mass and length) although the shell constitutes a smaller proportion of the total mass during the mid growth phase than in either the early or late growth stages (Fig. 13). On average the shell accounts for 19.1% (95% C.I. = 19.0–19.2%) of the mass of snails with hard lips to the shell aperture.

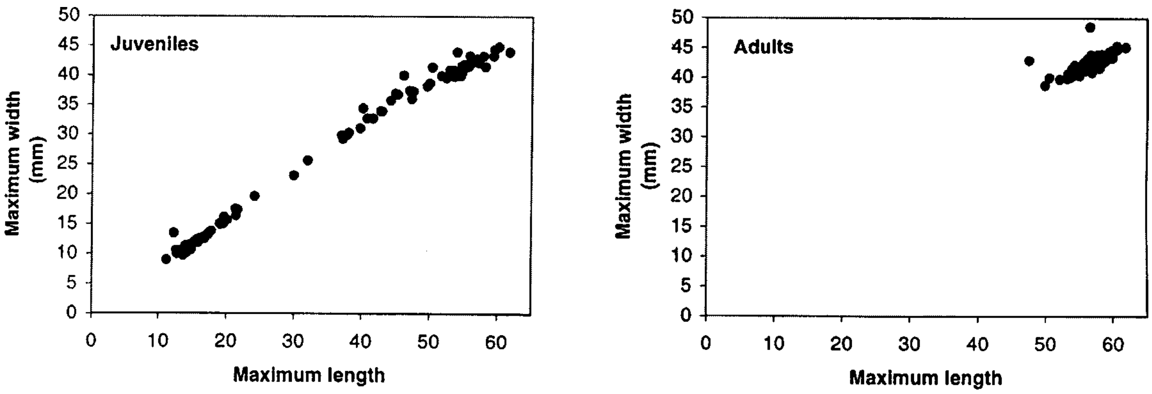


Figure 10. Relationship between maximum length and width of the shells of juvenile and adult *Paryphanta busbyi watti.*

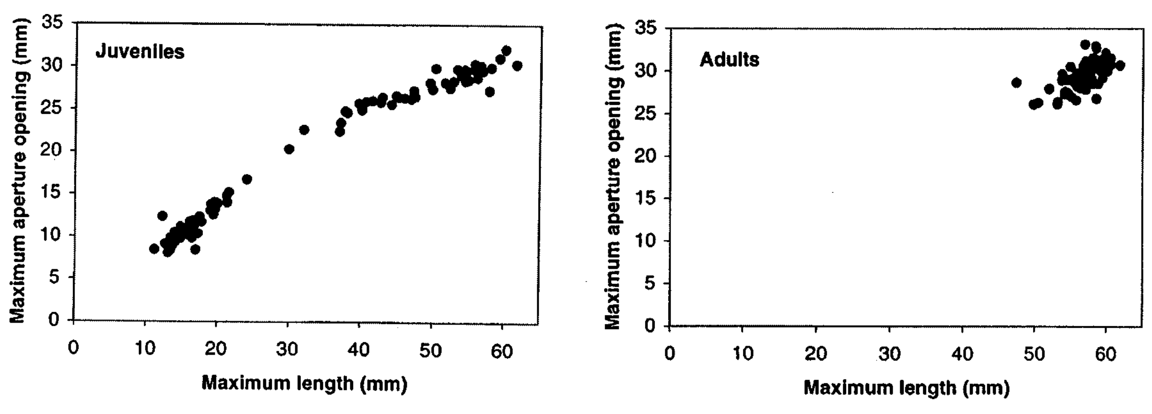


Figure 11. Relationship between maximum length and maximum opening of the aperture of shells of juvenile and adult *Paryphanta busbyi watti.*

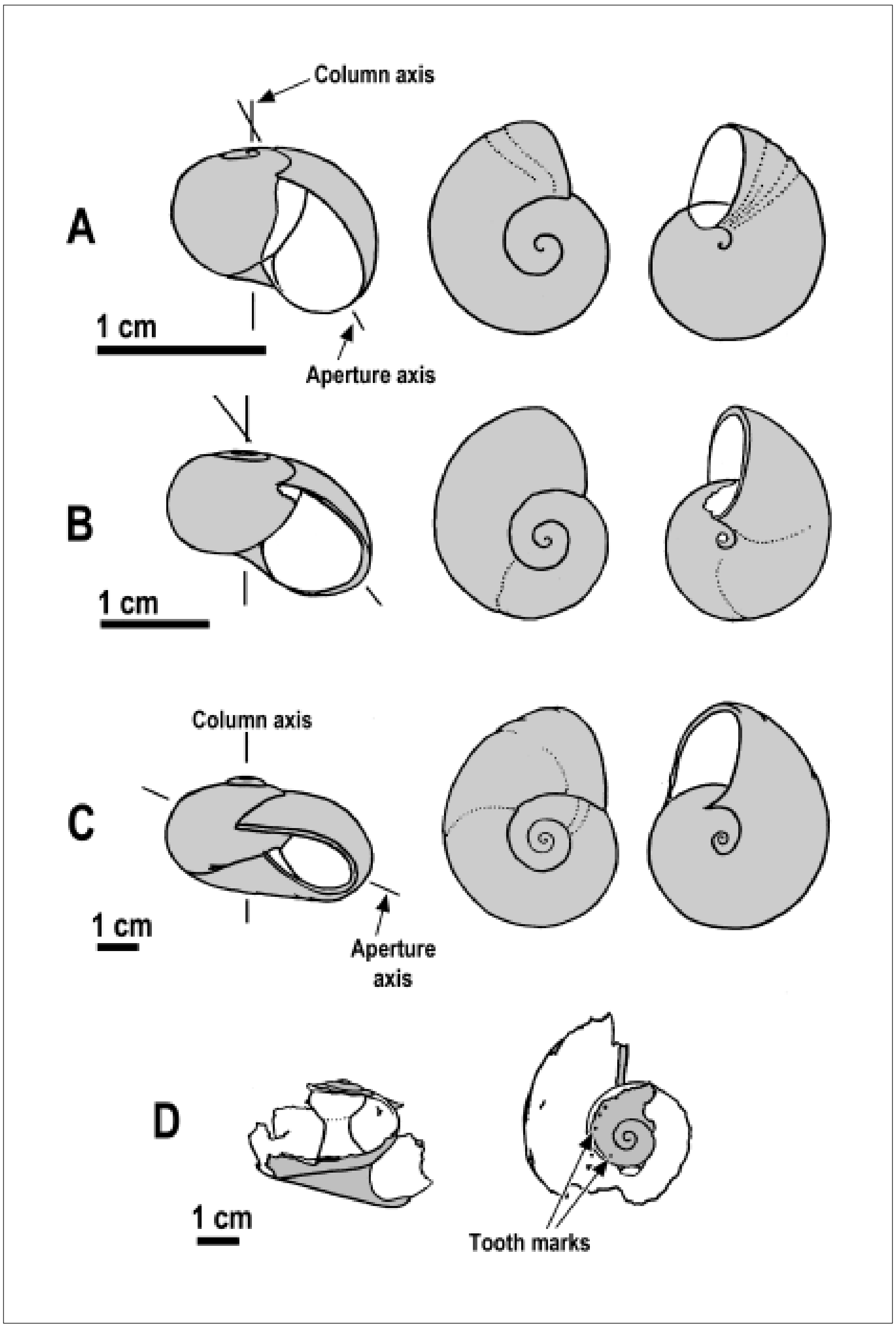


Figure 12. Diagrams of shells of *Paryphanta busbyi watti.*
A. Shell of a newly hatched snail.
B. Shell of a half grown snail.
C. Shell of an adult snail.
D. Shell after being attacked by a rat.
A, B, and C show dorsal, ventral and side views of shells, together with the axes through the column of the shell and through the maximum opening of the aperture. All diagrams were drawn from photographs.

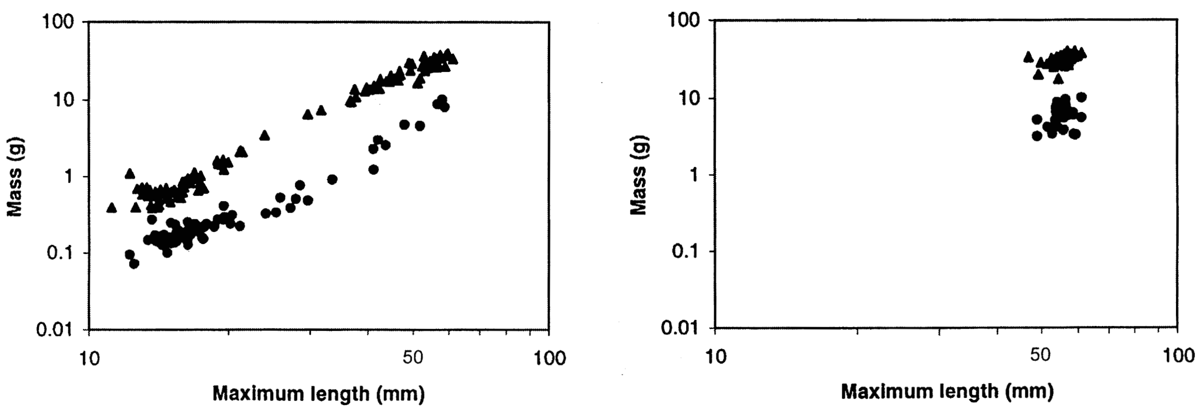


Figure 13. Relationship between maximum length of shells and the masses of the shells (dots) and of the total snails (triangles) for juvenile and adult *Paryphanta busbyi watti.*

4.4 LONG-TERM MOVEMENTS

Detailed movements of snails with transponders will be published at a later date but some preliminary information is given here. Over 97% of the snails with transponders were found again (Table 11), and most of these were found on subsequent searches (Table 12). However, some snails moved out of the search areas, and it was two to 10 visits before they were found again (Table 12). These absences varied from approximately two to 21 months (Table 13).

