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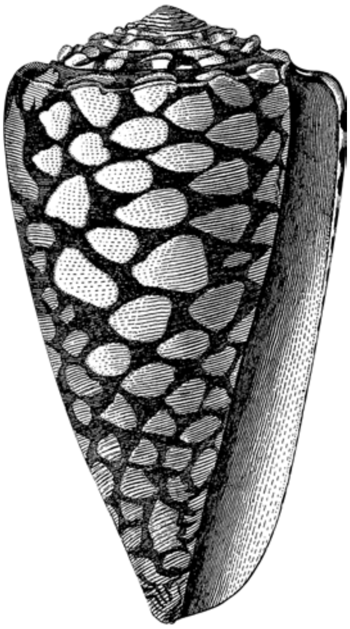

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Growth and development of the rare land snail *Paryphanta busbyi watti* (Eupulmonata : Rhytididae)

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Abstract

The rare carnivorous land snail *Paryphanta busbyi watti* was investigated by following marked snails over a study period of 6.3 years. Large snails were fitted with harmonic radar transponders to aid in locating them. This species is iteroparous and has determinate growth. Shells had maximum diameters of 49.6–61.2 mm. Two to eight large eggs, representing 5%–23% of the live weight of a snail, were laid at a rate of one to two per day over 2–5 days. These eggs were deposited in one to three holes dug in soil by the snails. A newly laid egg was surrounded by an adhesive membrane, which disappeared after a few days, exposing the calcareous shell. The eggs took 5–7.3 months to hatch and the young snails remained underground for a minimum of up to 2.8 months. The shells of these snails increased in size while underground. A non-linear mixed-effects model was used to combine data from 31 snails that were monitored for different lengths of time. Only an approximate estimate could be made of the development rate for young snails. Growth to the adult shell stage was estimated to take 3–4.3 years and fast-developing individuals tended to become larger adults. The maximum time that a snail with an adult shell was monitored was 4.1 years, whereas most snails with an adult shell were monitored for 1–2 years.

Additional keywords: egg incubation, landsnail, lifespan, Pulmonata.

Introduction

Paryphanta busbyi watti Powell, 1946 (Rhytididae) occurs only on the end of the Aupouri Peninsula, Northland, New Zealand (Fig. 1). It is a rare snail that is listed as a highest-priority species for conservation action by the Department of Conservation (Molloy *et al.* 1994). One other subspecies, namely *P. b. busbyi* (Gray, 1840), is widespread from Kaitaia to Warkworth in the upper part of Northland, where it occurs in forest and scrub. Both subspecies are large snails (up to 62 and 79 mm maximum shell diameter, respectively) that feed on earthworms and possibly other ground-living invertebrates (Powell 1979). Both subspecies are fully protected (Wildlife Act (New Zealand) 1953).

Information on *P. b. watti* is limited to its taxonomy (literature included in Powell 1979), distribution (Parrish 1992; Goulstone *et al.* 1993; Sherley 1993) and a description of one egg (Powell 1946). There is more information on the biology and egg of *P. b. busbyi*, but even this is, for the most part, sketchy (Hutton 1881; Powell 1930; O'Connor 1945; Ohms 1948; Dell 1955; Vause 1977; Ballance 1986; Meads 1990; Parrish *et al.* 1995; Montefiore 1996; Coad 1998).

The following research was started while working on the distribution and habitat of *P. b. watti* from 1994 to 1997 (Stringer and Montefiore 2000) and was completed in November 2000. The intention was to provide conservation managers with information on the incubation time, growth rates and longevity to help them make informed decisions relating to the species. For example, it is necessary to have data on the life history

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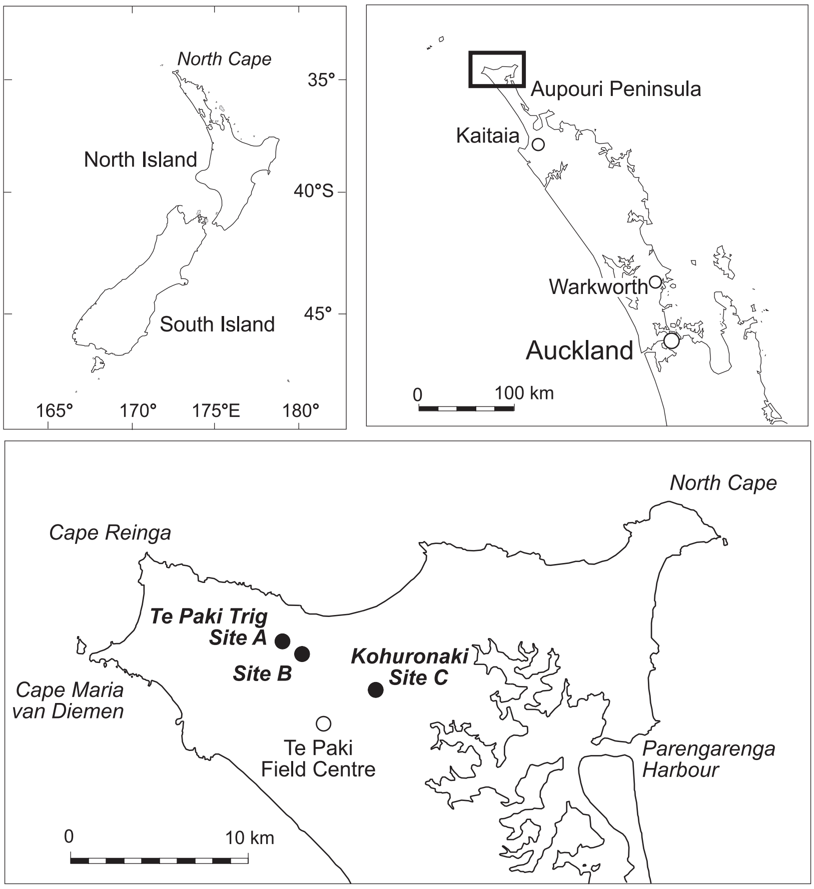

Fig. 1. Map of the North Island of New Zealand, showing the location of *Paryphanta busbyi watti*.

characteristics of *P. b. watti* to determine whether these rare snails are likely to become extinct and, if so, how to circumvent this. Information on the distribution, habitat, size-frequency distribution and observed mortality of *P. b. watti* are given in Stringer and Montefiore (2000), together with some preliminary information on the egg, the time of year when mating and egg laying occur and estimates of rates of movement and of site fidelity for large individuals. More detailed information on some of the latter aspects, together with some data on the age at first and subsequent reproduction and on movements will be published elsewhere.

