MORPHOLOGY, ECOLOGY AND DEVELOPMENT OF LEIOPELMATID FROGS (*LEIOPELMA* SPP.), IN WHAREORINO FOREST, NEW ZEALAND.

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ABSTRACT

Leiopelma archeyi, *L. hochstetteri* and a previously unrecognised leiopelmatid frog, Type A, occurred sympatrically in a small area of Whareorino forest when this was intensively surveyed between June 1996 and July 1997. *L. archeyi* was found predominantly along ridges. Large specimens were mostly under rocks whereas small ones were in grasses. This association was shown to be significant using canonical variate analysis. All *L. hochstetteri* were under rocks, logs or grasses and were associated with streams. Type A frogs were in small rock piles on ridges. Type A frogs were shown to be distinct from both *L. archeyi* and *L. hochstetteri* by canonical variate analysis. They could also be distinguished by morphological features. Overall they resemble *L. hochstetteri* but have less webbing between the toes, a distinct paratoid gland and a stouter body. These differences, together with their sympatry with *L. archeyi* and *L. hochstetteri*, indicate that the Type A frog is possibly a new species. It appears to be closest to the extinct *L. markhami*.

Two clutches of *L. archeyi* eggs were reared artificially at 11°C and 15°C. Ten hatched but one died 10 days later. The tails took 48-75 days to be absorbed. Parentage and temperature significantly affected the rate of tail reduction.

The gut contents of 8 frogs indicated that they eat a wider range of invertebrates than previously recorded. Their diet includes, in order of frequency of occurrence, Acari, insect larvae, Collembola, Amphipoda, Coleoptera, Araneae and Diptera. Unusual items were two diplopods, one ant and one gastropod. Large frogs with teeth ate a larger proportion of sclerotized prey. Small frogs lacked teeth and ate mostly small soft bodied invertebrates. However, they also took a wider range of prey. Potential prey was sampled using pitfall traps. Examples of all of the prey were caught but too few frog guts were analysed to indicate any relationship between pitfall trap catches and frog diet.

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Chapter 1

General Introduction - Native New Zealand Frogs

1.1 Introduction

New Zealand is a series of islands which separated approximately 80 million years ago from an ancestral continental landmass 'Gondwana' (Skipworth 1974, Stevens *et. al.* 1988). Due to this separation, the flora and fauna of these islands evolved in relative isolation, without mammalian predators, and hence many species developed into distinctive life forms, for example species of Weta (*Deinacrida*), the Kiwi (*Apteryx* spp.), the Tuatara (*Sphendon* spp.), and the native frogs (*Leiopelma* spp.) (Cooper and Millener 1993).

New Zealand has four extant species of endemic frog, *Leiopelma hamiltoni* McCulloch , *L. archeyi* Turbott, *L. hochstetteri* Fitzinger, and *L. pakeka*, (Bell, Daugherty and Hay 1998) which belong to the Leiopelmatidae. Leiopelmatid frogs are some of the most ancient of all extant frog species (Green and Cannatella 1993) because they retain many primitive anuran characteristics such as free ribs (not fused to vertebrae) and two tail-wagging muscles (m. pyriformis & m. caudalipuboischiotibialis) in adults. They also have amphicoelous vertebrae and nine presacral vertebrae and they lack the ear drums and vocal sac present in many other frog species. Despite the latter, leiopelmatids can produce chirps or squeaks when stressed or alarmed. Chirps have also been associated with breeding activities (Bell 1978a).

Many of the primitive characteristics seen in *Leiopelma* are shared with one other ancient North American frog, *Ascaphus truei* Fejervary. *Ascaphus* and *Leiopelma* historically were once placed together in the family Leiopelmatidae (Duellman and Trueb 1986), but genetic studies have recently led to their separation into Ascaphidae

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and Leiopelmatidae (Green *et. al.* 1989). The only other family of primitive frogs, the Discoglossidae, is not closely related to either of these (Zug 1993).

Leiopelmatid frogs are cryptic and nocturnal, and they retreat to moist sites under rocks and logs in forests during daylight. Breeding occurs in *L. hamiltoni* , *L. archeyi* and *L. pakeka* on land, where large eggs are laid in moist sites under rocks and logs, and tadpoles undergo intracapsular development to hatch as tailed froglets. Parental care is displayed by male frogs who brood the clutches of eggs till they hatch, and then permit the young to complete metamorphosis their backs (Bell 1985a). In *L. hochstetteri,* however, males have been found in association with egg clutches (Bell 1982b, 1985a) but they do not brood them and the tadpoles appear to have a brief aquatic phase. Such an adaptation to terrestrial living is generally considered typical of species that have had a long period of evolutionary development (Crump 1996).

The four extant species of *Leiopelma* are briefly described below.

1.2 Extant New Zealand leiopelmatids

1.2.1 *L. hamiltoni,* McCulloch 1919

Common name: Hamilton's frog

This is a totally terrestrial frog with a maximum snout-vent length of 50 mm. It was first discovered on Stephens Island, Cook Strait, in 1915, although it was not collected for description till 1919 by Mr H. Hamilton (Robb 1980). *L. hamiltoni* once existed throughout New Zealand and sub-fossil remains have been found at Punakaiki, Patarau, Takaka, and Mt. Owen in the South Island, and at Puketoi Range, Patoka and Waitomo in the North Island (Worthy 1987b) (Figure 1.1). However, *L. hamiltoni* now persists only on a small area of Stephens Island (Figure 1.2) known as the 'frog bank'. It is listed as '*endangered*' (Groombridge 1993) or vunerable (Bell 1997) and it is placed in 'Category A' of New Zealand's most threatened plants and animals (Molloy and Davis 1994). An estimated 150 - 200 individuals presently exist (Newman 1996). Breeding takes place from October to December when 2 to 19 eggs are laid under rocks where they are brooded by a male frog.

1.2.2 *L. archeyi,* Turbott 1942

Common name: Archey's frog

Often described as a smaller neotenic form of *L. hamiltoni* (Stephenson 1961), this frog has a maximum snout-vent length of 43.7 mm (Thurley and Bell 1994) and can be found in forest remnants throughout the Coromandel Ranges as well as Whareorino forest in the North Island (Figure 1.2). The past distribution of *L. archeyi* is unknown as sub-fossil material from this species has yet to be found (Worthy 1987b). It is classified as 'Category B' (Molloy and Davis 1994), and of '*low risk*' (Groombridge 1993). Recently Bell (1997) suggested that it should be classified as low risk - not threatened.

L. archeyi is a terrestrial frog which commonly dwells under rocks and logs but it can also use vegetation as a daytime retreat site (Thurley & Bell 1994). Individuals range in colour from bright green to brown, and often have bright orange[1] flashing on their legs. The eggs are laid in clutches of 1 to 13 eggs, under rocks or logs from September to November (Bell 1985a) and are brooded by an adult male until metamorphosis has been completed (Bell 1982a, 1985a).

1.2.3 *L. hochstetteri,* Fitzinger 1861

Common name: Hochstetter's frog

L. hochstetteri was first discovered in gold diggings in the Coromandel Ranges in 1852 (Thompson 1853), but formal description did not occur till much later (Fitzinger 1861). This is the only endemic semi-aquatic frog in New Zealand and it is found in association with streams throughout the top third of the North Island (Figure 1.2). Sub-fossil remains have also been found at Takaka Hill, Patarau, Karamea, and Punakaiki in the South island as well as at Waitomo and Hawkes Bay in the North Island (Worthy 1987b) (Figure 1.1). This frog is not listed as '*threatened*' and is considered to have a low risk of extinction and of least concern (Groombridge 1993, Bell 1997). However *L. hochstetteri* is at risk from further habitat degradation and has a 'Category B' listing in New Zealand (Molloy and Davis 1994). Adult *L. hochstetteri* have a snout-vent length of up to 50 mm are usually a brown colour although dark green morphs have been found (Whitaker 1996, and *pers. obs.*).

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[1] Thurley (1996) recognised this colour as 'pink'

Being semi-aquatic, this species is seldom found far from water (Stephenson and Stephenson 1957, Bell 1978a). Breeding sites are usually under rocks or vegetation in or around water seepages (Bell 1982a, 1985a). Clutch sizes range from 10 to 22 eggs which hatch as tailed swimming larvae. As previously stated, males may be found in association with an egg clutch but they do not incubate them as the other species do. Larvae do not, therefore, metamorphose on the back of the male, but disperse soon after metamorphosis (Bell 1985a).

1.2.4 *L. pakeka* n.sp. (Bell, Daugherty and Hay 1998)

Until recently the Maud Island and Stephens Island frogs were considered to be the same species. However, the Maud Island frog has recently been described as a separate species based upon electrophoretic evidence (Bell, Daugherty and Hay 1998).

L. pakeka grow up to 50 mm in snout-vent length, and are light to dark brown in colour. During November and December, they lay their eggs under rocks or logs in clusters of 7 to 19 eggs. These later hatch as tailed froglets (Bell 1995).

This species is currently known from a single population in the Malborough Sounds (Figure 1.2) and at present is listed as vunerable, with a New Zealand category B ranking, which may change now that it has been recognised as a distinct species which is known from only one population (Bell 1997, Bell *et. al.* 1998) .

Three other species of *Leiopelma*, *L. markhami* Worthy, *L. waitomoensis* Worthy and *L. auroraensis* Worthy are known only from sub-fossil remains and are therefore considered extinct (Worthy 1987a, Newman 1996) (Figure 1.1). Introduced mammalian predators and habitat fragmentation are likely reasons for both the decline of extant leiopelmatid species and the extinction of others (Worthy 1987b, Newman 1996).
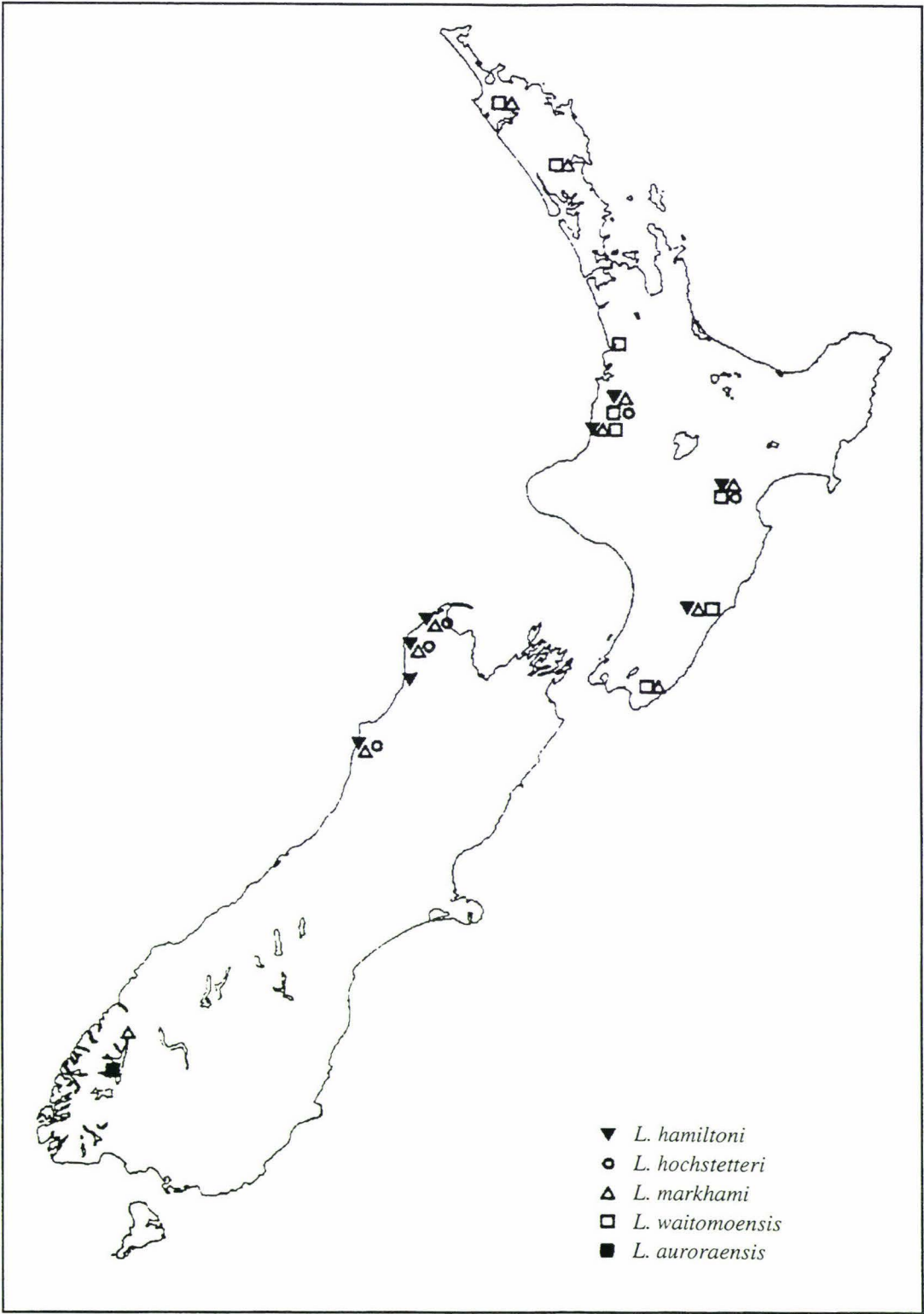
Figure 1.1 Sub-fossil distribution of leiopelmatid frogs in New Zealand
         After Newman (1996).
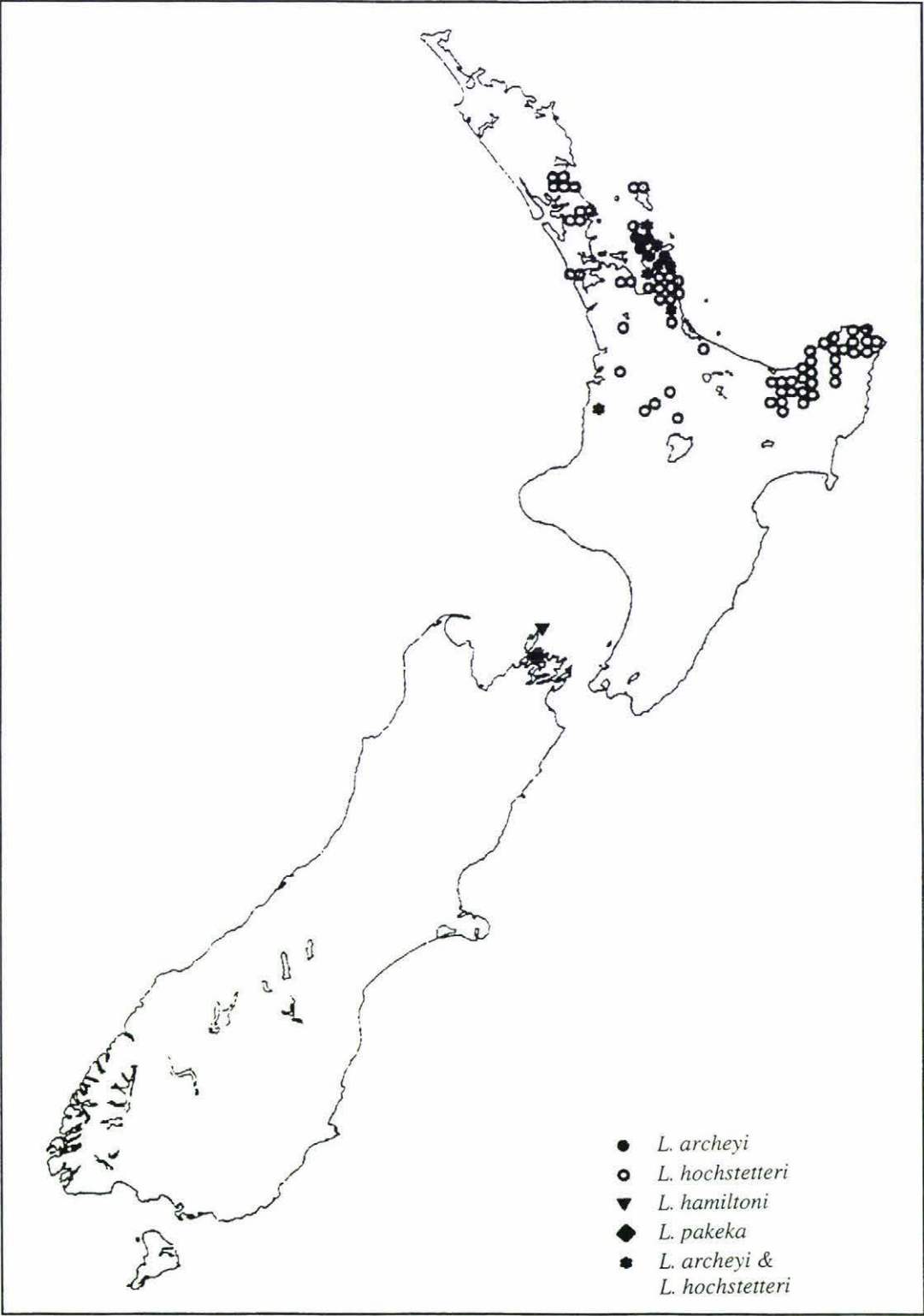
Figure 1.2 Present distribution of leiopelmatid frogs in New Zealand

After Newman (1996).

1.3 Previous Research

Early research on leiopelmatids was centered upon anatomical or taxonomic descriptions (Archey 1912, McCulloch 1919, Turbott 1937, 1942). This has recently undergone revision, particularly in regard to the relationship of the New Zealand frogs with their closest living relative *A. truei* (Green and Cannatella 1993). Terrestrial egg laying and larval development of native frogs have also attracted much interest, and several authors have described aspects of their general population ecology (Stephenson 1951, 1955, 1961, Barwick 1961, Robb 1980, Newman 1977a, 1990).

More recently genetic, karyotype and isozyme studies have been carried out on intra- and inter-population diversity (Stephenson *et. al.* 1972, 1974, Daugherty *et. al.* 1981, Green *et. al.* 1984, 1988, *et. al.* 1989, *et. al.* 1993, 1994) and physiological studies, particularly of water balance have also been published (Cameron 1974, Cree 1985a).

B.D. Bell has, for over 20 years, been the driving force in understanding the ecology of all four species of leiopelmatid frog. His published works include descriptions of larval development, reproduction, morphological variation, population demographics and conservation status of all species (Bell 1977, 1978a, 1978b, 1982a, 1982b, 1985a, 1985b, 1994, 1996, 1997, Bell *et. al.* 1998) and various aspects of these studies will be referred to in detail in the following chapters. B.D. Bell has also supervised a number of recent studies including analysis of diet in *L. hamiltoni* (Kane 1980); osteological comparisons and sub-fossil studies (Worthy 1986), population dynamics of the Maud Island frog, now *L. pakeka* (Bell 1995); the effect of 1080 on native frog populations (Perfect 1996); and the original survey and description of native frogs in Whareorino forest (Thurley 1996). This last study in particular will be referred to in the following chapters.

In 1996 the 'Frog Recovery Plan' for the Department of Conservation (DoC) was published. Prepared by D.G Newman, this document included a review of recent research and prioritised the needs for future research and management for all remaining frog populations (Newman 1996).

There remains, however, a need for more comprehensive description of leiopelmatid frog populations and their ecological relationships, particularly in Whareorino forest where the frogs have only relatively recently been discovered. This, and other mainland populations of native frogs, are currently under threat from predation and habitat deterioration, and detailed research into their ecology, demography and captive management is urgently needed (Newman 1996).

Most previous studies focused on large scale surveys of frog populations, but in contrast, my study concentrated on one limited area of Whareorino forest so that fine scale interactions between conspecifics and potentially related individuals could be examined closely.

My study also explored aspects of the development, early growth, population dynamics, inter- and intra-specific morphological variation, diet and habitat selection of leiopelmatid frogs which occur sympatrically in Whareorino forest. It is the first study in which multiple features of the ecology of sympatric native species have been assessed in such detail.

At Whareorino forest, two sympatric species of leiopelmatid frog, *L. archeyi* and *L. hochstetteri*, have been described (Bell 1993, Thurley and Bell 1994, Thurley 1996).

However, during this study a third group of unidentified frog was found within the main study site. These frogs are similar in appearance to *L. hochstetteri*, but have more robust limbs, are more terrestrial and have a distinct paratoid ridge similar to *L. archeyi*. These frogs are referred to in the following chapters as 'Type A' frogs.

1.4 Aims of this study

The primary aim of this study, is to closely examine the ecology of the native frogs in a small area of Whareorino forest, in an attempt to better understand the general ecology of leiopelmatids.

The findings of this thesis are presented in six chapters that follow.

Chapter 2 presents the results of surveys of native frogs within Whareorino forest. These results include data on the species present, their size distribution and their dorsal and ventral colours. Comparisons with previous research on leiopelmatid frogs are made.

Chapter 3 examines the habitat preferences (i.e. daytime retreat site selection) of native frogs and the relationship between retreat site to frog size is shown for *L. archeyi*.

Chapter 4 considers the complex morphology of *L. archeyi*, *L. hochstetteri*, and Type A individuals in Whareorino forest, and the variation which occurs between each. The relationship between intra-specific morphological variation and habitat selection is further explored for *L. archeyi* and the possible relationship of Type A frogs to both *L. archeyi* and *L. hochstetteri* is discussed.

Chapter 5 examines the captive development of *L. archeyi* larvae and their growth to juveniles. Techniques used in incubation and rearing are documented, and field observations of parental care are also included.

Chapter 6 describes the prey selection by leiopelmatid frogs in Whareorino forest. Comparisons of data on prey selection are made with the prey types and sizes available, as inferred by pitfall trap samples taken from Whareorino forest. Comparisons with the diet of other ground dwelling species of frog are also made.

Finally, *Chapter 7* documents the survey procedures and handling protocols used throughout this study. Key management issues for mainland frog populations, in light of the results from this study are discussed.

1.5 The study site - Whareorino forest

1.5.1 The study site

Whareorino forest is a designated Stewardship Area under the Conservation Act 1987. It is located on the western coast of the North Island approximately 50 km West-South-West of Te Kuiti (Figure 1.3). This study was concentrated in a small area of hillside where *L. archeyi*, *L. hochstetteri* and Type A frogs were relatively common. The exact location of this area can be obtained from the author, or Mr. C. Smuts-Kennedy, Dept. of Conservation, Hamilton. Research was conducted in three sites with most of the work concentrated at and immediately around an area termed P grid (680 m a.s.l.).

P grid (40 x 60 m), was divided into 24 10 m x10 m blocks that were repeatedly searched for frogs throughout the study. The location of all frogs found was mapped. Intermittent data were also obtained from individuals in areas adjacent to P grid, the locations of which can also be obtained from the author, or Mr. C. Smuts-Kennedy, Dept. of Conservation, Hamilton.
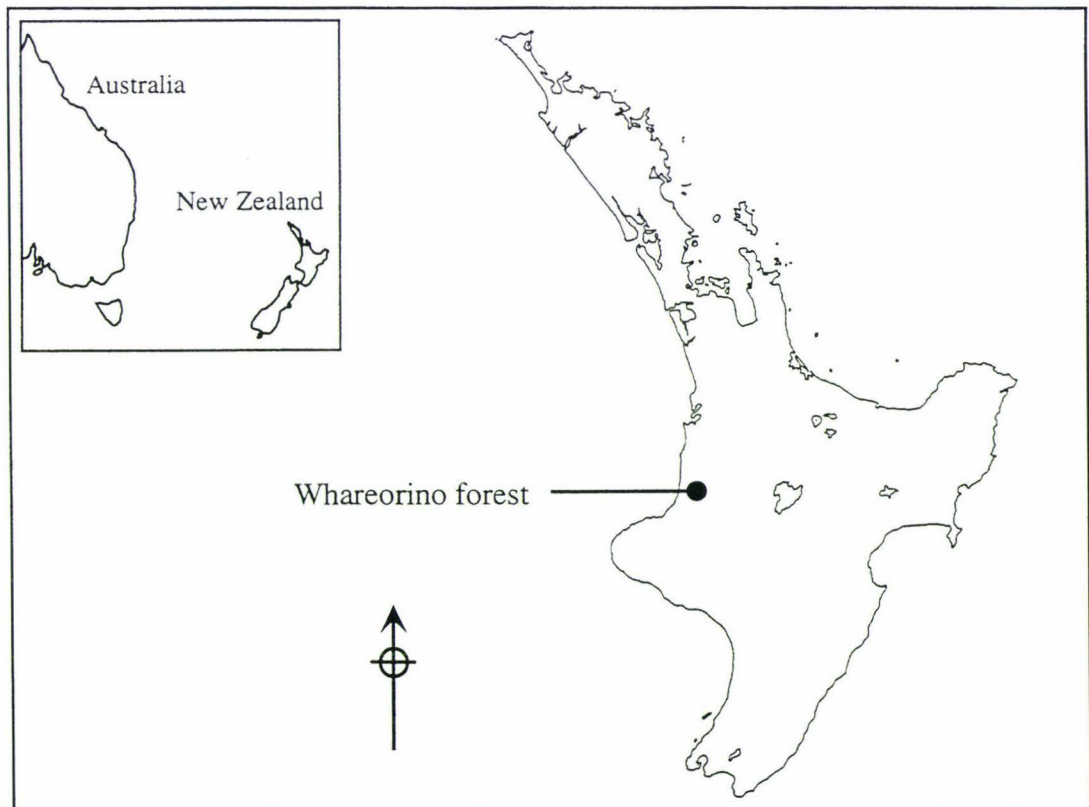
Figure 1.3 Location of Whareorino forest, Northern King Country, New Zealand.

1.5.2 Climatic variables

The climate of the northern King Country is fairly mild with an annual average temperature of 13°C (Ward 1985). It is typified by warm humid summers, mild winters, and an annual rainfall of 1500 to 2500 mm (Ward 1985). TFA Thermo-hygrometers were placed at two locations: P grid and stream 1, in the forest to measure ambient temperature, and humidity between samples.

Temperature

The limits of accuracy for each meter were - 15°C - + 49.9°C. The temperature was found to be consistently within this range. Temperature increased over summer (December - February) and decreased during winter (June - August) (Figure 1.4). The average maximum temperature was 15.2°C ± 0.99 [± S.E.], range 19.8°C to 9.3°C, and the average minimum temperature was 5.2°C ± 0.74, range 8.4°C to -1.6°C.

Humidity

Relative humidity (RH) readings were accurate between 30% and 90% but readings in Whareorino forest were commonly above 90 %. All such high readings were recorded as 95+ % humidity. Humidity was constantly greater than 90 % from April to September (Figure 1.5A), and varied between 95+ % and 68.5 % between September and April. Even during the summer months, December to February it was seldom less than 75 %. The forest atmosphere and environment was, therefore, moist most of the year.

Rainfall

Rainfall was measured using a Nylex® 1000 rain gauge, placed in a clearing in the forest. This was checked regularly to give a total monthly rainfall. The gauge was placed at a relatively low altitude (c 500 m a.s.l.) on the eastern edge of the forest, where there was little chance of accidental frog capture in the gauge. However this gauge only gave a value for this one particular point in Whareorino forest and it should be recognised that rainfall will vary in volume and intensity throughout a forest, especially with changes in altitude, hence this data may not reflect the actual rainfall at the study site, P grid.

Monthly rainfall is shown in Figure 1.5B. Most rain fell in August, November and April (242, 242.2 & 239 mm respectively) and the least fell in July (41 mm). Generally, however, rainfall was highest during late winter and spring (August to November) and lowest in late summer - early autumn (February and March).

The total rainfall recorded for the year July 1996 to June 1997 was 1788.88 mm.
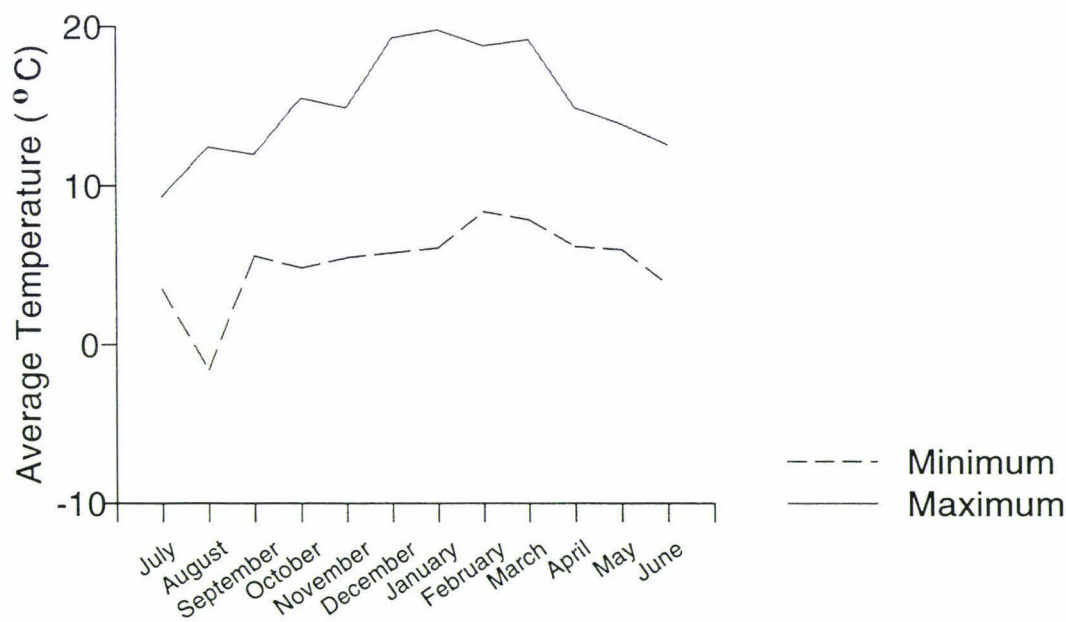
Figure 1.4 Average daily maximum and minimum temperature, for each month, recorded in Whareorino forest from July 1996 to June 1997.

A.

Month (1996-1997)
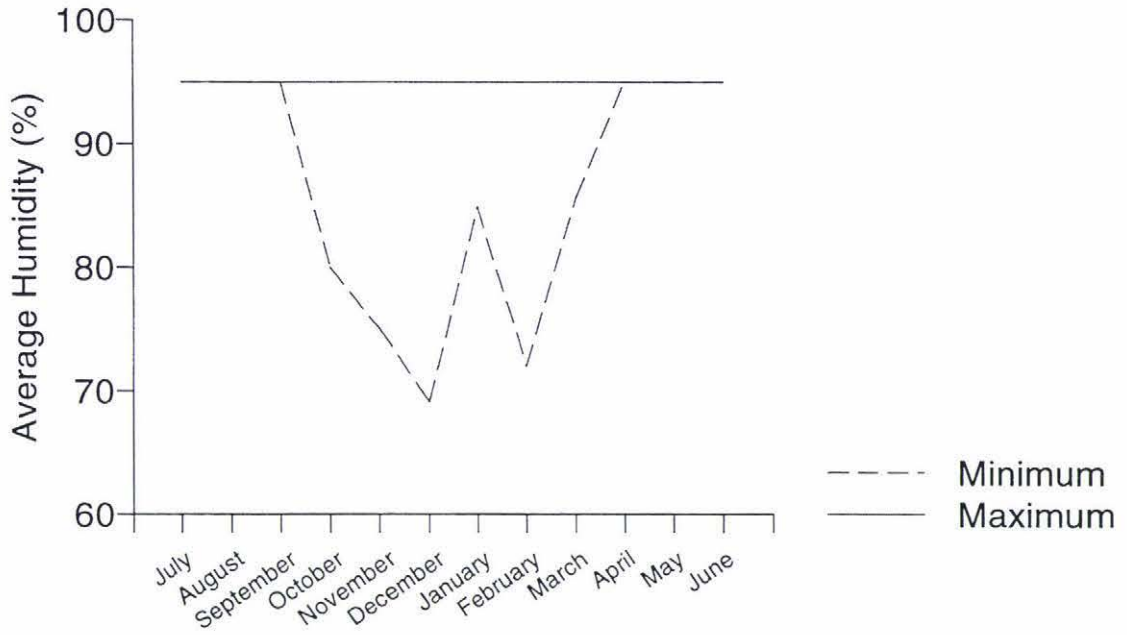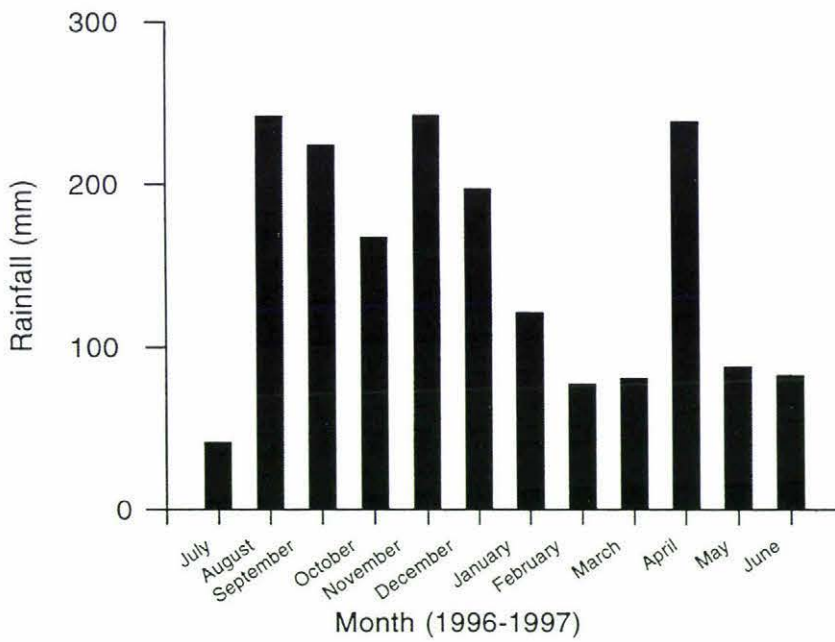
B.

Figure 1.5 (**A**) Average daily maximum and minimum humidity recorded for each month and (**B**) total rainfall per month in Whareorino forest from July 1996 to June 1997.

1.5.3 Substrate, Plant Cover and Mammals.

Sedimentary rocks, mudstones, sandstones and limestones form the principal components of the underlying strata of this area (Owen 1958). The forest floor of the study sites is characterised by soft soil and loose sliding surface rocks. The steepness and marked instability of the country has prevented development of the land for agriculture (Plate 1.1A).

Whareorino forest is a remnant broadleaf-podocarp forest which ranges in altitude from 300 m a.s.l. to the highest point of Maungamangero at 806 m a.s.l. At lower altitudes tree ferns (*Cyathea* spp. & *Dicksonia* spp.) were common. Broadleafs included Horopito/Pepper tree (*Pseudowintera* spp.), Tawhero & Kamahi (*Weinmannia* spp.) and species of *Quintinia.* Tawa (*Beilschmiedia tawa*), Toro (*Myrsine salicina*) and Rimu (*Dacrydium cupressinum*) were also present. *Quintinia* spp. and *Dracophyllum* also occurred at higher altitudes (Thurley 1996).

The secondary canopy is sparse in most places because of heavy browsing by introduced mammals such as possums (*Trichosurus vulpecula*) and feral goats (*Capra hircus*). However at lower levels rice grass (*Microlaena avenacea*), hook grass (*Uncinia uncinata*), tree fern, and button fern (*Pallaea rotundifolia*) are common(Plate 1.1B), as well as mosses such as *Dawsonia superba*, and liverworts. The forest supports a number of introduced mammals which indirectly, by herbivory or directly through predation, are likely to affect native frogs. These include possums, feral goats, feral pigs (*Sus scrofa*), rats (*Rattus rattus*), mice (*Mus musculus*), stoats (*Mustela erminea*) and feral cats (*Felis catus*) (Thurley 1996, *pers. obs.*).

The field work for this thesis began in April 1996 and was completed in July 1997 and what follows is a complete description of the methodology, results and conclusions of this study.