TABLE 11. NUMBER OF TIMES THAT EACH SNAIL WITH A TRANSPONDER WAS RECAPTURED. TOTAL NO. OF SNAILS WITH TRANSPONDERS = 69; DATA FROM AUGUST 1994 TO NOVEMBER 1999.

No. of times recaptured	0	1	2	3	4	5	6	7	8	10	11	12	14	15	16
No. of snails	2	9	17	8	4	4	8	2	7	2	1	2	1	1	1

TABLE 12. RELATIONSHIP BETWEEN THE NUMBER OF TIMES THAT SNAILS WITH TRANSPONDERS WERE RECAPTURED AND THE NUMBER OF CONSECUTIVE SEARCHES THAT WERE MADE BEFORE THEY WERE RECAPTURED. DATA FROM AUGUST 1994 TO NOVEMBER 1999.

No. searches before next recapture	1	2	3	4	5	6	8	10
No. of recaptures	245	40	22	10	4	2	1	1

TABLE 13. APPROXIMATE PERIODS WHEN SNAILS WERE ABSENT FROM THE SEARCH AREAS (± 0.5 MONTH).

Duration of absence (months)	2	3	4	5	6	7	8	9	10	17	18	19	21
No. snails absent	4	5	13	15	8	10	8	4	6	1	1	1	1

The positions where snails with transponders were recaptured at the three sites where marked quadrats were established are shown in Figs 3–5. Snails at site A were most frequently recaptured in an area of rank grass and low vegetation on the edge of kanuka bush, but they also formed a more dispersed group in the kanuka to the north west of this (Fig. 3). Other recaptures were widely dispersed over the rest of the search area except to the west of the western quadrat where few snails were found. An additional group of six recaptured snails was located near the site of a small temporary pond that formed during wet weather in the vehicle track. This was about 40 m to the east of the grass clearing and is not shown in Fig. 3. At site B, there was a slight tendency for snails to be recaptured more often towards the north of the search area but they were more evenly distributed elsewhere (Fig. 4). Recaptured snails were dispersed throughout the search area at site C although some formed a distinct band towards the south of the quadrat (Fig. 5). This latter band was not associated with any obvious feature of the habitat.

Individual snails with transponders were often found repeatedly in quite localised regions and six of these were selected for preliminary home range analysis. All six were found on more than 10 visits to the Aupouri Peninsula between August 1994 and June 1997 (Table 14). Only the positions where these snails were first found on each field trip were used for the analyses. Clearly, large juvenile and mature *P. b. watti* show site fidelity in that they mostly remain in areas of about 160 to 550 m² for up to 2.5 years. Many of the snails that were not used for home range analysis were either found too late in the study for them to be recaptured often enough to provide sufficient data points, or they were found on too few occasions for such an analysis to provide meaningful results.

TABLE 14. PRELIMINARY ANALYSIS OF PROBABLE AREAS OCCUPIED BY LARGE *Paryphanta busbyi watti* 50% AND 95% OF THE TIME (ADAPTIVE KERNEL METHOD). DATA USED INCLUDED FIRST CAPTURE AND SUBSEQUENT RECAPTURES BETWEEN AUGUST 1994 AND JUNE 1997.

Engraved snail no.	Location	No. of captures	Area (m^2) 50%	95%	Average dist. between recaptures (m)	Observation period (months)
T3	Site B	11	61.7	6.7	549.5	20
T5	Site B	12	44.2	8.5	327.7	30
T14	Site B	14	55.9	7.3	(230.7)*	29
2	Site A	15	111.8	8.1	487.7	31.5
6	Site A	16	23.3	6.6	159.9	31.5
K7	Site C	11	77.3	7.1	174.0	22

* 90% (not possible to estimate 95%).

4.5 SIZE DISTRIBUTION AND PREDATION

The largest (45–60 mm) and smallest (10–30 mm) size classes of live snails were most often found in temporary quadrats whereas intermediate sized snails were rare (Fig. 14). In contrast, small whole empty juvenile shells (10–30 mm) were most commonly found followed by large whole empty shells (45–60 mm) and, again, few intermediate sized whole empty shells were found (Fig. 15).

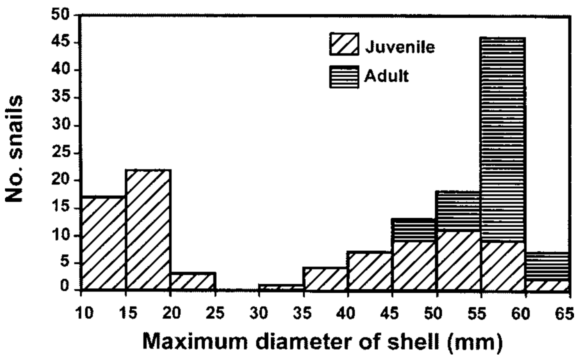


Figure 14. Numbers of live *Paryphanta busbyi watti* found in temporary quadrats at the end of the Aupouri Peninsula.

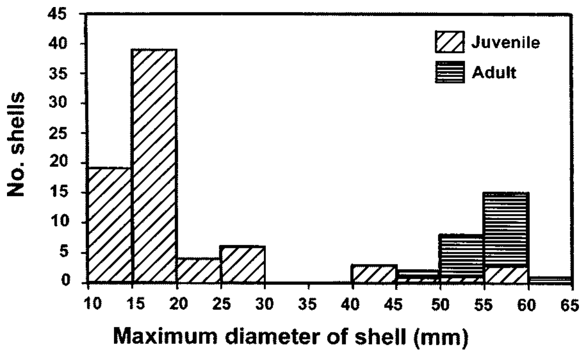


Figure 15. Numbers of whole empty *Paryphanta busbyi watti* shells found in temporary quadrats at the end of the Aupouri Peninsula.

The cause of death for the undamaged empty shells could not be determined. We found nine shells that had a broad spiral band of shell missing from the outer whorls leaving an irregularly edged spiral around the column (Fig. 12d). This was similar to typical damage done by Norway rats (*Rattus norvegicus* (Berkenhout)) to *Powelliphanta* shells as reported by Meads et al. (1984).

However, it is likely that the damage to *P. b. watti* shells was done by ship rats (*Rattus rattus* (L.)) because *Placostylus ambagiosus* shells were found at Cape Maria van Diemen with similar damage, and only ship rat and house mouse (*Mus musculus* L.) tracks were present in tracking tunnels there (Stringer & Parrish 1999). We were unable to measure the maximum lengths of the nine shells of *P. b. watti* that were damaged by rats but we estimate that all were larger than about 35 mm.

Eighteen shells of *P. b. watti* were found that were completely crushed and had evidence of molar marks or indentations on them and we assumed that they had been damaged by pigs. We were unable to measure their maximum lengths but estimate that all were larger than about 35 mm. The remains of one of these shells still had small amounts of fresh snail flesh adhering to it. We also found numerous fragments of *P. b. watti* shell in 21 of the temporary quadrats we searched. These either had evidence of pig rooting in them or there was such evidence nearby.

Vehicles probably damaged most of the other crushed shells that we found on the tracks but we did not record these. In two cases, cattle were probably responsible because the crushed shells were found amongst a large number of cattle hoof prints. Human damage was identified from one snail that we accidentally stood on while we were measuring out a temporary quadrat. The centre of the top of the shell was broken away from the outer whorl leaving most of the top of the shell open. Two other similarly damaged shells were found, one at site A and one on a path close to an illegal marijuana plot that had been abandoned (949959). Two empty shells with transponders were also found with similar damage although the transponders had prevented the tops of the shells from completely falling off. We assumed that these had been damaged underfoot by other visitors to the area. We ensured that we did not accidentally damage any snails with transponders in the areas where the marked quadrats were because we searched with harmonic radar as we entered them.

Shells with obvious predator damage formed 2.6% of the total number of empty juvenile shells and greater than 19.4% of empty adult shells. Both of these are minimum estimates because some of the large juvenile and adult snail shells were broken up and spread about, presumably by pigs, so that it was often impossible to tell how many original snails had been eaten. In addition, no small predator-damaged shells were found, so it is possible that predators completely destroyed the delicate shells of small snails or broke them into pieces that were too small to find. This suggests that the predation rate for juvenile snails is possibly much higher than we found. However, when only whole empty shells are considered, then small (less than 35 mm) and large (50–60 mm) *P. b. watti* experience the highest mortalities (Fig. 16). The true mortality rates cannot be estimated for different size classes of snails until we know the growth rate of these snails and how it varies with size, how long they live as adults, and how fast shells of different sizes decay. We have limited data on decay rates of adult shells which

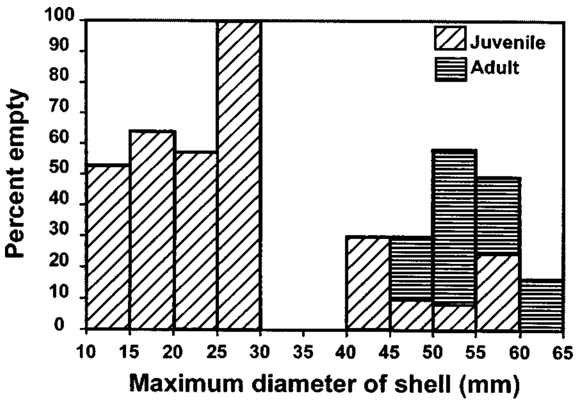


Figure 16. Apparent mortality of *Paryphanta busbyi watti* in relation to shell size as evidenced by whole empty shells.

indicate that the rate of deterioration rates varies considerably. Three empty adult shells, placed under leaf litter on the Te Paki trig ridge in October 1995 and examined once a year until 1999, did not deteriorate except for a small area of periostracum that lifted slightly between 1998 and 1999. In contrast, another snail (K4) at site C had half rotted away when it was recovered 232 days after last being seen alive. It was found in November 1996 in a pile of wet litter.