Paryphanta b. watti became rare when humans reduced its habitat to a few remnants of original forest at the end of the Aupouri Peninsula during the past 1000 years or so (Gardner and Bartlett 1980; Millener 1981; Goulstone *et al.* 1993; Brook 1999, 2000). During a recent survey, 45 live *P. b. watti* were found by searching through 13 954 m^2 of leaf litter in likely habitat (Stringer and Montefiore 2000). Introduced mammals, particularly feral pigs (*Sus scrofa*), prey on these snails. However, the vegetation where *P. b. watti* still occurs in Te Paki Farm Park has been slowly recovering since it was protected in 1966 and at least one population of snails now appears to be expanding into an area where pig numbers are reduced by frequent hunting (Stringer and Montefiore 2000).

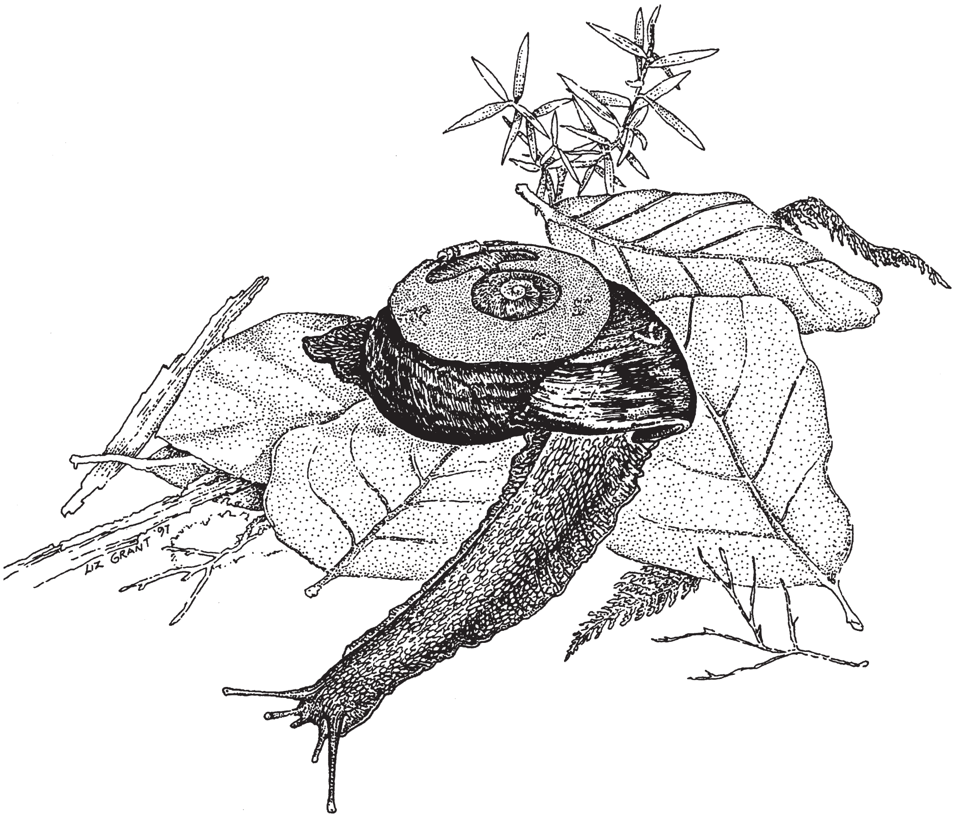

Fig. 2. Diagram of *Paryphanta busbyi watti* with a harmonic radar transponder attached to its shell. The transponder is a C-shaped copper disc with a Z3040 diode (visible at the rear) joining the ends to form a loop. Note the identification number 6 engraved through the periostracum of the shell. (Illustration by E. A. Grant for the cover of *New Zealand Journal of Ecology* **21**(2) (1997). With permission from the New Zealand Ecological Society.)

Materials and methods

Because *P. b. watti* is a protected species, special care was taken to ensure that no eggs or snails were harmed. Three sites in Te Paki Farm Park (Fig. 1) were chosen for the present study after a preliminary survey of the area (Stringer and Montefiore 2000). The snails occurred in relatively high densities (>100 ha^{-1}) in these sites and our activities were limited to areas of less than 2000 m^2 within each site so as to restrict any potential damage to the habitat. Sites A and B were on a ridge running off Te Paki hill and site C was on Kohuronaki Hill (Fig. 1). The exact positions are held by the New Zealand Department of Conservation to protect the snails from shell collectors. Meads *et al.* (1984) have outlined the effects that collectors have had on species of *Powelliphanta* (Rhytididae) in New Zealand.

Twenty six visits were made to the sites between August 1994 and November 2000. Three to six trips were made in January/February, April, June/July, August/September, October and November/December to ensure that samples were taken in all seasons.

Many of the snails were found the first time by searching marked quadrants that were established in each of the three study sites for other purposes (Stringer and Montefiore 2000). These were searched in October/November in most years by sorting through all the litter. Other snails were found for the first time up to 20 m away from these quadrants while searching for snails with harmonic radar transponders attached to them, as described below. Each time a snail was found, the maximum diameter of its shell was taken (Meads *et al.* 1984; Stringer and Montefiore 2000) and a note was made whether the shell was adult or juvenile. The periostracum at the edge of the aperture of adult shells was hard and rolled tightly inward.

The terms 'adult' and 'juvenile' were used following the convention of Johnson and Black (1991) because the snails probably became adult well before they acquired an adult shell with a hardened rolled inward periostome, but it was difficult to recognise when they were sexually mature prior to this (Stringer and Montefiore 2000). In contrast, the periostracum of juvenile snails projects at the edge of the aperture, giving the shell a soft lip (Stringer and Montefiore 2000). Snails found in November 2000 (at the end of the study) were released unmarked, whereas each snail found before this was marked the first time it was found with a unique number. A harmonic radar transponder was also fitted to the snail's shell if this was larger than approximately 20 mm in maximum diameter (Fig. 2). Individual numbers were engraved through the periostracum of shells greater than approximately 20 mm across using a battery operated engraver (Arlec; Dick Smith Electronics, Wellington, New Zealand). The prefixes 'T' and 'K' were added to numbers on shells from sites A and C respectively. The positions where these numbers were located are given in Stringer and Montefiore (2000). Small numbered labels used for marking queen bees (Christian Graze, Weinstadt, Germany) were glued on if the shells were smaller than 20 mm in diameter. Snails with such identification numbers were given the prefix 'red' below. Each shell was first dried with tissue paper and lightly buffed with fine carborundum paper, then the queen bee label was embedded in clear 5-min Araldite (Selleys, Auckland, New Zealand) on top of the protoconch. Descriptions of the harmonic radar transponders and how they were attached to snails are given in Lövei *et al.* (1997) and Stringer and Montefiore (2000). All snails were released exactly where they were found.