A.

B.

Plate 1.1 Whareorino forest, New Zealand. **A**: broadleaf-podocarp forest;
B: understorey vegetation.

CHAPTER TWO-

LEIOPELMATID FROGS OF WHAREORINO FOREST
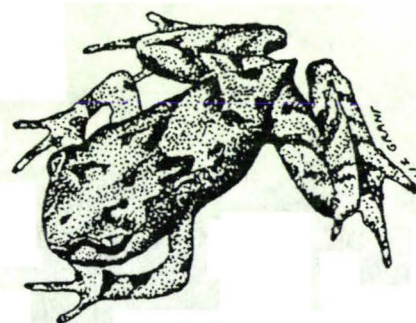
Chapter 2

Leiopelmatid Frogs of Whareorino Forest

2.1 Introduction

In 1993 Conservation Corps workers on track maintenance in Whareorino forest made the first recorded discovery of a native frog for the area (Bell 1993, Thurley and Bell 1994). Soon after, two species of *Leiopelma*, *L. archeyi* and *L. hochstetteri*, were identified after a broad survey of the forest had been undertaken (Thurley 1996). These were found to be coexisting sympatrically in an area of approximately 6 km². This location extended the known geographical range south-westwards for both species (Thurley and Bell 1994, Thurley 1996).

Archey's frog

L. archeyi is a small terrestrial frog which, until its discovery at Whareorino, was restricted to forest remnants in the Coromandel peninsular (*Chapter 1*). It has a range of colour morphs including green, brown and green, light brown and dark brown, although all individuals have black markings along the sides of the body, and on the legs (Stephenson and Stephenson 1957, Barwick 1961, Stephenson 1961).

Various estimates of maximum snout-vent length (SVL) have been reported for

L. archeyi. Stephenson and Thomas (1945) found that they reached 41 mm whereas Stephenson and Stephenson (1957) only found animals of this size in one population, on Tokatea Ridge, where SVL ranged from 28 mm to 41 mm. However at Mt. Moehau, SVL ranged from 19 mm to 34 mm. This intra-population size variation was clarified by Bell (1978a) who found that the mean SVL was 24.5 ± 0.8 mm on Mt. Moehau, whereas other Coromandel populations were significantly longer at 26.6 ± 0.6 mm. Bell (1978a), also noted that that the maximum SVL in Coromandel populations was 36 mm and this was the same maximum size as suggested by Robb (1980). Soon after Bell (1982a) revised the maximum SVL for *L. archeyi* to 37 mm, but recognised that there was some

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sexual dimorphism because females could have a maximum SVL of 37 mm and males only have a maximum SVL of 31 mm.

At Whareorino, Thurley (1996) found that *L. archeyi* ranged in SVL from 11.5 mm to 38.4 mm ($\bar{x}$ = 27.1 ± 0.3). Her results indicated therefore, that these frogs were larger on average than those in the Coromandel. Worthy (1987b) had suggested that such a geographic variation in size may occur. Thurley (1996) found that the range of colours in Whareorino frogs was similar to that of Coromandel frogs. The Whareorino animals, however, have a *'pinkish'* colour at the base of their limbs which is uncommon in Coromandel frogs (Thurley and Bell 1994).

Hochstetter's frog

L. hochstetteri was first described from the Coromandel (*Chapter 1*). They can be dull, light or dark brown frogs (Barwick 1961) but dark green or olive green frogs have also been found (Whitaker 1996).

Intra-population variation in SVL is not as apparent in *L. hochstetteri* as it is in

L. archeyi. The maximum SVL of *L. hochstetteri* was reported as 43 mm (Bell 1978a), or 45 to 46 mm (Bell 1981, McLennan 1985, Green and Tessier 1990, Slaven 1992). However, sub-fossil material indicates that individuals once reached a SVL of 50 mm (Worthy 1987a). Intra-population SVL varies from 15 mm to 46 mm (McLennan 1985), and the sexes differ in size with a maximum SVL for females of 45 mm and for males, 38 mm (Bell 1982b).

At Whareorino, Thurley (1996) found that *L. hochstetteri* were mainly brown individuals (93.9%), but individuals a combination of brown and green also occurred. One totally green individual was recorded during her study. She also recorded an average SVL for *L. hochstetteri* of 33.0 mm ± 0.8, (range 16.7 mm to 43.7 mm) which was not significantly different from other extant *L. hochstetteri* populations.

Type A frog

Frogs similar in size and appearance to *L. hochstetteri* also occur in Whareorino forest (*Chapter 1*). These frogs however have more robust rear and front limbs than either

L. archeyi or *L. hochstetteri*, and their limb musculature is more pronounced. Most were brown to light brown but some had greenish tints to their skin, refer *Chapter 4*. The webbing is reduced between the rear toes, and the front limbs and both the front and rear toes appear to be much longer than those in *L. hochstetteri*. A large parotoid ridge is present in most individuals. This extends from behind each eye to approximately half way down the dorsal surface. This gland is usually indistinct in *L. hochstetteri*, however is common to *L. archeyi* (Bell 1982b). Type A frogs were found under rocks, often with several similar individuals in close proximity. Two small post-metamorphic Type A individuals were also found in vegetation.

Leiopelmatid frogs are generally not sexually dimorphic[1], although differences in maximum SVL have been shown (Bell 1978a, Green and Tessier 1990). However as sexing of leiopelmatid frogs is not consistently reliable for all age classes and for all species, it was not considered during this project.

The Whareorino project

Previous descriptions of native frogs in Whareorino forest (Thurley and Bell 1994, Thurley 1996) were based on specimens found over the whole area. However, detailed description of the variation in size and colour for both species that occur within a small area had not been attempted. Such a study is important so that an appraisal of the community structure of groups of potentially related and/or interacting individuals can be made. For this reason, this study concentrated on a small area of Whareorino forest, P grid (*Chapter 1*). This study considered aspects of the broad morphology, size distribution and colour variation of all three groups of frog present in Whareorino forest. These aspects of frog size, morphology and colour will also be considered in subsequent chapters of this thesis. *Chapter 3* will examine habitat selection in leiopelmatid frogs and will show the relationship of habitat selection with frog colour and frog size. the following chapter, *Chapter 4* will closely examine the complex body morphology of the leiopelmatid frogs of Whareorino forest.

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[1] Differences in the 'thickness' of the radio-ulna between mature male and female *L. hochstetteri* have been found, however this is not consistent between sexes and cannot be detected for either juvenile or sexually immature individuals.

2.2 Methods

2.2.1 Field observations

Morphology

One hundred and fifty one *L. archeyi*, 27 *L. hochstetteri* and 28 Type A frogs were measured between June 1996 and July 1997 in Whareorino forest during random searches, transect searches, or casual surveys (*Chapter 3*). Seven morphological variables were measured to ±0.1 mm for each frog (Appendix 2.1) with vernier calipers, and recorded on standard morphological data sheets (Appendix 2.2).

Dorsal colour

The colour of the dorsum of each frog was assessed according to the amount of green pigment apparent; as follows:

1. 100 % green with no prominent brown colour. Commonly these animals displayed bright orange flashing on the legs and abdomen.

2. 75 % green without prominent areas of brown pigmentation. However patches of brown were usually apparent along limbs and along the sides of the abdomen. Orange flashing sometimes occurred on the legs or sides of the abdomen.

3. 25 % green with brown patches very prominent. These animals also had brown limbs as well as most brown sides and heads. Green pigmentation was in localised areas on the dorsal surface. Orange flashing were sometimes present along legs and the sides of abdomen.

4. 0% green. Totally brown or orange coloured frogs without green pigment on the dorsal surface. However orange flashing along the legs and sides of abdomen were still occasionally apparent.

The ventral colour and presence of any deformities were also recorded.

2.2.2 Data analysis

Data were compiled on Excel®, version 5.0, Microsoft Corporation, 1993-94 and graphics produced using SYSTAT® for Windows, version 6.0, SPSS Inc 1996. Statistical analysis was conducted using SAS® system for Windows, version 6.12, SAS Institute Inc., USA.

Morphology

Analysis of size distributions for each species and comparison of morphometric variables was based on the raw data. However individuals were grouped into size-based classes, following Green & Tessier (1990)[2] to examine the distribution of individuals within age-related classes: The size classes used are as follows:

<18 mm snout-vent length - juveniles

18.1 - 24 mm snout-vent length - subadults

24.1 - 30 mm snout-vent length - adults

30.1 - 35 mm snout-vent length - adults

35.1 - 40 mm snout-vent length - adults

(note that this classification into adults is arbitrary)

Dorsal colour variation

Analysis of the variation in dorsal colour was achieved for each frog group by separating them into the same five morphological size classes and the frequency of individuals in each size of each colour were calculated.

Ventral colour variation and deformities

The colour of the ventral surface and the nature of deformities were not recorded for all the frogs found. Therefore the results of these are discussed but are not quantified.

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[2] This categorisation was originally based upon *L. hochstetteri* data and may not be as accurate for *L. archeyi* and for Type A individuals due to probable differences in growth rates. However the use of the same classes does allow for comparison between groups.

2.3 Results

2.3.1 Morphology

Snout-vent length

The mean SVL for 151 *L. archeyi*, was 22.7 mm ± 0.63, [± S.E.] and ranged from 9.6 to 37.6 mm, (Figure 2.1A). In comparison mean SVL for 27 *L. hochstetteri* was 26.8 mm ± 1.08 and ranged from 9.1 to 40 mm, (Figure 2.1B). Type A frogs, mean SVL was 27.9 mm ± 1.03, n = 28, and ranged from 11.1 to 39.5 mm (Figure 2.1C).

Overall 33 % of *L.archeyi* were juvenile, based on their SVL (Table 2.1), 23.8 % were sub-adult, and fewer than half (43.2 %) were sexually mature. Sexually immature individuals were mostly (23.1 %) in the 24.1 - 30 mm SVL, and the fewest (7.3 %) were in the largest size group of 35.1 - 40 mm SVL. In contrast 52 % of *L. hochstetteri* were sexually immature (i.e. SVL < 24.0 mm) (Table 2.1). The remaining 48 % of frogs were evenly distributed within the mature size classes, although none had a SVL greater than 40.0 mm. The majority of Type A frogs were sexually mature with 32 % between 24.1 and 30.0 mm, 25 % between 30.1 and 35.0 mm and 14.0 % between 35.1 and 40.0 mm. Most juvenile/sub-adult individuals had a SVL between 18.1 and 24.0 mm.
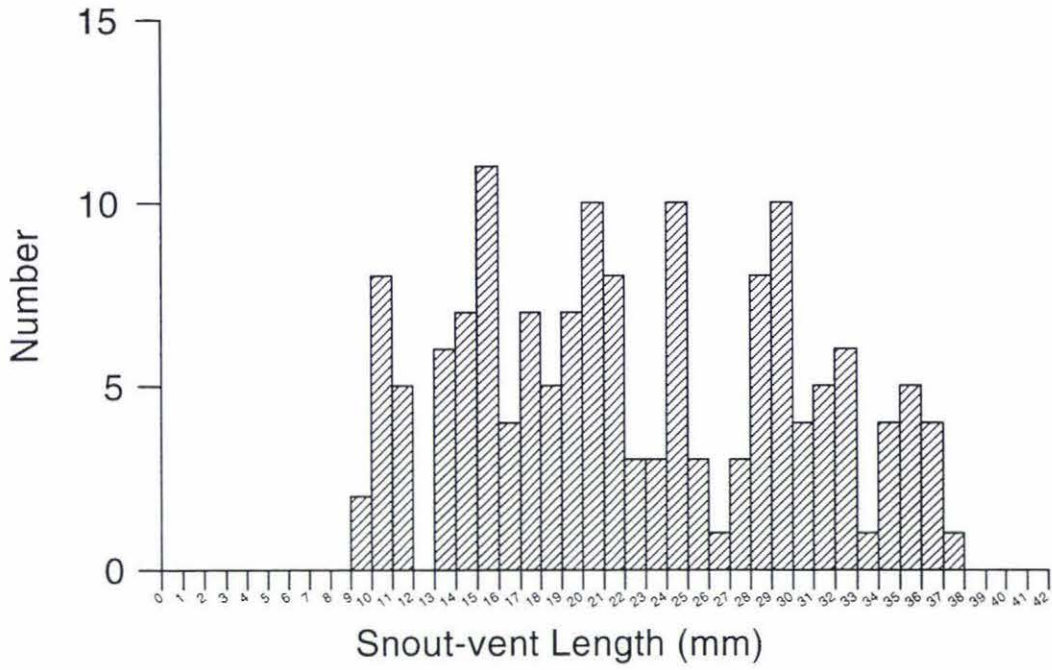
A.
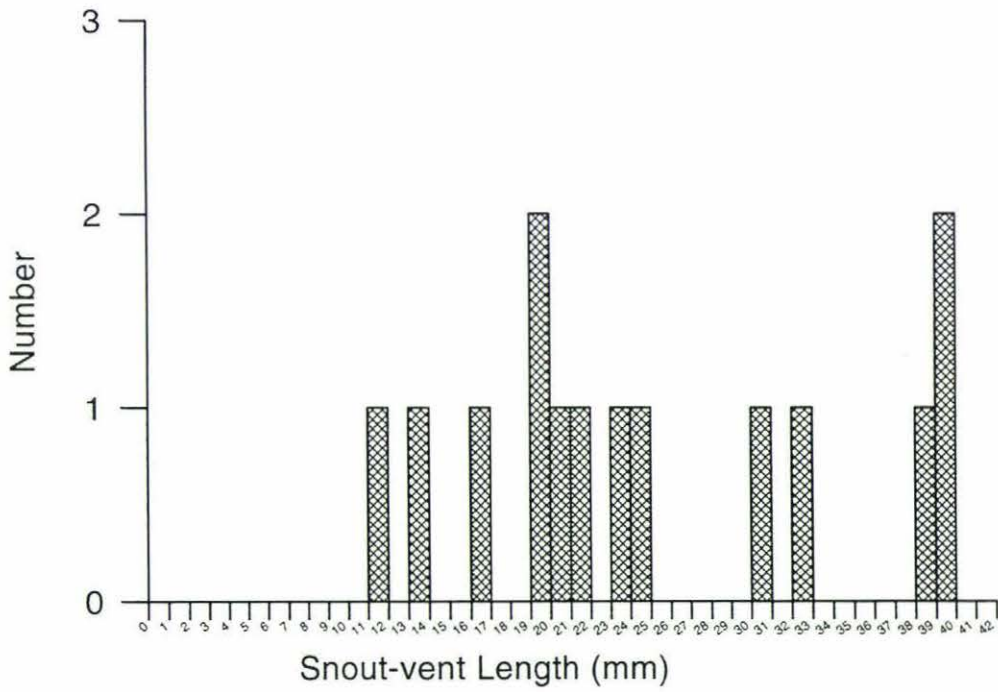
B.

Figure 2.1 Size distribution of frogs (SVL) from Whareorino forest. June 1996 - July 1997. **A**: *L. archeyi*; **B**: *L. hochstetteri*.
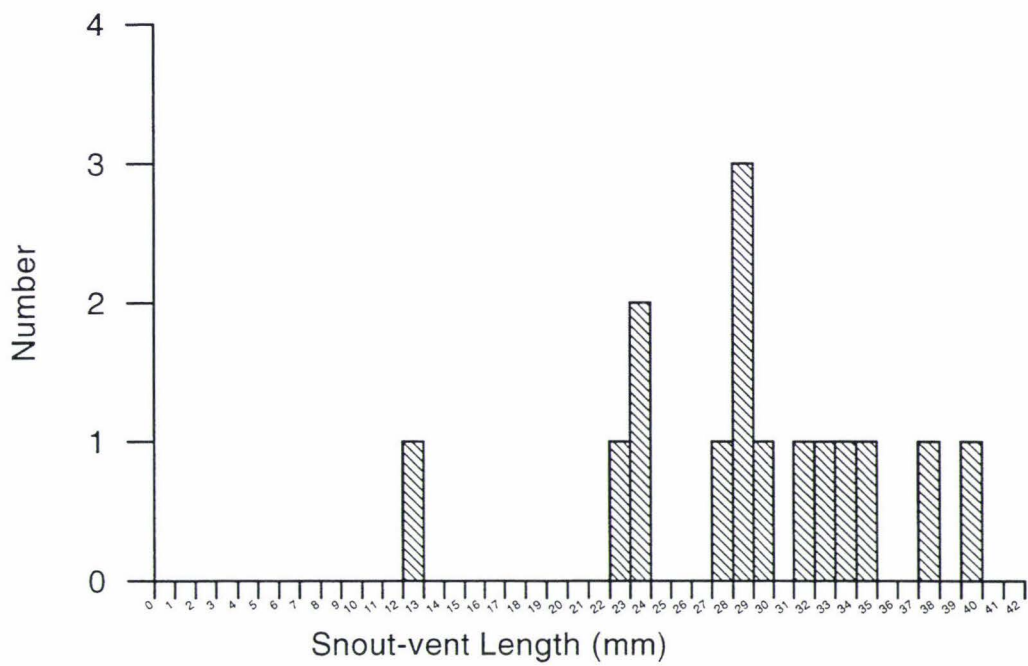
C.

Figure 2.1 Size distribution of frogs (SVL) from Whareorino forest,

June 1996 - July 1997. **C.** Type A frogs.

Table 2.1 Size distribution of leiopelmatid frogs from Whareorino forest,

June 1996 - July 1997.

	N	Size Classes (SVL) mm				
		- percentage of population in each class is given in brackets				
	N	<18	18.1-24.0	24.1-30.0	30.1-35.0	35.1-40.0
L. archeyi	151	50 (33.1)	36 (23.8)	35 (23.1)	19 (12.6)	11(7.3)
L. hochstetteri	27	4 (15)	10 (37)	3 (11)	4 (15)	6 (22)
Type A	28	2 (7)	6 (21)	9 (32)	7 (25)	4 (14)

Body Measurements

The dimensions of head width, right tibiafibula, rear fourth toe, right radioulna, right front third toe and weight for each of three types of leiopelmatid frogs at Whareorino forest are summarised in Table 2.2. *L. archeyi* and Type A frogs had significantly longer right front (3rd) toes than *L. hochstetteri*, 4.68 mm, 4.14 mm and 3.30 mm respectively. This highlights the short front toes in *L. hochstetteri*. *L. hochstetteri* was larger than *L. archeyi* in all other measurements but ranges of each dimension were less for *L. hochstetteri* than for *L. archeyi*. However, Type A frogs, had wider heads widths and longer radio-ulnas than both *L. hochstetteri* and *L. archeyi*. Lengths of the rear fourth toe were similar in all three groups.

Frog weight varied in a quadratic fashion with SVL in all three groups. On average, *L. archeyi* were the 'lightest' ($\bar{x}$ = 1.60 grams), followed by *L. hochstetteri* ($\bar{x}$ = 2.34 grams) and Type A frogs ($\bar{x}$ = 2.94 grams). The latter was apparent even though the range of weights for Type A frogs was wider than for either of the other frogs.

The proportion of head width, tibiafibula length, radio-ulna length and the length of the front (3rd) toe, to SVL were found to be significantly different between *L. archeyi* , *L. hochstetteri* and Type A frogs (Table 2.3) but rear (4th) toe lengths were found to be only significant between *L. archeyi* and Type A frogs.

Table 2.2 Dimensions of all *L. archeyi* (n = 151), *L. hochstetteri* (n = 27), and Type A (n = 28) frogs found in Whareorino forest, June 1996 to July 1997.

Measurement		Mean (± S.E)	Range
Head Width (mm)	*L. archeyi*	9.05 ± 0.24	4.1 - 19.0
	L. hochstetteri	10.73 ± 0.64	5.2 - 15.9
	Type A	12.27 ± 0.59	5.1 - 17.5
Right Tibiafibula (mm)	*L. archeyi*	9.29 ± 0.30	2.9 - 19.0
	L. hochstetteri	10.87 ± 0.88	4.3 - 18.6
	Type A	12.1 ± 0.58	4.5 - 16.9
Right Rear (4th) toe (mm)	*L. archeyi*	6.31 ± 0.22	2.0 - 13.2
	L. hochstetteri	6.61 ± 0.48	2.5 - 11.6
	Type A	6.69 ± 0.43	2.2 - 9.7
Right Radio-ulna (mm)	*L. archeyi*	7.44 ± 0.23	3.0 - 15.5
	L. hochstetteri	8.51 ± 0.59	3.6 - 14.0
	Type A	9.57 ± 0.49	3.9 - 14.3
Right Front (3rd) toe (mm)	*L. archeyi*	4.68 ± 0.17	1.4 - 9.6
	L. hochstetteri	3.70 ± 0.30	1.9 - 6.5
	Type A	4.14 ± 0.23	1.7 - 6.1
Weight (g)	*L. archeyi*	1.60 ± 0.11	0.08 - 5.4
	L. hochstetteri	2.34 ± 0.53	0.10 - 6.5
	Type A	2.94 ± 0.36	0.09 - 6.80

The correlation between SVL (as a measure of age) and other body measurements are shown for *L. archeyi*, *L. hochstetteri* and Type A frogs in Figure 2.2, 2.3 and 2.4, respectively. Every measure was highly correlated with SVL indicating that limb growth is directly proportional to SVL.
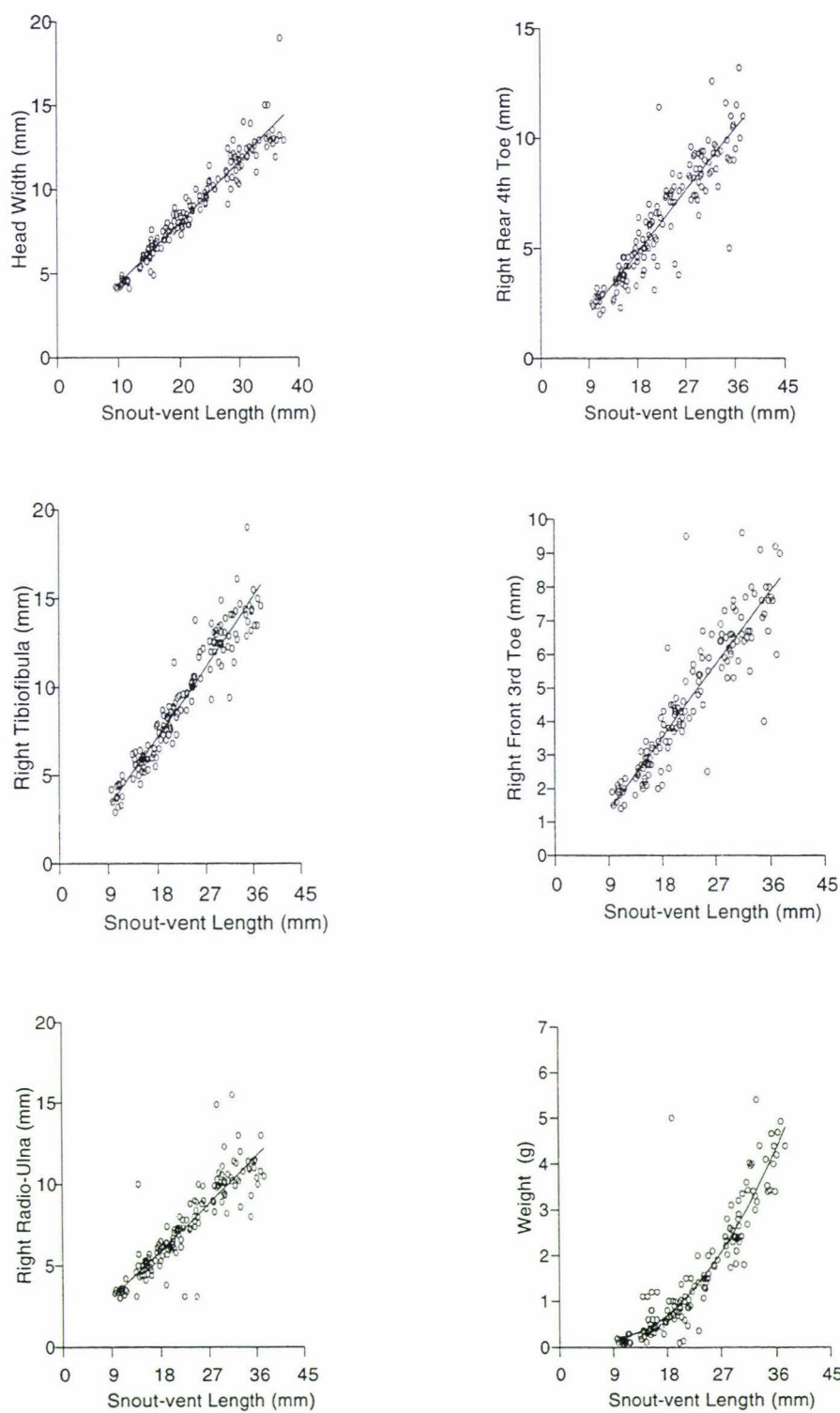
Figure 2.2 Relationship between measurements of leiopelmatid frogs and snout-vent length (SVL). **A**: *L. archeyi* .
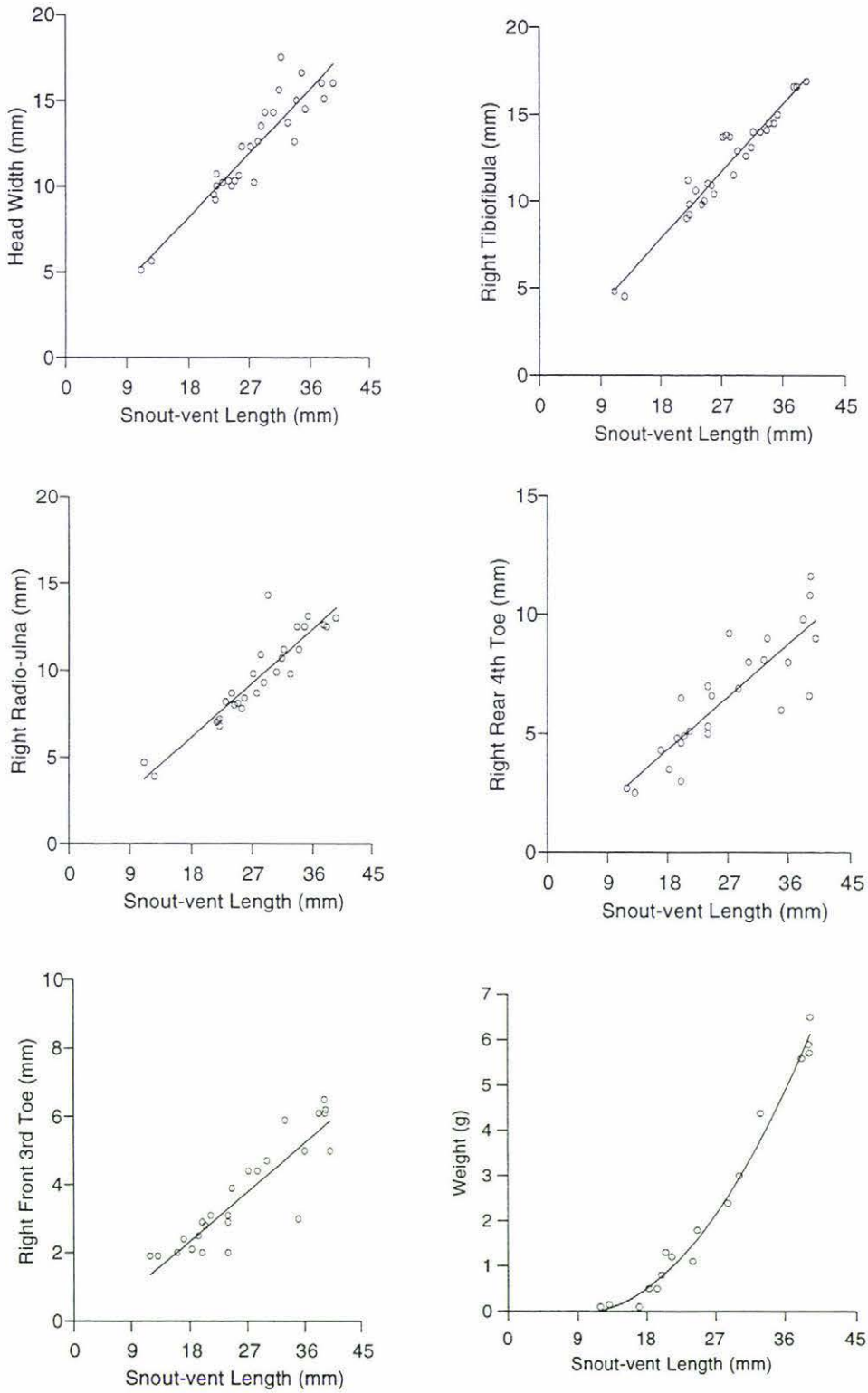
Figure 2.3 Relationship between measurements of leiopelmatid frogs and snout-vent length (SVL). **B**: *L. hochstetteri.*
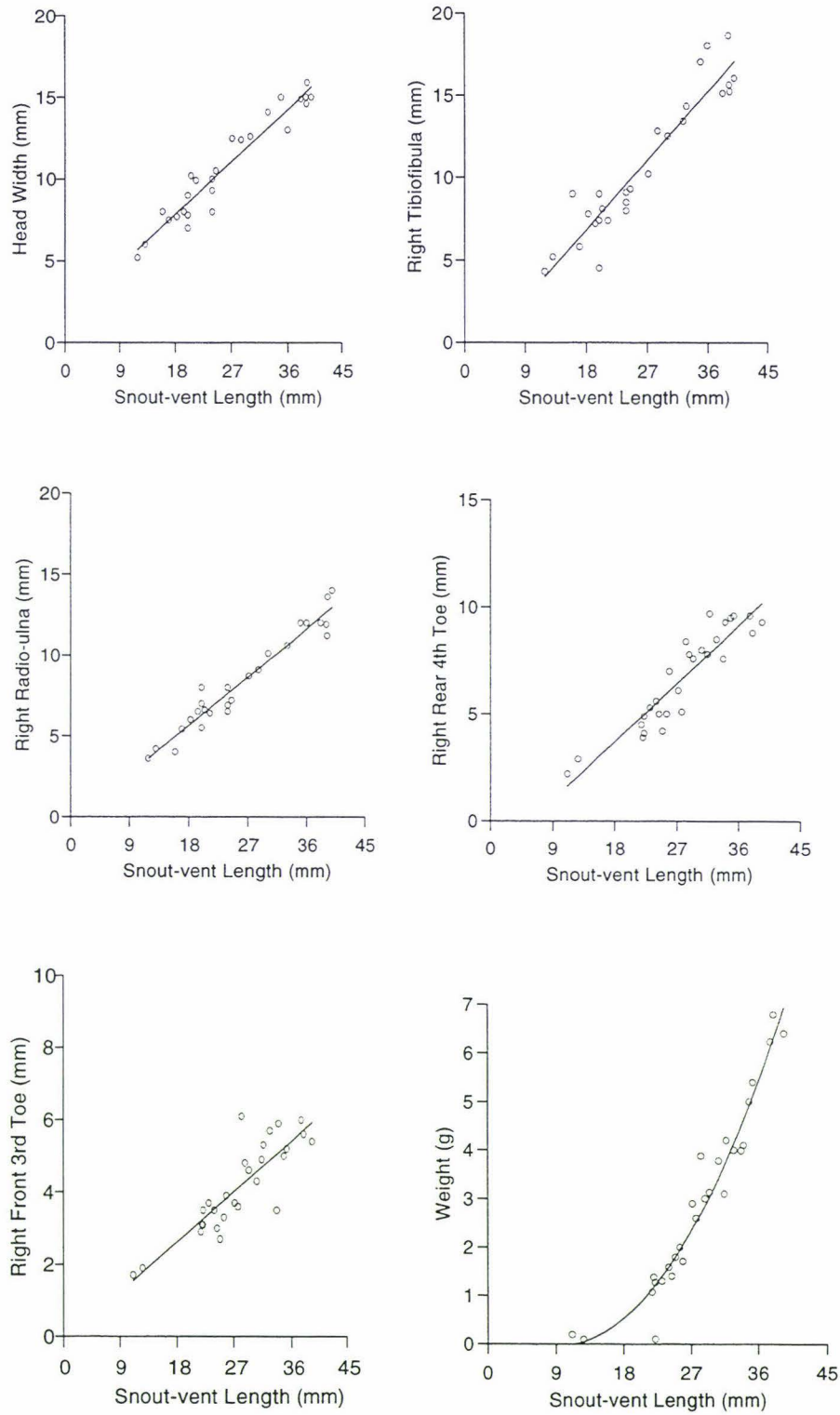
Figure 2.4 Relationship between measurements of leiopelmatid frogs and snout-vent length (SVL). **C**: Type A .

Table 2.3 Differences between regressions between *L. archeyi*, *L. hochstetteri* and
Type A frogs for five morphological variables, with respect to SVL.
$\alpha = 0.05$, DF = 197.
Comparisons from a Tukey's test, significant at the 0.05 level are indicated as ***'.

	Species Comparison	Lower Confidence limit	Difference between means	Upper Confidence limit	
Head Width (mm)					
	T - H	1.4104	1.8854	2.3608	***
	T - A	3.0288	3.3885	3.7483	***
	H - T	-2.3608	-1.8854	-1.4101	***
	H - A	1.1319	1.5031	1.8743	***
	A - T	-3.7483	-3.3885	-3.0288	***
	A - H	-1.743	-1.5031	-1.1319	***
Right Tibiafibula (mm)					
	T - H	1.2580	1.8327	2.4074	***
	T - A	2.5788	3.0179	3.4570	***
	H - T	-2.4074	-1.8327	-1.2580	***
	H - A	0.7393	1.1852	1.6311	***
	A - T	-3.4570	-3.0179	-2.5788	***
	A - H	-1.6311	-1.1852	-0.7393	***
Right Rear (4th) toe (mm)					
	T - H	-0.1430	0.4492	1.0414	
	T - A	0.0498	0.4979	0.9460	***
	H - T	-1.0414	-0.4492	0.1430	
	H - A	-0.4137	0.0487	0.5111	
	A - T	-0.9460	-0.4979	-0.0498	***
	A - H	-0.5111	-0.0487	0.4137	
Right Radio-ulna (mm)					
	T - H	0.9818	1.6148	2.2479	***
	T - A	1.8341	2.3133	2.7926	***
	H - T	-2.2479	-1.6148	-0.9818	***
	H - A	0.2040	0.6985	1.1930	***
	A - T	-2.7926	-2.3133	-1.8341	***
	A - H	-1.1930	-0.6985	-0.2040	***
Right Front (3rd) toe (mm)					
	A - T	0.12467	0.47109	0.81750	***
	A - H	0.71805	1.07548	1.43292	***
	T - A	-0.81750	-0.47109	-0.12467	***
	T - H	0.14684	0.60440	1.06195	***
	H - A	-1.43292	-1.07548	-0.71805	***
	H - T	-1.06195	-0.60440	-0.14684	***

Note: A = *L. archeyi*
      H = *L. hochstetteri*
      T = Type A.

2.3.2 Dorsal and Ventral Colours

Dorsal colour

The dorsal colour of *L. archeyi* ranged from bright green (Plate 2.1A) with orange flashing on the legs and sides of the abdomen (Plate 2.1B) to light or dark brown (Plate 2.1C). Light brown frogs also often had bright orange flashing, like those present in the bright green individuals. One large light brown/yellow frog escaped before photographs or body measurements could be taken. *L. hochstetteri* were commonly dark brown (Plate 2.1D), but individuals from relatively dry sites were typically light brown. Type A individuals were either brown or green/brown (Plate 2.1E *addendum*).

Relationship between dorsal colour and snout-vent length

In *L. archeyi*, 45.8 % of individuals less than 18.0 mm SVL had no green on the dorsum, and 31.3 % were completely green (Figure 2.5). The remainder of juvenile individuals, 22.9 % were a mixture of brown and green, dorsally.