4.6 GENERAL BIOLOGY

Small live snails were found most frequently between August and December during searches of quadrats (Fig. 17). However, we did not find sufficient numbers of live snails to demonstrate if there were any size cohorts that could be followed as they developed during the year.

Snails with transponders that had died were found most frequently during June to July and in January to February although some were also found in April (Fig. 18a). These snails would have died during the interval between the previous field trip and the field trip in which they were found dead.

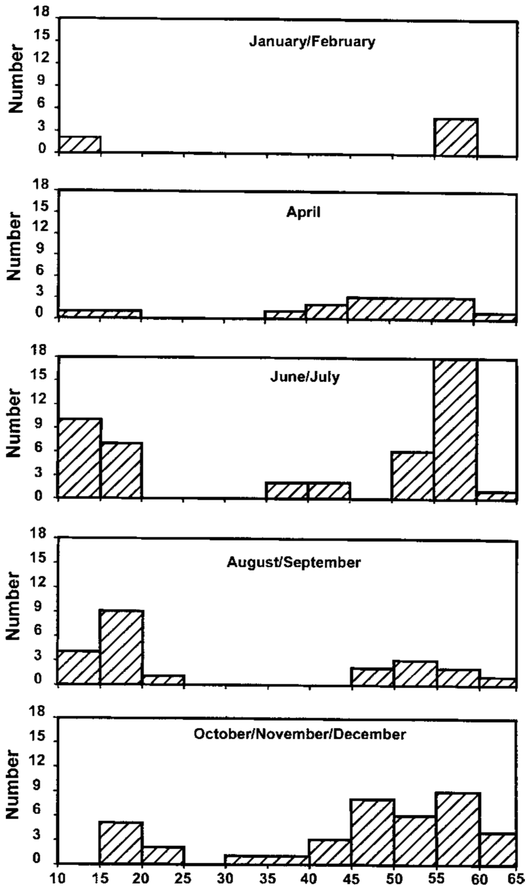


Figure 17. Relationship between the size distribution of shells of live *Paryphanta busbyi watti* and the time of year. The histograms show the total numbers of snails found in temporary quadrats between August 1994 and June 1997.

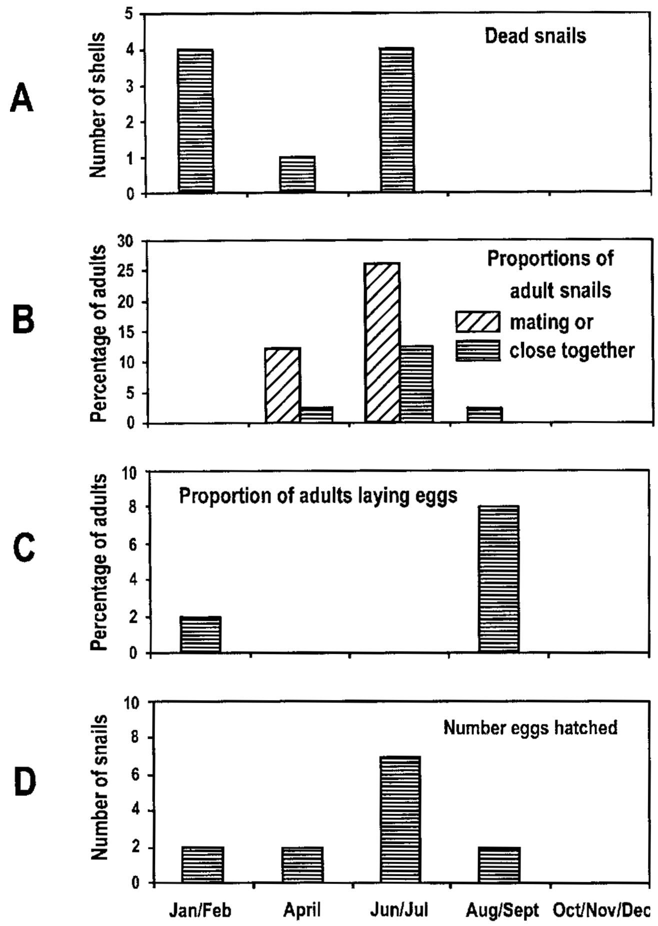


Figure 18. The times of year when snails died and reproduced. All data were taken from snails equipped with harmonic radar transponders. A. Time of year when dead snails were found. B. Time of year when snails were found within 5 cm of each other and when they were mating. C. Time of year when snails were found over nests containing eggs. D. Time of year when snails hatched from eggs.

Mating (Plate 1f) was most frequently observed amongst snails with transponders during the colder and wetter months and this was also the time of year when pairs of them were found closer together than 5 cm (Fig. 18b). Egg laying was observed during January to February and in August to September (Fig. 18c). Ovipositing snails were usually found above holes they had formed in soft soil and one was found over a hole formed in deep humus beneath bracken on Kohuronaki. One snail was also found alongside a hole that ran horizontally into a bank of soil. All holes were about 2 cm in diameter and 2–4 cm deep. On one occasion, a snail was found on three successive days above a new hole. These holes contained 2, 2, and 1 eggs respectively. Holes beneath other snails contained 3–6 eggs. The snails covered these holes over with soil when they left them.

Twenty eight eggs were found (Plate 1g), in 10 clutches of 1–6 eggs. Measurements were taken from 15 of the eggs. Most were ovoid but some were almost spherical. They weighed 1.103 ± 0.18 g (mean ± S.D.), and had maximum lengths of 14.22 ± 0.70 mm and maximum widths of 11.219 ± 0.80 mm. There is evidence that eggs may become lighter during development because four eggs that initially weighed 1.19 ± 0.15 g on 22 November 1995, weighed 1.06 ± 0.11 g the last time they were weighed on 8 April 1996. These eggs were laid with two others in a hole situated under grass by the road above the marked quadrat at site B. All successfully hatched by 9 June 1996 but all of the snails subsequently died in their hole. The probable cause of mortality was that a large clump of *Ghania* had died back, exposing the ground to the sun so it had dried up and hardened.

Nine of the shells of newly hatched snails were 13.30 ± 1.32 mm in maximum length. The snails remained underground for 2–3 months after hatching and two of them grew as already mentioned above. The incubation time is known for only one egg. This was found newly laid under a snail (K4) on Kohuronaki on 7 February 1995 and was checked again just as it was hatching 159 days later. The other eggs found in holes under snails all hatched after more than 4 months and less than 8 months so that newly hatched snails were found throughout the year, although most frequently during June and July (Fig. 18d).

Most snails with transponders were found buried beneath leaf litter when they were recaptured although 19.9% were found on the surface (Fig. 19). This differed from our subjective impression that live snails appeared to be rarely found on the surface when we were searching temporary quadrats for them. The shells of *P. b. watti* are, however, cryptically coloured and can easily be overlooked, especially if they are overhung by vegetation, or lying on leaf litter.

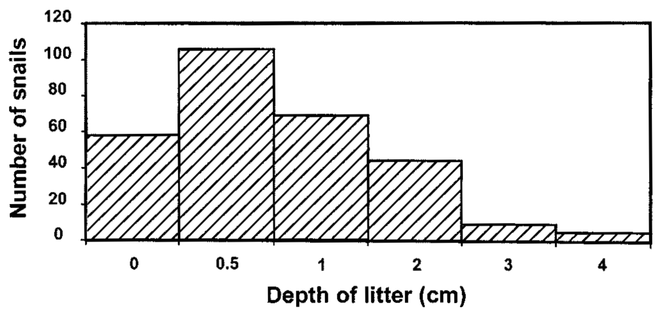


Figure 19. The approximate height of leaf litter found over snails with transponders when they were recaptured.

Two snails were found with the front of their bodies extended into empty shells of *P. b. watti* and they were apparently in the process of removing some of the ostracum. Both empty shells had ostracum missing from inside the last whorl when the snails were pulled from them. Empty shells of *P. b. watti* and *P. ambagiosus* were often found with most of the ostracum removed from the last whorl and this suggests that old shells are used as one source of calcium for these snails.

Two adult snails were observed in the process of eating juvenile *P. b. watti.* Both juvenile shells were partly pulled into the adult shells and orientated with their apertures towards the larger snails. When the smaller snails were removed for examination, a short string of fresh flesh was pulled out between the larger snails and the partly eaten juveniles. These were the only observations of feeding in *P. b. watti* although one snail was found with a faecal string that contained approximately 1 cm of earthworm. Coad (1995) often found that *P. b. busbyi* vomited entire earthworms while they were being handled, but *P. b. watti* never did this.

5. Discussion

Although we did not find any new populations of *P. b watti*, we greatly increased their known range. We established that those in Te Paki Farm Park form two distinct populations: one around Te Paki hill and the other around Kohuronaki hill. In both locations, the density of these snails increases significantly with increasing altitude but we do not know why they occur more frequently at higher altitudes. They often seem to be more frequent on steep slopes (up to 50°) where they are probably less likely to be eaten by pigs. However, susceptibility to pig predation is not the only factor in microhabitat selection because the densest concentration of snails was on an almost level area on Kohuronaki hill. The row of hills between Kohuronaki and Te Paki hill at between 150 and 250 m a.s.l. are frequently covered by cloud and this may provide enough moisture to prevent young snails from drying out during dry periods. Live snails are found down as low as 120 m a.s.l. while empty shells were found down to 55 m a.s.l. The snails also seem to be distributed quite widely to the west of Te Paki hill. Much of this area is low scrub and although they certainly do occur in this habitat they are probably only there in low densities. The area is popular with pig hunters, and it is likely that the snails have done well there because hunting has reduced the density of pigs.