Eggs were cleaned carefully with tissue paper to remove as much soil as possible, then their maximum length and width was taken with callipers. Eggs were weighed to the nearest 0.01 g using a portable electronic balance. Particular care was taken not to damage the fine membrane that surrounds newly laid eggs. The eggs were replaced carefully in the holes in which they were found and, when young snails were found in the process of hatching, they were replaced carefully next to the remnants of their eggshells. Soil was placed gently over them without compaction and the area was lightly sprinkled with water to prevent increased desiccation due to disturbance. Half the nests found were left alone after the first time they had been found because of the conservation status of this snail, but every second nest found was dug up each time the area was visited so that the eggs and young snails could be counted, measured and replaced.

Snails with harmonic radar transponders were located again using harmonic radar (Recco Rescue System; Recco AB, Lindingö, Sweden) each time the sites were visited. A grid pattern search was used with passes 3–5 m apart. This heightened the probability that each snail with a transponder in the search area was found (Lövei *et al.* 1997). The use of harmonic radar enabled us to quickly find any snail with a transponder and to narrow down its position to approximately 0.25 m^2 of forest floor. This reduced both the amount of hand searching required to find the snails and the disturbance to leaf litter.

The numbers of snails found at each study site during each field trip were too low to analyse separately, so data from all three sites were combined. All means are given with the SEM. The growth of snails with shells 25 mm or more in maximum diameter was described by a non-linear mixed-effects model fitted using S-Plus 5.1 (Mathsoft, Seattle, USA) for Unix.

Results

Overall, 126 live *P. b. watti* snails were found at the three study sites between August 1994 and November 1999. This includes 51 snails that were juveniles when first found and 13 snails that hatched from eggs (Table 1). Queen bee labels were attached to 33 juveniles and harmonic radar transponders were attached to 31 juveniles and 62 adults. There was no

Table 1. Maximum length (mm) of adult shells of snails fitted with harmonic radar transponders at three study sites in Te Paki Farm Park

Location	Maximum length of adult shells (mm)			
	Site A	Site B	Site C	All sites
Mean	56.10	56.84	56.42	56.51
SEM	0.69	0.45	0.75	0.34
Range	49.6–60.8	53.0–60.5	50.4–61.8	49.6–61.8
n	16	24	12	52

Table 2. Clutch size for *Paryphanta busbyi watti*

	Median	Range	Mean	SEM
No. eggs per nest	2	1-8	3.42	0.70
No. eggs per snail	5	2-8	5.40	1.03

significant difference between the maximum diameters of shells from adult snails at the three study sites (Table 1).

Development of the egg

A total of 41 eggs in 13 clutches produced by eight snails was found. Five of these snails were monitored for 2–5 days and laid an average of 5.4 eggs (Table 2). Two snails remained over their holes for 2–3 days and laid one to two eggs per night, whereas another snail laid one, two and two eggs in three different holes over 4 days. Data on clutch size are minimal because the snails may have laid eggs in other nests before they were found. The mass and size of snails in relation to the eggs they laid are given for three snails in Table 3. These were the only snails that were weighed on consecutive days while they were laying eggs.

One egg was found just after laying by snail T11. The front half of this snail was extended from the shell and the egg was partly enveloped by the ventral surface of the foot. The surface of the egg was smooth, but had a honeycomb pattern of white cells approximately 2 mm in diameter with darker centres. Another 17 newly laid eggs were also found either singly or among clutches of up to eight eggs (Table 2). Each was surrounded by a smooth and slightly adhesive tough white layer, which formed a loose membrane. This outer layer disappeared after 1–2 days, exposing the hard white calcareous shell.

The incubation time is known for only three eggs from different clutches (Table 4). These eggs were found just after they had been laid and the juvenile snails were subsequently found while they were in the process of hatching. Eggshells of mature eggs had a mosaic of fine cracks and broke apart as soon as they were touched. Two of these eggs were found when newly laid beneath snails with transponders and another was found during a casual search for snails approximately 40 m from site B. The eggs hatched 152, 213 and 221 days after being laid on 7 February 1995, 3 February 1996 and 8 April 1996 respectively (Table 4).

There is an indication that eggs may lose weight as they develop and that the rate of weight loss increases as incubation progresses (Fig. 3). However, individual eggs were not marked, so this could not be tested statistically. The mass of one egg that was monitored remained approximately constant during incubation, whereas five other eggs lost weight. Two of the

Table 3. Relationship between the dimensions of the snails (weighed after ovipositing) and the eggs they laid

Snail no.	Max. length snail (mm)	No. eggs measured	Max. length of eggs (mm)	Mass of eggs (g)	Mass of snail after laying (g)	Notes
20	60.18	1	–	1.01	43.5	Laid seven eggs (total 7.61 g) on 1 November 1997
K4	59.38	1	12.62	0.93	29.98	Laid two eggs by July 1997; second egg was not weighed
T25	56.18	5	14.54–14.99	6.26	28.52	Snail was 30.8 g after laying three eggs (3 eggs 3.90 g).

Table 4. Incubation period for eggs and the time spent by newly hatched snails underground in their nests

			Duration (days)			
		n	Mean	SEM	Median	Range
Eggs that died	Maximum time alive	4	135.3	18.7	149	81–163
Eggs that hatched	Known incubation time*	3	195.0	21.6	213	152–221
	Maximum incubation time	14	204.2	6.8	202	140–229
Snails that died	Maximum time alive	4	59.8	19.3	79	2–79
Snails that survived	Minimum time in nest	15	12.1	7.0	0	0–85
	Maximum time in nest	15	95.5	19.96	62	0–200

*Incubation times for eggs from an unmarked snail and from snails 3 and K4.

latter eggs subsequently died. Individual eggs were unable to be identified in the remaining three clutches of five to eight eggs, even though maximum lengths and widths were measured (Fig. 3). These measurements were difficult to take accurately because of the risk of damaging the fragile shell with the callipers. Overall, 82.8% of eggs hatched successfully and, of those that died, one was crushed by cattle and the remaining four died for unknown reasons.