In comparison, no *L. hochstetteri* individuals had green on their dorsal surface (Figure 2.6, B, C, D & E) and all Type A individuals, under 18 mm SVL were brown (Figure 2.7A).

In the sub-adult size class SVL 18.1 to 24 mm, the majority of *L. archeyi* individuals, had no green pigmentation (61.8 %) or had only small amounts of green (14.7 %) (Figure 2.5B). The remainder (23.5 %) were either predominantly or completely green on their dorsal surface.

One sub-adult Type A individual was green on its dorsal surface, whereas all other individuals had no green pigmentation (Figure 2.7B).

In the first adult size class, (SVL 24.1 to 30 mm) only 29.4 % of *L. archeyi* frogs were wholly or predominantly green on their dorsal surface (Figure 2.5C) whereas the majority (55.9 %) were totally brown. The remaining 14.7 % had only small areas of green. All Type A frogs in this class were without green dorsal pigmentation (Figure 2.7C).

In the second to largest size class, (30.1 mm to 35 mm), 78.9 % of *L. archeyi* individuals were totally brown or predominantly brown on their dorsal surface (Figure 2.5D). The remaining 21.0 % were either wholly or predominantly (i.e. 75 %) green. Totally brown Type A frogs (i.e. 0 % green) only were recorded in this size class (Figure 2.7D).

In the largest size class, (> 35.0 mm SVL), 60 % of *L. archeyi* individuals were totally brown, and the remainder were green, (Figure 2.5E). One Type A individual in this size class was dark green in colour, the remaining individuals were totally brown (Figure 2.7E).

Ventral colour

The ventral colour in most of the dorsally green individuals of *L. archeyi* ranged from black, to brown with yellow or red patterns or rings (Plate 2.2A & 2.2B). Individuals with black undersides had speckled green, blue and brown spots over the entire ventral surface.

L. hochstetteri individuals were commonly brown or tan on the ventral surface (Plate 2.2C) whereas Type A frogs ranged from light or mid brown to cream (Plate 2.2D *addendum*).

A.
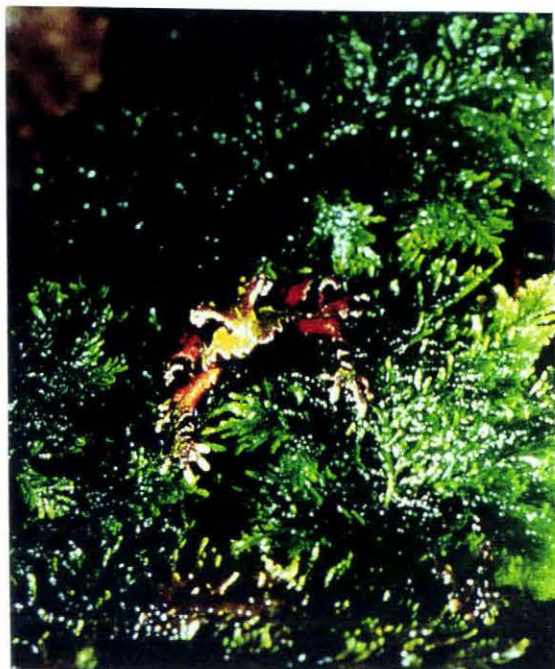
B.

C.

D.

Plate 2.1 Dorsal colour variation in leiopelmatid frogs, Whareorino forest.

A: *L. archeyi*, 100 % green; B: *L. archeyi*, orange flashing;

C: *L. archeyi*, 0 % green; D: *L. hochstetteri*, 0 % green.
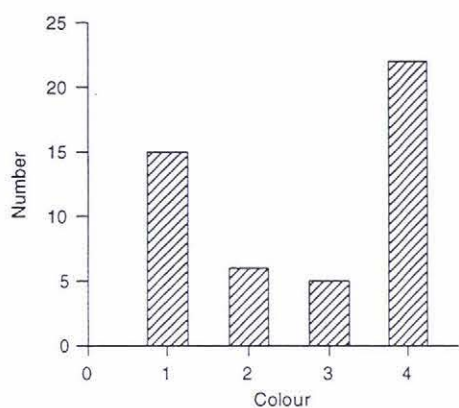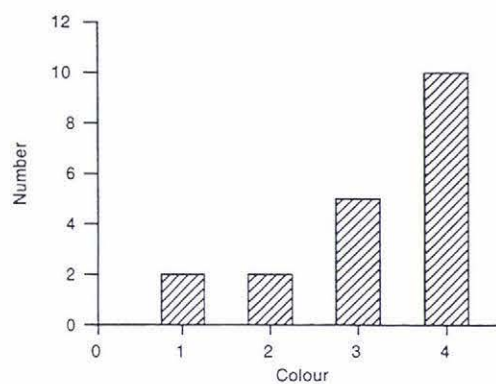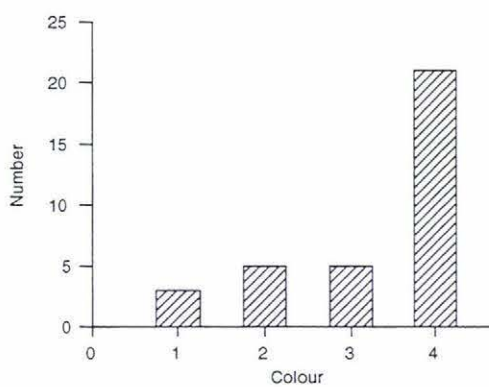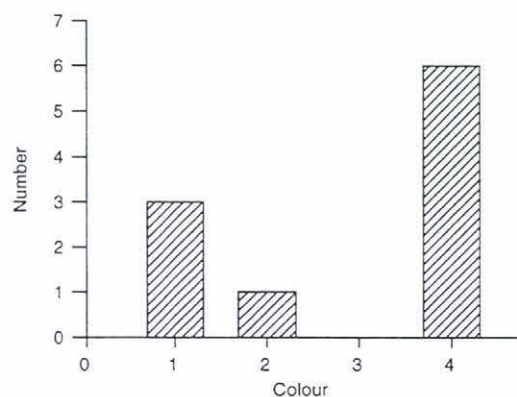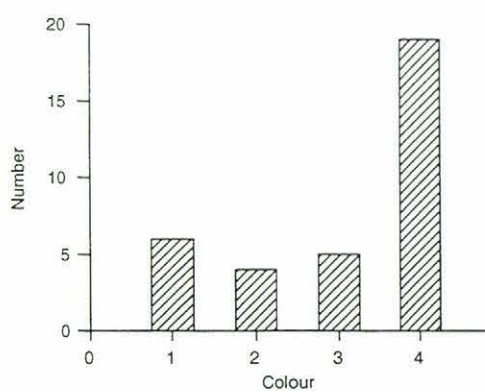
Figure 2.5 Colour variation in *L. archeyi* individuals, grouped according to snout-vent length. **A**: <18 mm; **B**: 18.1 - 24.0 mm; **C**: 24.1 - 30.0 mm; **D**: 30.1 - 35.0 mm; **E**: 35.1 - 40.0 mm.

A.

D.

B.

E.

C.
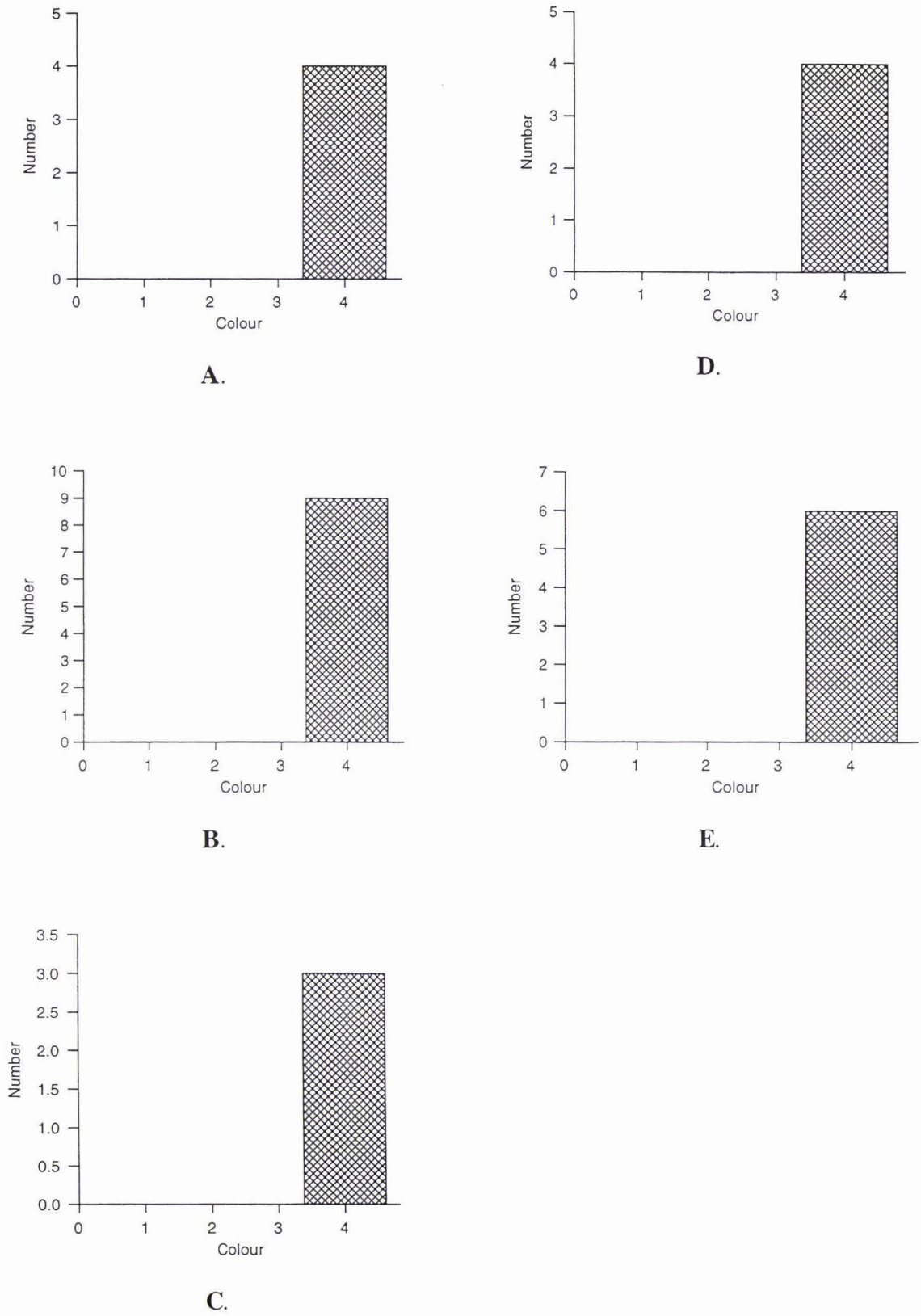
Figure 2.6 Colour variation in *L. hochstetteri* individuals, grouped according to snout-vent   length. **A**: <18 mm; **B**: 18.1 - 24.0 mm; **C**: 24.1 - 30.0 mm; **D**: 30.1 - 35.0 mm; **E**: 35.1 - 40.0 mm.
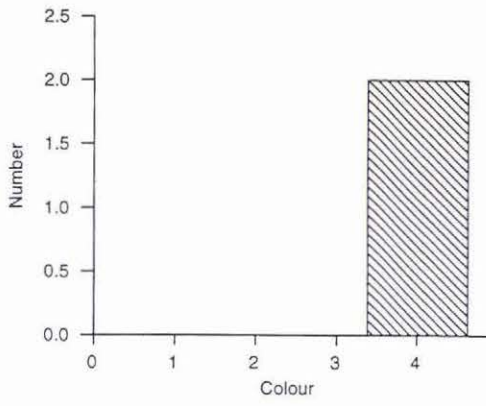
A.
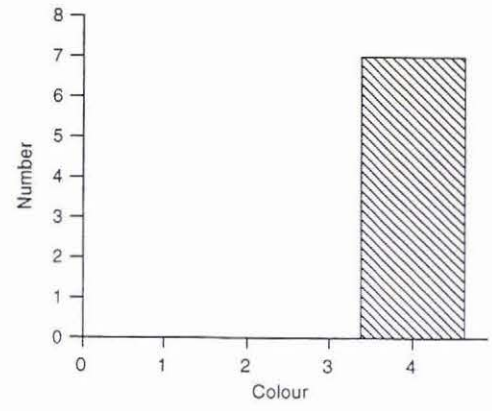
D.
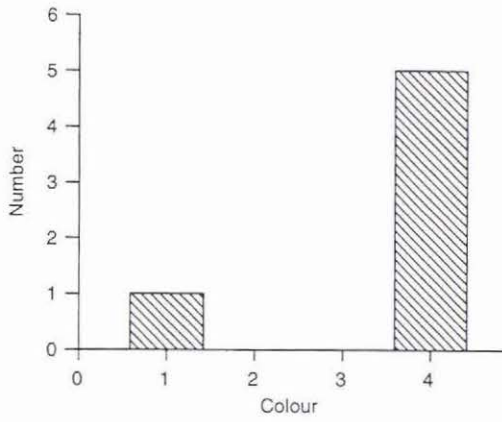
B.
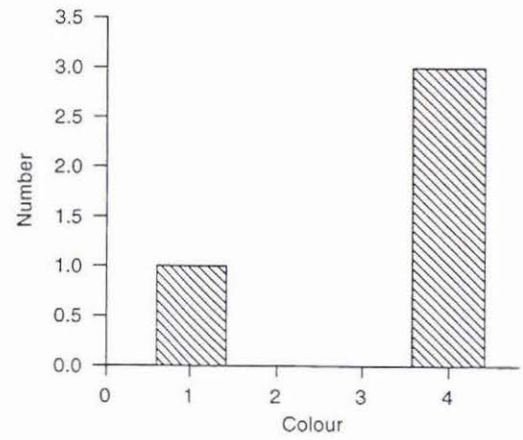
E.
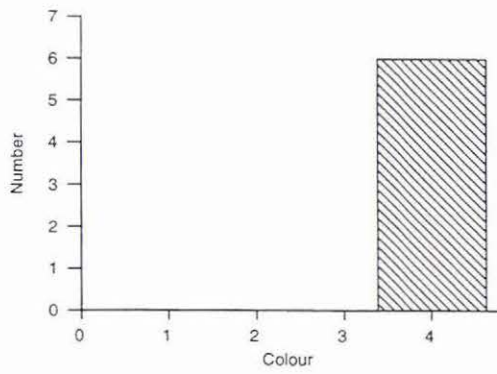
C.

Figure 2.7 Colour variation in Type A frogs, grouped according to snout-vent length.

A: <18 mm; B: 18.1 - 24.0 mm; C: 24.1 - 30.0 mm; D: 30.1 - 35.0 mm;

E: 35.1 - 40.0 mm.

A.

B.

C.

Plate 2.2 Ventral pigmentation in *L. archeyi* and *L. hochstetteri*, from Whareorino forest.

A. *L. archeyi*, speckled **B.** *L. archeyi*, mottled **C.** *L. hochstetteri*, tan

2.3.3 Deformities and injuries

Deformities occurred in 11 *L. archeyi*. They ranged from a severely damaged lower mandible to the entire loss of a front foot or loss of toes. Deformities of toes and fingers occurred as partial regrowth of the digits following an obvious earlier injury (Plate 2.3). Damaged or missing eyes were also found in 2 frogs. No *L. hochstetteri* were found that had obvious deformities but one Type A individual was found with a large facial scare.

Plate 2.3 Example of a regrown toe in *L. archeyi*.

2.4 Discussion

Size variation

Anuran growth rates are determined by age as well as climatic variables, particularly temperature (Duellman and Trueb 1986). Growth after metamorphosis is usually rapid, but slows during cooler seasons when amphibians are directly affected by ambient temperatures. When it is warm, growth continues through to sexual maturity and then it slows or stops (Zug 1993). Bell (1978a) suggested that leiopelmatid species may grow throughout their life and therefore exhibit indeterminate growth, although later growth is very slow.

L. archeyi

In this study at Whareorino forest *L. archeyi*, were found to be similar in size (SVL) to those from other localities, although the mean SVL ($\bar{x}$ = 22.7 ± 0.63 [± S.E.]), was much less than previously recorded. Thurley (1996) reported that the size range in Whareorino forest was 11.5 - 38.4 mm ($\bar{x}$ = 27.1 ± 0.3 mm). I did not find frogs in Whareorino forest larger than 37.6 mm, hence the calculated mean SVL is affected by a lack of large individuals. I sampled a wide range of individuals, within a small area of the forest, over half of which were sexually immature. The size (SVL) range of *L. archeyi*, however, indicates a selective absence of large (i.e. older) individuals which would normally be expected to be present in a stable population. Several reasons could contribute to this age structure. Larger individuals may have been taken by various mammal predators in Whareorino forest or died as a result of some unknown agent.

Alternatively there are differences in sampling technique between this study and both Thurley's (1996) and most other leiopelmatid surveys. This study concentrated on a small area of Whareorino forest where repeated searches for individuals were made. In comparison, most broad or transect surveys may be biased towards larger individuals as they are more apparent. Differences in habitat surveyed may also effect the size of frogs obtained. Thurley (1996) found that a difference occurred in its micro-habitat site selection between juvenile *L. archeyi* and adult *L. archeyi* as more juveniles were found in vegetation habitat than in any other habitat and adults were found primarily under rocks. Micro-habitat preference by leiopelmatid frogs found in this study is examined in

Chapter 3, where the results clearly show that juvenile and sub-adult *L. archeyi* do select for a different habitat from adult *L. archeyi* individuals.

L. hochstetteri

Of the 28 *L. hochstetteri* sampled, SVL ranged more widely than previously recorded at Whareorino (Thurley 1996) although the mean SVL was also much lower in my study. The largest frog recorded in Whareorino forest by me was 40.0 mm SVL, which is smaller than maximum *L. hochstetteri* recorded in previous studies (Bell 1978a, 1981, 1982, McLennan 1985, Green and Tessier 1990, Slaven 1992, Whitaker 1996). Worthy (1987a) found that sub-fossil evidence indicated that *L. hochstetteri* once reached up to 50 mm SVL.

The population mean SVL of this study for *L. hochstetteri* was 26.4 mm ± 1.7 [± S.E.], range 11.9 mm to 40.0 mm, which was smaller than $\bar{x}$ = 33.0 ± 0.8 mm, range 16.7 mm to 43.7 mm recorded by Thurley (1996). Thurley (1996), however encountered far fewer sub-adults and juveniles and proportionately more mature individuals than was found by me.

Several possible factors could effect the observed difference in *L. hochstetteri* measurements between the two studies. Firstly, Thurley's (1996) sample of *L. hochstetteri* was double the number I studied and therefore may be a better population estimate. Secondly, the frogs may vary geographically in size, or with climate (Heyer *et. al.* 1994). Thurley (1996) focused on sites that were at maximum 100 m higher in altitude than mine, so a large size effect would not be expected between sites. Thirdly, differences in the search methods used for the two studies may lead to sample bias. It may be that, similar to *L. archeyi* there is a difference in micro-habitat selection between young (smaller) and adult *L. hochstetteri*. An ontogenic shift in habitat selection has not, as yet, been indicated by stream surveys for *L. hochstetteri* (Slaven 1994, Whitaker 1996) Plant cover and other micro-habitat variables could all contribute to difficulties in finding well camouflaged frogs. Fourthly, the population may possibly change demographically over time so if it was expanding at present then juvenile frogs would make up a larger proportion. Such a situation could arise through predation. Alternatively, predation may selectively remove large frogs, or the present climate may

have improved reproductive success through increased levels of temperature, humidity or food.

The size profile of this population indicates that 52 % of frogs found were sexually immature which contrasts with the value of 13.2 % found by Thurley (1996). The results of the present study, although only a small sample size, suggest that a larger proportion of the population are immature. Whitaker (1996) found that over 5 years, the proportions of juvenile, sub-adult, and sexually mature individuals changed in an 'aging' population fashion in Coromandel *L. hochstetteri*. Four years separated the research conducted by Thurley (1996) and the present study. Thurley's population was skewed towards larger individuals. I found it was skewed towards smaller individuals. This can be caused by two main factors; changes in the population or different search methodology.

Type A frogs

I found juvenile, sub-adult and adult Type A frogs during my study. Most individuals were 24.1 to 30.0 mm (SVL) and few were in the minimum and maximum size classes. This suggests that the population size structure approached a normal distribution. The relative paucity of juvenile individuals may be due to my sampling technique, i.e. juveniles occur in a different habitat to the one sampled, or it may reflect a true lack of juveniles in the population. In contrast, the largest proportion of *L. archeyi* and *L. hochstetteri* were juvenile. One possibility is that Type A frogs consisted of an aging population (Whitaker 1996).

Dorsal and Ventral Colour

Leiopelmatid frogs are cryptic nocturnal frogs which are disruptively coloured, i.e. the patterns do not match the outline of the frog (Duellman and Trueb 1986). This is exemplified in both *L. archeyi* and *L. hochstetteri* by strong black bands that form distinct lines when the legs are folded. Such patterns can potentially help protect the frogs from predators.

The distribution of colour morphs of *L. archeyi* that I found were similar to that reported by Thurley (1996). She also found that more predominantly green frogs occurred in the smaller size classes and that there were few found in the largest size class.

All *L. hochstetteri* individuals that I found were totally brown and all but two Type A individuals were brown. The two individuals that were not brown, were a dull green colour and were 21.8 mm SVL and 35.3 mm SVL respectively. I found no *L. hochstetteri* or Type A frogs in the mid-colour ranges (i.e. categories 2 and 3).

L. archeyi, therefore, has a wider diversity of colour morphotypes than other groups of frogs in Whareorino forest. The reasons for colour variation and the pressures which lead to crypticity in *Leiopelma* are not well understood (Stephenson and Stephenson 1957, Slaven 1992). However Holdaway (1989) and Thurley (1996) suggest that the colours and patterns of leiopelmatid frogs could be a response to earlier predators such as the adzebill (*Aptornis* spp.) and the owlet nightjar (*Megaegotheles novazealandiae*). Thurley (1996) also considered that there may be a relationship between the colour of these frogs and their daytime retreat sites. The causes of distinct intra-specific variation in colour in *Leiopelma* are unknown and a clear association with habitat (e.g. substrate and plant cover), as has been shown for other species of frog, has not been demonstrated in *Leiopelma* (Stephenson and Stephenson 1957). Indeed, two differently coloured individuals were observed under the same rock on several occasions (Stephenson and Stephenson 1957, *pers. obs.*). Effects of genetics, and ambient light and temperature on body colour and any interaction of these factors with habitat variables, need clarifying.

Thurley (1996) demonstrated that there was a strong association between body size and "pink" colour (= orange in this study) at Whareorino. She found that the presence of pink pigmentation was related to the age of individuals, and was in sexually immature individuals (Thurley 1996). However, a major proportion of small individuals from the population she surveyed, were without pink pigmentation and so Thurley concluded that it was not a reliable aging criterion. In the present study orange was common in both brown and green frogs over a range of sizes. However I did not recorded the presence or absence of this colour in all frogs captured.

The variation in ventral colours qualitatively found in this study is difficult to understand. Colour patterning on body surfaces that touch the substrate are likely to be adaptively neutral, but the frequency of different forms of ventral surface patterning was not systematically surveyed so further research is required to examine the relationship of ventral surface patterning to size, micro-habitat, and sex.

Deformities

No major deformities, such as supernumerary limbs, were found in the frogs surveyed. Losses of limb extremities were found, only in *L. archeyi*. Such injuries could result from damage by predators (including other frogs) or from accidents such as rock movements on the unstable forest floor. An inter-habitat comparison of injuries sustained by frogs would be useful.

Conclusion

I have shown that several distinct groups of frogs exist in a small area of Whareorino forest. *L. archeyi* occurs in an array of colours and sizes and was common both in the main study sites and in other areas sampled. *L. hochstetteri* and Type A individuals were relatively uncommon in the study area, but my sampling methodology may not have included all relevant habitat types for these species.

The population of leiopelmatid frogs in Whareorino forest varies both in size, and in colour. The relationship of size and colour to each other and to the mircohabitat in which each frog occupies warrants further investigation on order to understand the variation.

The occurrence and causes of deformities in leiopelmatid frogs also require further investigation. Predators potentially may be having a major effect on mainland frog populations. In particular the relative absence of sexually mature individuals recorded in this study requires further investigation. Whether this population is seriously under threat (i.e. from predators) or whether it is an expanding population, will only be answered by further long term studies.

CHAPTER THREE-

HABITAT SELECTION BY LEIOPELMATID FROGS IN WHAREORINO FOREST
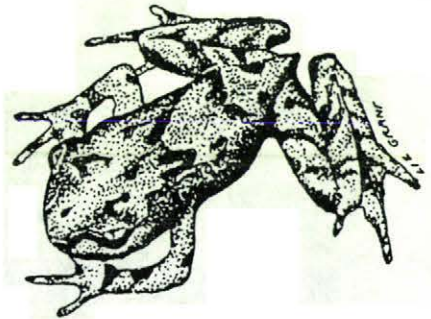
Chapter 3

Habitat Selection By Leiopelmatid Frogs In Whareorino Forest

3.1 Introduction

Frogs can inhabit a wide range of habitats in, aquatic, arboreal or terrestrial environments (Duellman and Trueb 1985). Most have an aquatic stage in their life cycle and all are dependent on a moist environment as they have an outer permeable skin layer (Bentley 1966).

Leiopelmatids are totally terrestrial or semi-aquatic nocturnal frogs which inhabit cool moist areas of the forest where they are commonly found under rocks and logs during the day (*Chapter 1*).

L. hochstetteri was first discovered in the Coromandel as a stream dwelling frog in 1852 (Thompson 1853). Since this first report several populations have been recorded both offshore, on Great Barrier Island, as well as throughout the top third of the North Island, where they have been estimated to occur as high as 50 frogs/100 m of stream bed (Green and Tessier 1990). Surveys have shown they prefer streams with rocky substrates (Bell 1978a) and low to moderate silting. McLennan (1983) reported that 79 % of

L. hochstetteri occur along the beds of streams in the upper tributaries of the Motu River. In comparison along the banks of the Motu River itself, frogs are found above the flood level and commonly 4 - 9 meters from water. However in situations where

L. hochstetteri occurs away from streams, such as on Tokatea Ridge it was noted that they tend to occupy much wetter sites, i.e. seepage's, in comparison to the sympatric terrestrial frog *L. archeyi* (Bell 1978a).

Thurley (1996), in an assessment of *L. hochstetteri* in Whareorino forest, found they were "almost exclusively" in stream beds, under rocks or logs.

L. archeyi, until recently, was only known from scattered populations throughout the Coromandel region where they predominantly are in daytime retreat sites under mossy rocks (Bell 1978a). Robb (1980) found that *L. archeyi* may occur near stream banks, or marshy areas (Mt. Moehau), but was more commonly found under rocks and logs on mountain ridges. Bell (1978a) found *L. archeyi* both in 'wet' sites, such as *Sphagnum* moss beds, as well as along ridges. However, occurrences of *L. archeyi* in streams have also been noted (Thurley 1996, *pers. obs.*). Hence *L. archeyi* occurs in a wide range of habitat sites. In Whareorino forest, Thurley (1996) reported that *L. archeyi* was more often in vegetation rather than under rocks or logs. A correlation between snout-vent length (SVL) and daytime retreat site showed that smaller frogs tended to be found in hook grass (*Unicinia uncinata*) and larger frogs were more commonly found under rocks and logs (Thurley 1996). Thurley (1996) also found that *L. archeyi* occurred in a wide range of habitats in Whareorino forest, including ridges, gully's, hillsides and hilltop's, in streams and away from streams, and amongst vegetation. She considered that Whareorino *L. archeyi* were widespread in comparison to *L. archeyi* in Coromandel, where they are mostly found on ridges (Thurley and Bell 1994, Thurley 1996).

L. hochstetteri and *L. archeyi* occur as sympatric species in parts of the Coromandel ranges as well as in Whareorino forest (Bell 1982b, Thurley and Bell 1994). Generally they are thought to segregate their resources by using different daytime retreat sites in the zones of overlap. This is because *L. hochstetteri* usually occurs in wetter areas and stream sites whereas *L. archeyi* are generally found in drier ridge top habitats. In Whareorino forest, *L. archeyi* and *L. hochstetteri* occurred throughout the forest, from c 300/350 m to 800 m a.s.l. *L. archeyi* were more common above 650 m a.s.l. whereas *L. hochstetteri* were found to be evenly distributed throughout the entire altitudinal range. Where the two species overlap, on a micro-habitat scale, individuals of both species occur in close proximity, even under the same rock (Stephenson and Stephenson 1957, Robb 1980, Bell 1982a,b).

I have described a third group of frogs, Type A frogs, which have not been previously recognised (*Chapter 1*). These frogs are commonly found within and in close proximity to P grid, in ridge top habitat, where they occur under rocks. Casual observation of these

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frogs suggest that they commonly occur together in 'clusters' or groups in rock piles. This is in contrast to *L. archeyi* which appears to be more widespread (*pers. obs.*).

My aim was to examine the community structure of leiopelmatid frogs in Whareorino forest. Communities can be structured in many ways. I choose habitat selection, as daytime retreat sites on which to assess community structure. Analysis of habitat selection is important for several reasons. Studies of a population whilst it is locally abundant can provide an 'image' or 'concept' of the ideal habitat of these frogs. This knowledge is important should the frogs or their habitat become endangered and require more intensive management. Such information has already proved useful, for example with the Stephens Island frog where new habitat was created to support a new population of frogs. Secondly, information on preferred habitat is important in captive management programs of leiopelmatid frogs, as this enables for the provision of optimal habitat in the captive situation.

For this reason I assessed the preferred habitats of leiopelmatid frogs in Whareorino forest to find the micro-habitats in which leiopelmatid frogs occurred and if there were any detectable differences between *L.* archeyi, *L. hochstetteri* and Type A frogs. The relationship of habitat selection to body morphology is further examined in *Chapter 4*, and the implications of habitat selection with frog diet is considered in *Chapter 6*.

3.2 Methods

Searches for leioplematid frogs were conducted in potential daytime retreat sites, during habitat surveys throughout Whareorino forest, from July 1996 to June 1997. General areas searched included 'ridge habitat', where searches were always conducted more than 40 m from the nearest stream, and 'water habitat' which included seepages and stream beds and banks.

Survey methods used were line transects, quadrat sampling and random sampling. Details of these methods are given in *Chapter 7*.

All potential (i.e. without a frog present) or actual (i.e. frog present) retreat sites were recorded and the following were measured; the length of the rock or log (visible from the surface), the basal diameter of vegetation (i.e. grass habitat), the height of tree ferns. All data were recorded on a standard habitat data sheet (Appendix 3.1).

Frogs found during habitat surveys were measured to ± 0.1 mm snout-vent length (SVL) refer *Chapter 2*. The association of snout-vent length with daytime retreat site selection is considered.

All data were graphed using Systat® version 6.0, for Windows®, SPSS Inc. Chicago.

Correspondence analysis was run on SAS® system version 6.12, for Windows®. 1989-1996, SAS Institute Inc. USA.

3.3 Results

3.3.1 General frog habitat

All *L. archeyi* in this study were found along ridges whereas of the 17 *L. hochstetteri* recorded 16 were found in stream beds (Table 3.1). One *L. hochstetteri* was found recorded along a ridge. Type A individuals (n = 30) were all recorded on ridges.

Table 3.1 General habitat selection by *L. archeyi, L. hochstetteri* and Type A frogs in Whareorino forest.

General Habitat	*L. archeyi*	*L. hochstetteri*	Type A	Total
Ridge Habitat	144	1	30	175
Water Habitat	0	16	0	16

3.3.2 Micro-habitat selection

A total of 1450 potential daytime retreat sites were searched for frogs in Whareorino forest. Potential retreat sites searched included ground ferns (e.g. button fern *Pallaea rotundifolia*), rice grass *Microlaena avenacea* and hook grass *Uncinia uncinata*, logs, leaf litter, rocks, tree fern *Cyathea smithii* and crown ferns *Blechnum discolor*. One hundred and ninety-one frogs were found in a variety of retreat daytime retreat sites in or under rocks, logs, hook grass, rice grass, leaf litter, and ground ferns. Frogs were not found in tree ferns or crown fern. The number of sites searched and number of habitat types with frogs is shown in Table 3.2. Of these 191 frogs, 20 occurred as pairs within the same retreat and at one site three individuals occurred.

Table 3.2 Occurrence of leiopelmatid frogs in different habitats, in Whareorino forest.

Figure in bold type is percentage of total.

Habitat	Number of retreats without frogs	Number of retreats with frogs	Total
Ground ferns	37	1	38
	2.55	**0.07**	**2.62**
Rice grass *Microlaena avenacea*	182	50	232
	12.55	**3.45**	**16.00**
Hook grass *Uncinia uncinata*	113	16	129
	7.79	**1.10**	**8.90**
Log	33	6	39
	2.28	**0.41**	**2.69**
Leaf litter	7	4	5
	0.07	**0.28**	**0.34**
Rock	878	114	992
	60.55	**7.86**	**68.41**
Tree Fern *Cyathea smithii*	15	0	15
	1.03	**0.00**	**1.03**
Total	1259	191	1450
	86.83	**13.17**	**100.00**

Of those sites that had a frog, 59.69 % were rocks and 26.18 % were rice grass (Table 3.3). Frogs were also found in leaf litter, hook grass and under logs. Frogs were not found in tree ferns and one frog only was found in a ground fern.

Table 3.3 Habitat selection by leiopelmatid frogs in Whareorino forest
Figure in plain type is number
Figure in bold type is percentage of total number

Habitat	*L. archeyi*	*L. hochstetteri*	Type A	Total
Ground ferns	1	0	0	1
	0.52	**0.00**	**0.00**	**0.52**
Rice grass	45	3	2	50
Microlaena avenacea	**23.56**	**1.57**	**1.05**	**26.18**
Hook grass	16	0	0	16
Uncinia uncinata	**8.38**	**0.00**	**0.00**	**8.38**
Log	5	0	1	6
	2.62	**0.00**	**0.52**	**3.14**
Leaf litter	3	1	0	4
	1.57	**0.52**	**0.00**	**2.09**
Rock	74	13	27	114
	38.74	**6.81**	**14.14**	**59.26**
Tree Fern	0	0	0	0
Cyathea smithii	**0.00**	**0.00**	**0.00**	**0.00**
Total	144	17	30	191
	75.39	**8.90**	**15.71**	**100.00**

Of the three groups of frog in Whareorino forest, *L. archeyi* was found in the greatest range of retreat sites (Table 3.3, Figure 3.1). It was found in ground ferns, rice and hook grass, in leaf litter and under rocks and logs. *L. hochstetteri* were found under rocks, in rice grass habitat and in one individual was recorded in leaf litter. Type A individuals were found mostly under rocks, however two individuals were recorded in rice grass and one individual was recorded in leaf litter.
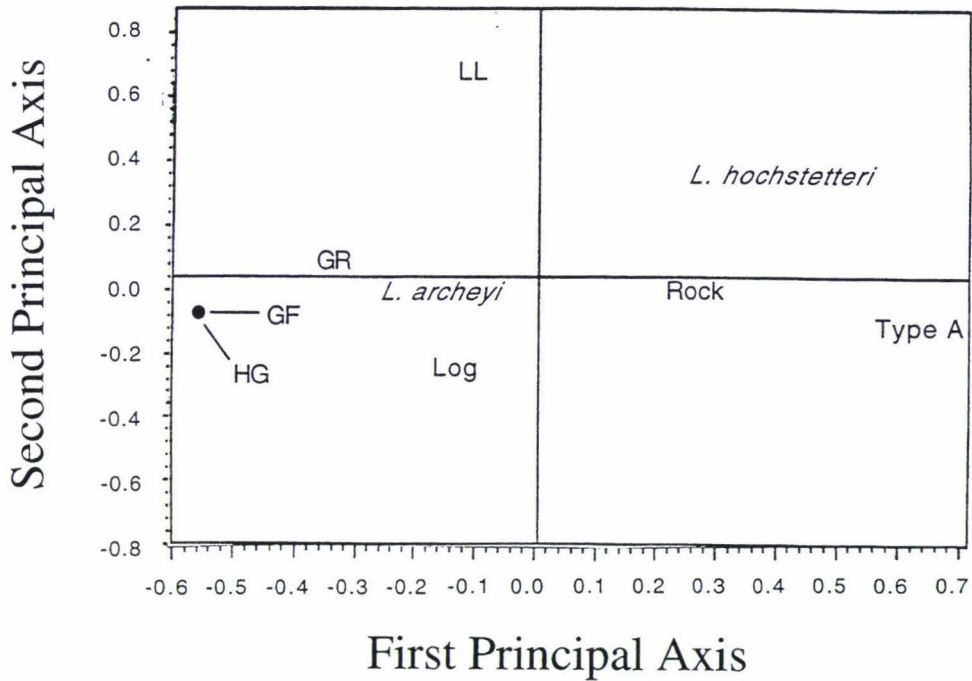
Figure 3.1 Correspondence analysis of *L. archeyi* , *L. hochstetteri* and Type A frogs

in relation to micro-habitat sites in which they were found.