The sizes of the two populations of *P. b. watti* in Te Paki Farm Park are hard to estimate from our data because our sampling was designed only to survey the area. A very approximate estimate was made by using the density of live snails found in each 50 m altitudinal range of each vegetation type within the snail's likely distribution. We suggest that there are about 5500 snails spread over a maximum area of about 10.5 km^2 in the vicinity of Te Paki hill and about 5000 snails within a maximum area of 5 km^2 in the vicinity of Kohuronaki hill. These estimates are only approximate because they depend on our subjective choice of the boundaries between vegetation types. We also estimate that the areas over which these snails occur are larger than the areas that we sampled (Fig. 6). The data that the estimates are based on are not suitable for estimating confidence intervals. We did not search the area around Unuwhao extensively enough to give any estimate of the area that these snails probably occupy there.

We do not have complete data on the time taken for snails to grow to adult because no snails with shells smaller than 24 mm in maximum diameter were recaptured except for those that had hatched from eggs and were still underground. The variability in growth that occurs both during the development of individual snails and between different snails makes it difficult to find evidence that the youngest snails of *P. b. watti* grow fastest and that growth slows with increasing size, except that this does occur as the final shell size is approached (Fig. 7). However, the fastest growth certainly does seem to occur in the youngest snails of *P. b. busbyi* (Coad 1998), so it is also likely to occur in *P. b. watti.* If we assume that the snail's growth rate is about the same as the growth rates of snails 18 and K5 when they were small, then young snails should take between 10 and 15.5 days to add one millimetre to their shell diameter. The young snails probably leave their nests when they are about 15 mm long so they would then take between 160 and 260 days to grow to a maximum length of 30 mm. If this is added to the 2.2 years that snail 18 took to grow from 29 mm to almost adult size then this gives a total of 2.6 to 3 years required to reach maturity. Using the same calculations, snail 29 would have taken 384–439 days to reach a shell length of 53.5 mm. These estimates are, of course, very approximate because we do not know the growth pattern of young *P. b. watti*. However, if our extrapolated growth rates are true, then *P. b. watti* grows very much faster than the seven or so years that Dell (1955) estimated for *P. b. busbyi* to reach adult size. His estimate was based on an examination of growth ridges on shells, and on the assumption that these ridges were the result of slowed growth during summer when it was hot and dry (Dell 1955). We found that such growth ridges are not necessarily formed annually in *P. b. watti* because many snails that we followed as juveniles did not develop any recognisable deformities during summer, and many empty shells lacked such deformities altogether (Table 10). Using annual growth rings to estimate the age of pulmonates can also be unreliable for a variety of reasons that are discussed by Williamson (1976), Oosterhoff (1977), and Comfort (1957).

The change in shape that occurs after the shell of P. *b. watti* reaches a maximum diameter of 40–45 mm (the points of inflection in the plots for juvenile snails in Figs 10 and 11) is similar to that reported for other land snails with determinate growth. The reproductive organs begin to develop when other snails reach this inflection point, indicating that they are becoming sexually mature (e.g. Williamson 1976; Solem & Christensen 1984; Staikou & Lazaridou-Dimitriadou 1990; Lazaridou-Dimitriadou 1995). It is likely that the same occurs in *P. b. watti* snails when their shells reach diameters of about 40 mm but we did not confirm this by dissection because these snails were too rare to justify killing them. The shells of *P. b. watti* subsequently continue to increase a further 20 mm or so in diameter before they form a hard aperture lip and cease further growth. However, it is possible that the snails may become fully mature before their shells stop growing as can sometimes happen in other pulmonates (Chatfield 1968). However, all the snails that we found mating and ovipositing had shells with hard aperture lips.

The numbers of snails and empty shells found in the marked quadrats differed significantly from those found in the majority of nearby temporary quadrats that were searched (Table 15). Initial searches of the marked quadrats had relatively high densities of live snails but relatively low densities of empty shells in comparison to nearby temporary quadrats (Fisher's exact test, $p = 0.38$). The marked quadrat sites were chosen because they had high densities of snails but this does not explain why they had relatively fewer empty shells. One possible explanation is that these sites may have been locally more moist than elsewhere and, as discussed below, this may have both favoured higher densities of live snails whilst allowing empty shells to decay faster. It may also be possible that the ostracum is more likely to be removed from empty shells by other live snails when there is a higher density of live snails and this would also increase the rate of decay of empty shells.

TABLE 15. DENSITIES OF LIVE AND EMPTY *Paryphanta busbyi watti* IN MARKED QUADRATS AND TEMPORARY QUADRATS NEARBY.

Results are for initial searches of marked quadrats. Standard errors given with means.

	No. quadrats	No. live juveniles/ha	No. live adults/ha	No. whole empty shells/ha	
				juveniles	aults
Temporary quadrats	22	47 ± 22	50 ± 21	143 ± 62	81 ± 26
Marked quadrats*	4	11 ± 11	300 ± 33	9.1 ± 9.1	6.1 ± 6.1

*The two quadrats at site A were treated as one combined quadrat.

The size distribution of whole undamaged shells of *P. b. watti* at Te Paki Farm Park was quite different from the size distributions that Coad (1998) reported for *P. b. busbyi* in either Trounson Park or Katui Scenic Reserve, Northland. Coad (1998) found that the numbers of whole empty shells at Trounson Park increased more or less uniformly with shell size up to adult whereas no empty shells smaller than 30 mm were found at Katui Scenic Reserve but shells larger than this were more frequently found the larger they were. Balance (1985), however, found no intermediate sized shells of *P. b. busbyi* in a small collection in pine forest near Waipoua. The differences between the size distributions of empty shells at Trounson and Katui were partly attributed by Coad (1998) to there being intensive rat and other predator control at Trounson and no predator control at Katui. In contrast to both of these sites, we found numerous small juvenile and large empty *P. b. watti* shells at Te Paki but very few shells between 30 and 45 mm long (Fig. 15). Small *P. b. watti* evidently suffer a high mortality which is unrelated to rodent predation, and this could be at least partly caused by desiccation. It seems unlikely that the lack of shells in this mid-size range was due to drought prior to our study because there was sufficient time during our study for some of the smaller snails to grow to this size, and because there is no evidence of increased mortality amongst similar sized *Placostylus ambagiosus* nearby during this period (Sherley et al. 1998). The end of the Aupouri Peninsula certainly appears to be drier than Waipoua Forest, the nearest location to Trounson Park and Katui Scenic Reserve where meteorological records are kept (Waipoua is about 6 and 14 km NW

TABLE 16. MEAN ANNUAL TEMPERATURE, HUMIDITY AND RAINFALL FOR THE FAR NORTH AND AT WAIPOUA FOREST. DATA FROM NEW ZEALAND METEOROLOGICAL SERVICE (1983).

Location	Mean annual temperature (C)	Mean annual rel. humidity (%)	Mean total sunshine hours	Mean annual rainfall (mm)
Cape Reinga	15.5	85	-	992
Te Paki Station	15.2	78	2118	1440
Waipoua Forest	14.1	83	1692	1651

respectively from these). The average rainfall, humidity and sunshine hours all indicate that the Te Paki area is probably drier than these others (Table 16). However, it is likely to be wetter above altitudes of 200–250 m on the hills at Te Paki than where the meteorological records were taken (at an altitude of 40 m) because cloud often covers these hills. We took some temperature and relative humidity records at ground level at site B and some rainfall data from between sites A and B (Appendix 2) but no official meteorological records were taken at Te Paki during this period so we cannot give any indication of how much the climate at the snail study sites differ from that at the official Te Paki weather station. Meads et al. (1984) also note that species of *Powelliphanta,* which are closely related to *Paryphanta*, are more common in moist high-altitude forest than in drier forests at lower altitudes because they are prone to dehydration, and cannot survive dry conditions. However, the altitudinal ranges where *Powelliphanta* are found in the South Island and lower North Island of New Zealand are very much greater (up to at least 1500 m) than those where *P. b. watti* occur.

A possible explanation for the paucity of small empty shells reported by Coad (1998) at Trounson Park and at Katui Scenic Reserve could be that they decay rapidly under the damper conditions there. We certainly found that large *P. b. watti* can decay much more rapidly under moist leaf litter than when in apparently drier conditions. Small shells might also decay faster than larger shells because they are thinner walled.

Why were so few live snails and empty shells found of *P. b. watti* in the intermediate size range? A possible explanation is that perhaps they grow relatively rapidly through this size range so they are relatively rarely encountered. The snails may then survive for some time once they are large because of their long adult life span, at least 2 to 2.5 years (Table 8, Figs 8, 9), and because the empty shells usually decay slowly. However, this explanation seems unlikely in view of the size distribution of whole empty shells of *P. b. busbyi* that was found by Coad (1998). She reported that live intermediate sized *P. b. busbyi* were relatively common at least in pine forest at Mangakahia (Coad 1998), so either the growth patterns for these two subspecies are very different or there is some other difference between these locations that causes this. Another possibility is that the shells of small to medium sized *P. b. busbyi* were completely destroyed by predators such as mice, rats or pigs so that few damaged shells remained to be found. The number of rats at Trounson Park were reduced by poisoning using bait stations on a 100 × 100 m grid, and this may have resulted in increased numbers of mice (Innes et al. 1995). Mice could have attacked some of the smallest snails and completely destroyed them, but it is unlikely that they damaged larger snails because they seem unable to eat intermediate sized *Powelliphanta* which have thinner shells than *Paryphanta* (K.J. Walker, pers. comm.). We cannot be sure of the possible role that mice may have played at Te Paki because we did not sample rodents where *P. b. watti* were found. Obvious predation by rodents on large juveniles and adults of *P. b. watti* (2.1% of empty shells) was similar to that reported by Coad (1998) at Katui Scenic Reserve (3.7%) and both were much lower than she found at Mangakahia Forest (14.5%) or at Trounson Park (29.9%). No predator control was being done at either Mangakahia Forest or Katui Scenic Reserve whereas there was intensive mammal control at Trounson Park as already mentioned. Pigs were the major obvious predators of both *P. b. watti* at Te Paki Farm Park and of *P. b. busbyi* at Katui Scenic Reserve although the pig predation rate at Te Paki (7.8%) was considerably lower than at Katui (48%) (Coad, 1998). However, it is quite possible that intermediate sized *P. b. watti* could have been eaten whole by pigs so that no evidence of this remained. We found no recognisable predation of *P. b. watti* by possums (*Trichosurus vulpecula* (Kerr)), mustelids or birds (particularly thrushes, *Turdus philomelos* C.L. Brehm) even though they are present at Te Paki and were reported to eat *P. b. busbyi* (Coad, 1998) and species of *Powelliphanta* (Meads et al. 1984).