Growth

Only fragmented data were obtained on the growth rate of *P. b. watti* and on the length of time that adults live. After hatching, the snails remained underground in their nests on average for a minimum of 12 days and a maximum of 95 days (Table 4). However, 12 snails were never seen alive because their nests were checked after they had left, so this minimum period is conservative. The minimum periods that the three snails were seen alive in their

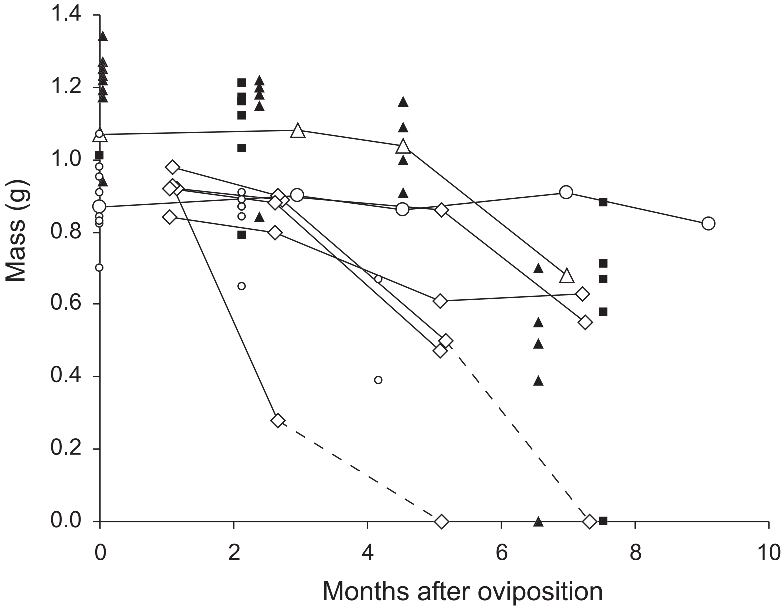

Fig. 3. Changes in the mass of the eggs during incubation. Symbols indicate eggs in the same clutch.

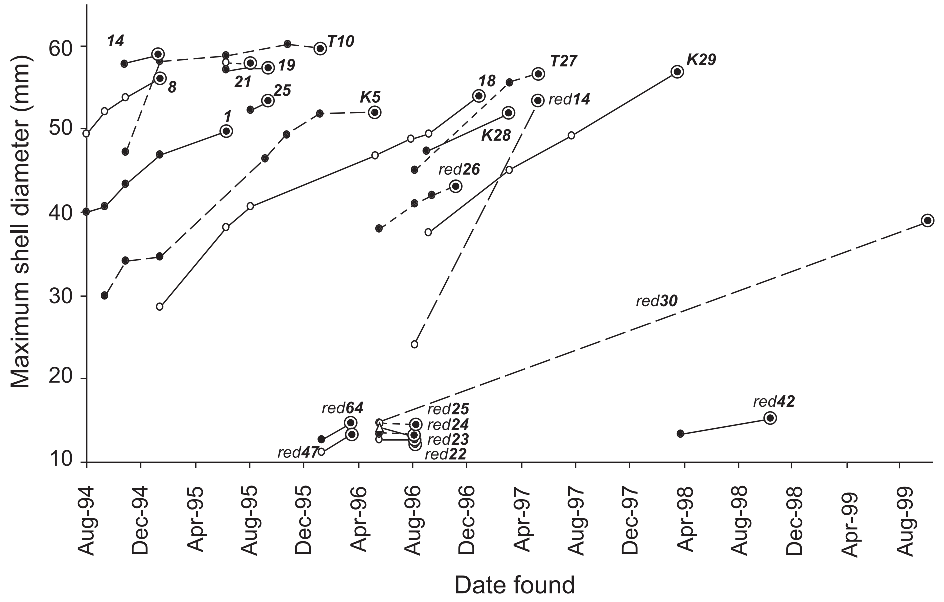

Fig. 4. Growth of juvenile *Paryphanta busbyi watti*. Data are for snails that did not develop adult shells during the study. Labels are identification numbers of snails.

nests were 32, 65 and 85 days. None of the six snails that hatched within the study sites and survived was found again after leaving the nest.

The shells of young snails in nests were difficult to measure because the edge of the aperture was very delicate and flexible. However, the shells of all six snails that were measured in the study sites grew because their apertures extended beyond a slight deformity that marked the edge of the protoconch at hatching. Five of these snails died while underground; however, the shell of one had clearly increased in size, whereas three other shells were approximately the same size and the last shell had, apparently, become smaller. The shell of the snail that survived (red-47) clearly increased in diameter (Fig. 4) and increased in mass from 0.39 to 0.47 g.

Juvenile snails that had left the nest grew at widely differing rates, although they tended to slow down as they approached adult size (Figs 4,5). Only one snail (red-30) was recaptured after being first found with a shell slightly larger than a newly hatched snail. This snail grew from an initial maximum shell diameter of 14.9 mm to 39.1 mm over 1241 days (Fig. 4). Three other snails with initial shell diameters of less than 30 mm and two with shells between 30 and 40 mm in diameter were monitored until they were almost mature. Twenty-four larger juveniles were recaptured at least twice and 13 of these were monitored until they were adults (Figs 4–6). A further 33 juvenile and 28 adult snails were not recaptured.

Estimation of growth rate

The early stages of growth were particularly difficult to estimate because only one snail was recaptured that, when first found, was approximately the size of snails that emerge from nests, one snail was recaptured that was initially one-third grown and another four snails were recaptured that were initially less than two-thirds grown. Thus, there are not sufficient

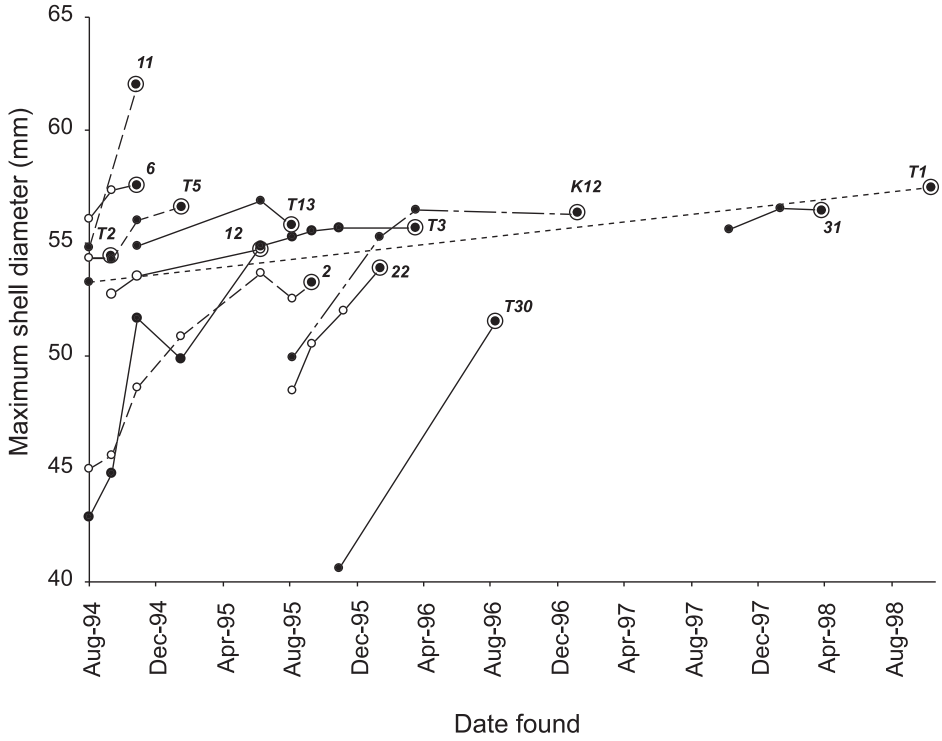

Fig. 5. Growth of snails that developed adult shells. Labels are identification numbers of snails.