Key :   LL = leaf litter
          GR = rice grass
          GF = ground fern
          HG = hook grass
          Rock = rock sites
          Log = log sites

3.3.3 Inter-specific habitat selection

Daytime retreats for *L. archeyi* were strongly associated with frog snout-vent length
(SVL) *L. archeyi* in vegetation were, on average smaller (SVL $\bar{x}$ = 19.8 mm, range 9.8 -
37.6 mm) than those under rocks (SVL $\bar{x}$ = 27.3 mm, range 13.5 - 37.0 mm) (Figure
3.4).
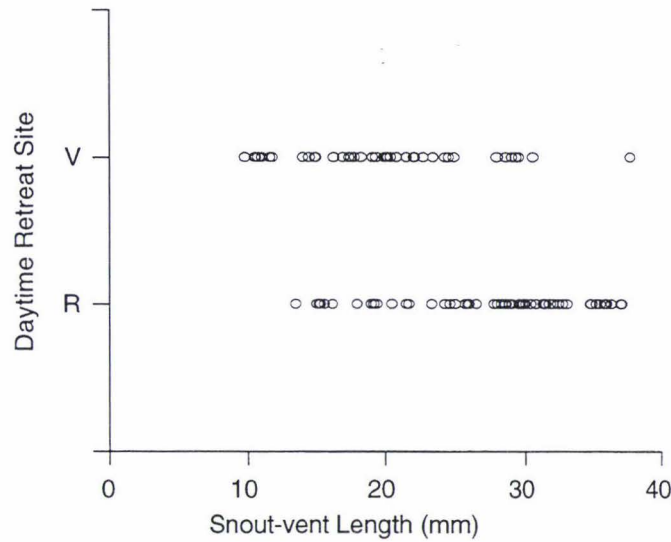
Figure 3.4 Relationship between snout-vent length (mm) and habitat selection in
  L.archeyi.
  Key: V= Vegetation: R = Rock.

3.4   Discussion

The ability for competitive species to utilise their available resources is termed 'resource
partitioning' (Schoener 1965). How resource partitioning determines the abundance,
diversity and distribution of organisms is one focus for ecologists in studies of
community structure (Toft 1985). There are three major categories of resources which
are able to be partitioned. These are habitats, food and time (Schoener 1974, Pianka
1975).

Variation in habitat selection, as a measure to reduce competition have been shown in
many species, such as shrews (Neet and Hausser 1990, Dickman 1995), fossorial lizard
species *Typhlosaurus* spp. (Huey *et. al.* 1974), and *Anolis* lizards (Schoener 1968,
Moermond 1979). Ontogenic changes in amphibian taxa are accompanied by shifts in
diet or habitat and can give rise to major differences in resource use within the same
population of the same species (Learm 1974, Wissinger 1992).

Resource partitioning in *L. archeyi* and *L. hochstetteri* is known to occur in areas of sympatry, as species which overlap occupy different habitats (Bell 1985). In this study I found that the frog community of Whareorino forest was segregated, and frogs occurred in both semi-aquatic and ridge dwelling habitats. True sympatric overlap was noted to occur as one *L. hochstetteri* was recorded in ridge dwelling site. However other individuals had been found but were not recorded (*pers. obs.*). After habitat surveys had been completed, 2 *L. archeyi* were found at the edge of a stream in Whareorino forest. One of these *L. archeyi* was sitting in the same vegetation site as a *L. hochstetteri*.

Further a third group of frogs, 'Type A' were also found to occur in Whareorino forest. These frogs were commonly found under rocks, along ridges, in the same habitat as *L. archeyi*. However Type A frogs appeared to exist in a patchy or clumped distribution in whereas *L. archeyi* were distributed more randomly (*pers. obs.*). I have shown therefore that three distinct groups of frogs appear as a true sympatric population in Whareorino forest. These frogs occupy distinct micro-habitats however a degree of overlap is apparent between all three. This is the first time that a sympatric population of three distinct frog groups has been identified for leiopelmatid frogs.

Further to habitat selection between groups or species of frogs, an ontogenic change within one species of frog was also shown. Differences in habitat selection for adult and sexually immature *L. archeyi* are clear. However the abiotic and or biotic mechanisms that promote this separation within the one species are, at this stage unknown.

Heatwole (1959, 1966) demonstrated that in salamanders and geckos, habitat selection may be based upon the properties of perch surfaces or substrates. Heatwole (1966) found that there was a correlation between the properties of micro-habitats and habitat selection for both intra- and inter- specific groups of frog. Potential mechanisms which would promote this variation in habitat selection for *L. archeyi* may be abiotic, such as differences in humidity, or biotic such as prey preferences. Prey preferences in leiopelmatid frogs will be discussed further in *Chapter 6*.

Intra-specific variation in frog species have been shown. For example; the round frog *Arenophyryn rotunda* (Roberts 1985) occurs in sandy habitats as well as amongst vegetation, i.e. shrub woodland, dense heath and low mixed woodland and at an inter-

specific level retreat sites under rocks and logs is common for terrestrial frogs. An example is *Assa darlingtoni* (Ehmann and Swann 1985). However *A. darlingtoni* has also been found in leaf litter, as were leiopelmatid frogs during this study. This is important daytime retreat site to acknowledge as few monitoring surveys for leiopelmatid frogs include leaf litter surveys (McLennan 1983, McNaughton and Greene 1994, Greene *et. al.* 1995, Whitaker 1996) .

What this means for habitat conservation though is clear. It is simply not just rocky or stream areas that need protection but the whole habitat. Hadden and Westbrooke (1996) suggested that amphibian and reptilian species, particularly terrestrial species are more likely to be affected by changes in habitat rather that fragmentation and reduction of areas. Hadden and Westbrooke (1996) note that detrimental habitat alteration is caused by such factors as such as grazing and/or removal of understory vegetation. In Whareorino forest, many introduced browsers occur, including feral goats *Caprus hircus*, pigs *Sus scrofa*, and possums *Trichosurus vulpecula* and from time to time cattle *Bos taurus* from a local farm occur in part of the frogs range. Therefore, the destruction of the frogs micro-habitat by the action of any of these browsers may be seen as a crucial problem for the potential survivourship of North Island leiopelmatid frog populations.

Conclusion

This study therefore has shown the leiopelmatid frogs occur in a wide range of habitats within the one ecological area. This variation in habitat selection occurs both at an intra-specific and an inter-specific level, which suggests that in monitoring surveys of leiopelmatid populations a wide range of micro-habitats should be searched and that searching in any one particular habitat may bias the results.

CHAPTER FOUR-

MORPHOLOGICAL VARIATION IN LEIOPELMATID FROGS OF WHAREORINO FOREST
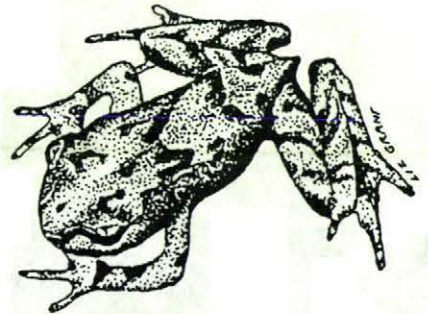
Chapter 4

Morphological Variation in Leiopelmatid frogs Of Whareorino Forest.

4.1 Introduction

The goal of many recent studies on vertebrate populations has been to estimate the amount of variation within or amongst two or more groups. Such variation occurs as morphological, behavioural or genetic differences, and hence variation may be detected within a population by a variety of means. It is important to assess the variation in both natural and manipulated populations because selection occurs on this, and therefore evolutionary adaptation and change depend upon it (Duellman and Trueb 1986, Arnold and Bennett 1988, Weir 1996). Analysis of the 'level' of variation in different populations can also provide evidence of past evolutionary events through which a population has passed (Weir 1996).

Morphology is defined as the form, structure and/or function of an individual (Darwin 1928) and the natural morphological variation between individuals is termed 'morphological diversity' (Roy and Foote 1997). Morphological variation is commonly assessed because it is straight forward and easy to do, both from live and preserved specimens (Hillis 1987). Morphology, however, can also change during growth and development and some animals undergo drastic structural and behavioural alteration during their lifecycles. This is particularly so for species which undergo metamorphosis, i.e. invertebrates and amphibians (Duellman and Trueb 1986). During growth and development, the overall morphology of a species or population is affected by genetic and environmental factors that relate to its ancestry, the ecological niche that it occupies, climatic variables, development and sex (Crome and Richards 1988, Collette 1961,

Thompson and Withers 1997). Evaluation of intra- and inter-populational or intra- and inter-specific variation can therefore provide clues about the abiotic and biotic effects upon a natural population. A close link occurs between morphological and genetic structure, although it has been suggested recently that ecological factors may have a stronger effect on morphological structure, whereas genetic factors are probably more involved in the development of post-zygotic mating barriers (Tregenza and Bridle 1997).

In terms of evolutionary history, relationships within and between taxonomic levels, i.e. 'phylogeny' (Allaby 1992), are hinged upon estimates of relative morphological distance between populations (Roy and Foote 1997). Phylogenetic studies are enhanced by both morphological and molecular studies and this leads to the generation of hypotheses and suggested evolutionary pathways of groups or species (Hillis 1997). However, the relationship between morphological and phylogenetic measures is not interdependent, so it is important to study both factors if the evolutionary history of a population is to be determined (Roy and Foote 1997).

Morphological divergence between species, (inter-specific) and within species (intra-specific) has been a long acknowledged feature of natural populations because of the ability of species to evolve and occupy new niche types. Many factors, however, can initiate and permit the development of intraspecific variation. Such factors include sexual, geographic (i.e. clinal variation or isolation), age-related, ecological or behavioural differences. Maret and Collins (1997) suggest that competition for one or more of these factors can initiate morphological differentiation and if, during any stage, a reproductive isolating mechanism arises, then speciation may occur (Smith 1990, Bush 1994, Losos 1997, Svensson 1997, Tregenza and Bridle 1997). Speciation occurs in three major steps according to Krebs (1985). Reproductive isolation occurs by the development of a physical, or geographic separation within a population, which then evolved independently and adapts (e.g. morphological divergence) and a reproductivly isolating mechanism arises.

Recently, however, evolutionary biologists recognised that speciation can occur in the absence of geographic isolation. Bush (1994) defined speciation in the presence of geographic variation as 'allopatric speciation', which included dichopatric speciation where the groups are physically separated, and peripatric speciation, which results from inbreeding, selection or a morphological or ecological shift. Allo-parapatric speciation, also occurs if initial speciation processes occur due to isolation, but are completed in sympatry. Non-allopatric speciation occurs in the absence of geographic isolation. This can occur as parapartic speciation, i.e. the evolution of sister species during adaptation to continuous but spatially segregated habitats, or sympatric speciation if new sister species evolve within the dispersal range of offspring from a single deme. Hence, in recent years, there has been a shift in evolutionary thought from regarding speciation as a result of random change in populations to the understanding that speciation is a result of adaptation by individuals to a new environment (Tregenza and Bridle 1997).

The leiopelmatid frogs of Whareorino forest

Three distinct groups of leiopelmatid frog exist in sympatry within Whareorino forest (*Chapter 2*). Two of these are the recognised species, *L. archeyi* and *L. hochstetteri*. Both are also known to occur sympatrically in the Coromandel (*Chapter 1*).

L. archeyi are found primarily under rocks and in vegetation along ridge tops, (*Chapter 3*, Bell 1978a) whereas *L. hochstetteri*, a semi-aqautic frog, is commonly found in or near streams. So called 'terrestrial' dwelling individuals have been recorded but the latter are usually within 10 m of water (Bell 1982a, Perfect 1996). Type A frogs, are similar in colour and markings to *L. hochstetteri*, but they lack webbing between their rear toes, have a cream/white ventral surface and a more robust limb structure than *L. hochstetteri* (*Chapter 2*). Type A frogs were found as groups in rock plies or rock 'trails[1]' (*Chapter 3*).

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[1] In Whareorino forest, long 'trails' of rounded mossy rocks often occur between patches of rice grass.

A detailed examination of the complex morphology of leiopelmatid frogs in this forest was conducted as part of my study into the community structure of the frogs of Whareorino forest. This was done to compare the morphology of different frogs, in different habitats, and to show the probable identity of Type A frogs.

4.2 Methods

Field and laboratory research

Twenty-one anatomical features were measured from all leiopelmatid frogs caught during habitat surveys (*Chapter 3*) in Whareorino forest, from March to April 1997. The measurements that were taken are listed below, and are shown in Appendix 4.1.

1. Snout-vent length, from tip of snout to vent (SVL).
2. Head width from right shoulder to left shoulder, perpendicular to snout-vent length (HD).
3. The length of the right radio-ulna to the tip of third toe (RRST).
4. The length of the right astragalus and calcaneum to the tip of fourth toe (RFST).
5. Length of the right femur (FEM*).
6. Length of the left tibio-fibula (TIBF*).
7. Length of the left fourth toe, from 1st meta-tarsal joint to the tip of the toe (rear foot) (R4T*).
8. Length of the left fifth toe, from 1st meta-tarsal joint to the tip of the toe (rear foot) (R5T*).
9. Length of the left humerus (HUM*).
10. Length of the left 4th toe, from 1st meta-tarsal joint to the tip of the toe (front foot) (F4T*)
11. Length of the front 3rd toe, from 1st meta-tarsal joint to the tip of the toe (front foot) (F3T*)
12. Width of the gap between the closest anterior points of the eyes (ANTE).
13. Width of the gap between the closest posterior points of the eyes (POTE).
14. Width of radio-ulna, closest to joint with humerus, but perpendicular to line of radio-ulna (RADU).
15. Distance from humerus/shoulder joint to the tip of the snout on right side, (SNT*)
16. Length of the left femur (FEM*).
17. Length of the right tibio-fibula (TIBF*).
18. Length of the right fourth toe from the 1st meta-tarsal joint to tip of the toe (rear foot) (R4T*).
19. Right side, third toe length, from the 1st meta-tarsal joint to tip of the toe (front foot) (F3T*).
20. Length of the right humerus (HUM*).
21. Distance from humerus/shoulder joint to the tip of the snout on left side (SNT*).

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*Measurements averaged for analysis

Measurements were obtained to the nearest 0.5 mm directly from frogs in the field, using vernier callipers.

Data was recorded on a standard morphological data sheet (Appendix 4.2). Each individual was then photographed and released where it was captured. The location of each capture/release site was recorded and is deposited with the Department of Conservation (Waikato Conservancy). Some additional measurements were obtained from photographs of frogs caught in Whareorino forest before this part of the study commenced. The calculation of magnification was obtained from comparison of standard measurements recorded at the time the photograph was taken, and their length on the photograph (*Chapter 2*).

Potential observer effects were avoided by having the same observer take the measurements from all frogs during this research. The same observer also read and recorded the data which was obtained from photographs.

The raw morphological data is included as Appendix 4.3.

Micro-habitat information was recorded at the point of capture for both field and photograph measured frogs. Frogs in their daytime retreat sites were assigned to the categories as detailed in *Chapter 3*.

This was: *L. archeyi* in either 'vegetated' (AV) sites or sites under rocks or logs (AR).

L. hochstetteri around streams (HO) and ridge dwelling Type A individuals (TA).

Data analysis

Limb measurements taken from the left and right side of each individual were combined to give an average limb length.

A canonical variate analysis was used to determine if there were any difference between measurements taken in the field and those obtained from photographs.

Inter-specific morphometric variation between the groups of frogs (*L. archeyi, L. hochstetteri* and Type A) was examined using Canonical Variate Analysis (CVA). Intra-specific variation in *L. archeyi* only, was examined because insufficient *L. hochstetteri* and *L. archeyi* individuals were found. For analysis, identical variables taken from the left and right side of the frog were combined and an average of the two used. Also any variable found to be non-significant during analysis was discarded.

All analyses were conducted by using SAS® version 6.12, for Windows®, 1989-1996, SAS Institute Inc. USA.

4.3 Results

4.3.1 Comparison of field and photograph data

Canonical variate analysis of four morphological variables, snout-vent length (SVL), head width (HD) tibia-fibula length (TIBF) and femur length (FEM), were used to show that data obtained in the field and data obtained from photographs was not significantly different (Duncan's Multiple Range Test; α = 0.05, field data $\bar{x}$ = -0.0920, n = 95; photograph data $\bar{x}$ = 0.2081, n = 42) (Figure 4.1).
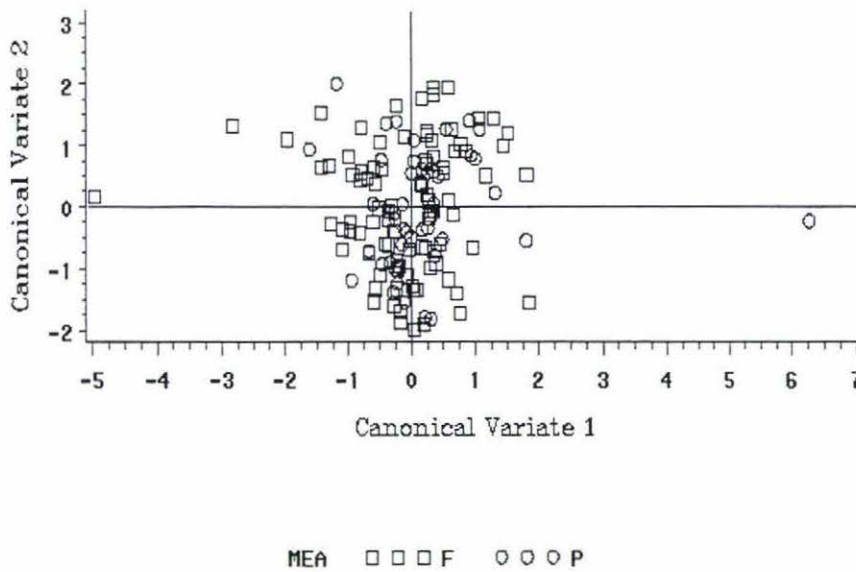
Figure 4.1 Canonical variate analysis of leiopelmatid frogs measured in the field and those measured from photographs.

Key: = individuals measured in the field
O = individuals measured from photographs

4.3.2 Morphological variation between *L. archeyi, L. hochstetteri* & Type A frogs.

The three groups of leiopelmatid frog found in Whareorino forest separated out significantly (Wilks' Lambda = 0.1894, D.F. = 42, F. = 5.6985, p = 0.0001) when their morphological measurements were subjected to a canonical variate analysis (Figure 4.2, Table 4.1). A high degree of overlap occurred between *L. archeyi* found in rock habitat and these found in vegetation. However, little overlap occurred between Type A individuals and either of the *L. archeyi* groups or between Type A individuals and *L. hochstetteri*. Little overlap also occurred between *L. hochstetteri* and either of the *L. archeyi* groups. The separation of these groups occurred principally because of their snout-vent length (SVL), head width (HD), head length (SNT), tibia-fibula length (TIBF), femur length (FEM), and distance between the eyes at the anterior (snout) end (ANTE) (Table 4.2). The pooled within canonical structure and the pooled within-class standardised coefficients are given in (Appendix 4.4 and 4.5).

Separation along the first canonical variate accounted for 71.6 % of the variation between groups (Table 4.3), and the means of their canonical scores were significantly different (Tukey's Studentised Range test; $\alpha = 0.05$). The second canonical accounted for 22.5 % of the variation.

The difference between the three groups is significant so that the first canonical variate provides a very good means of identifying which group each frog belongs to. Discriminant analysis of the data using a linear function provided correct classification of 81.0 % of *L. archeyi*, 53.3 % of *L. hochstetteri* and 73.68 % of Type A individuals (Table 4.4).
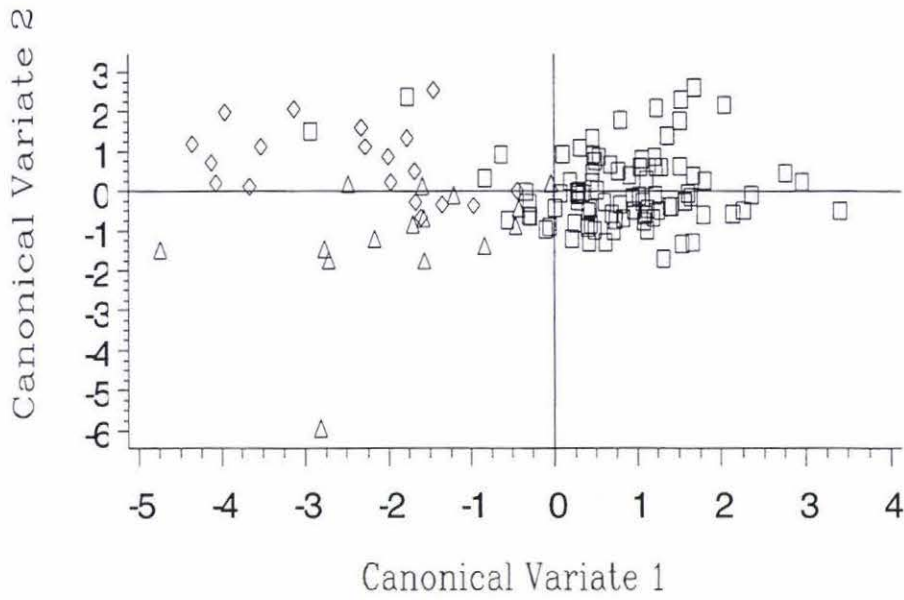
Figure 4.2 Canonical variate analysis of the complex morphology of *L. archeyi*,

L. hochstetteri, and *Type A* frogs from Whareorino forest.

Key:☐ = *L. archeyi*
    Δ = *L. hochstetteri*
    ◊ = Type A frogs

Table 4.1 Class means for the canonical structure of morphological variation in *L. archeyi*,

L. hochstetteri and Type A frogs (as shown in Figure 4.2)

Spp	CAN1	CAN2
L. archeyi	0.816759990	0.037384534
L. hochstetteri	-1.808740612	-1.155890911
Type A	-2.440909995	0.735460822

Table 4.2 Table of parallel discriminant ratio coefficients for canonical variate analysis.

Variable	CAN1	CAN2
SVL	0.307871329	-0.738098702
HD	0.448781206	0.448795819
RRST	-0.012630133	0.642447995
RFST	-0.084275623	0.294164319
TIBF	0.200256283	-0.525094664
FEM	-0.137019477	0.060472328
POTE	-0.007883866	-0.189910603
ANTE	0.175702055	0.552185971
SNT	0.047125068	0.736339591
RADU	0.105313163	-0.335191591
R5T	-0.017725313	0.197999403
F4T	-0.000789084	-0.066583096
F3T	-0.000194811	0.135014282
R4T	0.089138416	-0.208526354

Table 4.3 Eigenvalues from a CVA of frogs from Whareorino forest.

	Eigenvalue	Difference	Proportion	Cumulative
1	1.8785	1.2873	0.7163	0.7163
2	0.5912	0.4384	0.2254	0.9418
3	0.1527	.	0.0582	1.00

Table 4.4 Cross-validation of species classifications by a linear discriminant analysis.
Number in brackets is percentage of total

From SPP	*L archeyi*	*L. hochstetteri*	Type A	Total
L. archeyi	81	5	4	90
	(90.00)	(13.73)	(4.44)	(100.00)
L. hochstetteri	3	8	4	15
	(20.00)	(53.33)	(26.67)	(100.00)
Type A	1	4	14	19
	(5.26)	(21.05)	(73.68)	(100.00)
Total	85	17	22	124
	(68.55)	(13.71)	(17.74)	(100.00)

4.3.3 Canonical variate analysis of *L. hochstetteri* and Type A frogs

The appearance of Type A individuals in the field was most similar to *L. hochstetteri* so a further canonical variate analysis was conducted to confirm the degree of morphological similarity between the two groups. This analysis confirmed that *L. hochstetteri* and Type A individuals are morphologically distinct (Figure 4.3). This was significant on a Tukey's Studentised Range test; $\alpha = 0.05$; *L. hochstetteri*, $\bar{x} = -1.5059$; Type A, $\bar{x} = 1.1889$, D.F. = 32.
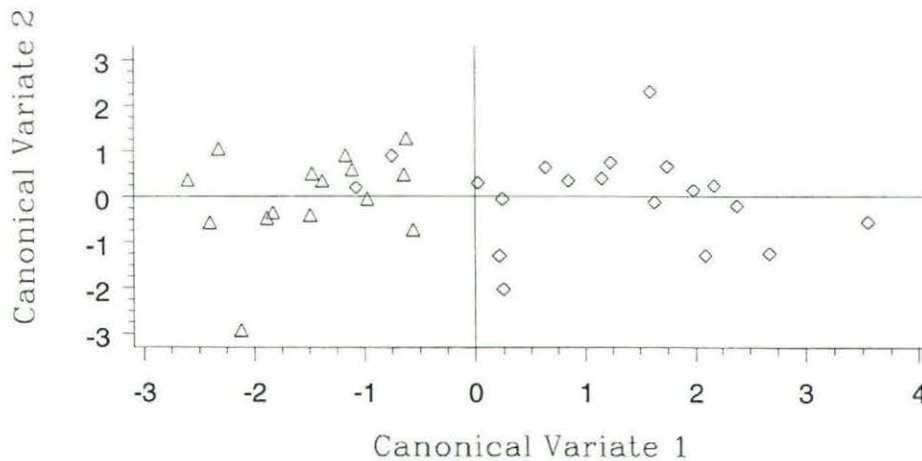
Figure 4.3 Canonical variate analysis of morphological variation between *L. hochstetteri*; n = 14, and Type A individuals, n = 19, from Whareorino forest.

Key: Δ = *L. hochstetteri*,
$\lozenge$ = Type A frogs

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4.3.4 Intra-specifc morphological variation

L. archeyi

Canonical Variate Analysis of *L. archeyi* morphological data showed the relationship that occurs between morphology and habitat selection. *L. archeyi* individuals found in vegetation clustered to one end of the first canonical variate ($\bar{x}$ = -0.8583, n= 40) and individuals that were found under rocks or logs at the other end of the first canonical variate (1st canonical $\bar{x}$ = 0.6835, n= 50) (Figure 4.4). This morphological difference was significant (Tukey's Studentised Range test; α = 0.05, *L. archeyi* - rock dwelling,

$\bar{x}$ = 0.6866, n = 50; *L. archeyi* - vegetation dwelling, $\bar{x}$ = -0.8583, n = 40). This trend has been correlated with frog size (SVL) (*Chapter 3*), as smaller frogs are generally found in vegetation and larger frogs more often occur under rocks.
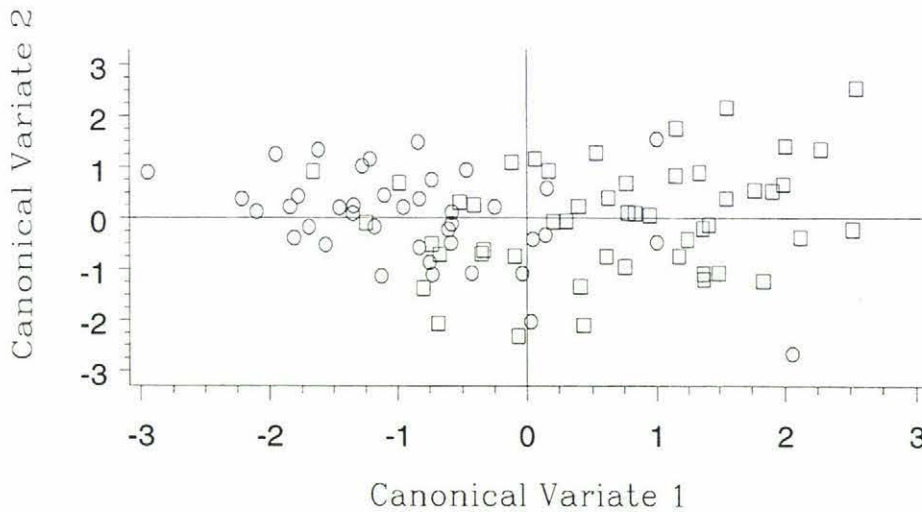
Figure 4.4 Canonical Variate Analysis of morphology within *L. archeyi* individuals from two habitats in Whareorino forest.

Note:☐ = *L. archeyi* individuals found under rocks or logs

○ = *L. archeyi* individuals found within or associated with vegetation

Source = Spp, DF = 1, Mean Square = 53.04, F Value = 53.04, Pr > F = .0001.

4.4 Discussion

The leiopelmatid frogs of Whareorino forest were only recently discovered in 1991 (Bell 1993, Thurley and Bell 1994). However the potential of finding another species of frog, is remote, but it cannot be discounted particularly, while description of the New Zealand biota is still new. In recent years a new species of Tuatara *Sphendon guntheri* and new species of skinks *Leiolopisma* spp. have been described (Daugherty *et. al* 1990, Patterson and Daugherty 1990, Cree *et. al.* 1995) so there is the potential to find new species. The cryptically similar Maud Island and Stephen's Island frogs have only recently been recognised as distinct species after many years of research on both populations (Bell *et. al.* 1998). In recent years authors have queried the apparent lack of diversity within the genus *Leiopelma*, given that a lack of mammalian predators and a long period of evolutionary development would have permitted such diversification. This is certainly true for species of geckos and skinks (Daugherty *et. al.* 1993b).

This study has clearly shown that three morphologically distinct groups of leiopelmatid frog do exist in a small area of Whareorino forest studied. Two are described species, the third poses a complex ecological question and awaits further study and an explanation. From the results of my study, the most probable explanations for this frog group is that either a new species of leiopelmatid frog or an extant population of a frog previously thought to be extinct.

Comparison of Whareorino frogs with other leiopelmatid frog populations

The ratio of femur length to length of tibia-fibula in adult frogs suggests that all Whareorino frog populations are different from all other known native frogs in New Zealand. This may in part be because I only measures live individuals whereas Worthy (1987a,b) used subfossil material as well as data from live individuals.

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Cluster analysis of femur to tibia-fibula length ratios suggest that Type A frogs ($\bar{x} = 0.9898$) are most closely related to *L. markhami* ($\bar{x} = 0.99$), an extinct species. *L. archeyi* and *L. hochstetteri* both grouped separately from Type A individuals, as did the extinct frog *L. auroraensis* ($\bar{x} = 0.9836$, $\bar{x} = 0.9993$, $\bar{x} = 1.03$ respectively). Other populations of *L. archeyi* and *L. hochstetteri* both clustered closely with *L. hamitoni* data[2] and these were distantly similar to *L. waitomoensis*.

Comparison of radio-ulna length

Comparison of the mean, maximum and minimum length of the radio-ulna in leiopelmatid frogs gave a clear separation of Type A individuals from other Whareorino frog species. Type A frogs ($\bar{x} = 11.633$) were found to separate from both other Whareorino frog as well as other extant frog populations. Significantly Type A frogs were found to cluster most strongly with two groups of *L. markhami*. However it is noted that the use of 'live' material does confound this cluster analysis. This is evident by the clustering of Whareorino *L. archeyi* with *L. auroreansis* .

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[2] *L. hamiltoni* data includes both *L. pakeka* and *L. hamiltoni* morphological data
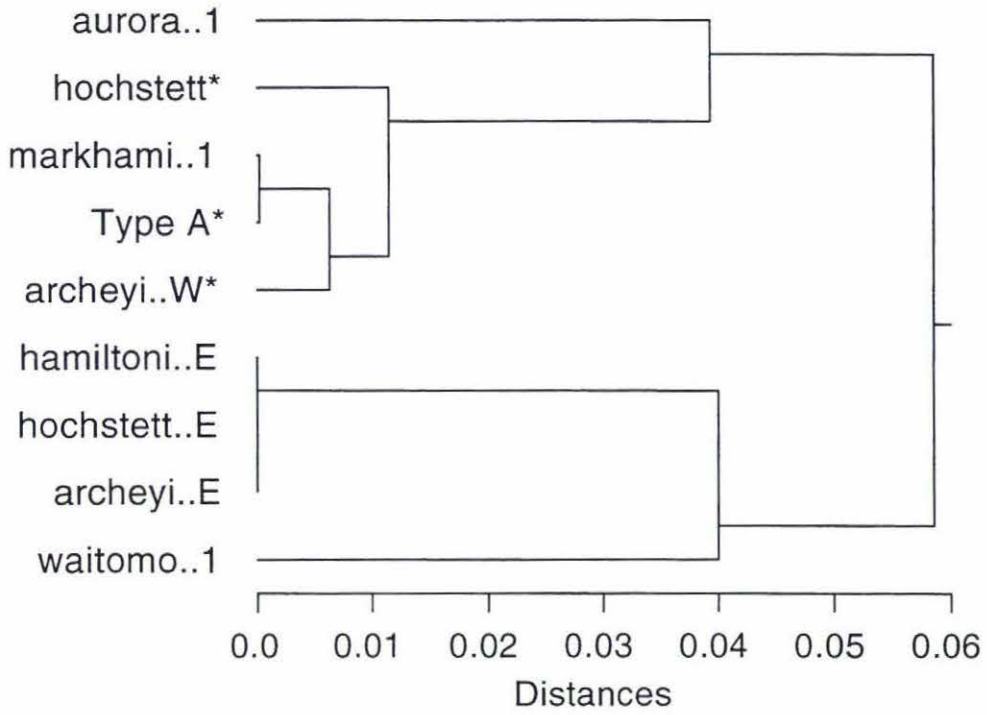
Figure 4.5 Ratio of femur to tibia-fibula length in extinct and extant leiopelmatid frogs.

aurora..1 = *L. auroreansis*

hochstett* = *L. hochstetteri*, Whareorino population

markhami..1 = *L. markhami*

Type A* = Type A individuals, Whareorino population

archeyi..W* = *L. archeyi*, Whareorino population

hamiltoni..E = *L. hamiltoni*, extant population

hochstett..E = *L. hochstetteri*, extant population

archeyi..E = *L. archeyi*, extant population

waitomo..1 = *L. waitomoensis*
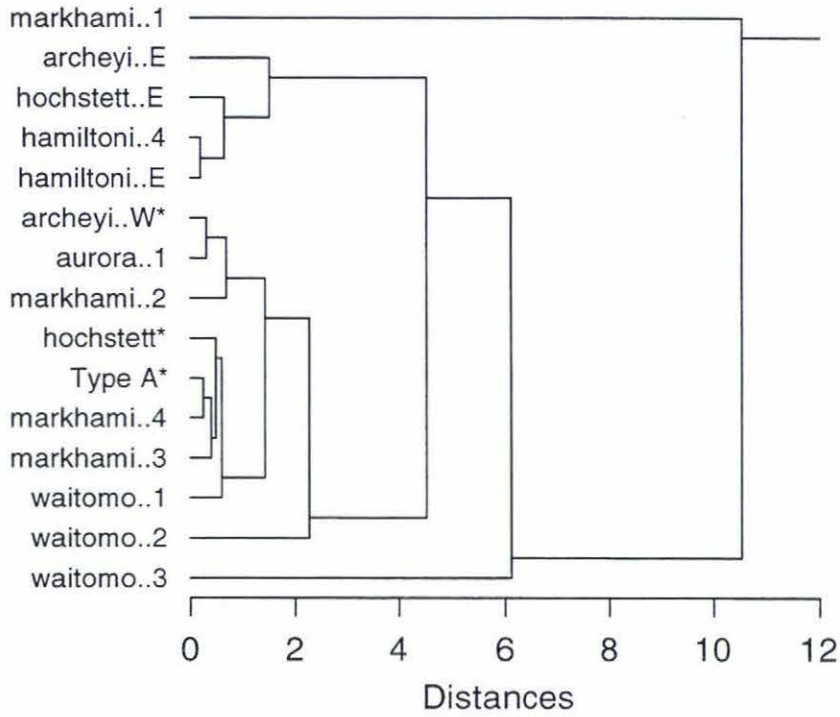
Figure 4.6 Comparison of radio-ulna length in extinct and extant leiopelmatid frogs.
aurora..1   = *L. auroreansis*
hochstett* = *L. hochstetteri*, Whareorino population
markhami..1 = *L. markhami*
Type A* = Type A individuals, Whareorino population
archeyi..W* = *L. archeyi*, Whareorino population
hamiltoni..E = *L. hamiltoni*, extant population
hochstett..E = *L. hochstetteri*, extant population
archeyi..E = *L. archeyi*, extant population
waitomo..1 = *L. waitomoensis*
(Note: variables 1,2,3 or 4 after a species name refer to samples from different sites in Worthy 1987a or b)

This therefore suggests that Type A frogs may be more likely to be related to *L. markhami* than to any extant species. The possibility that Type A frogs are either *L. hamitoni* or *L. pakeka* is discounted at this stage. The closeness of *L. archeyi* and *L. auroreansis* may be partially due to the Whareorino frog, *L. archeyi*, being morphologically larger than other *L. archeyi* populations (Thurley and Bell 1994).