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7. References

Ballance, A.P. 1985: *Paryphanta* at Pawakatutu. *Tane* 31: 13–18.

Chatfield, J.E. 1968: The life history of the helicid snail *Monacha cantiana* (Montagu), with reference also to *M. cartusiana* (Müller). *Proceedings of the Malacological Society of London* 38: 233–245.

Coad, N. 1998:The kauri snail (*Paryphanta busbyi busbyi*), its ecology and the impact of introduced predators. MSc thesis, University of Auckland. 161 p.

Comfort, A. 1957: The duration of life in molluscs. *Proceedings of the Malacological Society of London* 32: 219–241.

Dell, R.K. 1955: A contribution to the study of rates of growth in *Paryphanta busbyi* (Gray), (Mollusca, Pulmonata). *Records of the Dominion Museum* 2: 145–146.

Devine, D.C. 1997: Some aspects of behaviour and ecology in the land snail *Powelliphanta traversi traversi* Powell (Rhytididae: Rhytidinae). MSc thesis, Massey University. 137 p.

Goulstone, J.F.; Mayhill, P.C.; Parrish, G.R. 1993: An illustrated guide to the land Mollusca of the Te Paki Ecological Region, Northland, New Zealand. *Tane* 34: 1–32.

Innes, J.; Warburton, B.; Williams, D.; Speed, H.; Bradfield, P. 1995: Large-scale poisoning of ship rats (*Rattus rattus*) in indigenous forests of the North Island, New Zealand. *New Zealand Journal of Ecology* 19(1): 5–17.

Johnson, M.S.; Black, R. 1991: Growth, survivorship, and population size in the land snail *Rhagada convicta* Cox, 1870 (Pulmonata: Camaenidae) from a semiarid environment in Western Australia. *Journal of Molluscan Studies* 57: 367–374

Kie, J.G.; Baldwin, J.A.,; Evans, C.J. 1994: CALHOME: A Home Range Analysis program. http://nhsbig.inhs.uiuc.edu/wes/calhome_info.html.

Lazaridou-Dimitriadou, M. 1995: The life cycle, demographic analysis, growth and secondary production of the snail *Helicella* (*Xerothracia*) *pappi* (Schutt, 1962) (Gastropoda Pulmonata) in E. Macedonia (Greece). *Malacologia* 37: 1–11.

Lövei, G.L.,; Stringer, I.A.N.; Devine, C.D.; Cartellieri, M. 1997: Harmonic radar—a method using inexpensive tags to study invertebrate movement. *New Zealand Journal of Ecology* 21: 187–193.

Meads, M.J.; Walker, K.J.; Elliott, G.P. 1984: Status, conservation, and management of the land snails of the genus *Powelliphanta* (Mollusca: Pulmonata). *New Zealand Journal of Zoology* 11: 277–306.

Molloy, J.; Davis, A.; Tisdall, C. 1994. *Setting priorities for the conservation of New Zealand's threatened plants and animals.* (2nd edn) Department of Conservation, Wellington. 64 p.

New Zealand Meteorological Service. 1983: Summaries of Climatological Observations to 1980. *NZ Meteorological Service Miscellaneous Publication 177*. 177 p.

Ohms, P.G. 1948: Some aspects of the anatomy of *Paryphanta busbyi.* MSc thesis, University of Auckland.

Oosterhoff, L.M. 1977: Variation in growth rate as an ecological factor in the landsnail *Cepaea nemoralis* (L.). *Netherlands Journal of Zoology* 27: 1–132.

Parrish, R.; Sherley, G.; Aviss, M. 1995: Giant land snail recovery plan *Placostylus* spp., *Paryphanta* sp. *Threatened Species Recovery Plan No. 13*. Department of Conservation, Wellington. 13 p.

Powell, A.W.B. 197: *New Zealand Mollusca.* Collins, Auckland.

Sherley, G.H.; Stringer, I.A.N.;Parrish, G.R.; Flux, I. 1998: Demography of two land snail populations (*Placostylus ambagiosus,* Pulmonata: Bulimulidae) in relation to predator control in the far north of New Zealand. *Biological Conservation* 84: 83–88.

Solem, A.; Christensen, C.C. 1984: Camaenid land snail reproductive cycle and growth patterns in semiarid areas of North-Western Australia. *Australian Journal of Zoology* 32: 471–491.

Staikou, A.; Lazaridou-Dimitriadou, M. 1990: Aspects of the life cycle, population dynamics, growth and secondary production of the snail *Monacha cartusiana* (Müller, 1774) (Gastropoda Pulmonata) in Greece. *Malacologia* 31: 353–362.

Williamson, P. 1976: Size–weight relationship and field growth rates of the land snail *Cepaea nemoralis* L. *Journal of Animal Ecology* 45: 875–885.

Worton, B.J. 1989: Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168.

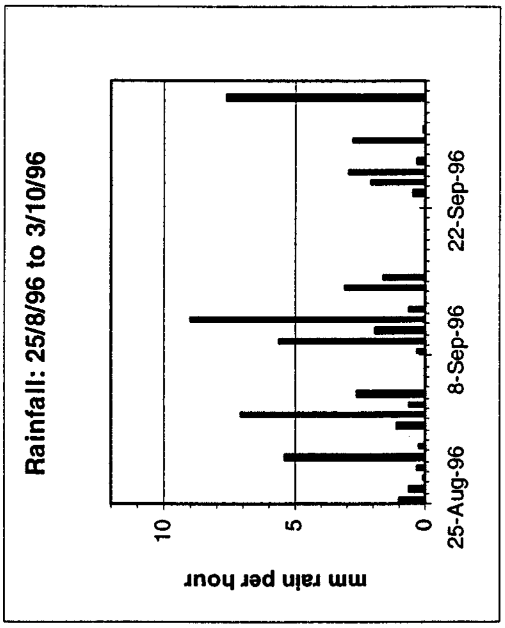
Appendix 1. Data from searches of marked quadrats

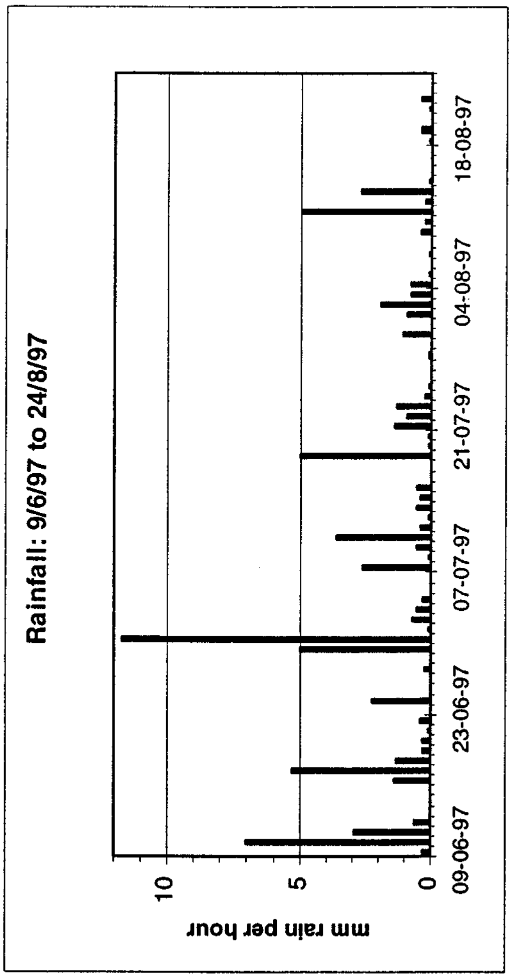
Date	Site	Search method	No. live adults	juvs	No. with transponders adults	juvs	No. live marked snails found	No. bee-labelled juvs found	Hatched juvs	No. snails on eggs	No. of eggs	No. marked empty shells	No. empty juvs	No. empty adult
Aug-94	A	casual	6	4	6	.	0	.	.	.	.	.	.	.
Aug-94	B	casual	.	4	.	4	.	.	.	.	.	.	.	.
Oct-94	B	radar	2	1	2	1	.	.	.	.	.	.	.	.
Oct-94	A	hand	1	2	1	2	5	.	.	.	.	.	.	.
Oct-94	C	hand	4	1	4	1	.	.	.	.	.	.	.	1
Nov-94	A	radar	2	1	2	.	8	.	.	.	.	1	.	.
Nov-94	B	hand	3	2	3	1	.	.	.	.	.	.	.	.
Feb-95	A	radar	.	.	.	.	8	.	.	.	.	1	.	.
Feb-95	B	radar	.	.	.	.	10	.	.	.	.	.	.	2
Feb-95	C	radar	.	.	.	.	5	.	.	1	2	.	.	.
Jul-95	A	radar	2	2	2	2	6	.	.	.	.	.	.	.
Jul-95	B	radar	4	6	2	.	6	1	.	.	.	.	.	.
Aug-95	A	radar	1	3	1	.	5	2	.	1	5	.	.	.
Aug-95	B	hand	1	4	1	.	1	3	.	.	.	.	.	.
Aug-95	C	radar	2	1	1	.	.	.	2	.	.	.	.	.
Sep-95	B	radar	.	.	.	.	3	.	.	1	1	.	.	.
Oct-95	C	radar	.	.	.	.	7	.	.	.	.	.	.	.
Oct-95	A	radar	.	.	.	.	4	.	.	.	.	.1	.	.
Nov-95	B	radar	.	1	.	1		.		2	12	.	.	.
Nov-95	A	radar	2	.	2	.		.		.	.	.	.	.
Feb-96	A	radar	.	.	.	.	4	.	1	.	.	1	.	.
Feb-96	B	radar	.	.	.	.	6	.	1	.	.	2	.	.
Feb-96	C	radar	.	.	.	.	6	.	.	.	.	.	.	.
Apr-96	A	radar	.	.	.	.	4	.	2	.	.	.	.	.
Apr-96	B	radar	.	.	.	.	5	.	.	.	.	.	1	.
Apr-96	C	radar	1	.	1	.	5	.	.	.	.	.	.	.
Jun-96	A	radar	1	1	1	.	3	1	.	.	.	.	.	.
Jun-96	B	radar	1	.	1	.	4	.	6	.	.	.	1	.
Jun-96	C	radar	.	.	.	.	6	.	.	.	.	.	.	.
Aug-96	A	radar	.	1	.	1	7	1	.	.	.	.	.	.
Aug-96	C	radar	3	.	3	.	4	.	.	.	.	.	2	.
Aug-96	B	radar	.	1	.	1	6	.	.	.	.	.	.	.
Aug-96	B	hand	1	3	1	.	.	3	.	.	.	.	8	.
Aug-96	A	hand	1	.	1	.	2	.	.	.	.	.	2	1
Oct-96	B	radar	1	1	1	.	5	1	.	.	.	.	.	.
Oct-96	C	radar	.	2	.	2	3	.	.	.	.	.	.	.
Nov-96	A	radar	1	.	1	.	5	1	.	.	.	1	.	.
Nov-96	B	radar	1	.	1	.	6	.	.	.	.	.	.	.
Nov-96	C	radar	.	.	.	.	4	.	.	.	.	1	.	.
Jan-97	A	radar	.	.	.	.	3	.	.	.	.	.	.	.
Jan-97	B	radar	2	.	2	.	5	.	.	.	.	.	.	.
Jan-97	C	radar	.	.	.	.	4	.	.	.	.	.	.	.
Apr-97	A	radar	.	.	.	.	4	.	.	.	.	.	.	.