data to estimate growth rates reliably for snails until they are approximately three-quarters grown (shells 40–45 mm across). The low recapture rates for small snails resulted because of relying on finding them either by chance encounters or during annual searches of marked quadrants. Only when the snails were large enough to have a harmonic radar transponder attached to their shells were they recaptured more frequently.

Growth through the development period of the juvenile phase (i.e. snails with shells less than 45 mm in maximum diameter) was estimated first. A morphometric change in shell shape occurs at approximately 45 mm in *P. b. watti* (Stringer and Montefiore 2000), which is usually associated with reproductive organ development in other pulmonates and is indicative of a change from juvenile to adult growth (e.g. Williamson 1976; Solem and Christensen 1984; Lazaridou-Dimitriadou 1995). In addition, there is also evidence that the growth rate of juvenile snails may differ from that of adults in some species (e.g. Baur 1989; Lazaridou-Dimitriadou 1995).

Two different methods were used to estimate growth rate. First, the minimum and maximum times to reach a shell size of 45 mm were estimated by adding together the growth curves of each snail, starting with the smallest (red-30) and adding the others in order of their initial size. The growth curve for each snail was started at the point where its size corresponded with the estimated sizes of the respective growth curves of the fastest and slowest snails previously added (Fig. 7). This method gave a minimum of 674 days and a maximum of 1107 days to reach 45 mm. The average developmental time was then estimated by averaging the developmental times of both growth sets (fastest and slowest

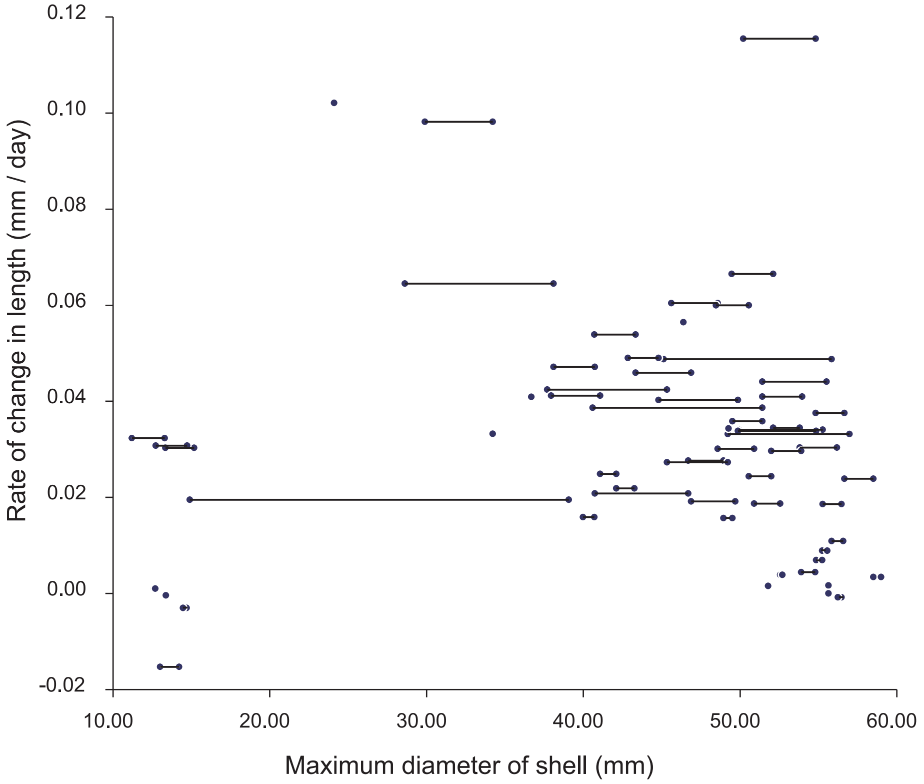

Fig. 6. Growth rates of snails. The daily rate of change in maximum shell diameter is shown in relation to the increase in shell size between recaptures for all snails shown in Figs 3 and 4.

growth patterns). This gave an average time of approximately 910 days to reach a shell diameter of 45 mm (Fig. 8).

The second method was to add the growth pattern of each successively larger snail to the others at the point where its initial size corresponded with the average time taken for all smaller snails to reach this size. For example, the growth patterns of the two smallest snails were added together, as shown in Fig. 7, then the average time was estimated for these to reach the initial size of the third-largest snail. The growth pattern for the latter was then added at this point and the process was repeated for subsequent snails. This method gave an estimated average time of 937 days for snails to reach a shell size of 45 mm (Fig. 8).

Neither of these two methods makes any assumptions about the shape of the growth curve. Figure 6 suggests that, although there is considerable variability, for maximum diameters of approximately 30 mm and above the growth rate decreases with increasing maximum shell diameter, which implies a curve that approaches an asymptote exponentially as described below:

Maximum length l of shell i at time t after marking $= A_i(1 - e^{-B(t+Ti)})$ if the shell has a soft lip at t

or

Maximum length l of shell i at time t after marking $= A_i$ if the shell has a hard lip