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The extinct leiopelmatid frogs have been described from sub-fossil remains found in deposits (caves) throughout the North and South Islands of New Zealand. Some of these are as recently as 300 years ago (Worthy 1987a,b, *Chapter 1*).

The suggestion is that *L. markhami*, *L. auroreansis*, and *L. waitomoensis* may have become very recently extinct and this may have been linked to the arrival of mammals to New Zealand (Towns and Ballantine 1993). Worthy (1987b), suggested that all three species were terrestrial frogs.

Of the extinct species, *L. auroraensis* is only known from one specimen. This was found in Aurora Cave near Lake Te Anau, and (Worthy 1987b) suggested that this has only recently become extinct. *L. markhami*, was found in both the South Island and from Haggas Hole, near Whareorino forest, as well as from various other localities in the North Island (*Chapter 1*). The most recent sub-fossil deposit where it is found is dated as approximately 2350 years b.p.

Type A frogs look very different from both *L. archeyi* and *L. hochstetteri*. They have muscular limbs, and are more robust. However when it was first found it was identified as *L. hochstetteri* (Eggers *et. al.* 1997). Therefore if this frog is not a new species, then it maybe a morphological variant of *L. hochstetteri* because they were more similar to this than any other frog. It is necessary to consider how such variation could occur in order to examine this hypothesis.

Resource partitioning (Schoener 1965) refers to the way in which species differ in their use of resources such as habitat, food and time (Pianka 1975). Toft (1985) recognised that ecologists are interested in this partitioning because of how it affects the distribution, abundance, and diversity of organisms. Adaptation occurs within organisms to allow them to efficiently use resources in their environment, and morphological variation that is due to this adaptation has been termed 'ecomorphology' (Birt *et. al.* 1997). Such ecomorphological variation has been shown in African finch bills, *Pyrenestes* (Smith 1993), tongues of Australian bats (Birt *et. al.* 1997) and anurans dentition (Das and Coe 1994).

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Ecomorphology can also be related to variation in maximum size and this can occur both within and between species. In the former it reduces competition for resources between sexes, examples are, head size in hooded seals *Cystophora cristata* (Whg 1985), body size in sugar and squirrel gliders (Quin *et. al.* 1996) and morphological variation in fossorial lizards (Huey *et. al.* 1974). Sexual differences in maximum body size also occur in amphibians, as females are often larger than males (Zug 1993). Such dimorphism is thought to have been evolved to facilitate the laying of larger eggs or clutch sizes (Duellman and Trueb 1986).

Intra-specific variation can also occur as a result of geographic variation. Commonly this occurs in widespread species where individuals or groups of individuals experience variation in climatic regimes (James 1970). An example is Bergmann's ecogeographic rule. Such size variation within a species was initially thought not to have adaptive significance, but later evidence suggested that increased mass provides a physiological advantage with respect to cold tolerance, particularly in homeotherms (James 1970, 1983). Bergmann's ecogeographic rule applies to many species and examples include house sparrows *Passer domestics* (Murphy 1985) and other birds (James 1970), as well as mammals, such as raccoons *Procyon lotor* (Kennedy and Lindsay 1984), suger and squirrel gliders *Petaurus breviceps* & *P. norfolcensis* (Quin *et. al.* 1996) and kangaroo rats, genus: *Dipodomys* (Baumgardner and Kennedy 1993). However such latitudinal effects can also be due to other factors such as seasonality, prey availability, and/or competition levels (Yamazaki *et. al.* 1983, Zeloff and Boyce 1988, Baumgardner and Kennedy 1993).

Previously, a strong correlation was found between individual morphology and niche utilisation, e.g. Learm 1974. Similarly ecomorphs within several species of Anolis lizards have also been described (Moermond 1979). However, the properties which prevent intra-specific groups from occupying different or the same areas often remain unknown.

Cases also exist where morphological variation between geographically separate populations occur, but the causes are unknown. Such variation was reputed for brushtail

possums *Trichosurus caninus* (Lindenmayer *et. al.* 1995) where no consistent pattern explained the observed morphological and colour variations.

Few studies have been published which consider intra-specific morphological variation of anuran species. One study, however, of isolated (island) populations of the Seychelles treefrog *Tachycnemis seychellensis* showed that a high level of intra-population geographic variation occurred both within and between all populations of this frog. A suggestion was that variation resulted from rapid divergence in each of the isolated populations (Nussbaum and Wu 1995).

A study of the morphological variation in corroborree frogs, *Pseudophyne corroborree* combined morphological analysis with genetic analysis of two populations which clarified the observed morphological variation as actual speciation (Osbourne *et. al.* 1996). Another recent anuran study considered the ecomorphological colouration and patterning of some species of dendrobatid frogs. A vast array of colour and pattern variation occurs in one species *Dendrobates pumilio*, and this contrasts with two other sympatric species, where there is little such variation (Summers *et. al.* 1997). Morphological variation was combined with a genetic comparison of the three species, and resulted the hypothesis that neutral divergence had occurred in the sympatric species whereas divergence had arisen in the allopatric species. In contrast Austin and Knott (1996) found that the observed morphological variation in freshwater crayfish may not always be correlated with variation at the genetic level but it is more related to ecological factors which affect the individual.

Divergence can occur within a population if individuals are presented with the opportunity to adapt or evolve to a new resource. An example of one such resource is habitat. Clearly similarities between the semi-aquatic frog, *L. hochstetteri* and the terrestrial Type A frog occur and these include similar colours and leg patterning. Differences, however, occur in the body shape and the intra-toe webbing. It could thus be suggested that these observed differences are the result of adaptation of *L. hochstetteri* to a more terrestrial environment. This is supported by an evolutionary hypothesis which proposes that occupation of a

terrestrial habitat is a result of evolutionary adaptation, in order to avoid competition or predation in the aquatic of semi-aquatic habitat (Crump 1996) .

Previous research on *L. hochstetteri* (Slaven 1992, Perfect 1996) noted individuals which occurred away from stream populations. Perfect (1996) found that the terrestrial *L. hochstetteri* were significantly larger than those in streams. This could result if smaller individuals are limited to the moist environment because of their larger body size to surface area ratio, (Bentley 1996). Apart from their snout-vent length the complex morphology of these terrestrial individuals has not been studied till now.

In Whareorino, Type A frogs were found in distinct clusters, indicating that re-location away from stream habitat has not occurred as a chance event but as an adaptation of individuals into another habitat. This may have arisen over along time if some *L. hochstetteri* became isolated, and independent evolution occurred.

L. hochstetteri, may once have occurred over a much larger range throughout a forest, such as Whareorino, at a time when more 'wet' areas occurred, i.e. streams and swamps. For example, during the late Cretaceous, New Zealand had a cool or cold-temperate climate (Cooper and Milliner 1993). During the Paleocene and Eocene, however, there was rapid warming towards subtropical temperatures, associated with an increase in rainfall. Cooling occurred during the late Eocene to Oligocene epohs, till warming occurred again during the early Miocene. Throughout the late Miocene, the Pliocene there was again cooling (Cooper and Milliner 1993). During these periods of warming and cooling, the amount of rainfall on New Zealand was affected as the New Zealand 'group' become wetter during the warmer periods, and drier during the cooler periods.

During these wetter periods, there would have been more streams, swamps and wet areas than what presently exist. Possibly the 'rock trails' of rounded[3] mossy rocks which occur throughout Whareorino forest are evidence of such previously wet areas.

It may be possible for individuals to have become isolated in these areas, by dry land as the climate changed. Isolated individuals would then have, interbred and possibly evolved and

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[3] rounded rocks often have often been linked to a stream habitat, as the action of the water flow, and the tumbling of the rocks creates smooth rounded rocks.

adapted to a more terrestrial habitat. Adaptation would include the development of larger limb structures and the loss of webbing from between the toes (Duellman and Trueb 1986). Assumptions of this 'dry-land barrier' hypothesis is that, firstly, the formation of dry land areas were impassable to semi-aquatic frogs, and secondly that the rate of climatic change was equal to or slower than the rate of evolutionary change in the frogs. If one of these did not hold, then the frogs would have died out.

Support for this hypothesis is found in the variation within salamanders of the *Ensatina eschscholtzii* complex Wake (1997). Wake (1997) suggested that they have undergone long periods of range contraction, isolation and differentiation. However, such strongly defined ecomorphological types are uncommon in closely associated (i.e. sympatric) populations, because the chance of interbreeding is high. If such interbreeding occurred between these two groups then it would then be expected that an intermediate morphological version of Type A and *L. hochstetteri* individuals would show on a canonical variate analysis as an intermediate group. None, however, occurred in this study although only a small number of frogs were found.

Hybridisation

A third major suggestion that could explain Type A frogs in Whareorino forest, is that they are a hybrid between *L. hochstetteri* and *L. archeyi*. The potential for interbreeding between these two species does exist because both species are occasionally found together in the same daytime retreat site (Stephenson and Stephenson 1957). However recent studies have shown that *L. hochstetteri* and *L.archeyi* have sufficiently different chromosomal structures which would prevent successful interbreeding. Both species also have different reproductive behaviour and early development and these may also prevent interbreeding (Bell 1985). Therefore interbreeding seems unlikely is unlikely between the two species, and it is unlikely that Type A individuals are the product of hybridisation.

The suggestion that Type A frogs are different from *L. archeyi* and *L. hochstetteri* at the sub-specific or specific level is supported by two main field observations;

1. There is little morphological overlap, although habitat overlap occurs between stream-dwelling *L. hochstetteri* and terrestrial Type A individuals. For instance, *L. hochstetteri* frogs have been found in terrestrial areas, although close to streams where Type A individuals also occur.

2. Difference in habitat (*Chapter 3*) and morphology are clear, so if *L. hochstetteri*, and Type A frogs are the same species then this raises questions about the reproductive biology of *L. hochstetteri*. *L. hochstetteri* is semi-aquatic and has very different breeding behaviours from terrestrial leiopelmatids. *L. hochstetteri* eggs are not brooded by a male frog, although occasionally a frog has been found near clutches, and the larvae undergo a brief aquatic stage (Bell 1985). Both behaviours would probably prevent successful terrestrial breeding by *L. hochstetteri* away from streams.

Intra-specific morphological variation

I also found morphological variation within *L. archeyi*. This was found to be related to habitat selection (*Chapter 3*).

L. archeyi individuals occur in two main daytime retreat sites; under rocks or in clumps of grass. Individuals were also occasionally found in other habitats such as under logs or in leaf litter (*Chapter 3*). Comparison of daytime retreat with morphology of the frogs found there was a strong correlation between daytime retreat site and individual size, as determined by snout-vent length (SVL). Young individuals, therefore, hatch as terrestrial larvae under rocks and logs and appear to develop as juveniles and sub-adults in vegetation, principally rice grass *Uncinia uncinata*, and return to rock (and log) habitat at sexual maturity. It is under these rock/log retreat sites that mating, egg deposition and attendance occurs (*Chapter 5*).

Such separation of juvenile and sexually mature individuals can evolve in a population for several reasons, including competition, resource selection, and micro-habitat preference (Moermond 1979). Exclusion due to competition have been a long acknowledged component of populations (Hutchinson 1968, Pianka 1973, 1975). This exclusion can

occur either directly, such as by predation, or indirectly, as for example by competitive exclusion where the adults of a population fill all the available habitat sites. In this example the adults occupy the rock and log daytime retreat sites, and juveniles are thereby forced to use other sites. Other factors such as resource selection may also lead to intra-specific age-related distribution. Vegetated sites may, for example be the areas where appropriately sized prey occur or they may be the sites where micro-habitat variables, such as humidity are more suitable.

Conclusion

I have clearly shown that the morphology in leiopelmatid frogs is variable, both between and within species or groups. Further research is required to address the questions raised by my study, particularly in regard to the taxonomic status of the morphologically different Type A frogs. Further studies are also required in other populations so that clearer pictures of native frog community structures can be obtained.

CHAPTER FIVE-

EARLY DEVELOPMENT IN
L. ARCHEYI
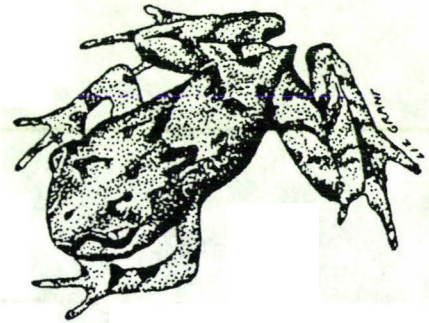
Chapter 5

Early Development in *Leiopelma archeyi*

5.1 Introduction

The first endemic frog to be described in New Zealand was a specimen of *Leiopelma hochstetteri*, by A. S. Thomson in 1852 (Fitzinger 1861). Since this description, three extinct (Worthy 1987a), and four extant species of endemic frog have been identified (Bell *et. al.* 1998).

All New Zealand frogs belong to the endemic genus *Leiopelma* (Anura: Leiopelmatidae). They possess many distinguishing features which indicate that they are ancient in palaeobiological terms (Worthy 1987b). These include the presence of nine presacral vertebrae and the retention of free ribs and two tail-wagging muscles in adults. They also have small clutches of very large eggs, and no vocal sac or ear drums. These frogs are terrestrial or semi-terrestrial, and amplexus, egg laying and parental care of eggs and tadpoles all take place on land.

Of the four extant species, *L. hamiltoni* and *L. pakeka* (Bell *et. al.* 1998) occur as single isolated island populations at the top of the South Island (*Chapter 1*). *L. archeyi* is restricted to isolated populations in the Coromandel region and in the Northern King Country, where it can occur sympatrically with the more widespread *L. hochstetteri* (*Chapter 2*). The latter, a semi-aquatic species, is present in scattered populations throughout the top third of the North Island (Green & Tessier 1990, Newman 1996).

The terrestrial reproduction of leiopelmatid frogs has drawn much interest since Gilbert Archey (1922) first documented the early development in what he believed to be *L. hochstetteri*. However, Turbott (1942) described Archey's specimens as a new species, *L. archeyi*. Archey, along with others noticed that breeding in this species occurred under

rocks or logs in cool damp areas of forest (Archey 1922, Stephenson 1951, Stephenson & Stephenson 1957, Stephenson 1961, Bell 1978a, 1982b) during November and December. Clutches of eggs have also been recorded in vegetation, such as in crown ferns *Blechnum discolour* (Thurley & Bell 1996). Amplexus occurs in the pelvic position after which the female may lay up to 14, 4 - 5 mm eggs, which have large unpigmented yolks (Stephenson 1961, Bell 1985). These eggs are then are guarded throughout incubation by a brooding male frog. Bell (1978a, 1985) noted that a male frog may be present at a breeding site months before oviposition occurs. Male association with egg clutches, such as occurs in *Leiopelma*, has been discussed by several authors. Salthe and Meechan (1974) suggest that males agitate the eggs either to help diffusion of oxygen and wastes around the eggs, or to prevent the yolks from stratifying in the early stages of development. Other suggestions are that the presence of the male ensures external fertilisation, that the males' urine may provide water to the larvae and/or prevent contamination of the eggs by pathogens, and that the males may guard/protect the eggs from natural predators (Stephenson 1961, Bell 1982a, Zug 1993, Stebbins & Cohen 1995).

Leiopelma archeyi hatch after 8 or 9 weeks (Bell 1978a) when the larvae *'pierce the capsule with rotating movements of their tails'* (Stephenson 1961). The newly hatched froglets then stay with the remains of the egg capsule for some days before climbing onto the back of the brooding male. Here they remain until they metamorphose six to nine weeks after hatching (Bell 1978a, 1980, 1985). During this period the tail becomes progressively reduced and the limbs develop fully. The entire time from when the eggs are laid until metamorphosis is complete takes between 14 and 19 weeks (Bell 1978a).

Biotic and abiotic factors such as competition, predation, pathogens, ambient temperature, rainfall and day length can affect amphibians at various stages of their development (Berven 1990, Cohen & Alford 1993, Williamson & Bull 1994). To further understand the population dynamics of a species with a complex life cycle, such as an amphibian, it is necessary to know the rate of growth and survival of individuals during each life-history stage (Cohen & Alford 1993).

Because leiopelmatid frogs are small, cryptic, nocturnal species that often persist in remote forest remnants, the ideal situation in which to observe and measure rates of growth of these species is in captivity. As yet, however, captive rearing of leiopelmatid frogs to the sub-adult stage has met with limited success (B. D. Bell *pers. comm.*). There is therefore a need to improve techniques for rearing and maintaining individuals in captivity. This is especially important in case the remaining wild populations of leiopelmatid frog, which are threatened at present decline further (Groombridge 1993, Newman 1996).

The aim of this study was, therefore, to comprehensively document the early development and growth of one species of leiopelmatid frog, and to further develop captive incubation, rearing and maintenance techniques.

Definitions

Most frogs go through an egg, aquatic tadpole and terrestrial or semi-terrestrial adult phase during their lifecycle (Duellman & Trueb 1986, Zug 1993). However, the tadpole phase in leiopelmatid frogs is completed within the egg. Here I use the following terms to refer to the main stages of development:

Larva - larva undergo development within the egg and the stage ends at hatching.

Froglet - this stage starts immediately after hatching when the tail is still present, and ends when the tail is completely absorbed, the limb buds develop into complete limbs, and the oral ingestion of food begins.

Frog - In this stage food is ingested and individuals are independently mobile. In *Leiopelma* the young frog is referred to as a juvenile then a sub-adult till sexual maturity occurs at 3-4 years of age (Bell 1978a).

5.2 Methods

5.2.1 Intra-capsular development

Ten *L. archeyi* eggs were gathered on 19 December 1996 from two separate egg clusters found under the same rock in Whareorino forest. Each egg cluster was brooded by a different coloured male frog.

Cluster A; Initially incubated by a green male, this cluster consisted of eleven eggs, all of which were held within a gelatinous matrix. The matrix was cut and six eggs removed. These six eggs were maintained throughout incubation as a single cluster.

Cluster B; Initially incubated by a brown male, this cluster consisted of nine eggs. However, it had been damaged, so that four of the eggs had been physically separated from the others. Only these separated eggs were removed. They comprised a pair of eggs bound together by gelatinous matrix and two separate, single, eggs. The pair of eggs were labelled as Group B1 and the single eggs as, Group B2 and Group B3.

Each group of eggs was transported to controlled temperature cabinets in the laboratory in an individual large specimen vial lined with damp capillary matting and cotton wool. Initially the groups of eggs were incubated on damp capillary matting in individual glass containers at 13°C without light (Plate 5.1). Holes covered with filter paper provided for ventilation. The eggs were washed once a day with chilled distilled water (15°C) and the capillary matting and glass containers were cleaned with distilled water every seven days.

The anti-fungal agent, Stress-coat®was occasionally added to the distilled water (2 drops of agent per 500 ml water). This appeared to have no effect on the eggs, larvae or froglets at any stage of their development.

The eggs were weighed and photographed at weekly intervals until they hatched. The diameter of each egg was calculated separately from the photographs, by averaging two measurements taken perpendicular to each other.

Post-larval development

After hatching the froglets were kept in individual glass containers. Ventilation was provided by vent holes covered with filter paper. The floor of each container was lined with damp capillary matting and rehydrated Crystal Rain® crystals. The latter helped maintain a high humidity. The froglets were incubated at either 15°C or 11°C for 150 days after hatching. Thereafter they were maintained in the same controlled temperature room at 14°C - 15°C. (Table 5.1).
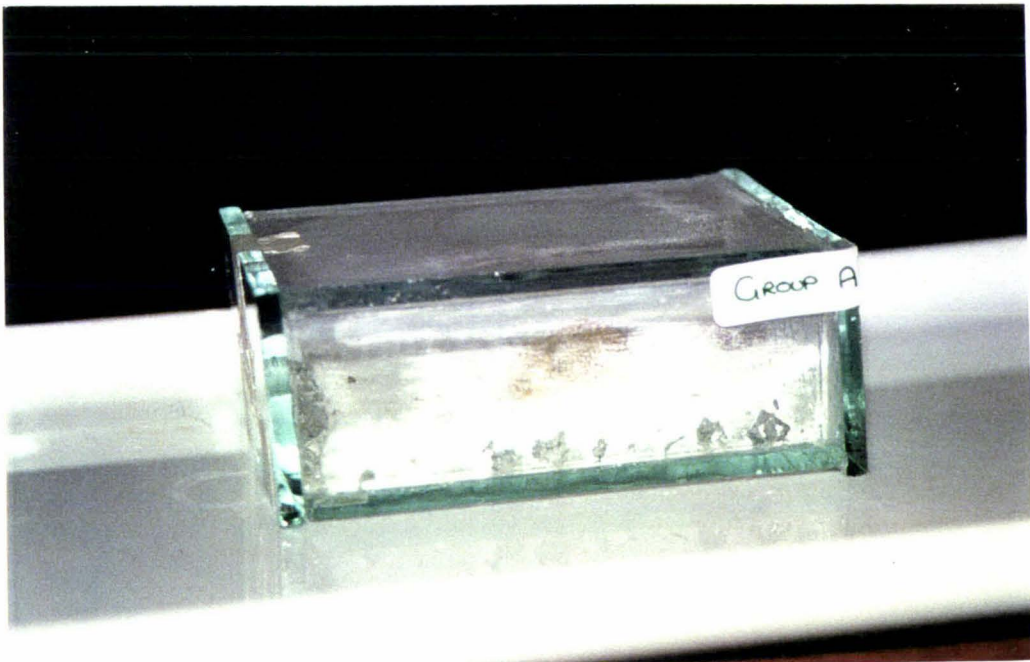
Plate 5.1 Glass container, with damp capillary matting used to incubate *L. archeyi* eggs.

(Dimensions 14 cm long x 5.5 cm high x 9.5 cm wide)

Table 5.1 Temperatures used to incubate captive *L. archeyi* froglets which hatched in
January 1997.

	Incubation Temperature	
	11°C	15°C
Group A (Individuals 1,2,3,4,5 & 6)	4 , 5 , 6	1 , 2 , 3
Group B1 (Individuals 7 & 8)	7	8
Group B2 (Individual 9)	9	
Group B3 (Individual 10)		10

The froglets, and frogs were weighed weekly to the nearest 0.0001 g, and measured with
dial callipers.

Measurements taken were:

- snout-vent length (from tip of snout to vent).

- tail length (from tip of tail to vent), froglets only.

Once the froglets had metamorphosed and begun to feed they were fed on laboratory reared
Drosophila, plus other small invertebrates (i.e. amphipods) collected in leaflitter from
Bledisloe Park, Palmerston North.

Data analysis

Egg Data

Egg weight and diameter data were graphed and 95 % confidence intervals obtained using Systat® version 6.0, for Windows® , SPSS Inc., USA 1996.

Post-larval development

Data were graphed on Systat® version 6.0, for Windows® , SPSS Inc., USA 1996.

Tukey's Studentised Range Test was done using GLM with SAS®version 6.12, SAS Institute Inc. USA.

- Variation in the rate of tail adsorption was calculated when 10mm, 4mm, and 2mm of the tail was present (Appendix 5.1)

- variation in snout-vent length at 30, 60, 90 and 120 days after hatching (Appendix 5.2) variation in weight at 30, 60, 90 and 120 days after hatching (Appendix 5.3)

  All photographs were taken by the author unless otherwise stated

5.3 Results

5.3.1 *Larval development*

When first collected, each larva appeared as a long thin translucent body wrapped around a large pale yellow yolk sac positioned on its ventral surface between the pectoral and pelvic girdles (Plate 5.2). The heart was visible immediately anterior to the yolk sac. Small brown eye spots were also present at the anterior end of the dorsal surface.

During larval development the head widened and the eye spots enlargened and darkened (Plate 5.3A). The body thickened along the spinal column and the yolk sac became a deeper yellow.

After three weeks in captivity the larvae become darkly pigmented. Pigmentation developed initially in the anterior head region and progressed towards the base of the tail (Plate 5.3B). The larvae were very active within their egg capsules throughout incubation and if they were disturbed or moved, they would rotate using their long tails in a 'side to side' whip-like action.
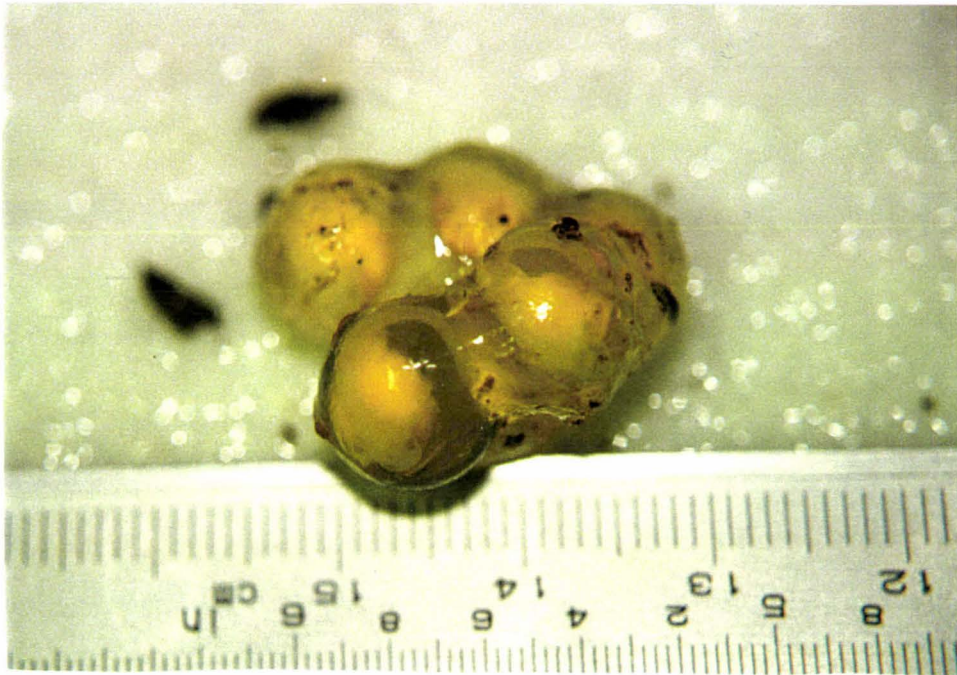
Plate 5.2 Cluster of *L. archeyi* eggs (Group A) in captivity, 8 days after collection from Whareorino forest.

A.

B.

Plate 5.3 Developmental stages of *L. archeyi*. **A:** 22 days and **B:** 35 days before hatching in captivity.

Egg Weight

The average weight per egg differed between the clusters when first brought into captivity (Table 5.2). Initially egg B3 had the lowest egg weight (0.3326 g) but this may be due to the loss of intra-capsular fluid which occurred due to damage sustained before being brought into captivity. Eggs in group A had a significantly lower initial average egg weight (0.4886 g) compared with either B1 or B2 groups (0.6003 & 0.6964 g respectively). However after three weeks in captivity eggs in group A reached the same weight that B1 & B2 had when they were first collected. This suggests that group A eggs may have been laid approximately two weeks later than group B eggs.

Each egg cluster lost 20.5 %-60.7 % of their weight during the first seven days in captivity but all eggs, with the exception of B3, later regained some weight. Only one group of eggs, Group A, exceeded its initial average egg weight before larvae started to hatch on day thirty-seven (Figure 5.1A). Group B1 and B2 recovered 18.4 % and 26.5 % of their initial average egg weight respectively before hatching after 30 and 27 days respectively in captivity (Figure 5.1B & 5.2A). Egg B3, however, lost 50.4% (0.1677g) of its initial weight after fourteen days in captivity and hatched prematurely on day eighteen (Figure 5.2B).

Table 5.2 Average egg weights for eggs of *L. archeyi*, incubated in the laboratory.

See Table 5.1 for incubation temperatures

Recording ceased when eggs hatched.

It was not possible to weigh attached groups of eggs individually so standard errors are not included.

Group	No. of Eggs	Average weight per egg (g). (% weight change from initial weight)					
		Initial weight	7 days	14 days	21 days	28 days	35 days
A	6	0.4886	0.3694 (-24.3%)	0.4097 (-16.1%)	0.6432 (+31.7%)	0.743 (+52.1%)	0.694 (+42.0%)
B1	2	0.6003	0.2941 (-30.1%)	0.4163 (-18.4%)	0.4838 (-11.7%)		
B2	1	0.6964	0.2736 (-60.7%)	0.3171 (-54.5%)	0.4585 (-34.2%)		
B3	1	0.3326	0.2643 (-20.5%)	0.1649 (-50.4%)			

A.

B.
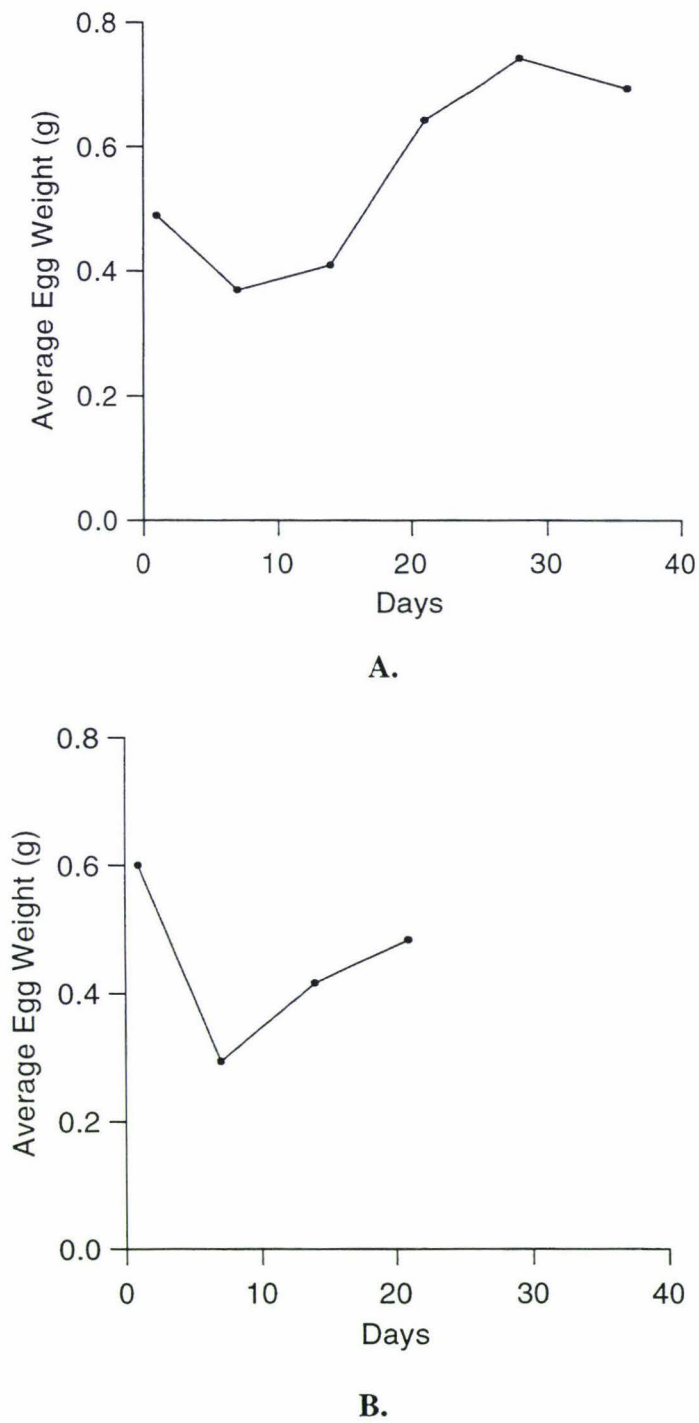
Figure 5.1 Changes in average weight of *L. archeyi* eggs in captivity from collection until hatching. **A**: Group A eggs, n=6, **B**: Group B1 eggs, n=2. Incubation temperature 13°C.
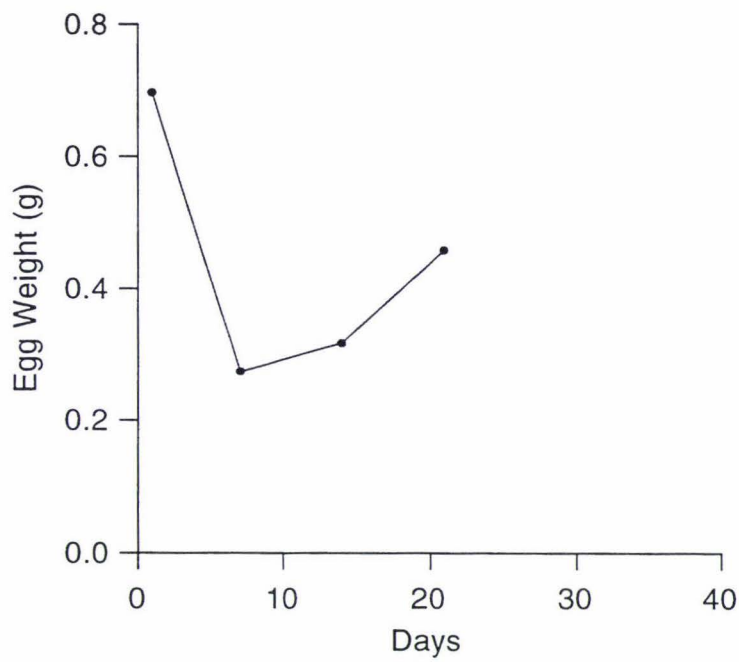
A.
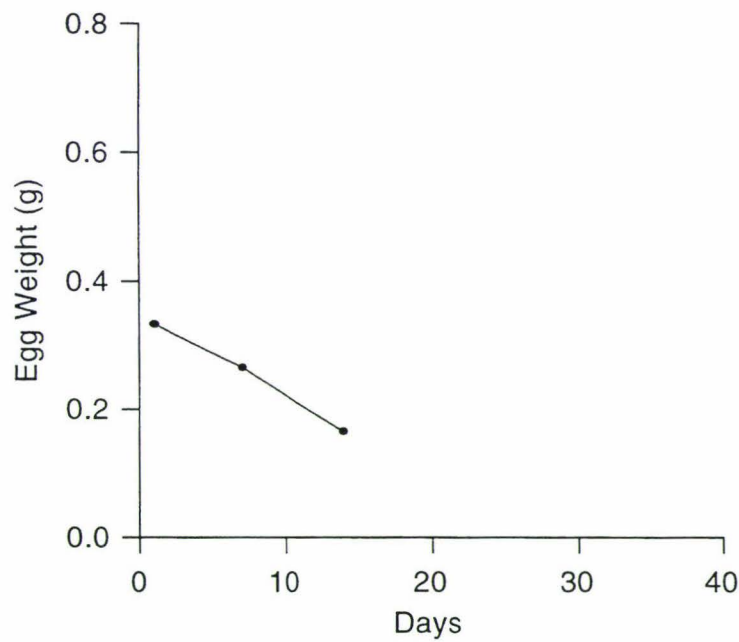
B.