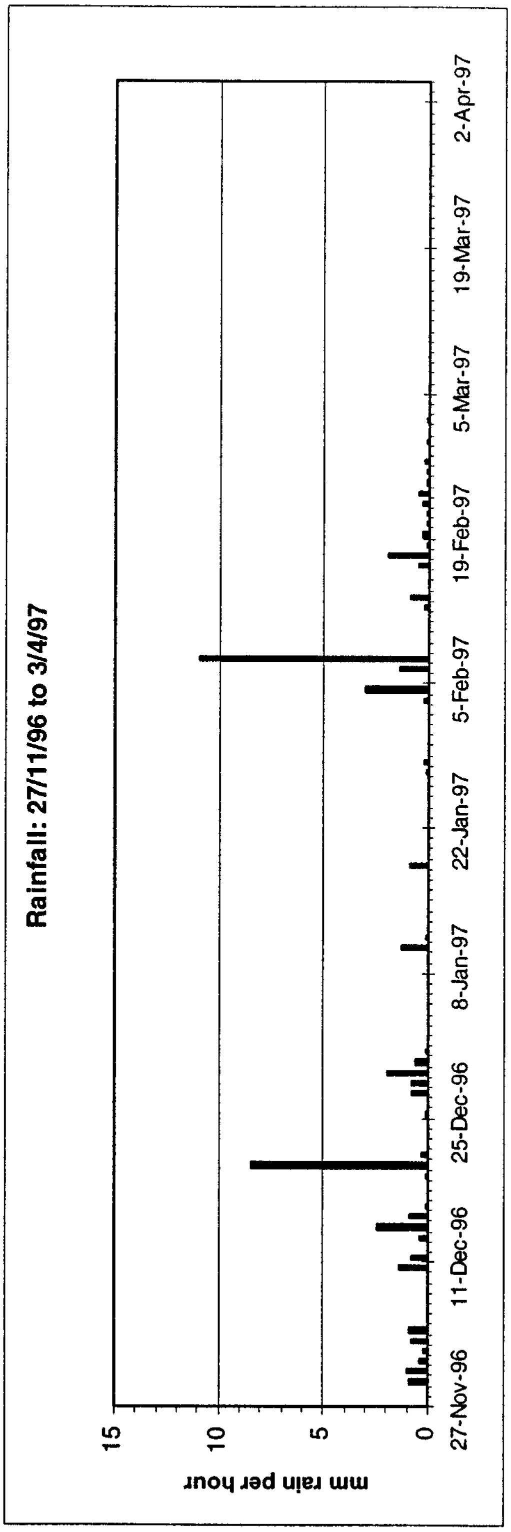
Date	Site	Search method	No. live adults	juvs	No. with transponders adults	juvs	No. live marked snails found	No. bee-labelled juvs found	Hatched juvs	No. snails on eggs	No. of eggs	No. marked empty shells	No. empty juvs	No. empty adult
Apr-97	B	radar	1	.	1	.	8	.	.	.	.	.	.	.
Apr-97	C	radar	1	.	1	.	7	.	.	.	.	.	.	.
Jun-97	A	radar	3	.	2	.	4	.	.	.	.	.	.	.
Jun-97	B	radar	2	1	2	1	8	.	.	.	.	1	.	.
Jun-97	C	radar	2	.	2	.	4	.	.	.	.	.	.	.
Aug-97	A	radar	.	.	.	.	3	.	.	1	7	2	.	.
Aug-97	B	radar	.	.	.	.	3	.	.	.	.	.	.	.
Aug-97	C	radar	.	1	.	1	3	.	.	.	.	.	.	.
Nov-97	A	radar	.	1	.	1	2	.	.	.	0	.	.	.
Nov-97	B	radar	.	.	.	.	4	.	.	.	.	.	.	.
Nov-97	C	radar	.	.	.	.	4	.	.	.	.	.	.	.
Feb-98	A	radar	.	.	.	.	2	.	1	.	.	.	.	.
Feb-98	B	radar	1	.	.	.	4	.	.	.	.	.	.	.
Feb-98	C	radar	.	.	.	.	5	.	.	.	.	.	.	.
Jul-98	A	radar	.	.	.	.	2	.	.	.	.	.	.	.
Jul-98	B	radar	.	.	.	.	3	.	.	.	.	1	.	.
Nov-98	A	hand	3	.	.	.	1	.	.	.	.	.1	.	.
Nov-98	B	hand	.	5	.	.	5	5	.	.	.	1	14	2
Nov-98	C	hand	7	.	.	.	2	.	.	.	.	1	7	.
Oct-99	A	hand	1	3	.	.	1	.	.	.	.	.	.	.
Oct-99	B	hand	2	6	.	.	4	.	.	.	.	.	9	1
Oct-99	C	hand	5	3	.	.	.		.	.	.	.	2	.
	TOTAL		71	61	48	19	248	18	13	6	27	15	46	

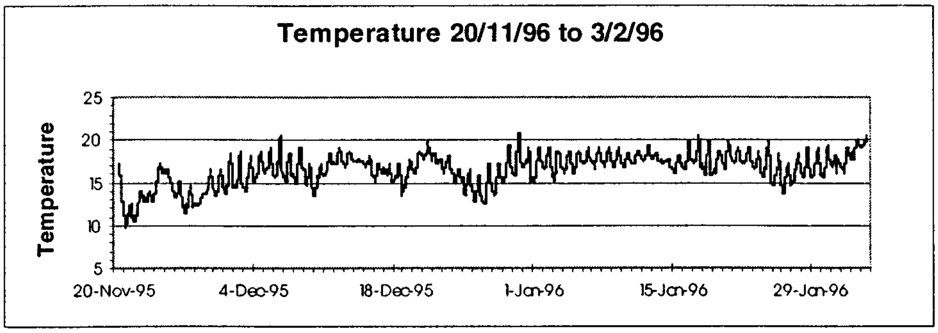
Appendix 2. Meteorological data from site C on Te Paki ridge

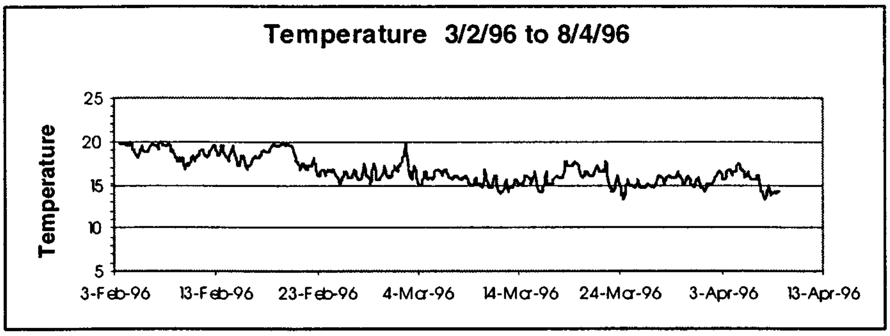
Temperature was recorded using a "Hobo" data logger (Hastings data Loggers, Wauchope, Australia) with an external probe. The probe was positioned on the leaf litter between rocks near site B where it would never be in direct sunlight. Relative humidity and rainfall were measured with "Tinytag" data loggers (Gemini Data Loggers (UK) Ltd, Chichester, England). The relative humidity data logger was accurate to 95% and all reading above 95% were converted to 100% in the following graphs. This data logger was placed in a protective box next to the temperature data logger at site B with the sensor exposed and positioned 2–3 cm above the leaf litter. The rain gauge was placed about halfway between sites A and B in a small clearing in low scrub. Here it had wide uninterrupted exposure to the sky and protection from the wind.