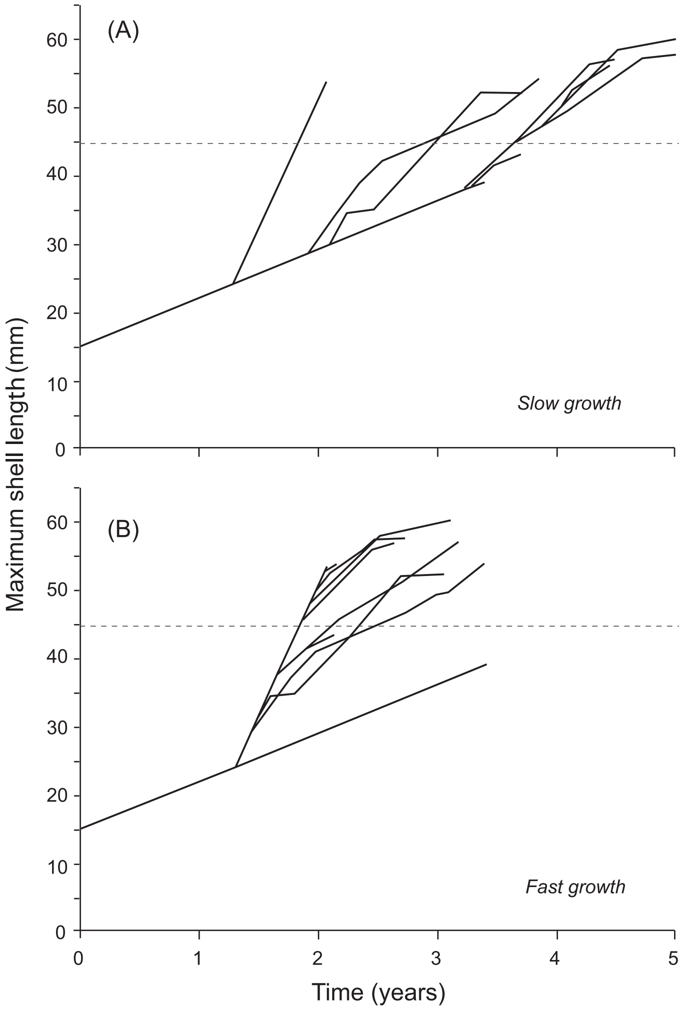

Fig. 7. Growth patterns of *Paryphanta busbyi watti* up to a maximum shell diameter of 45 mm. The growth pattern of each successively larger snail was added at the point where its initial size corresponds to the estimated size that an initially smaller snail had grow to in order to provide (*a*) the fastest overall growth rate and (*b*) the slowest overall growth rate.

where A_i is the ultimate diameter of the i^{th} shell, (estimated mean (± SEM) 55.8 ± 1.2 mm; estimated standard deviation 3.4 mm) and the mean of A_i is the mean maximum diameter of adult shells, B is the growth rate, assumed constant for all snails, of 0.0051 ± 0.0006 and T_i is an adjustment for the age of the i^{th} snail when first marked (estimated mean (± SEM) 318 ± 48 days).

The snails found were assumed to be a random sample from a population of snails over which A_i and T_i vary. The parameter T_i, using a non-linear mixed-effects model, slides the growth curve horizontally for an individual snail to fit the overall curve, thereby aligning the curves for different snails on the one plot (Fig. 9). In practice, this

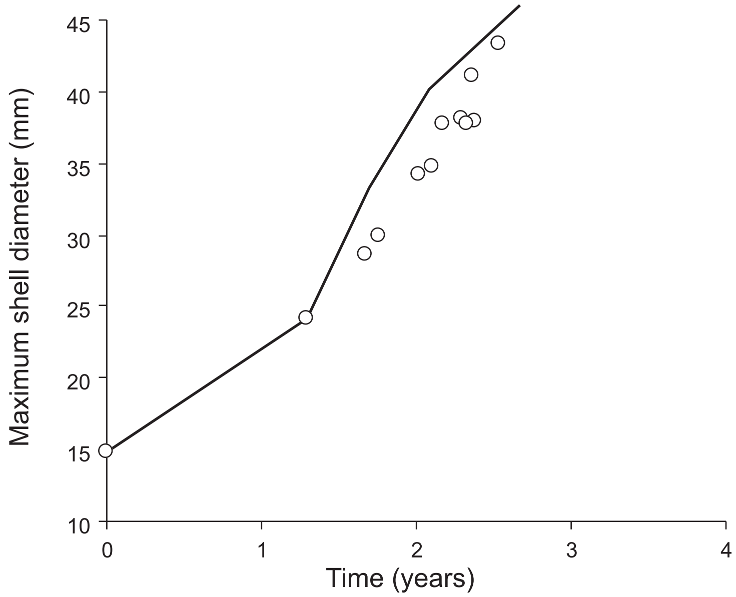

Fig. 8. Average developmental growth patterns of *Paryphanta busbyi watti* up to a maximum shell diameter of 45 mm. The open circles indicate average developmental times from Fig. 7*A*,*B* combined; the solid line indicates average developmental times of snails when the developmental pattern of each successively larger snail was started off at the average time taken for all other snails to reach its initial size.

means that snails with only a few points can be made to fit any curve and five points were needed per snail to enable the model to be fitted. Note that $T = 0$ does not correspond to any particular stage of snail development because the model will not fit earlier growth.

On average, snails 45 mm across took a further 430 days before they acquired adult shells (at Day 746 on the graph in Fig. 9). Overall, the average time taken for *P. b. watti* snails to develop full adult shells was estimated as 3.7 years and they could conceivably grow to this stage anywhere between approximately 3.0 and 4.3 years. This is an estimate of the maximum developmental period because it is based on the times when the shell of each snail was first observed to have a hard aperture lip. The minimal developmental period (the time when each snail was last observed with a soft-lipped shell) is, on average, 0.61±0.26 years (median 0.36 years) earlier than this.

Lifespan of the adult

Ten juvenile snails developed adult shells. Four were subsequently found dead and the others were recaptured at least once before they moved out of the search areas. The periods when the snails were known to be alive are given in Table 5. Another 39 snails were first found with adult shells. Fourteen of these died, another 23 were recaptured at least once before they moved out of the search areas and two were found alive during the last search. The periods that they were known to be alive are given in Table 5.