Figure 5.2 Changes in the egg weight of single eggs of *L. archeyi* eggs incubated from collection until hatching. **A**: Group B2 eggs, n=1, **B**: Group B3 eggs, n=1. Incubation temperature 13°C.

Change in egg diameter during incubation in captivity

All eggs expanded as larval development progressed. The 6 eggs in Group A, which were maintained as a single cluster, had an average diameter of 9.18 mm when brought into captivity (Figure 5.3). This increased to 9.77 mm after fourteen days in captivity and by the time they were about to hatch (after 35 days) the average diameter was 11.43 mm.

Group B eggs (B1, B2 & B3) had been separated naturally from their original egg mass before collection. They were possibly damaged because B2 and B3 appeared to have enlargened blood vessels on the yolk mass and they hatched earlier than other eggs from the same clutch. It was therefore considered inappropriate to use Group B egg data.
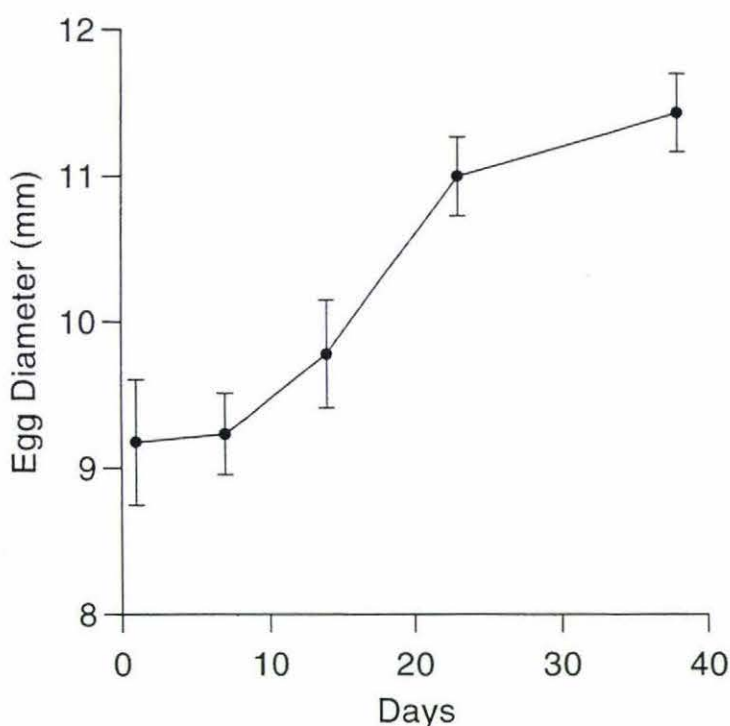
Figure 5.3 Change in average egg diameter of 6 *L. archeyi* eggs (group A), from collection until hatching. Incubation temperature 13°C.

The bars are 95 % Confidence Intervals.

5.3.2 *Hatching and post intra-capsular development of the froglet*

Hatching

Hatching began when the egg wall was pierced by the end of the tail of the larva. A series of vigorous flicks of the tail caused the tail to protrude further out of the egg till the egg wall ruptured. The larvae and other contents of the egg then to spilled out (Plate 5.4).

Hatching was first observed in number 10 after 18 days in captivity. However eggs from the same original egg mass hatched much later, number 9 hatched after 27 days and both number 7 and number 8 hatched on the 30th day of captivity. This contrasted with Group A, froglets number 1, 2, 3, 4, 5 & 6 where all larvae hatched on the same day, over a period of approximately twelve hours. This occurred after 37 days in captivity although no two eggs hatched at the same time. After hatching these larvae remained clustered together in a tight group on the egg remnants till they were physically separated and put into individual containers. Each froglet at hatching, had only partial limb development (Plate 5.5A). A long tail was present, which the froglets used to move their body with strong, vigorous movements, or flicks (Plate 5.5B).

Plate 5.4 Hatching in *L. archeyi* (Group B1) after thirty days in captivity at the Department of Ecology, Massey University.
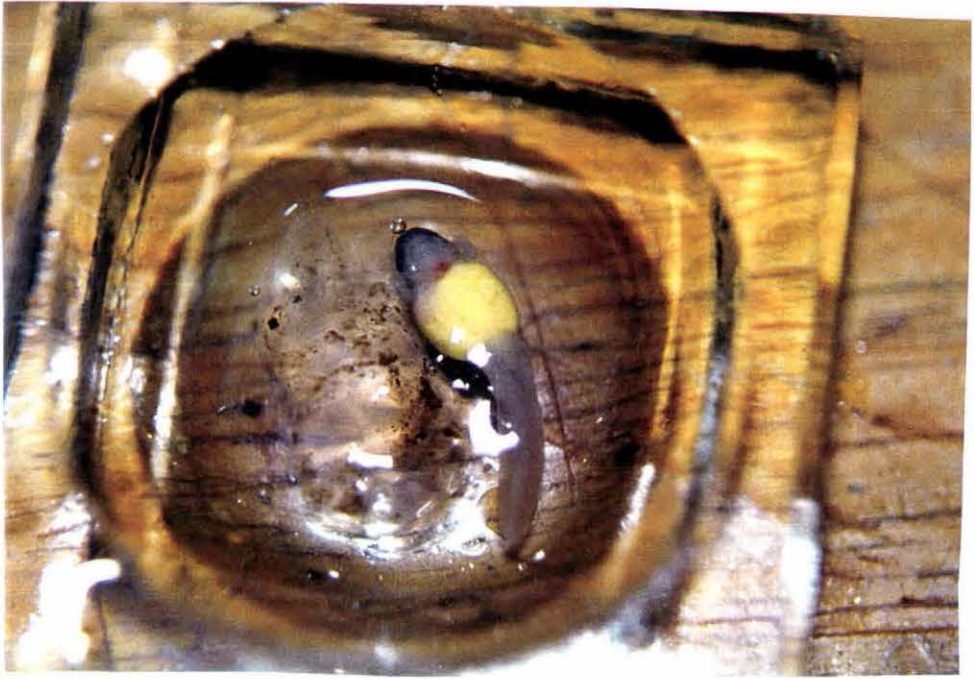
A.

B.

Plate 5.5 Early limb development in captive *L. archeyi*. Individual No. 8. **A**: 6 days after hatching; ventral view. **B**: 12 days after hatching; dorsal view.

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5.3.1.1 Tail Reduction

Tail reduction began immediately after hatching and the tails took an average 56 days to disappear. At this stage metamorphosis was complete. However, significant differences were found in the rate of tail adsorption between individuals in group A and group B, and also in individuals incubated at 15°C and those incubated at 11°C as detailed below.

The effect of parentage on the rate of metamorphosis

The number of days taken for individuals in group B to absorb their tails to a length of 10mm was significantly longer than for group A individuals ($\bar{x}$ = 19.8 days ± 1.26 [± S.E.] & $\bar{x}$ = 31.7 days ± 1.76 respectively) (Table 5.3) and at the stage where 4 mm of tail remained to be absorbed, a 12.8 day difference existed between the two groups (Figure 5.4A & 5.4B), with group A being significantly faster ($\bar{x}$ = 35.2 ± 1.69 days) than group B ($\bar{x}$ = 48.0 ± 2.35 days).

At a late stage of metamorphosis, when the tail length was 2mm, the difference in time taken to reach this point between the two groups had further increased to 13.6 days (group A $\bar{x}$ = 39.7 ± 1.09 days & group B $\bar{x}$ = 53.3 ± 1.52 days).

The effect of temperature on the rate of metamorphosis

Temperature had no significant effect of temperature on the number of days taken to reduce the tail to 10 mm in length when froglets kept at 15°C ($\bar{x}$ = 24.4 ± 1.37 days) and were compared with froglets raised at 11°C ($\bar{x}$ = 23.0 ± 1.49 days) (Table 5.3). However, by a later stage (Figure 5.5A & 5.5B) when the tail was 4mm long a significant difference was apparent between individuals incubated at the two different temperatures (15°C; $\bar{x}$ = 37.0 ± 1.84 days, 11°C; $\bar{x}$ = 42.5± 2.00 days). This difference was maintained between the individuals at these temperatures until metamorphosis was complete.

Table 5.3 ANOVA results showing the effect of temperature and male parentage on tail reduction in two clutches of *L. archeyi* eggs.

Tail Length	Source of Variation	DF	MEAN SQUARES	F VALUES	PR>F
10mm					
	Parent	1	284.6282051	59.71	0.0006
	Temperature	1	2.8846154	0.61	0.4718
	Parent*Temperature	1	9.3461538	1.96	0.2203
4mm					
	Parent	1	434.0512821	50.87	0.0008
	Temperature	1	172.5128205	20.22	0.0064
	Parent*Temperature	1	52.5128205	6.15	0.0558
2mm					
	Parent	1	507.7051282	142.35	0.0001
	Temperature	1	254.8846154	71.46	0.0004
	Parent*temperature	1	61.0384615	17.11	0.0090
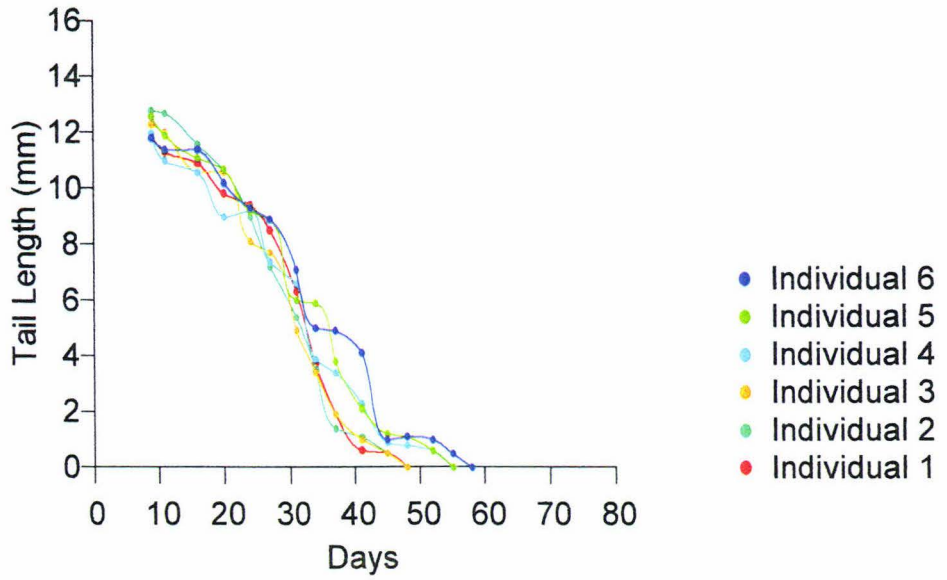
A.
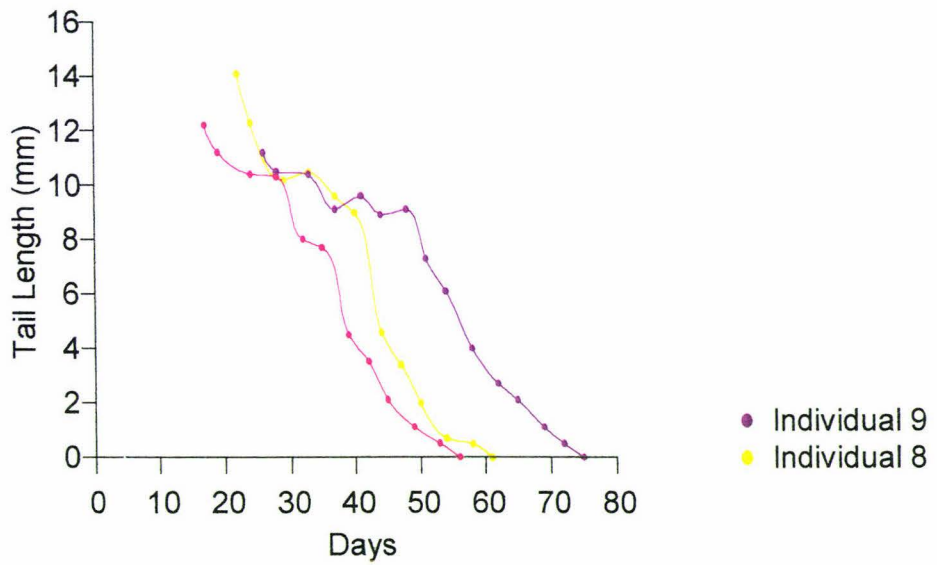
B.

Figure 5.4 Change in tail length during metamorphosis of *L. archeyi* individuals held at different temperatures in captivity. **A:** Group A, n=6. Individuals 1, 2 & 3 incubated at 15°C. Individuals 4,5 & 6 incubated at 11°C. **B:** Group B, n=3. Individuals 8 & 10 incubated at 15°C. Individual 9 incubated at 11°C.

Individual No. 7 died soon after hatching and is not included in Figure 5.4B.
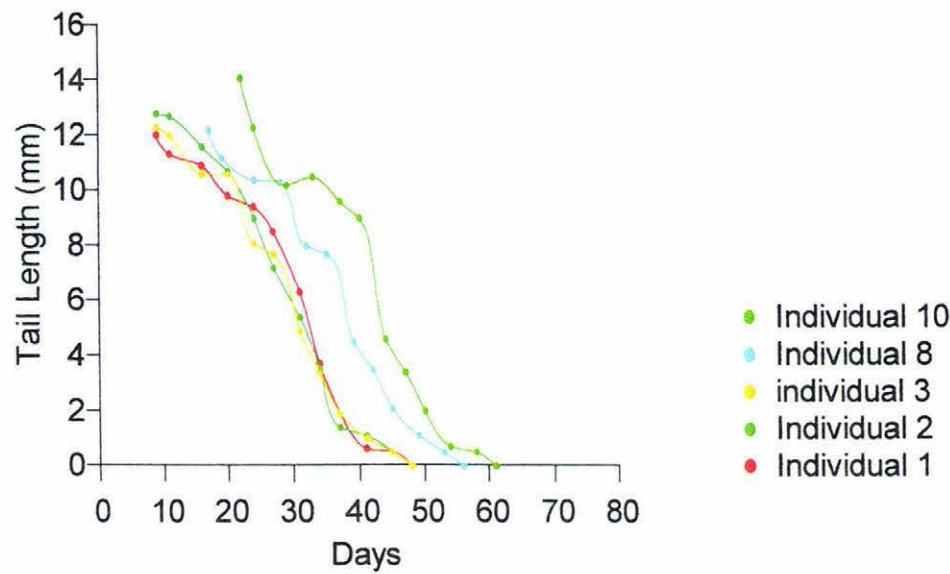
A.
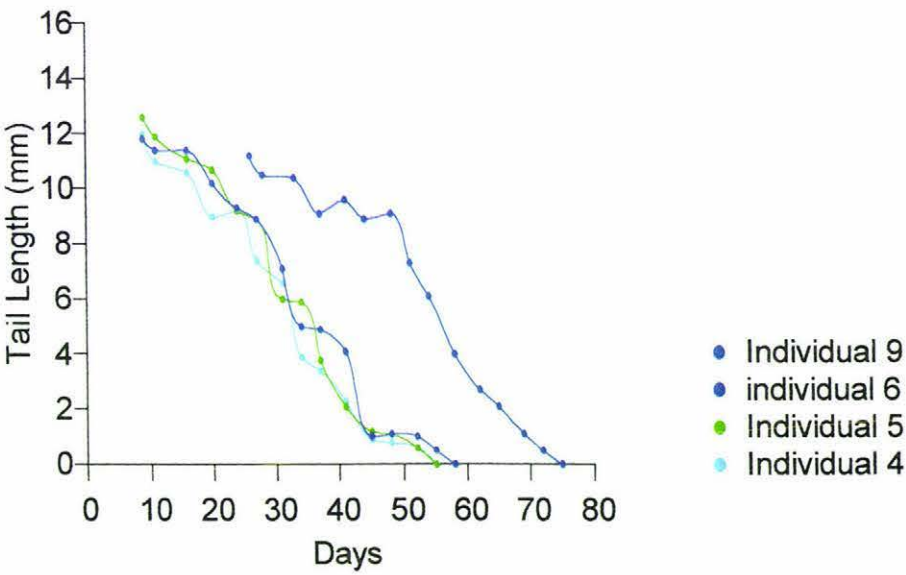
B.

Figure 5.5 Change in tail length during metamorphosis of *L. archeyi* individuals held at different temperatures in captivity. A: Individuals incubated at 15°C, n=5.

B: Individuals incubated at 11°C, n= 4.

Individual No. 7 died soon after hatching and is not included in Figure 5.5B.

Morphometric development of the froglet

Measurements of snout-vent length was varied throughout development for all individuals in captivity (Figure 5.6A - E, Table 5.4) Temperature had no effect on the growth rate of individuals, as indicated by snout-vent length, at any stage during the first 150 days of development (Table5.5, Appendix 5.5). However, a significant difference occurred between group A and group B individuals around the period of metamorphic climax at 60 days. This difference was still apparent 90 days after hatching but was no longer apparent after 120 days.

Table 5.4 Snout-vent lengths of captive *L. archeyi* for the first 120 days of development, showing the effects of parentage and temperature.

	Average snout-vent length (mm) ± standard errors			
	after 30 days	after 60 days	after 90 days	after 120 days
Group A	9.27 ± 0.12	9.62 ± 0.18	9.38 ± 0.14	8.94 ± 0.24
Group B	9.10 ± 0.18	8.81 ± 0.18	8.67 ± 0.09	8.38 ± 0.32
	after 30 days	after 60 days	after 90 days	after 120 days
11°C	8.93 ± 0.17	9.12 ± 0.17	8.95 ± 0.13	8.77 ± 0.30
15°C	9.39 ± 0.13	9.30 ± 0.13	9.10 ± 0.10	8.52 ± 0.26

Weight

As with snout-vent length, individual weights of the froglets varied throughout development (Appendix 5.5, Figure 5.6 A - E, Table 5.5). Temperature significantly effected on the weight of individual froglets during the first 30 days of development after hatching (Table 5.7). This effect was gone 60 days after hatching, but occurred again after 90 days. There was no significant difference between weights of individuals at 15°C and 11°C after 120 days of development.

A significant difference in weight between group A and group B individuals was shown to occur after both 60 and 90 days of development but, as with snout-vent length, the significant difference between the two groups of froglets disappeared after 120 days.

Table 5.5 Post-intracapsular weight change in captive *L. archeyi* during the first 120 days of development showing the effects of parentage and incubation temperatures.

	Average weight (g) ± standard error			
	after 30 days	after 60 days	after 90 days	after 120 days
Group A	0.1085 ± 0.001939	0.1227 ± 0.003217	0.1134 ± 0.002744	0.1095 ± 0.006147
Group B	0.1065 ± 0.002908	0.1058 ± 0.004818	0.1025 ± 0.001830	0.09346 ± 0.008247
	after 30 days	after 60 days	after 90 days	after 120 days
15°C	0.1117 ± 0.002168	0.1167 ± 0.003591	0.1114 ± 0.002045	0.1015 ± 0.006733
11°C	0.1030 ± 0.002742	0.1048 ± 0.004542	0.1017 ± 0.002857	0.09753 ± 0.007775
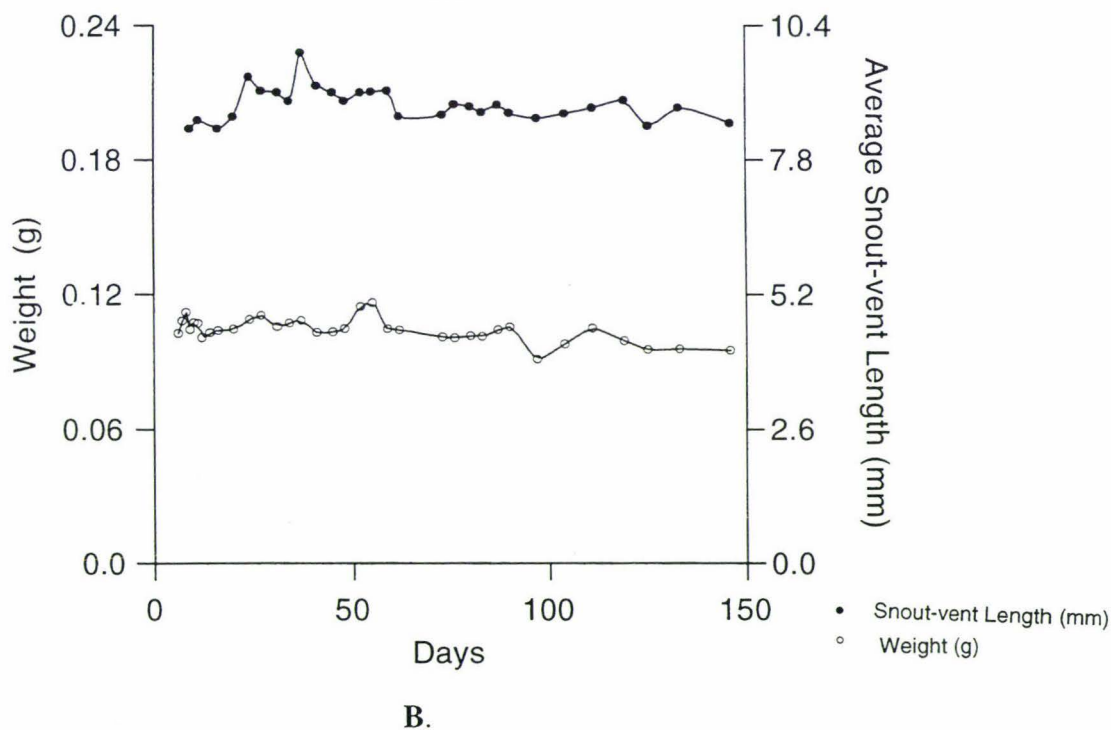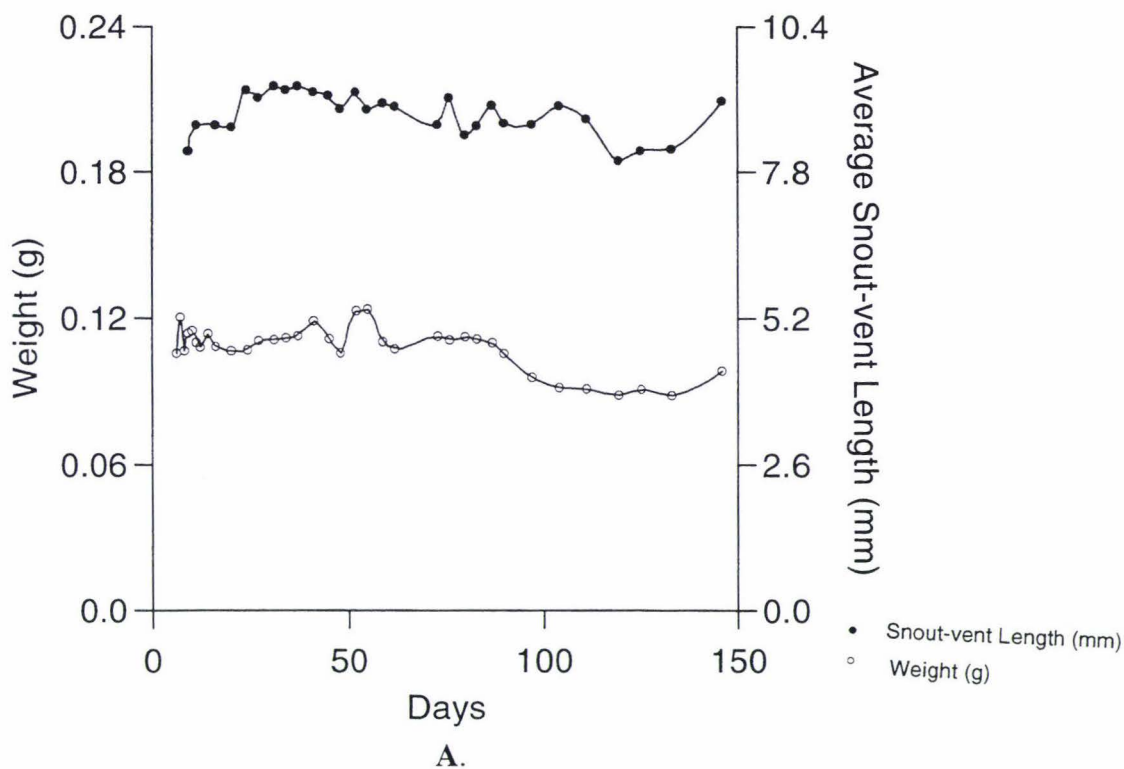
Figure 5.6 Change in snout-vent length and weight during early development in captive

L. archeyi. **A**: Average of individuals 1, 2, & 3. **B**: Average of individuals 4, 5, & 6.

Day 0 = hatch day

Individual weights and individual snout-vent lengths are shown in Appendix 5.6 & Appendix 5.7
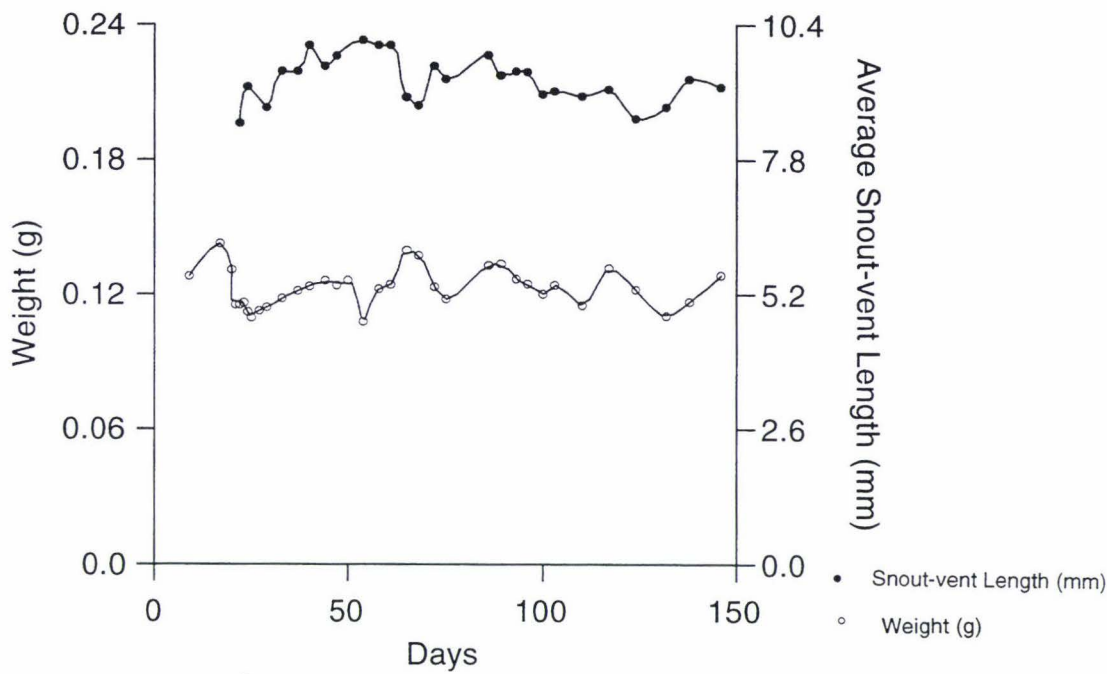
C.
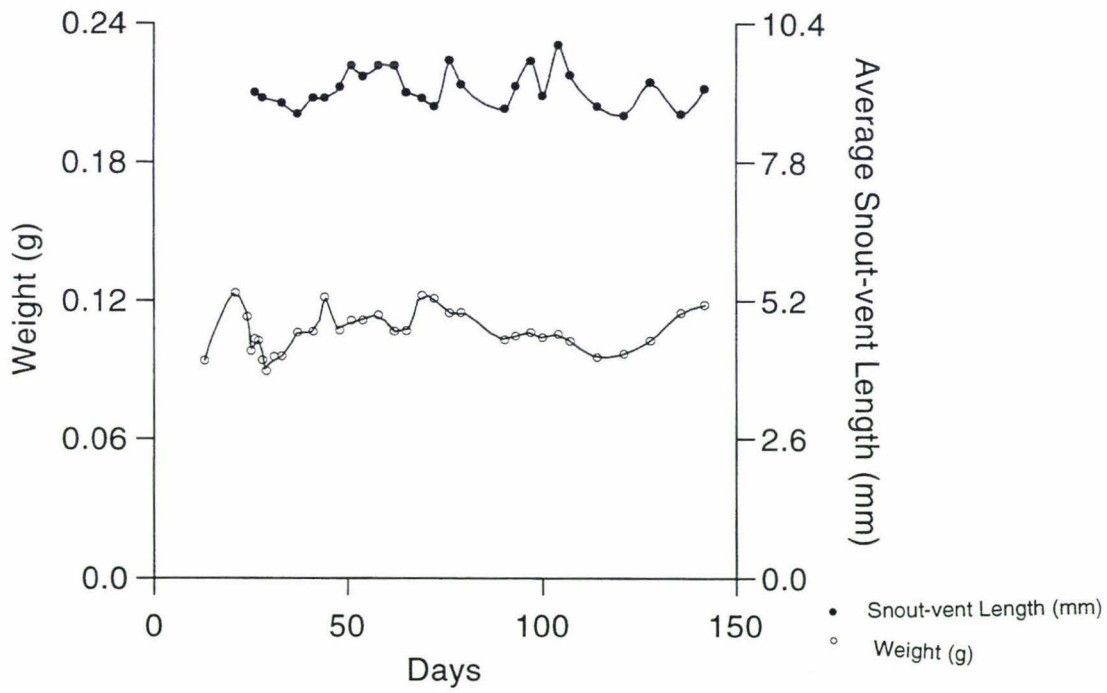
D.

Figure 5.6 Change in snout-vent length and weight during early development in captive

L. archeyi. **C**: Individual number Eight; **D**: Individual number Nine.

Day 0 = hatch day.
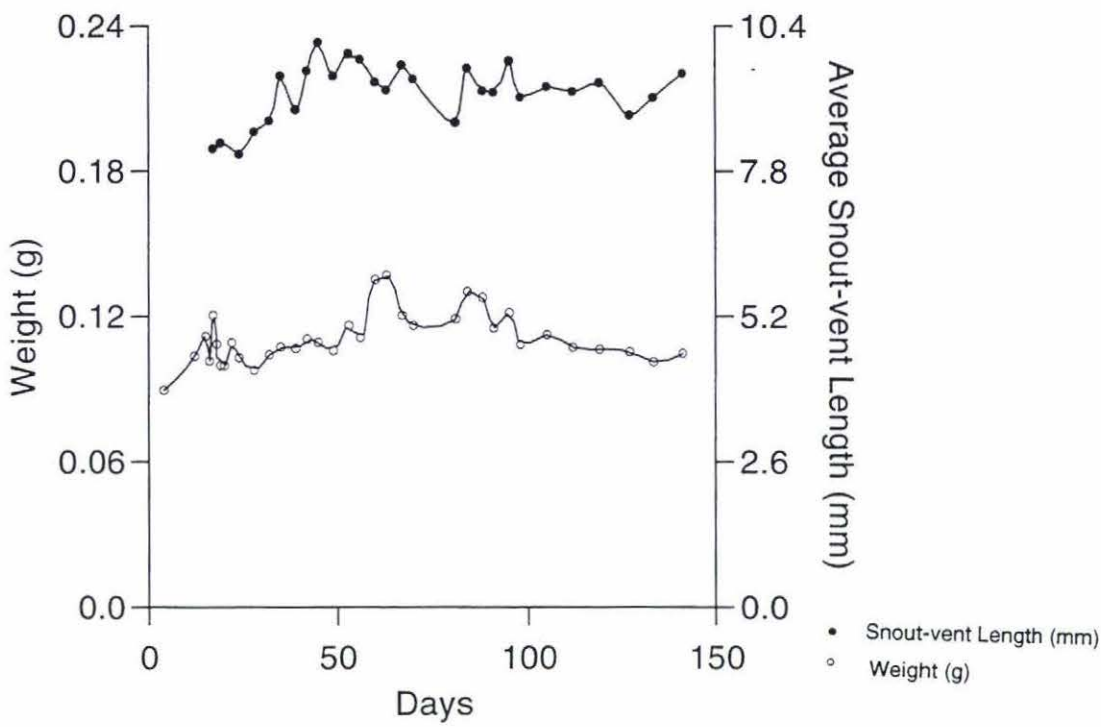
E.

Figure 5.6 Change in snout-vent length and weight during early development in captive *L. archeyi*. **E**: Individual number Ten.

Day 0 = hatch day

Table 5.6 ANOVA for snout-vent lengths of captive *L. archeyi* during the first 150 days after hatching.

	Source	Df	Mean Square	F Values	Pr>F
30 days after hatching	Parent	1	0.08935385	1.03	0.3571
	Temperature	1	0.40205128	4.63	0.0842
	Parent*Temperature	1	0.05128205	0.59	0.4771
60 days after hatching	Parent	1	1.20379615	14.12	0.0132
	Temperature	1	0.0516538	0.68	0.4464
	Parent*Temperature	1	0.04293464	0.50	0.5096
90 days after hatching	Parent	1	0.94380000	18.82	0.0074
	Temperature	1	0.04435385	0.88	0.3902
	Parent*Temperature	1	0.05026154	1.00	0.3628
120 days after hatching	Parent	1	0.64662976	2.32	0.2026
	Temperature	1	0.11220119	0.40	0.5605
	Parent*Temperature	1	0.06914405	0.25	0.6448

Table 5.7 ANOVA for weight of captive *L.archeyi* during the first 150 days after hatching.

	Source	Df	Mean Square	F Values	Pr>F
30 days after hatching	Parent	1	0.00004035	1.79	0.2387
	Temperature	1	0.00023124	10.25	0.0239
	Parent*Temperature	1	0.00004358	1.93	0.2233
60 days after hatching	Parent	1	0.00031200	5.04	0.0747
	Temperature	1	0.00031446	5.52	0.0656
	Parent*Temperature	1	0.00019586	3.16	0.1354
90 days after hatching	Parent	1	0.00021968	10.94	0.0213
	Temperature	1	0.00020257	10.08	0.0247
	Parent*Temperature	1	0.00008726	4.34	0.0916
120 days after hatching	Parent	1	0.00034648	1.91	0.2391
	Temperature	1	0.00002242	0.12	0.7429
	Parent*Temperature	1	0.00026288	1.45	0.2950

Limb structure

At hatching, individual froglets had rudimentary limbs but fingers and toes were not apparent (Plate 5.4). The froglets did not use their limbs for locomotion and the limbs lacked obvious muscle development. Limb development was rapid during the first fourteen days post-hatching (Plate 5.5A) and muscular limbs were completed well before tail reduction had finished (Plate 5.5B). During this phase individuals were found to associate with the alkasorb crystals provided in each enclosure. The froglets would rest at the highest point of the crystals and if disturbed they would crawl or wriggle to the top of the nearest alkasorb crystal, using their tail to aid movement.