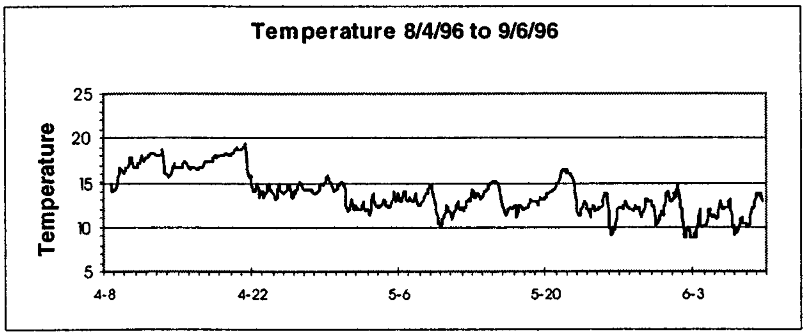

Rainfall: 25/8/96 to 3/10/96
mm rain per hour
10
5
0
25-Aug-96
8-Sep-96
22-Sep-96

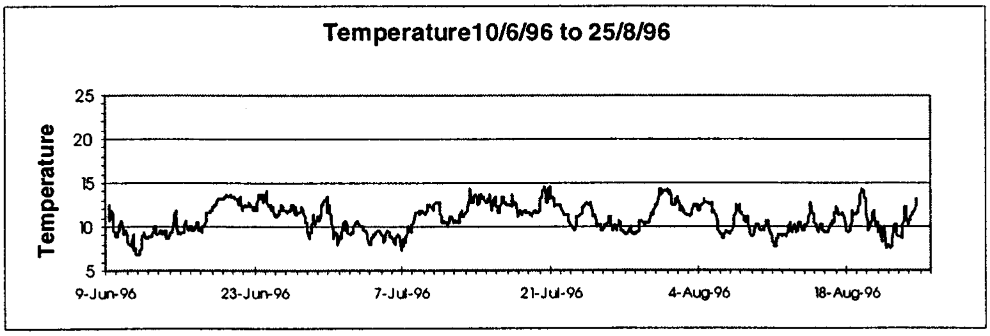

Rainfall: 9/6/97 to 24/8/97
mm rain per hour
10
5
0
09-06-97
23-06-97
07-07-97
21-07-97
04-08-97
18-08-97

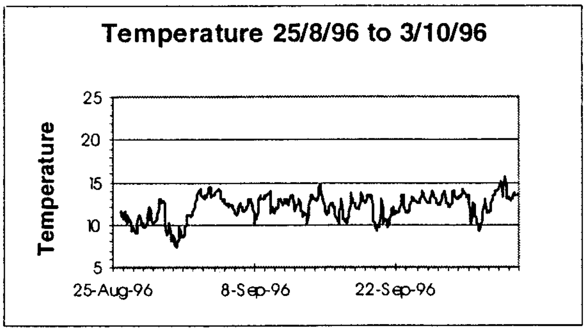

Rainfall: 27/11/96 to 3/4/97
mm rain per hour
15
10
5
0
27-Nov-96
11-Dec-96
25-Dec-96
8-Jan-97
22-Jan-97
5-Feb-97
19-Feb-97
5-Mar-97
19-Mar-97
2-Apr-97

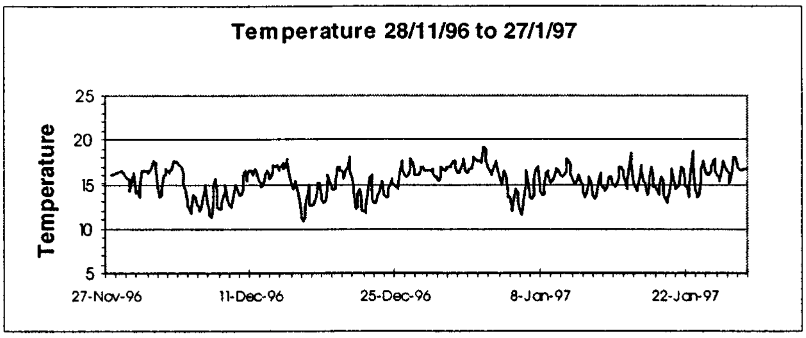

Temperature 20/11/96 to 3/2/96
Temperature
25
20
15
10
5
20-Nov-95
4-Dec-95
18-Dec-95
1-Jan-96
15-Jan-96
29-Jan-96

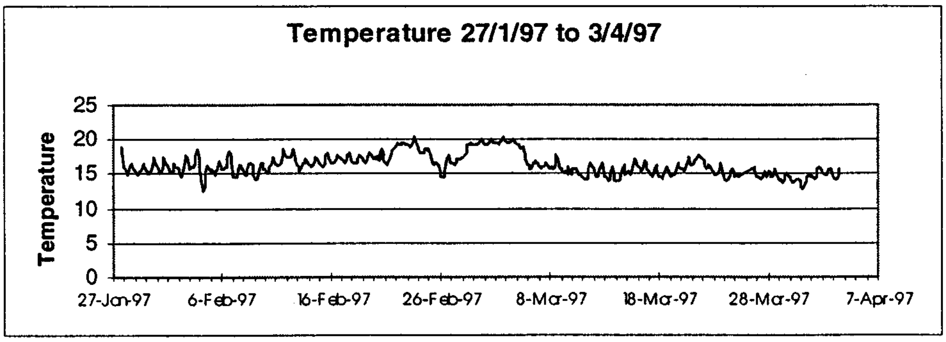

Temperature 3/2/96 to 8/4/96
Temperature
25
20
15
10
5
3-Feb-96
13-Feb-96
23-Feb-96
4-Mar-96
14-Mar-96
24-Mar-96
3-Apr-96
13-Apr-96

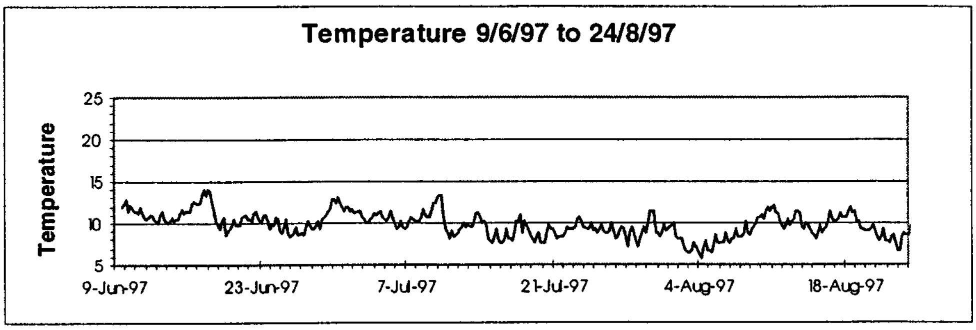

Temperature 8/4/96 to 9/6/96
Temperature
25
20
15
10
5
4-8
4-22
5-6
5-20
6-3

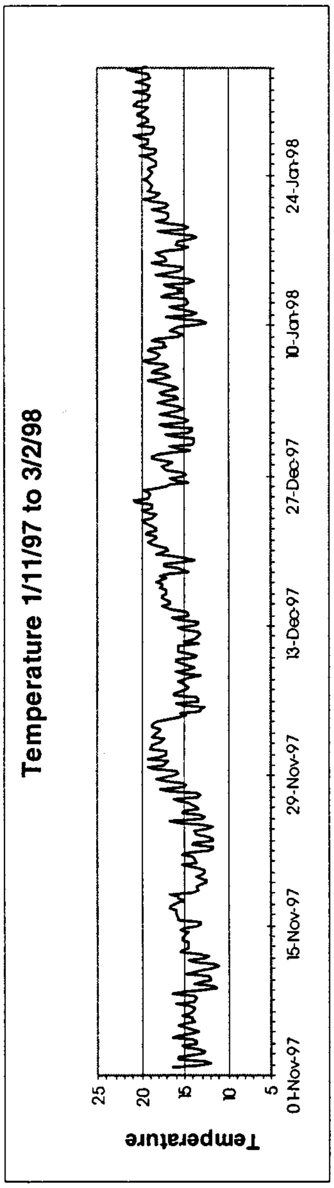

Temperature10/6/96 to 25/8/96
Temperature
25
20
15
10
5
9-Jun-96
23-Jun-96
7-Jul-96
21-Jul-96
4-Aug-96
18-Aug-96

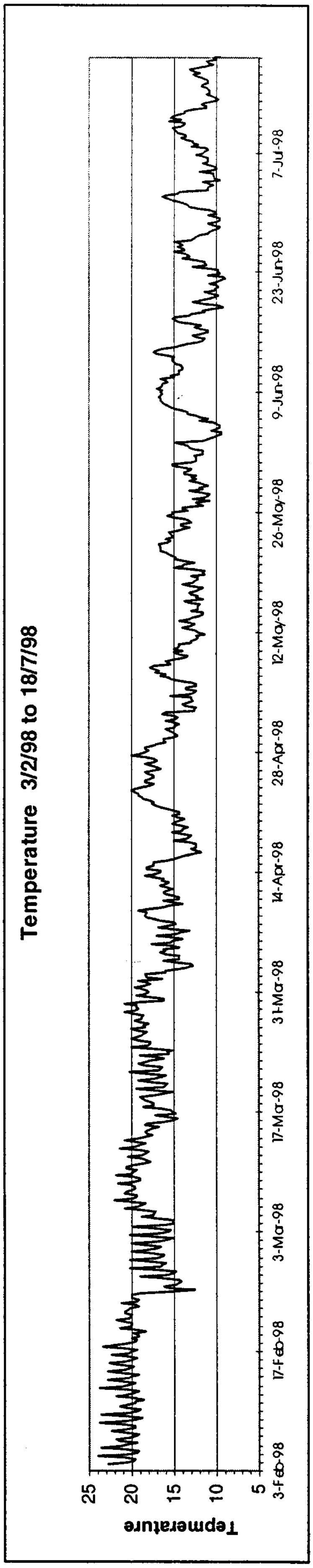

Temperature 25/8/96 to 3/10/96
Temperature
25
20
15
10
5
25-Aug-96
8-Sep-96
22-Sep-96