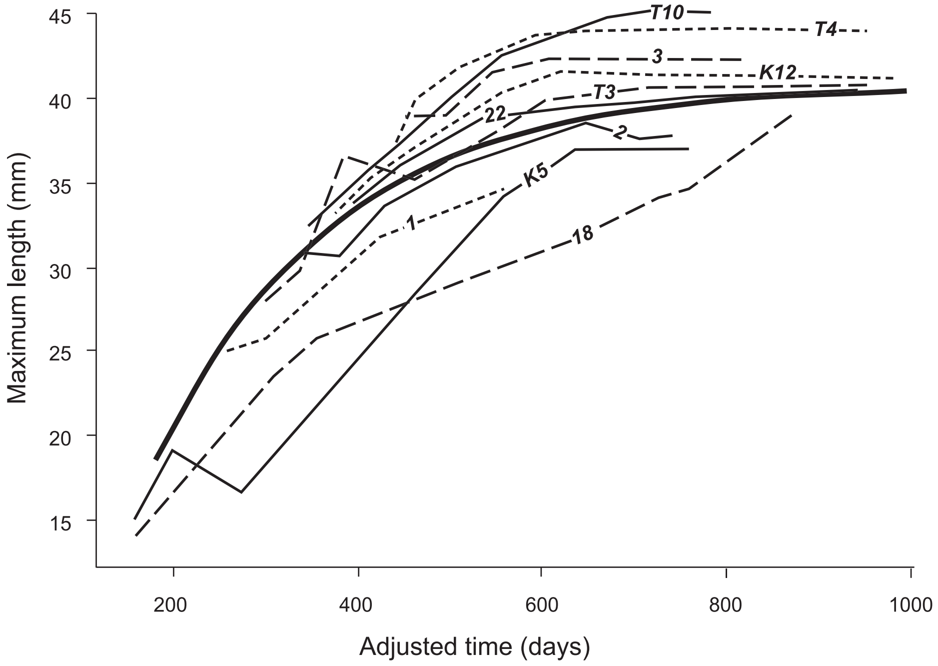

Fig. 9. A non-linear mixed-effects growth model (see text for details) fitted to data for snails that were found five or more times. The thicker curved line shows the growth of an average snail and the lines around it are growth curves for individual snails. Labels are identification numbers of snails.

Discussion

The life history of *P. b. watti* has been sketched out from a series of observations of portions of individual life histories taken from many different snails. This is partly because the snails are both relatively long lived and develop slowly in relation to the time span of our study and partly because of the low numbers of these rare snails that were monitored.

Table 5. Observed life expectancy of adult snails

The minimum period is the time taken from when snails were last seen alive and the maximum period is taken to when they were found dead

Category of adult snail	*n*	Minimum period (years)			Maximum period (years)		
		Mean ± SEM	Median	Range	Mean ± SEM	Median	Range
Found as juvenile, died as adult	4	0.65 ± 0.38	0.60	0–1.42	1.13 ± 0.23	1.19	0.53–1.59
Found as adult and died	12	1.24 ± 0.26	1.04	0–2.35	1.84 ± 0.32	1.71	0.26–3.18
Found as juvenile, lost as adult	6	0.56 ± 0.47	0.58	0.38–2.75	–	–	–
Found as adult, moved out of area	27	1.07 ± 0.19	0.49	0.18–3.19	–	–	–
Found as adult and alive on last search	2	1.97	–	1.55–2.40	–	–	–

Egg development

The incubation period of between 5.5 and 7.5 months for the eggs of *P. b. watti* is close to the 5 months or more reported by Coad (1998) for three eggs of *P. b. busbyi*. These incubation periods are long in relation to most pulmonates that do not have egg dormancy, but they are similar to those of species of *Powelliphanta*, which take 2–6 months (K. J. Walker, personal communication). Species of *Wainuia* (Rhytididae) are much smaller than *Paryphanta* or *Powelliphanta* and take approximately 2 months to hatch (Meads 1990).

Much of the apparent variability in incubation periods for the eggs of *P. b. watti* is due to the long periods between monitoring them. Even the incubation periods for the three eggs that were found in the process of hatching are probably approximate because it appears that these snails hatch gradually as the eggshells progressively crack and break up towards the end of incubation. It is also likely that these snails were released prematurely because the eggshells broke up as they were examined. However, all three snails subsequently survived. Some of the variability in incubation times may be due to differences in the temperatures that the eggs experienced during incubation. Thus, of the three eggs that were observed in the process of hatching, one laid in February (summer) had an incubation period that was 66%–71% as long as the incubation period for eggs laid in July and August. However, our sampling intervals were too far apart to demonstrate this effect with other eggs.

Both O'Connor (1945) and Powell (1979) reported that eggs laid by species of *Powelliphanta* have a glossy membranous 'cuticle' that is a pale buff colour, but they did not observe this in either *Paryphanta busbyi busbyi* and other rhytidid genera. Newly laid eggs of *P. b. watti* do possess such a membrane, although it is white, but it subsequently disappears within a few days to expose the hard calcareous eggshell.

The shells of adult snails account for 19.0%–19.2% of the total mass of the snails (Stringer and Montefiore 2000); therefore, the individual eggs laid by snails 20 and K4 represent 2.8%–3.1% and 3.7%–4.1% of the live mass of these snails before oviposition, respectively. Snail T25 lost 21.5%–23.3% of its original live mass by laying five eggs (Table 3). The average weight loss during oviposition is estimated as 23.2 ± 4.5% from the average masses of complete adult snails (31.60 ± 0.50 g), their shells (6.04 ± 0.32 g) and eggs (1.10 ± 0.05 g), together with the average number of eggs laid (Table 2).

Growth period

Newly hatched *P. b. watti* snails remain underground at the nest site after they hatch and the shells of some of these snails clearly grow while they are underground. In contrast, it is doubtful whether the three newly hatched snails of *P. b. busbyi* observed by Coad (1998) remained underground for long because all had left the nest within 9–18 days after the eggs were observed in the process of hatching. It is not known whether newly hatched snails of *P. b. watti* feed while underground, but no evidence of faecal matter was found with the snails. Thus, the 20% gain in mass that one of them experienced while underground may have been due to water uptake, whereas the increase in shell size could have been supported by reserves within the snails themselves.

What is the advantage for young snails of remaining underground? Juveniles of *Helicella pappi* (Schütt, 1962) also remain buried for some time and Lazaridou-Dimitriadou (1995) suggested that it may be safer for them to do so until environmental factors are suitable for their activity. This may be especially appropriate during the harsh winters that *H. pappi* experience in Greece. Moisture seems to be the most important environmental factor for young *P. b. watti* snails, yet the period these snails remained underground seems unrelated to this. Summer at Te Paki is dry and this is when the area has the lowest number of rain days (approximate summer monthly averages: 91 mm rain, 8 rain days), whereas winter is the wettest season (164 mm rain, 18 rain days; New Zealand Meteorological Service 1983). However, the period spent underground by young snails seems unrelated to whether they hatched in summer, autumn or spring. Possibly, there is some other protective advantage for young *P. b. watti* remaining underground yet to be discovered.

Stringer and Montefiore (2000) found that no size cohorts were evident among juvenile snails because of the relatively low numbers of snails found and because *P. b. watti* has widely overlapping generations. Therefore, Stringer and Montefiore (2000) were unable to estimate the growth period by following size cohorts, as has been done for other snails (Williamson 1976; Johnson and Black 1991 and references therein). Attempts were not made to estimate growth rates by using annual growth deformities on the shell because these were often hard to recognise and many shells lacked them altogether. This method may also be unreliable, as discussed below. The only data that were collected for estimating the growth period are portions of growth patterns from different snails.