Froglet survival

All of the original ten eggs collected from 2 different adult frogs in Whareorino forest hatched successfully in captivity. This occurred even though two eggs (B2; Individual 9 & B3; Individual 10) were brought into captivity in a damaged state. Individual 9 hatched well before the other eggs and was placed in 'toad ringer solution'(Appendix 5.8) for 7 days, in order to attempt to simulate the intra-capsular fluid. This solution appeared to have no adverse effect on the young froglet, which was successfully raised to a frog. Individual 7 was the first froglet to die. It stopped moving 9 days after hatching and was found to be dead 24 hours later. The next death was accidental, and occurred in May when Individual 3 escaped from its container and was found desiccated in the controlled temperature cabinet. Sudden deaths occurred amongst some the remaining captive individuals during June, August and September. Individual 2 (16 June 1997) and Individual 6 (21 June 1997) were found dead, on their ventral surface and in a bloated state. Individual 8 (6 August 1997) and Individual 10 (14 August 1997) were also found upside down; both had swelling in their rear limbs, but were not completely bloated.

Individual 4 died shortly after leaf litter with invertebrates was introduced to the enclosures. Possibly the young froglet had been attacked as one rear limb was found swollen and disfigured.

Swelling in a live individual, Individual 6, was only noted once prior to its death two days later. All other individuals showed no apparent signs of any illness before death.

Frog Development

Three of the 10 eggs survived to provide 12 months of data, and although these data could not show significant differences between individuals from within or between clutches, they show clear trends in the early development of *L. archeyi*.

Individual 1 fluctuated in weight and snout-vent length throughout its early development (Figure 5.7A). Changes in both weight and snout-vent length occurred in the same direction, suggesting a degree of correlation between the two measures. After metamorphosis (48 days+) this individual varied little in either snout-vent length or weight until a distinct increase in both measures occurred 240 days after hatching. Between 240 and 293 days, the weight of this frog increased 75.4%, from 0.1194 g to 0.2094 g, which corresponded to an increase in snout-vent length.

The weights and snout-vent length of Individual 5 (Plate 5.6), did not vary as much as those of the other froglets during the early phase of its development (Figure 5.7B). This individual had a similar weight after metamorphosis as it did during the tail reduction phase. However, an increase in body weight occurred approximately 170 days after hatching.

This was much earlier than what occurred for Individual 1. This continued till measurement ceased on day 365. Snout-vent length declined slightly between 100 and 160 days but increased later, at around 300 days.

Dimensions for Individual 9 were variable before and after metamorphosis occurred (Figure 5.7C). Significant increases in weight did not occur till after 200 days after hatching. Snout-vent length measurements were also variable, but a significant increase in snout-vent length occurred 200-300 days after hatching.

Plate 5.6 Individual 5, 298 days after hatching in captivity.
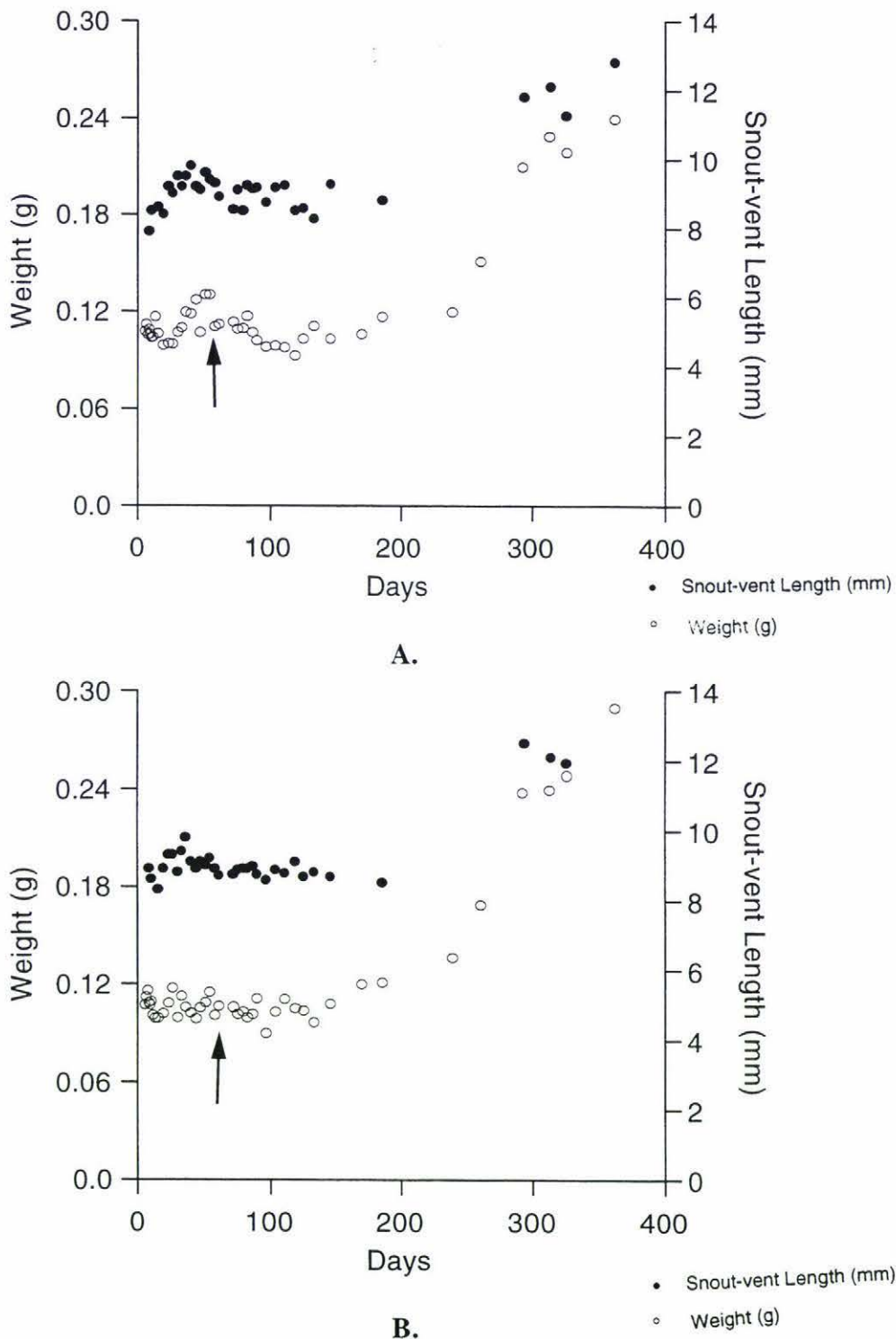
Figure 5.7 Changes in weight and snout-vent of *L. archeyi*, during the first 365 days after hatching. Completion of metamorphosis (ie. tail absorption) is indicated by (→).
A: Individual 1; **B**: Individual 5.
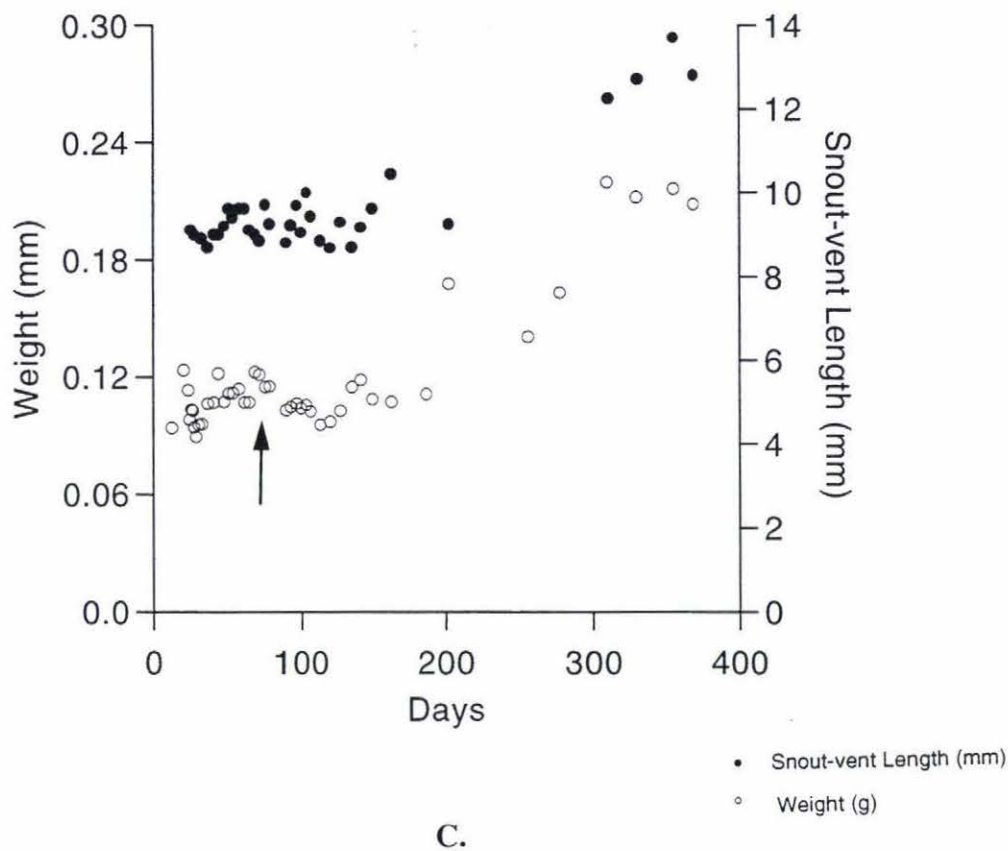
Figure 5.7 Changes in weight and snout-vent of *L. archeyi*, during the first 365 days after hatching. Completion of metamorphosis (ie. tail absorption) is indicated by (→).
C: Individual 9.

5.3.2 Observations on Incubation and Development in the Field

On 14th November 1996 a large orange male *L. archeyi* was found brooding a clutch of approximately 10 fertile eggs under a small rock in Whareorino forest. When first discovered this male was sitting upright, holding its body over the cluster of eggs, in the typical frog brooding stance (Bell 1985) (Plate 5.7A). The eggs rested on leaf litter immediately under the frogs' stomach. This frog was observed every 2 weeks for three months, brooding its egg clutch.

As the eggs developed, the number of eggs in the clutch diminished. Sometimes an egg or pair of eggs, were found separated from the main clutch, lying beside the brooding male, and infected by a white fungus. These eggs would decay rapidly, in about 48 hours, and disappear.

By 9 January 1997, 8 weeks after the brooding male was first discovered, approximately half the clutch was gone. However the clutch had appeared to stay approximately the same overall size, due to swelling of the eggs and occupied approximately the same space under the frog. It is possible that this observed reduction of eggs occurred as a response to either the increasing size of individual eggs, and an inability of the male to incubate all the large eggs, or the eggs may have been attacked by a fungus and discarded as a result.

On 13 January 1997, 8 and a half weeks after being found, two froglets had hatched, and lay as tailed froglets, on the back of the brooding male. No eggs or other juveniles were seen. Five weeks later, 18 February 1997, the froglets were at Gosner stage 46 (Gosner 1960), and therefore had nearly completed metamorphosis. However small tail remnants, approximately 4 mm - 5mm remained (Plate 5.7B). Both juveniles were dark green/brown in colour, fully mobile but still resident on the back of the male frog. When disturbed the male frog jumped which caused the young to fall off his back but, both froglets quickly jumped back onto the male frog. This is the first documented record of the development, hatching and metamorphosis of an entire leiopelmatid frog clutch in the wild. Two weeks

after this last observation the metamorphosed juveniles and the brooding male were gone from the nest site.

A.

B.

Plate 5.7 Egg brooding and late froglet development in *L. archeyi*. **A**: egg brooding behaviour in *L. archeyi*; **B**: adult with metamorphosed young, 1st froglet is on the back of the male, 2nd froglet by the left eye.

5.4 Discussion

Egg and larval development

Werner (1986) suggested that woodland habitats were suitable environments for the development of terrestrialism in amphibians. Full terrestrialism requires that direct development occurs, which in turn gives a species freedom from the uncertain aquatic environment. A species that typifies such development is the ancient endemic frog *Leiopelma archeyi*.

Leiopelmatid frogs have characteristics which are typical of terrestrial species (Duellman & Trueb 1986, Werner 1986, Zug 1993, Crump 1996). These include a small number of relatively large eggs, that are usually laid under rocks and logs, and care of the young throughout their development (Stephenson 1955). Egg clutch size from observations of six egg clutches in Whareorino forest found that an average of approximately 9 eggs per clutch occurred, (six clutches of 11, 9, 10, 8, 7 & 10 eggs, *pers. obs.*). Thurley (1996), however, found egg clusters of 4, 5 and 6 eggs only. Combined this data gives an average clutch size of 7.8 eggs per clutch. This is a small number compared with other terrestrial amphibians such as *Platymantis hazelae*, which has direct developing young, and lays 31 - 40 eggs per clutch (Brown and Alcala 1982) and the marsupial frog, *Assa darlingtoni*, which has a maximum snout-vent length 18 mm, and has an average egg clutch size of approximately 13 eggs per clutch (Ehmann and Swann 1985). However the eggs of leiopelmatid frogs are larger, (see below), and this constrains the number of eggs produced.

The size of anuran eggs varies tremendously. The largest known capsular diameter is 14mm in *Gastrotheca cornuta*, a hylid marsupial frog whose development, including metamorphosis from larvae is direct. The smallest egg produced by an amphibian is that of a pipid frog *Hymenochirus boettgeri* which has a capsule size of 1.5 mm (Duellman & Trueb 1986). In comparison *Leiopelma* eggs are close to some of the largest known eggs. For example, *L. hamiltoni* eggs which initially are 8-10 mm in diameter, swell to 12-14 mm before hatching. *L. hochstetteri* eggs are laid at 12-16 mm an enlarge to 20mm in diameter at hatching (Bell 1982b). *L. archeyi* eggs raised in captivity in this study were 9.18 mm

when first brought into captivity and reached a maximum diameter of 11.43 mm before hatching.

One suggested advantage to terrestrial amphibians of larger egg sizes has been identified as a reduced surface area to volume ratio for the egg and therefore fewer problems associated with water loss (Crump 1996). Large eggs also enable larger, more robust individuals to enter the environment (Salthe and Duellman 1973). More robust individuals have an advantage in environments where juvenile mortality from predation could be high (Howard 1978). In Whareorino forest many carnivorous ground dwelling invertebrates such as peripatus, large carabid beetles, large centipedes, and ground spiders, may prey on *Leiopelma* individuals in the juvenile stage. Carabid beetles have been known to prey upon eggs of *Assa darligtoni*, (Ehmann and Swan 1985), in Australia, which may also occur here.

After hatching, growth of the captive individuals was rapid during the first year. The data therefore support Werner's (1986) model which showed that the majority of growth occurs during the terrestrial stage of anuran lifecycles. Newman (1989) suggested that temperature may influence development by affecting rates of physiological processes. In this study, however, the overall rate of growth, from hatching to year 1, did not vary with temperature. Longer-term studies, with larger samples, and over different temperatures are required to show how growth is affected by temperatures. Certainly a temperature effect, particularly in geographically separated populations has been suggested for other amphibian populations, (Gollmann and Gollmann 1996, Osbourne *et. al.* 1996). The effect of low temperatures may be related to geographic variation in body size and this might partially explain the present differences in body size apparent between extinct and extant populations of leiopelmatid frogs (Worthy 1987b, Thurley and Bell 1994).

Soon after this population was discovered in Whareorino forest, a pair of *L. archeyi* were taken into captivity, where a clutch of eggs was produced, from which nine young were raised (Thurley and Bell 1994). Comparison of the snout-vent lengths of individuals, immediately after metamorphosis, found that Whareorino *L. archeyi* were larger than

Coromandel *L. archeyi* of the same age, 10.6 mm and 8.7 mm respectively. However the results from this study also found that immediately after metamorphosis, the average snout-vent length of all individuals was 8.96 ± 0.16 [S.E.], $n = 9$, which is only slightly larger than Coromandel *L. archeyi* however much smaller than the average snout-vent length for Whareorino type measured by Thurley and Bell (1996). I have shown however that variation in tail length, weight and snout-vent length can occur between different clutches of the same species which may explain the differences between the averages in my results, from those of Thurley and Bell (1996). Indeed if Group A, $n = 6$ and Group B, $n = 3$ are compared to each other, there is a significant difference in snout-vent length, immediately post-metamorphosis for the groups, $\bar{x} = 8.78 \pm 0.15$ and $\bar{x} = 9.33 \pm 0.31$, respectively. There is a need for more comprehensive research using larger sample sizes under control conditions so that better comparisons between populations at any stage of growth can be made.

Metamorphosis

Metamorphosis is the rapid transformation of morphological characteristics which occurs naturally during the life cycle of an animal (Rowe and Ludwig 1991) . It is particularly obvious in insects and amphibians. Metamorphosis involves a series of post-embryonic structural, physiological, biochemical and behavioural changes of an individual to equip it to a new mode of life (Duellman and Trueb 1986). These authors also recognised three main changes during metamorphosis:

1) regression of some structures and functions that are significant only to the larva;

2) transformation of other larval structures into the adult form;

3) development of new structures and functions that did not previously exist, but which are essential for adulthood.

Metamorphosis in amphibians is a complex process regulated by both external (environmental) and internal (hormonal) processes. The rate of change between life history stages during metamorphosis in frogs is regulated by many ecological factors, such as

temperature, food levels, tadpole densities and sizes, pond evaporation (desiccation) rates and the presence of predators (Kaplan 1980, Cohen and Alford 1993, Hayes 1997).

In *Leiopelma* metamorphosis was described as being direct and entirely intra-capsular (Stephenson 1955). Bell (1980), however recognised that only some larval development is carried out in the egg and that further development takes place after hatching before metamorphosis is complete. His view was supported by my study of *L. archeyi* individuals raised in captivity. Most larvae hatched at Gosner stage 42-45[1] (Gosner 1960), with protruding forelimbs and developed mouth structures. After hatching, however, the final stage(s) of metamorphosis (i.e. tail absorption - Gosner stage 43-46), took on average 56 days to complete.

Leiopelma archeyi is not, therefore, a 'complete direct developing' amphibian, as categorised by several authors (Stephenson 1955, Stephenson and Stephenson 1957, Stephenson 1961, Goin, *et. al.* 1978, Duellman and Trueb 1986). It should more appropriately be categorised as an 'incomplete direct developing' species because it lays terrestrial eggs which hatch as froglets which then undergo further development in the nest (Zug 1993).

Premature Hatching

Individual 9 hatched prematurely, nine days before the other individuals from the same clutch did. However, this individual was well developed, when it hatched, Gosner stage 42, and had developed to Gosner stage 45, 96 hours after hatching (Gosner 1960). This was comparable to the stage of development of the other individuals from the same clutch, when they hatched 9 days later. The ability of the premature individual to hatch at the same Gosner stage as the other froglets from the same clutch, suggests that hatching may be determined by the stage of development reached rather than the time elapsed since laying.

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[1] The assumption made here is that terrestrial amphibians follow the same mode of development as the aquatic amphibin, *Bufo valliceps* at 25°, that Gosner based his diagrammatic series upon.

When brought into captivity this individual had a ruptured egg capsule and had lost most its intra-capsular fluid. The influence of this fluid loss on development is unknown. Photographs of intra-capsular development show that major changes in growth and development occurred during the 10 days prior to hatching, indicating that an individual could not hatch prematurely and be at the same level of development as individuals from the same clutch. However amphibians are well known for plasticity during development (Denver 1997), and some are known to be able to change their rate of development in response to environmental variables such as temperature, evaporation rates, population density and food availability (Wilbur and Collins 1973, Wilbur 1977, Pfennig *et. al.* 1991, Hayes *et. al.* 1993, Goater 1994, Denver 1997). Crump (1996) states that the land environment represents an inhospitable environment for amniotic eggs, thus developmental plasticity would be an advantage for terrestrial larvae which are immobile.

An increased rate of larval development in an individual could allow it to shorten the time spent in the most vulnerable stage of its lifecycle and permit entry to the terrestrial environment before other individuals of the same nest. Indeed, survival rates for amphibian metamorphs of *Crinia signifera* are higher in individuals that metamorphose earlier than other individuals (Williamson and Bull 1996). Early metamorphosis would be particularly important if competition for food resources or habitat, particularly daytime retreat sites, were limited. The response of a brooding male frog to premature hatching is unknown. Brooding males remain at the nest throughout development of the eggs and, after hatching, the juveniles develop further on his back (Bell 1985 & *pers. obs.*). This study showed that eggs in an intact clutch will hatch simultaneously, showing the same degree of development, and the froglets will undergo metamorphosis at the same rate. My field observations of *L. archeyi* juveniles support these captive results. It could be possible however that, if one individual was more advanced than the others and metamorphsed early the brooding male may be stimulated to leave the nest site, abandoning the less developed young.

Parental Care

Examples of parental care are found in all three orders of the class Amphibia. It occurs in 240 species or 6% of the total number of 3967 species (Crump 1996). Crump 1996, recognised parental care as being the 'derived character state' common to many primitive amphibia. It could be expected, therefore, that ancient leiopelmatid frogs would display parental care, and indeed it occurs in every species (Bell 1985). Parental care can take the form of egg attendance or transport, tadpole attendance, transport or feeding or even internal ingestion, and incubation (Crump 1996). In *Leiopelma*, egg attendance, tadpole attendance, and transport of tadpoles all occurs. The possible functions of egg attendance, such as protection from predators and or pathogens, aeration and/or hydration of eggs, or prevention of developmental abnormalities by preventing yolk stratification, have been recognised by many authors. However, very few studies exist that show the effect of parental care, and hence this remains a poorly understood area of amphibian biology. Therefore the reasons for egg attendance in Leiopelma are therefore not yet completely understood. Larvae newly hatched in captivity, displayed strong tendencies to crawl, or wiggle to the nearest high point suggesting that movement upward is a reflex action in the froglets. This behaviour may help them avoid potential predation from other ground dwelling carnivores. Metamorphosis is completed on the back of brooding male frog and when and where the male frog goes and what initiates movement away from the nest site is not yet known. It is also not known whether the young leave with, or independently of, the male. Other research (*Chapter 3*) has shown that sub-adult frogs, aged 1-3 years, are most commonly found in vegetation, such as rice grass *Microlaena avenacea*, They then move into a rocky habitat once sexual maturity is reached.

During this thesis, *L.archeyi* were successfully raised in captivity and this chapter clearly describes the early development of this species. Development was found to be affected by temperature, and there was also a genetic effect based on parentage. The techniques used in this study have also been described and thus are available for future studies of early frog development. Such studies should be conducted, as possible as the captive rearing and

maintenance of individuals is a useful tool to obtain further scientific information on frog species, as well as to aid in threatened species recovery.

CHAPTER SIX-

THE DIET OF LEIOPELMATID FROGS IN WHAREORINO FOREST
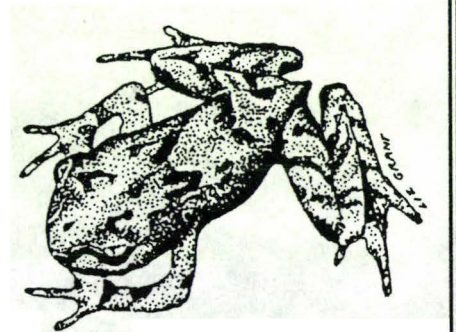
Chapter 6

The diet of leiopelmatid frogs in Whareorino forest.

6.1 Introduction

Post-metamorphic amphibians are feeding opportunists, and as such their diet reflects the availability of food in their environment. This is principally invertebrate species such as arthropods, molluscs, and worms (Zug 1993), although large amphibians are capable of eating vertebrates such as mice, rats and snakes (Duellman and Trueb 1986). Frogs are also gape limited predators so the size of prey they are able to injest is determined largely by the size of the frog, because this correlates with mouth size (Clarke 1974, Tyler 1976, Pianka 1983, Lima and Moreira 1993). Most species of frog are also cannibalistic (Zug 1993) and prey selection changes as the frog grows (Lima and Moreira 1993).

Duellman and Trueb (1986) suggested that amphibians have a low level of food discrimination, but Stebbins and Cohen (1995) stated that prey attributes, such as size, movement, palatability and nutritive value, affect food choice. In general, amphibians have two kinds of foraging strategy; a sit-and-wait (sedentary) strategy, common to anurans, and an active foraging strategy, common in salamanders and caecilians. Sedentary foragers typically select prey of a larger relative size. Such prey, including beetles and spiders generally occur as solitary individuals in the environment (Pough and Taigen 1990, Toft 1981, 1985, Lima and Moreira 1993).

Anurans often have well developed structures specialised for particular prey. For instance *Rhinophrynus dorsalis*, a large toad, is able to project the tip of its tongue forward, unlike other frogs. This allows it to catch ants and termites efficiently (Trueb and Gans 1983). Das and Coe (1994) examined the dentition of various Indian anurans,

bodied invertebrates, whereas those with more prominent teeth commonly fed on larger hard-bodied invertebrates.

Major studies on the actual diet of leiopelmatid frogs have been limited to a study by Kane (1980) who compared the diet of hamilton's frog (*L. hamiltoni*) with the whistling frog *Litoria ewingi*. Kane (1980) found that Hamilton's frog ate more mites and flies than the whistling frog which ate predominantly amphipods and spiders. He also examined feaces from *L. archeyi* and *L. hochstetteri* and found that beetles were an important component of the leiopelmatid diet. However studies of rare species are often restricted because individuals cannot be killed to obtain the contents of their digestive systems. In addition soft-bodied invertebrates do not show in feacal analysis. I used pitfall traps to sample the ground-dwelling invertebrates to find the potential food of leiopelmatid frogs in Whareorino forest. During sampling, however, 8 leiopelmatid frogs became accidently caught in the traps and died. The stomach contents from these frogs were then able to be compared to the data obtained from pitfall traps.

Such studies of the dietary requirements of a species are important in understanding the ecology of the frogs. An understanding of the dietary requirements of leiopelmatid frogs is an important prerequisite in establishing new populations and for rearing frogs in captivity.

6.2 Methods

Potential and actual diet

Samples of ground dwelling invertebrates were taken from Whareorino forest over a 12 month period, from August 1996 to July 1997. Invertebrates were collected in pitfall traps. Each trap consisted of a round plastic food container, with a diameter of 9 cm and a depth of 5 cm. Each trap was set into the ground so that the opening was level with the leaf litter. Each trap was surrounded by a selective net fence, with $1cm^2$ mesh and protected by a large white cover. A 10 - 15 cm gap was allowed between the protective cover and the trap.

Samples were collected by placing glycerol solution (75 %) in each trap to a depth of about 1 cm. This served as a temporary preservative for any animals that fell in. The contents of the traps were then subsequently collected 14 nights later. Invertebrates were recovered from the glycerol solution, in the laboratory, and stored in 70 % alcohol til further laboratory analysis.

Six traps, were operated in two groups during August, September and October 1996, and nine traps were subsequently run, as three groups from November 1996 til July 1997.

The stomach and rectal contents from each frog were obtained by dissection. The contents were stored in 70 % alcohol solution.

Invertebrate identification

Invertebrates from pitfall traps were recovered using a 0.5 mm sieve. Insects were sorted to family. The body length of each specimen was measured to 0.5 mm, and this was recorded on a standard invertebrate record sheet (Appendix 6.1). Representitive specimens of each family were retained as a reference collection at Massey University. A list of these is provided in Appendix 6.3.

Specimens were identified using;

- Borror, D.J., Tripplehorn, C.A., and Johnson, N. F. (1989) - An introduction to the study of insects (6th ed.). Saunders College Publishing, Chicago. pp 895.

- Klimaszewski, J.,Watt, J.C. (1997) Coleoptera: family group review and keys to the identification of the fauna of New Zealand. No. 37. Manaaki Whenua Press, Canterbury. pp 199.

- Fly species (Diptera) were identified by Dr. Ian Andrews (Biochemistry Department, Massey University)

Analysis of frog stomach and rectal contents was conducted in the laboratory by identifiying whole or parts of invertebrate and plant material. The body lengths of complete prey items were measured to 0.5 mm and recorded on a standard stomach content record sheet (Appendix 6.3). Partial specimens, such as a leg or wing were identified as far as practical. Usually this was to genus or family level, and an approximate body length was obtained by comparison with specimens from the

pitfall trap samples. A complete record of the items identified from the stomach and rectal contents are included in Appendix 6.4

Data Analysis

Specimens from pitfall trap samples were grouped according to the month of sampling, invertebrate family and the body length (size) of the specimen.

Size categories used were:

- < 1 mm length
- 1.5 - 3 mm length
- 3.5 - 5 mm length
- 5.5 - 7 mm length
- 7.5 - 9 mm length
- 9.5 mm and larger individuals

Graphs of percentage composition of prey species, were produced using Systat® version 6.0 for Windows®, SPSS Inc., Chicago.

6.3 Results

6.3.1 Stomach and rectal content analysis

Eight leiopelmatid frogs were caught in pitfall traps during pifall trap sampling. Three were caught in the 14 day sampling period collected on 6 August 1996, (frog number 10, 11 and 12). Frog number 39 was caught in a sample collected on 25 December 1996, and number 133, 134 and 135 were in samples collected on 6 March 1997 and frog number 136 was collected on 16 June 1997.

The stomach and rectum contents of these 8 frogs, contained a wide range of forest floor invertebrates as summarised in Table 6.1. Each frog had some invertebrates in its gut indicating that they are seldom entirely empty of food. The most commonly eaten invertebrate were mites (Acari: 23.7 %), Collembola (20.4 %) and insect larvae (18.3 %). Amphipods (7.5 %) and beetles (Coleoptera: 8.6 %) were also eaten, as well as a wide range of other invertebrates. These included Araneae, Diptera, Diplopoda, Isopoda, Hymenoptera, Psuedoscorpione, Hemiptera, Formicidae and one gastropod. Comparison of the invertebrate diversity within individual frogs with frog size showed that small frogs (i.e <20.0mm SVL) ate several species of invertebrate which were not eaten by larger frogs. These included invertebrates such as Isopods, Pseudoscorpiones, Hymentopterans and Hemipterans. Smaller frogs, however, did contain many of the same species which occur in larger frogs, but the size of the invertebrates within smaller frogs was also generally smaller than those in large frogs (Figure 6.1).

The highest invertebrate diversity and the largest number of invertebrates per frog, were recorded in frog number 133, (SVL 15.9; Figure 6.2A and B). The diet of this frog included 12 Collembola, 8 insect larvae, and several Diptera, one of which was 10.0 mm long. This frog also had proportionately the largest invertebrate relative to its snout-vent length of any frog sampled (Figure 6.3). The average number of invertebrate groups per frog was 6.8 groups (ie. 7 groups) with the grestest diveristy recorded in three of the small sub-adult frogs (Figure 6.2A). An average of 11.6

(ie. 12) invertebrates per frog was recorded. There was no apparent trend visable between frog size and the number of invertebrates eaten (Figure 6.2B), however this may not be visable due to the limited samples of frogs. The range in ratio of snout-vent length to length of the largest invertebrate eaten was from 62 % - 20 %, Figure 6.3.

Table 6.1 Invertebrates in stomach and rectum contents of eight leiopelmatid frogs from Whareorino forest.

Frog Number	Snout-vent Length (mm)	Invertebrate Group	Number of Invertebrates	Percentage of Sample
39	9.1	Acari	8	72.7
		Insect Larvae	1	9.1
		Araneae	1	9.1
		Collembola	1	9.1
		Total	11	
136	11.3	Acari	4	66.7
		Insect Larvae	2	33.3
		Total	6	
134	11.1	Acari	3	21.4
		Insect Larvae	3	21.4
		Collembola	4	28.8
		Amphipoda	1	7.1
		Microsnail	1	7.1
		Pseudoscorpione	1	7.1
		Coleoptera	1	7.1
		Total	14	
135	10.0	Collembola	2	50.0
		Coleoptera	1	15.0
		Hemiptera	1	15.0
		Total	4	
133	15.9	Acari	2	6.3
		Insect Larvae	8	25.0
		Araenae	2	6.3
		Collembola	12	37.5
		Pseudoscorpione	2	6.3
		Isopoda	1	3.1
		Diptera	4	12.5
		Hymenoptera	1	3.1
		Total	32	
12	20.0	Acari	2	22.2
		Insect Larvae	2	22.2
		Amphipoda	1	11.1
		Araenae	1	11.1
		Formicidae	1	11.1
		Coleoptera	2	22.2
		Total	9	

Table 6.1 *continued*

11	35.0	Acari	2	28.6
		Insect Larvae	1	14.3
		Amphipoda	2	28.6
		Coloeoptera	1	14.3
		Araneae	1	14.3
		Total	7	
10	40.0	Acari	1	10.0
		Amphipoda	3	30.0
		Coleoptera	3	30.0
		Diplopoda	2	20.0
		Diptera	1	10.0
		Total	10	
Summary Statistics : **All frogs**				
		Acari	22	23.7
		Insect larvae	17	18.3
		Collembola	19	20.4
		Amphipoda	7	7.5
		Microsnail	1	1.1
		Pseudoscorpione	3	3.2
		Coleoptera	8	8.6
		Isopoda	1	1.1
		Hymenoptera	1	1.1
		Hemiptera	1	1.1
		Araneae	5	5.4
		Diptera	5	5.4
		Diplopoda	2	2.2
		Formicidae	1	1.1
	Total	14 Groups	93 Individuals	
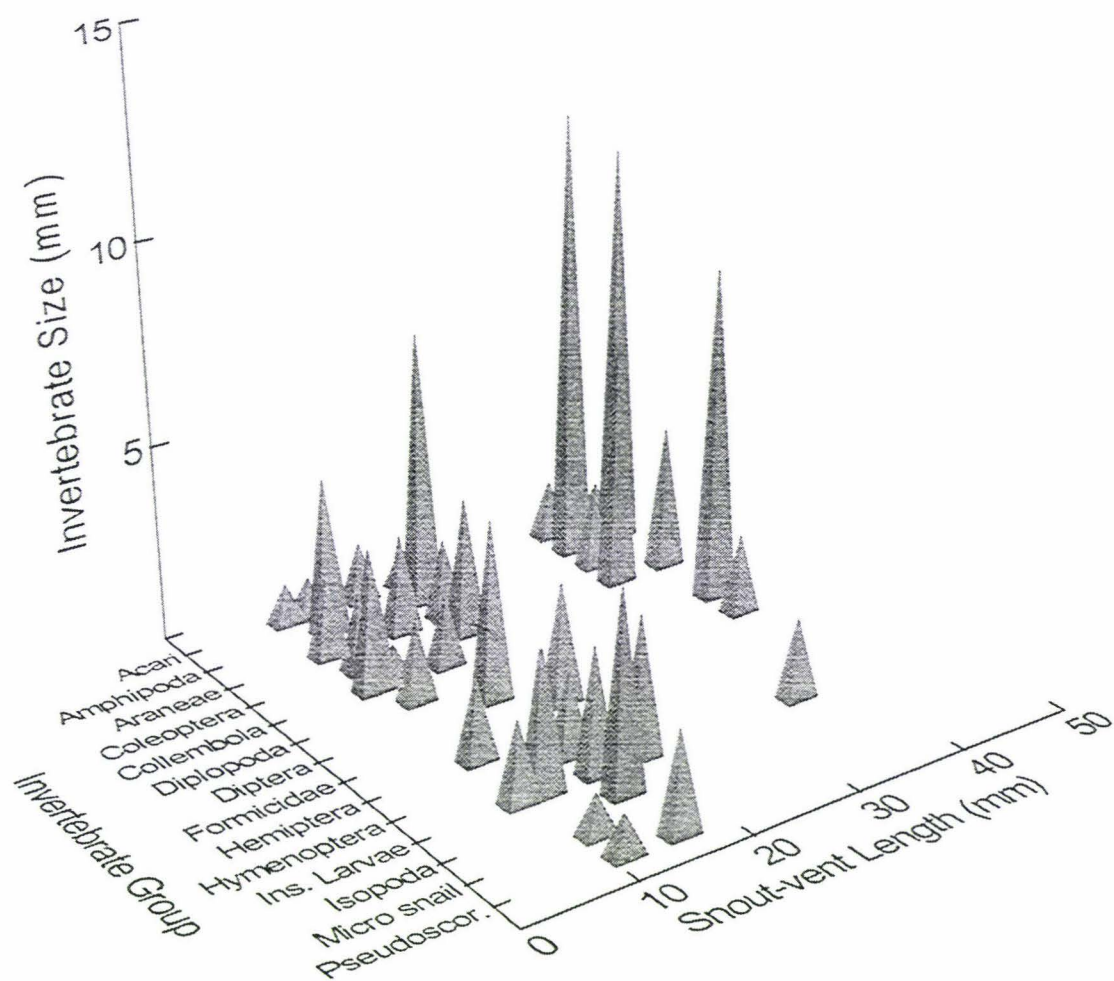
Figure 6.1 Invertebrates recorded in the stomach and rectum contents of 8 leiopelmatid frogs from Whareorino forest.
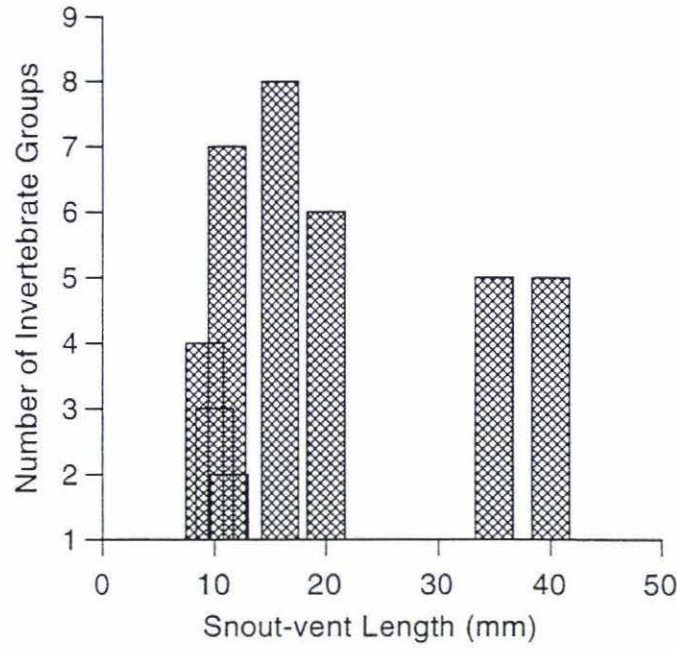
A.
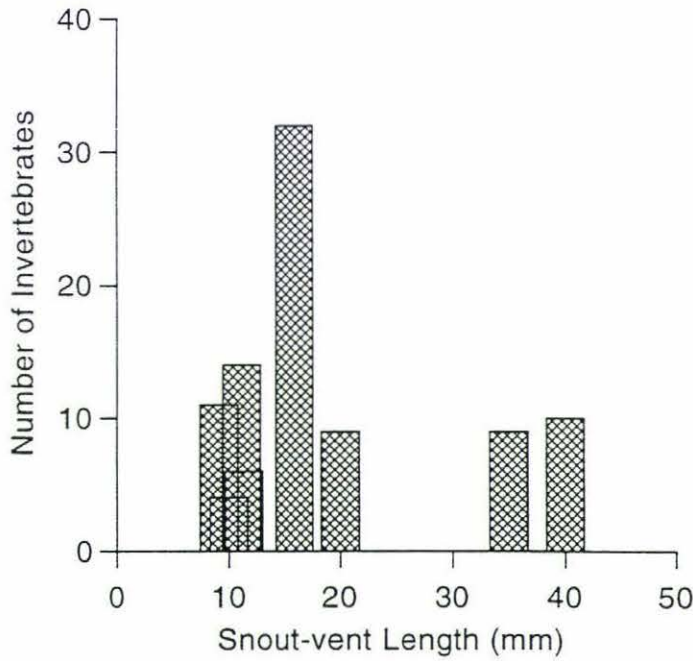
B.