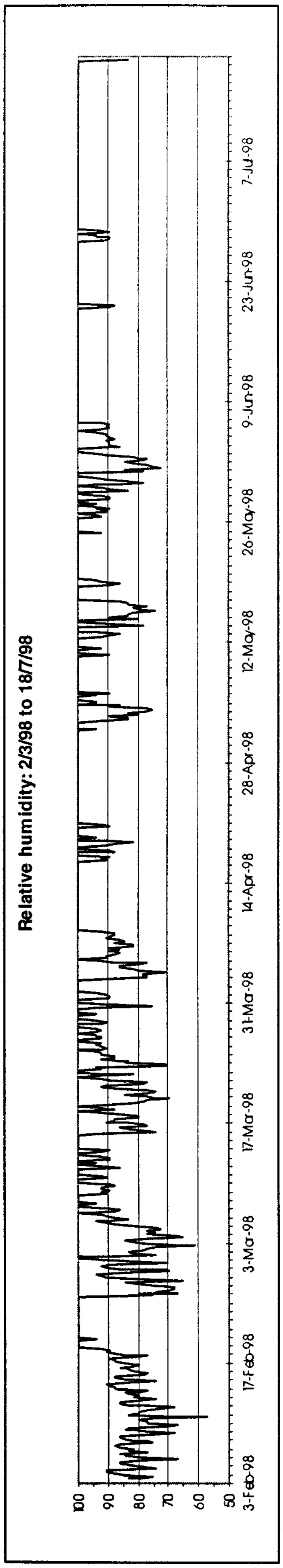

Temperature 28/11/96 to 27/1/97
Temperature
25
20
15
10
5
27-Nov-96
11-Dec-96
25-Dec-96
8-Jan-97
22-Jan-97

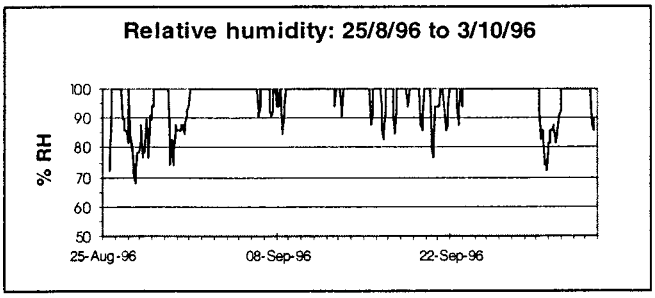

Temperature 27/1/97 to 3/4/97
Temperature
25
20
15
10
5
0
27-Jan-97
6-Feb-97
16-Feb-97
26-Feb-97
8-Mar-97
18-Mar-97
28-Mar-97
7-Apr-97

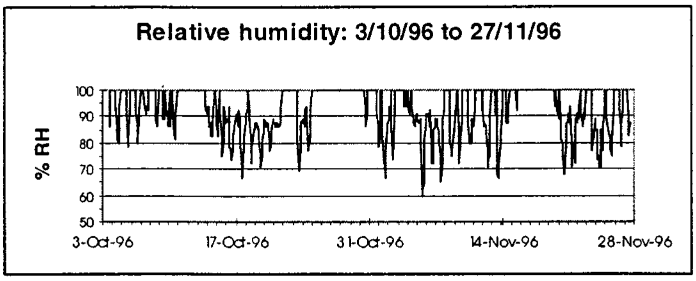

Temperature 9/6/97 to 24/8/97
Temperature
25
20
15
10
5
9-Jun-97
23-Jun-97
7-Jul-97
21-Jul-97
4-Aug-97
18-Aug-97

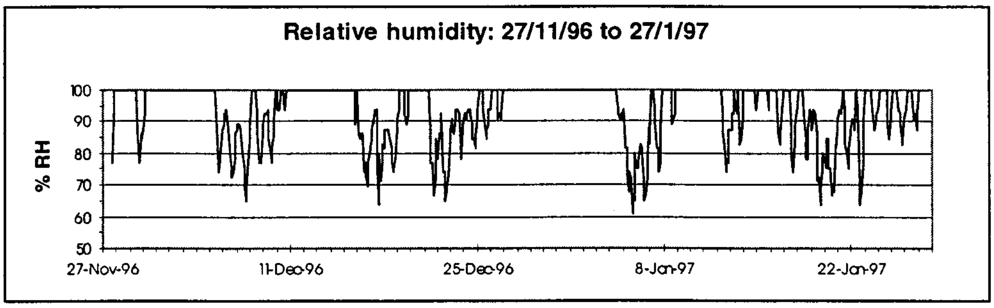

Temperature 1/11/97 to 3/2/98
Temperature
25
20
15
10
5
01-Nov-97
15-Nov-97
29-Nov-97
13-Dec-97
27-Dec-97
10-Jan-98
24-Jan-98

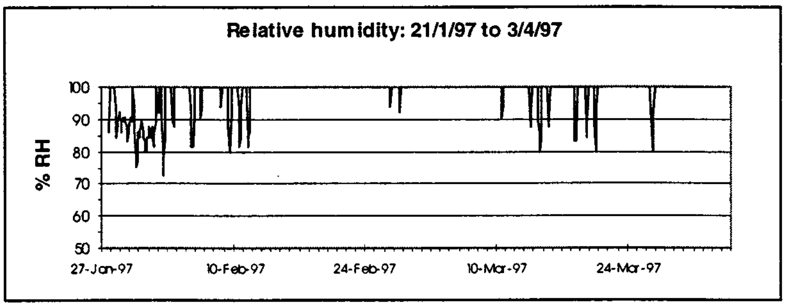

Temperature 3/2/98 to 18/7/98
Tepmerature
25
20
15
10
5
3-Feb-98
17-Feb-98
3-Mar-98
17-Mar-98
31-Mar-98
14-Apr-98
28-Apr-98
12-May-98
26-May-98
9-Jun-98
23-Jun-98
7-Jul-98

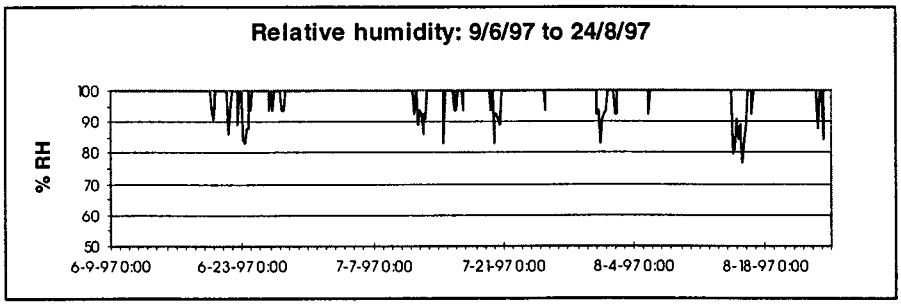

Relative humidity: 2/3/98 to 18/7/98
100
90
80
70
60
50
3-Feb-98
17-Feb-98
3-Mar-98
17-Mar-98
31-Mar-98
14-Apr-98
28-Apr-98
12-May-98
26-May-98
9-Jun-98
23-Jun-98
7-Jul-98

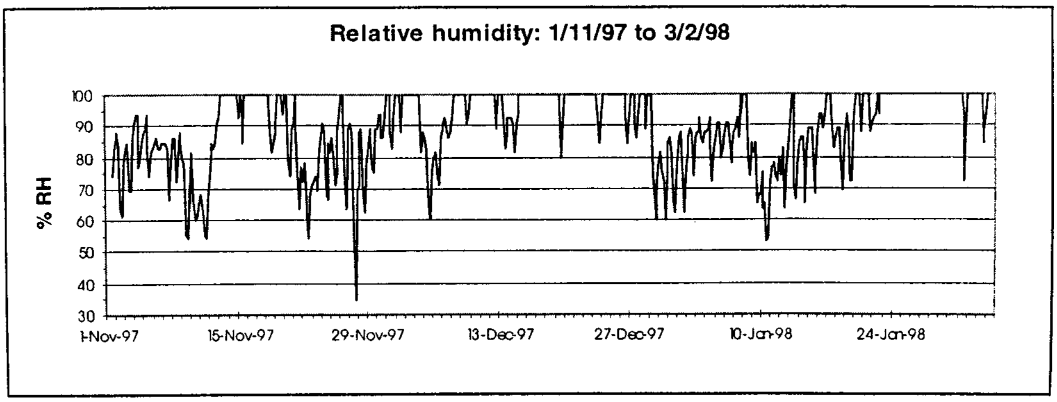

Relative humidity: 25/8/96 to 3/10/96
% RH
100
90
80
70
60
50
25-Aug-96
08-Sep-96
22-Sep-96


Relative humidity: 3/10/96 to 27/11/96
% RH
100
90
80
70
60
50
3-Oct-96
17-Oct-96
31-Oct-96
14-Nov-96
28-Nov-96


Relative humidity: 27/11/96 to 27/1/97
% RH
100
90
80
70
60
50
27-Nov-96
11-Dec-96
25-Dec-96
8-Jan-97
22-Jan-97


Relative humidity: 21/1/97 to 3/4/97
% RH
100
90
80
70
60
50
27-Jan-97
10-Feb-97
24-Feb-97
10-Mar-97
24-Mar-97


Relative humidity: 9/6/97 to 24/8/97
% RH
100
90
80
70
60
50
6-9-97 0:00
6-23-97 0:00
7-7-97 0:00
7-21-97 0:00
8-4-97 0:00
8-18-97 0:00


Relative humidity: 1/11/97 to 3/2/98
% RH
100
90
80
70
60
50
40
30
1-Nov-97
15-Nov-97
29-Nov-97
13-Dec-97
27-Dec-97
10-Jan-98
24-Jan-98