The two methods used to estimate the time for snails to reach a maximum shell size of 45 mm gave similar results. However, one method indicated a gradual decrease in growth rate with increasing size, whereas the other method indicated a gradual increase in growth rate with increasing shell size up to 45 mm. The first pattern appears to correspond with the growth pattern that Coad (1998) found for *P. b. busbyi* at Trounson Park. This is the usual growth pattern for most gastropods (Wilbur and Owen 1964). Coad (1998) reported that the smallest snails (16 mm) had the fastest growth rate and that growth rate progressively decreased with increasing shell size. Coad's (1998) data set ($n = 79$) was larger than the one presented here and included six snails with shells between 16 and 30 mm across and another 27 snails with shells up to 30 mm across. Therefore, Coad's (1998) estimates of overall growth are correspondingly better than ours. Despite this, we believe that the growth rates of small *P. b. watti* may very well be depressed because Te Paki is drier (lower rainfall, fewer rain days, lower average relative humidity and higher average temperature; New Zealand Meteorological Service 1983) than Trounson Park. Thus, small *P. b. watti* snails would experience fewer nights that were moist enough for them to be active compared with young *P. b. busbyi*. Another possible indication that the environment at Te Paki is harsher than at Trounson Park is that young *P. b. watti* experience a much higher mortality rate than young *P. b. busbyi* at Trounson Park (Stringer and Montefiore 2000).

Stringer and Montefiore (2000) gave a rough estimate of 2.6–3 years for *P. b. watti* to grow to maturity. However, the three smallest snails they found had shells 24, 29 and 30 mm in diameter, so they had to base their growth estimate on the assumption that snails smaller than this grew at the same rate as the initial growth rate of these three snails. This was justified by Coad's (1998) observation that the growth rate of *P. b. busbyi* was fastest when it was small (shell diameter of 15 mm) and decreased with increasing shell diameter. Coad (1998) estimated that *P. b. busbyi* takes approximately 3 years to grow to the stage where its shell has a hard lip, whereas Dell (1955) estimated that *P. b. busbyi* takes 7 years to reach full adult size from an examination of growth ridges on the shells. Dell (1955) assumed that these ridges were caused by annual dry periods during the summers and estimated that the shells increased in diameter from 4 to 12 mm each year, but this is a low annual increment in relation to Coad's (1998) observed increases of approximately 15–19 mm each year. However, Dell's (1955) collection site was open scrub, where there were probably high temperatures and a lack of moisture during summer. The use of annual growth rings to estimate the age of pulmonates can also be unreliable for a variety of reasons (see Comfort (1957), Oosterhoff (1977) and Williamson (1979) for a discussion), even though other authors have used this method to estimate pulmonate age (Pollard *et al.* 1976; Oosterhoff 1977).

Overall, the growth rates of *Paryphanta* seem relatively fast in relation to other large rhytidid snails that occur further south in New Zealand. The shells of three *Powelliphanta hochstetteri obscura* (Beutler, 1901) increased in diameter by approximately 1.5 mm per year in captivity (Meads *et al.* 1984) and Devine (1997) found that the shells of marked individuals of *Powelliphanta traversi traversi* (Powell, 1930) increased, on average, by 2.6 mm per year (range 0.5–10.7 mm) in forest near Levin. In contrast, species of *Wainuia* reach adult size in approximately 6–12 months (Meads 1990), although they only grow to maximum shell diameters of 11.5–38 mm (Efford 1998). Compared with pulmonates that live elsewhere in temperate regions, a growth period of 3–4.6 years seems higher than average, but not by any means extreme. Most have annual or biennial life cycles if they do not undergo periods of dormancy. Larger tropical pulmonates may mature within 1–3 years (Comfort 1957; Peake 1978; Mead 1979; Cain 1983; Solem and Christensen 1984). Exceptions include medium-sized camaenids from Puerto Rico and small Hawaiian achatinellids, which take 3–6 and 4–7 years, respectively, to reach adult size (McLauchlan 1951; Heatwole and Heatwole 1978; Hadfield and Mountain 1980; Hadfield 1986).

In pulmonates, a wide variation in the size of shells of mature snails (e.g. Oosterhoff 1977; Vermeij 1980; Kemp and Bertness 1984; Johnson and Black 1991) and in growth rate (e.g. Heatwole and Heatwole 1978) is quite usual. Also, it is not unusual that faster-growing individuals may often become larger adults (Wolda 1970) and this appears to hold for *P. b. Watti* (Fig. 9). The growth rates of pulmonates, as well as the final adult size of their shells, can be affected by many environmental factors, but moisture seems to be the most important factor at times when the snails are not in cold-induced dormancy. Lack of moisture, in particular, may reduce growth indirectly by preventing the snails from being active (Potts 1975; Oosterhoff 1977; Solem and Christensen 1984; Goodfriend 1986; Johnson and Black 1991; Lazaridou-Dimitriadou 1995). Differences in growth rate and the resulting changes in adult size could affect both juvenile mortality rate and reproductive rate and, thus, affect population density (Oosterhoff 1977). Therefore, such variations in growth rates may have far-reaching consequences for population dynamics and evolution (Heatwole and Heatwole 1978)

Total lifespan

Adult *P. b. watti* are known to be able to live at least 4.1 years, although the average time all adult snails were monitored (including those that died) was 1.1 ± 0.1 years. When this is added to the average growth period, this gives an average lifespan for *P. b. watti* after hatching of approximately 4.8 years. This estimate is conservative because it includes the lifespans of those snails already adult when first found and the adult periods used are minima (time to last found alive). In contrast, by using the estimated maximum growth period and the maximum known adult period, an individual snail could, conceivably, live for at least 8.8 years. Such a lifespan seems relatively short in comparison with the suggestions proposed by Powell (1946) that there are at least 15 years between generations of *Powelliphanta* and by Meads *et al.* (1984) that larger species of *Powelliphanta* (60–70 mm) may live 40 years or more. In relation to other temperate-zone pulmonates, the lifespan of *P. b. watti* seems to be long, but not extreme, because larger temperate-zone pulmonates usually have a lifespan of several years and some can live 10 years or more (Comfort 1957, Staikou *et al.* 1988; Lazaridou-Dimitriadou 1995).

Overall, *P. b. watti* are large snails that are relatively long lived, are slow developing and probably have a low reproductive rate. Such life history traits are commonly associated with the absence of predatory mammals and are among the features that characterise the New Zealand fauna (Daugherty *et al.* 1993).

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