Figure 6.2 Number if invertebrates in stomach and rectum contents of 8 frogs from Whareorino forest, in relation to the snout-vent lengths of each frog.
A: Number of invertebrate groups. **B**: Number of invertebrates.
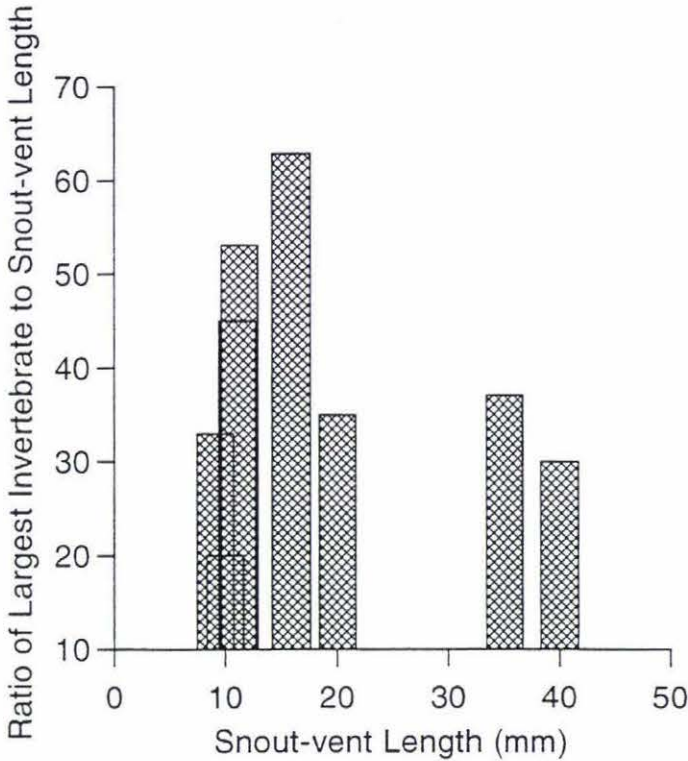
Figure 6.3 A comparison of the ratio of the largest invertebrate found in the
stomach or rectum to the snout-vent length of eight frogs from Whareorino
forest.

6.3.2 Invertebrates found in Whareorino forest

The invertebrates caught in pitfall traps in Whareorino forest varied in family groups and the numbers and abundance of indivudals present changed throughout the field work year. A brief summary of the major results are included below, and the raw data is included as Appendix 6.5.

Invertebrates less than 1 mm long.

Collembola and mites (Acari) were the the dominant invertebrates in this size class throughout the year (Figure 6.4). However the composition of other invertebrates changed during the year, Microsnails and Pseudoscorpiones were the two main invertebrate groups caught during late winter and early sping whereas Coleoptera appeared, ie Staphylinidae and Carabidae in December. Insect larvae were first recorded in October and were present till the end of the sampling period (July 1997). The super-family Entomobryidea (Collembola) were very abundant during March but were not recorded in large numbers during any other month.

Invertebrates 1.5 mm to 3.0 mm long.

The greatest variety of invertebrate families occurred in this size range, indicating that in terms of biodiversity this size class was the most prolific.

During August, September and October, 21 different groups of invertebrates were recorded (Figure 6.5). Collembola were the most abundant, followed by Diptera, Acari and insect larvae. However, in September mostly ants (Formicidae), Carabid beetles, and insect larvae were present. Insect larvae continued to be prominent to February, along with Amphipods, Entomobryidae, Coleopteran beetles and some microsnails. Samples collected during March, however, were dominanted by Collembola, Sphaeroceridae (Diptera) and amphipods.

During Autumn and winter months, (April to July) the invertebrate fauna in this size class was dominated by Entomobryidea, Insect larvae and amphipods.

Invertebrates 3.5 mm to 5.0 mm long.

Invertebrates in this size range varied a lot between monthly samples. In August,

40 % were Collembola, and 20 % were amphipods whereas in September, for example, Coleoptera comprised 40 % of the sample and Eucinemidae (Coleopetera). Insect larvae, Tipulidae, microsnails, and amphipods were also present in the samples. Amphipods were the most abundant species in October and November but many other invertebrate groups were present in relatively low numbers. These included Coleoptera, Diptera, insect larvae, Araneae, Entomobryidea, isopods, and microsnails. December to Februaury was dominated by amphipods, as well as Coleoptera. Several Diptera were recorded. Formicidae were also abundant during the summer months, but after February the comprised less than 10 % of the samples. In March, Coleopterans and amphipods acccounted for most of the inveretebrates, although other groups were present but recorded in lower numbers. Coleoptera were the most abundant invertebrates in Winter months of May, June, and July, although from April, amphipods were also abudant. Many other groups were also present during these months, such as Entomobryidea, Isopoda, Araneae, and insect larvae, however were not often present in a high abundance.

Invertebrates 5.5 mm to 7.0 mm long.

This size category yielded an obviously lower diversity of groups than in the previous size categories with all months except June having fewer than 10 invertebrate groups (Figure 6.7).

From August to November, no particular group was dominant and only 13 invertebrates were caught in total, from all nine traps. These included amphipods, an ant (Formicidae), a fly (Mycetophilidae), a curculionid (Coleoptera) and a microsnail. However during the summer months of December to February, beetles (Coleoptera) and amphipods were usually the dominant groups. Microsnails were also caught every month, but in low numbers. The Autumn months of March to May, however, were very different from each other. In March, predominantly ants (Formicidae), Amphipods and Coleoptera were caught. The April samples consisted of Amphipods, mostly and the May samples contained a mixture of insect larvae, Coleoptera, an Amphipod and a centipede (Diplopoda). Mainly Coleoptera and

Amphipoda as well as insect larvae, isopods and ants were caught in June whereas isopods, an amphipod, a carabid beetle and a large insect larvae were caught in July.

Invertebrates 7.5 mm to 9.0 mm long.

Samples in this large size class were mostly dominated by amphipods throughout 1996 to 1997 (Figure 6.8). Coleoptera, such as carabids and curculionids were often presnt as well as micorsnails. During the summer months a diplopod, an opilione and insect larvae were present, although during Autumn to Winter months consistently fewer than 5 groups of invertebrates were caught, with amphipods and insect larvae dominating the invertebrate fauna.

Invertebrates 9.5 mm or longer

During the late winter and early spring months (August to November) 17 invertebrates were caught in this size range, 10 of which were amphipods, and 2 were insect larvae, 2 were diplopods and 2 were oligocheates. A phoridae and an entomobryid were also collected (Figure 6.9).

From December to March, 14 groups of invertebrates were caught, Amphipods being the most common but carabid beetles were abundant during the summer months. The later comprised 47.1 % of the invertebrates caught during May. Other groups were also present as one or two individuals including 7 oligocheates found from December to March, 6 *Paraphanta* snails, 4 millipeds (Diplopoda), and 4 Staphylinidae (Coleoperta).

After April, amphipods were the most common group followed by *Paraphanta* snails. Oligocheates, insect larvae, microsnails, chilopods, diplopods, coleopterans and isopods.

Figure 6.4 Relative proportion of invertebrates of body length < 1.0 mm, per month collected from Whareorino forest.

LEGEND

- Trichoceridae
- Tipulidae
- Tenebrionidae
- Staphylinidae
- Sphaeroceridae
- Simuliidae
- Sciaridae
- Scarabaeidae
- Psychodidae
- Pseudoscorpione
- Platygastridae
- Phoridae
- Paraphantidae
- Opiliones
- Oligocheate
- Mymaridae
- Mycetophilidae
- Muscidae
- Micro-snail
- Melandryidae
- Leiodidae
- Isopoda
- Insect Larvae
- Hydrophilidae
- Hydraenidae
- Formicidae
- Eucinemidae
- Entomobryidea
- Diplopoda
- Diapriidae
- Delphacidae
- Curculionidae
- Collembola
- Coccoidea
- Chysomelidae
- Chironomidae
- Chilopoda
- Carabidae
- Araneae
- Aphididae
- Amphipoda
- Acari

Figure 6.5 Relative proportion of invertebrates of body length 1.5 - 3.0 mm, per month collected from Whareorino forest.

LEGEND

Trichoceridae
Tipulidae
Tenebrionidae
Staphylinidae
Sphaeroceridae
Simuliidae
Sciaridae
Scarabaeidae
Psychodidae
Pseudoscorpion
Platygastridae
Phoridae
Paraphantidae
Opiliones
Oligocheate
Mymaridae
Mycetophilidae
Muscidae
Micro-snail
Melandryidae
Leiodidae
Isopoda
Insect Larvae
Hydrophilidae
Hydraenidae
Formicidae
Eucinemidae
Entomobryidea
Diplopoda
Diapriidae
Delphacidae
Curculionidae
Collembola
Coccoidea
Chysomelidae
Chironomidae
Chilopoda
Carabidae
Araneae
Aphididae
Amphipoda
Acari

Figure 6.6 Relative proportion of invertebrates of body length 3.5 - 5.0 mm, per month collected from Whareorino forest.

LEGEND

Trichoceridae
Tipulidae
Tenebrionidae
Staphylinidae
Sphaeroceridae
Simuliidae
Sciaridae
Scarabaeidae
Psychodidae
Pseudoscorpione
Platygastridae
Phoridae
Paraphantidae
Opiliones
Oligocheate
Mymaridae
Mycetophilidae
Muscidae
Micro-snail
Melandryidae
Leiodidae
Isopoda
Insect Larvae
Hydrophilidae
Hydraenidae
Formicidae
Eucinemidae
Entomobryidea
Diplopoda
Diapriidae
Delphacidae
Curculionidae
Collembola
Coccoidea
Chysomelidae
Chironomidae
Chilopoda
Carabidae
Araneae
Aphididae
Amphipoda
Acari

Figure 6.7 Relative proportion of invertebrates of body length 5.5 - 7.0 mm, per month collected from Whareorino forest.

LEGEND

- Trichoceridae
- Tipulidae
- Tenebrionidae
- Staphylinidae
- Sphaeroceridae
- Simuliidae
- Sciaridae
- Scarabaeidae
- Psychodidae
- Pseudoscorpione
- Platygastridae
- Phoridae
- Paraphantidae
- Opiliones
- Oligocheate
- Mymaridae
- Mycetophilidae
- Muscidae
- Micro-snail
- Melandryidae
- Leiodidae
- Isopoda
- Insect Larvae
- Hydrophilidae
- Hydraenidae
- Formicidae
- Eucinemidae
- Entomobryidea
- Diplopoda
- Diapriidae
- Delphacidae
- Curculionidae
- Collembola
- Coccoidea
- Chysomelidae
- Chironomidae
- Chilopoda
- Carabidae
- Araneae
- Aphididae
- Amphipoda
- Acari

Figure 6.8 Relative proportion of invertebrates of body length 7.5 - 9.0 mm, per month collected from Whareorino forest.

Figure 6.9 Relative proportion of invertebrates of body length > 9.5 mm, per month collected from Whareorino forest.

LEGEND

Trichoceridae
Tipulidae
Tenebrionidae
Staphylinidae
Sphaeroceridae
Simuliidae
Sciaridae
Scarabaeidae
Psychodidae
Pseudoscorpione
Platygastridae
Phoridae
Paraphantidae
Opiliones
Oligocheate
Mymaridae
Mycetophilidae
Muscidae
Micro-snail
Melandryidae
Leiodidae
Isopoda
Insect Larvae
Hydrophilidae
Hydraenidae
Formicidae
Eucinemidae
Entomobryidea
Diplopoda
Diapriidae
Delphacidae
Curculionidae
Collembola
Coccoidea
Chysomelidae
Chironomidae
Chilopoda
Carabidae
Araneae
Aphididae
Amphipoda
Acari

Whareorino invertebrate fauna: size range comparison.

The size distribution of invertebrates on the forest floor of Whareorino forest varied little throughout the year (Figure 6.10). The smallest size category, < 1 mm, were always the most dominant group and their abundance varied between 31.0 % of the June invertebrates to 85.9 % of the August sample. The next size category (1.5 mm to 3 mm), was often the next most abundant group, except in both October, and June, when the 3.5 to 5 mm size category was the second most abundant group.

Invertebrates in the largest size category were more abundant than the two smaller size categories, (5.5 mm to 7.0 mm and 7.5 mm to 9.0 mm), except in June when inverst in the 5.5 mm to 7.0 mm size category (13.8 % of the June sample) was much greater.

June was an 'unusual' month, because the abundance of invertebrates in the 6 size categories were close to each other.
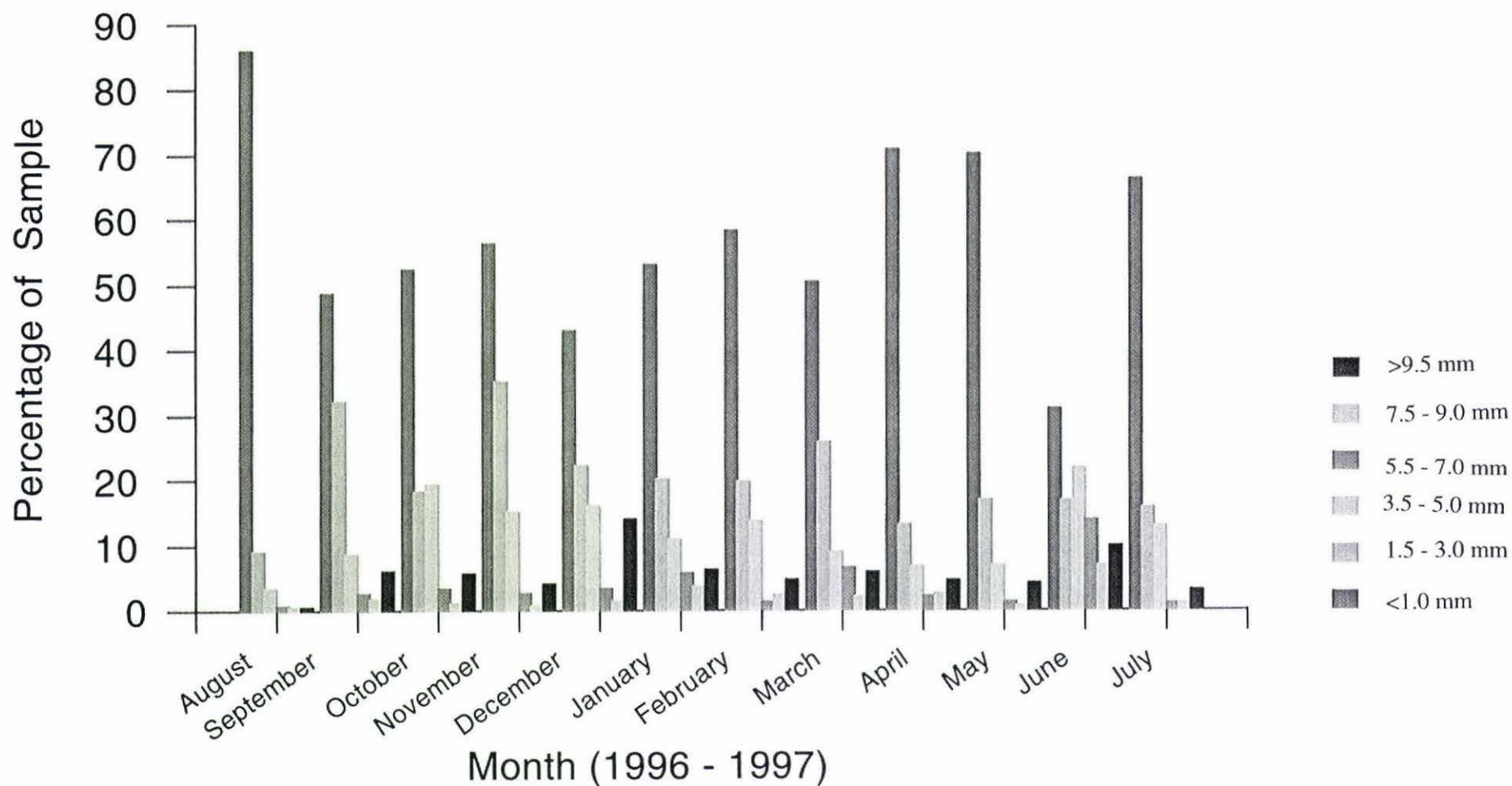
Figure 6.10 Invertebrate fauna abundance for the six size categories of invertebrate, during the year, in Whareorino forest.

6.4 Discussion

Leiopelmatid frogs employ a sit-and-wait strategy to capture food (*pers.obs.*). To capture prey, a frog will orientate itself towards a prey items that has been visually detected. When the prey becomes within 'leaping' range the frog makes a single leap and swallows the prey. Occasionally if a prey item is missed, then a second leap may occur (*pers. obs.*). Captive *L. archeyi* have also been found to use their front legs and toes to help guide prey into the mouth, particularly if appendages or wings of the prey are not taken into the mouth in the first gulp. Alternatively, a front arm may be 'wiped' over the mouth to ensure that everything is in the mouth. Gray *et. al.* (1997) termed these respective behaviours as 'scooping' and 'wiping', and suggested that they were common to ancient amphibian species.

A sit-and-wait strategy for prey capture possibly reflects the sedentary lifestyle that leiopelmatid frogs have and is important, for example, whilst brooding as adult males frogs spend several months under the same rock incubating eggs and probably do not forage beyond the nest site for food (*pers. obs.*).

Simon and Toft (1991) recently found that mites (Acari) were eaten by few species of anuran. They suggested that such small items were unprofitable for many frogs to eat unless they themselves were small. An example of one such small species is *Colostethus stepheni* (Lima and Moreira 1993). I found that mites (Acari) in this study were common food in all but 1 of the 8 frogs examined. The mites in relation to snout-vent length of the frog certainly suggest that more mites are found in smaller frogs (Figure 6.11) but to few frogs were used in this study to confirm this.
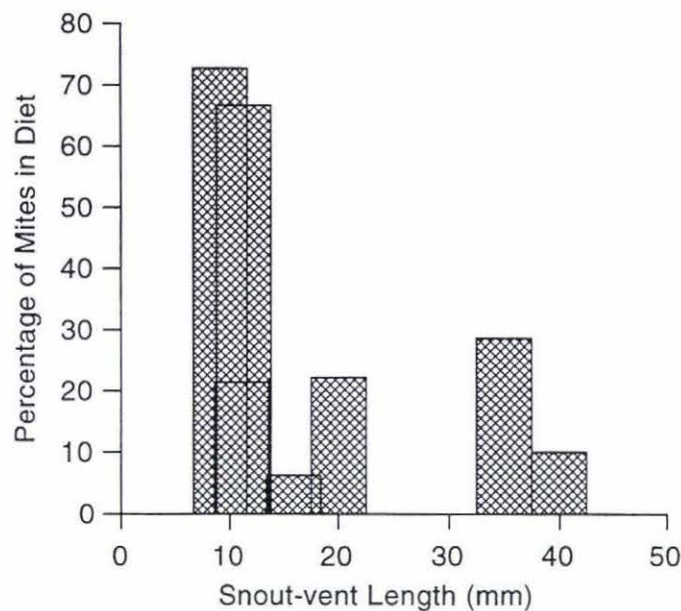
Figure 6.11 The percentage of mites in the diet of 8 leiopelmatid frogs, from Whareorino forest, in relation to snout-vent length of the frog.

Lima and Moreira (1993), showed that there is a similar tendency with other small prey items such as Collembola. In the leiopelmatid frogs, I only found Collembola in immature individuals (i.e. less than 25.0 mm SVL), and this does indicate a possible change in prey selection with age

Das and Coe 1994, studied the invertebrates eaten by 8 anuran species in India and found that Coleoptera were the most commonly eaten prey. Small terrestrial species (i.e. *Microhyla ornata*, *M. rubra*) had a narrow diet range(n_{groups}[1] = 5, n_{groups} = 2, respectively), whereas larger aquatic or terrestrial frogs, (i.e. *Tomopterna rolandae, Rana crassa, R. hexadactyla*) were found to have a wider range of prey types (n_{groups} = 10, n_{groups} = 17, n_{groups} = 10, respectively) (Das and Coe 1994). By comparison, I found that leiopelmatid frogs ingested an average of 5 invertebrate groups each, (range 2 - 8 groups), and no difference was detected between the smaller immature individuals (< 24.0 mm SVL) and the larger mature individuals (> 24.5 mm SVL)[2]. I suggest therefore that the diet range for leioplematid frogs is relatively wide and this which is especially likely considering that I only examined eight individuals. Such a wide diet may be in

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[1] n_{groups} = the number of invertebrate groups.
[2] refer *Chapter 2* for size categories of leiopelmatid frogs.

part due to the abundance of prey types available (groups), particularly in the smaller size categories.

I found that the range of leiopelmatid diet in individuals from Whareorino forest was much wider than previously reported for leiopelmatid frogs (Kane 1980). In his study Kane (1980) compared the diet of *L. hamiltoni* with the introduced frog *Litoria ewingii* using faecal analysis. Mites (Acarina) and Collembola were found to be the most common prey eaten by both species, (*L. hamiltoni*, 74 % mites, 14 % Coleoptera, *Litoria ewingii*, 21 % mites, 34 % Coleoptera). Diptera, Hymenoptera, Araneae, Hemiptera, Lepidoptera, Amphipoda and Gastropoda were also eaten by both species. Kane (1980) also compared the diet of *L. hamiltoni* with faecal samples from *L. archeyi* and *L. hochstetteri*. He found that no mites, Hemiptera or Leiopidoptera were present in the diet of *L. hochstetteri*. However, the diet of *L. hochstetteri* is likely to differ from the other species as *L. hochstetteri* occupies different habitat. Samples of stream water invertebrates were taken as part of my study but as yet have not been analysed. Kane (1980) in his examination of *L. archeyi* found that their diet consisted predominantly of mites (Acari) and Coleoptera, whilst Hymenoptera and Araneae were also strong components of the diet. Although, again Hemiptera and Leipidoptera were absent.

Several groups were identified in this study of the diet of leiopelmatid frogs, which were not reported by Kane (1980). These included insect larvae, Collembola, Pseudoscorpiones, Isopoda, Diplopoda, and Formicidae. These together, constituted 46.3 % of the invertebrates in Whareorino frogs. Some of the differences between the two studies, could be due to the methods because Kane (1980) used faecal analysis, and I used preserved stomach and rectum contents. Soft-bodied groups, such as insect larvae are not well preserved, in faeces although the remains of sclerotised groups, such as Pseudoscopions and ants (Formicidae) would perhaps would have been expected to be present.

Das and Coe (1994) found that frogs which primarily eat soft bodied invertebrates, such as insect larvae have very few or no teeth whereas those that commonly eat larger prey had various forms of teeth. They suggested that this is a response to having to either grip the prey or to break it up before ingestion (Das and Coe 1994). I found that large leiopelmatid frogs have well developed teeth, as described by Worthy (1987a) but teeth were absent in small (juvenile) individuals. A sub-adult individual, (number 12), that I

examined had teeth that were not as fully developed as in sexually mature individuals. I therefore suggest that tooth structure in leiopelmatid frogs develops as the frog ages and that it may be related to the change to sexual maturity. This observation may partially explain the ontogenic change in diet that I found in leiopelmatid frogs. I suggest that frogs with reduced or no teeth select for soft-bodied invertebrates whereas those individuals with well developed teeth select for harder bodied prey (Das and Coe 1994). I have also shown that the small immature terrestrial leiopelmatid frogs predominantly select daytime retreat sites in vegetation (*Chapter 3*) whereas larger mature individuals predominantly occupy daytime retreat sites under rocks and logs (*Chapter 3*, *Chapter 4*). I suggest that there may also be a correlation between daytime retreat site and prey available at the sites and this may help in understanding the complex habitat occupancy of the Whareorino frog community.

Comparison of the relative abundance of invertebrates caught in pitfall traps with that actual diet of the 8 leiopelmatid frogs examined, suggest that pitfall traps are a reliable method to assess diet from. The bulk of the invertebrates found in either the stomach or rectum of the 8 leiopelmatid frogs examined, were less than 3.0 mm (body length) (Figure 6.12). This correlates well to the size range of invertebrates during most months of the year (refer Figure 6.10).

At an invertebrate 'group' level pitfall trap sampling did reflect the prey eaten by the frogs, however the pitfall traps did yield a greater range of invertebrates. For example in the smallest size class, (individuals < 1 mm) groups which were caught in pitfall traps were Collembola, mites (Acari), Coleoptera, Diptera, and insect larvae, which compares well to the prey items of leiopelmatid frogs in the same size class (mites, insect larvae, Collembola, Diptera, Microsnail and Pseudoscopione).

The second size category yielded a vast range of invertebrate fauna from the pitfall trap samples, which was not reflected by such a wide diversity of frog prey. However, frogs may be selective with their prey, especially considering their habitat preferences and level of tooth development as discussed earlier. Such prey selectivity, where a community of animals does not prey resources proportionate to their availability in the environment, was shown by a comparable study conducted in New South Wales (Webb 1995). This study found that some invertebrates that were abundant in the pit-fall trap samples (i.e. earwigs, scorpions, centipedes and millipedes) were not eaten by the herpetofauna species, and other invertebrates were not eaten in proportion to their

abundance on the forest floor. Differences in prey selectivity because of foraging behaviours and habitat preferences are known to occur (Crome 1981).
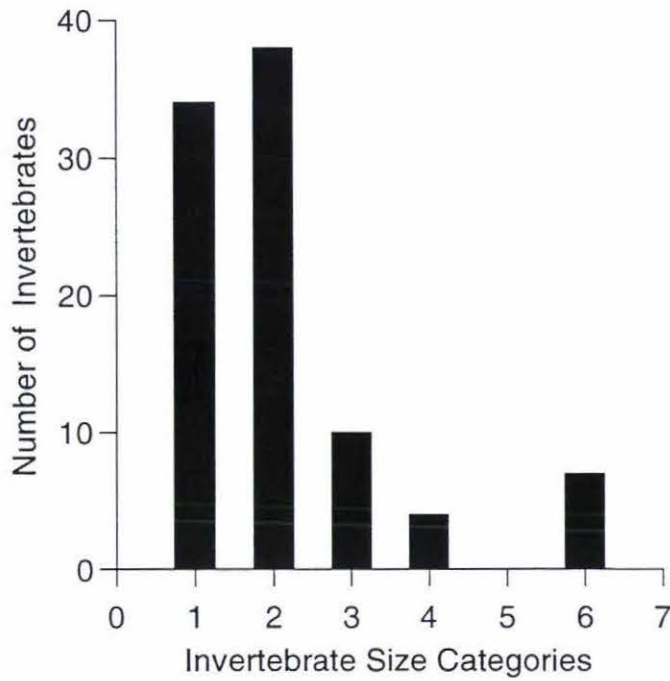
Figure 6.12 The invertebrate diet of leiopelmatid frogs in Whareorino forest, categorised according to invertebrate size[3].

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[3] refer to methods section for size categories of invertebrates.

Conclusion

The results of this study have shown that leiopelmatid frogs eat a wider range of prey types than what has been shown in previous studies. This was potentially due to differences in sampling methods. The range in food types as well as the species eaten was found to alter with the size of the frog which indicated an ontogenic shift in diet for these frogs. This shift in prey selection has been suggested to be related to two factors, tooth structural development as the frog ages and differences in habitat selection between young and sexually mature frogs. The results of this study are important for use with captive colonies of frogs so that ideal food types are provided.

CHAPTER SEVEN-

NATIVE AMPHIBIAN SURVEY PROTOCOLS, HANDLING TECHNIQUES AND KEY MAINLAND MANAGEMENT ISSUES
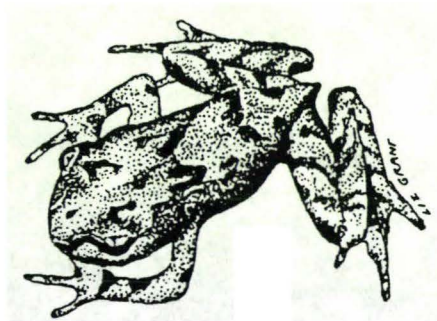
Chapter 7

Native amphibian survey protocols, handling techniques,

and key mainland management issues.

New Zealand leiopelmatid frogs have been a studied component of the endemic fauna since the first ones were described in 1853 (Stephenson 1961). They are recognised in texts as ancient and highly evolved anurans which have retained many primitive characteristics (*Chapter 1*). Sub-fossil remains of these frogs have been found throughout the North and South Island of New Zealand indicating that species of *Leiopelma* were once more widely distributed, and more diverse (Worthy 1987a). Currently, only two species of leiopelmatid frog are known to occur in the North Island, and no extant native frog has been found in the South Island (*Chapter 1*).

There two places on the North Island where *L. hochstetteri* and *L. archeyi* occur sympatrically (Thurley and Bell 1994, Newman 1996). My study concentrated on one of these places, Whareorino forest, near Te Kuiti. Here a number of aspects of a small proportion of the total population of leiopelmatid frogs were studied, including habitat selection, general population dynamics, complex body morphology and diet. The early development of *L. archeyi* was followed and described.

My study was conducted in Whareorino forest for several reasons. Firstly, this population was only discovered in 1991, and therefore information on these frogs is limited to the initial survey work and to a comprehensive study by Thurley (1996). Secondly, this population was the closest and most accessible mainland population to Massey University, where I was based. Also, no study had as yet considered two sympatric leiopelmatid frogs in detail, and these in Whareorino forest provided the opportunity to consider an amphibian community where leiopelmatid frogs were locally abundant (Thurley and Bell 1994).

The main research for my study was conducted in a small study site, P grid (*Chapter 1*). Research in such a small area had several advantages. Firstly, it allowed the same habitat to be frequently re-surveyed, and presented the opportunity for the re-capture of marked individuals. Secondly the observation of the same individuals occurred over time. An example is the brooding male *L. archeyi* in *Chapter 5*. Thirdly, frequent examination of unusual characteristics amongst and between individuals enabled a unique or 'unusual' group of individuals to be recognised.

My study therefore, bridged a gap in the scientific knowledge of the community structure of native New Zealand amphibians. However, an additional aim of this study was to test and develop monitoring techniques suitable for long term studies of other native frogs.

The responsibility for management and monitoring amphibian species is currently held by the New Zealand Department of Conservation *Te papa atawhai*. The Department of Conservation formulate 'Recovery Plans' for species or groups of species, in which guidelines for future management are stated. In 1996 the entire native frog genus *Leiopelma* was included within a 'Frog Recovery Plan', which was developed by Don Newman. The main emphasis of management was to establish further populations of *L. hamiltoni* and *L. pakeka*, as well as to develop adequate and standardised monitoring techniques for populations of native frogs. This was done particularly for those frogs in the North Island where research and management is not as concentrated (Newman 1996). It was also recognised that further scientific research is required and adequate husbandry techniques developed so that successful captive rearing and maintenance of all species of native frogs is possible.

This five year plan effective from February 1996. It is due for revision in 2001.

During the field work phase of my study several volunteers assisted with the field research. However, as many people were involved, I developed protocols for handling live amphibians to minimise the possible deleterious effects to individual frogs. This protocol is outlined below, so that it is available to future field researchers.

In addition, survey techniques were developed for sampling the local amphibian community. A broad outline of these survey techniques has also been included below as a reference or guide for future field studies.

Handling protocols

Field techniques

The following protocol of handling techniques was established to minimise the stress to animals, both during habitat surveys and during handling.

General protocol

Before going into the study site(s), researchers and assistants were instructed not to apply suncreen, or any other chemical based substance using their hands. If sunscreen or insect repellent was required, roll-on application was used. This ensured that no chemical residue could be unintentionally wiped onto the frogs.

All equipment, including calipers, toe-clip scissors, weigh bag and the balance tray were wiped with 70 % alcohol at the conclusion of each day in the field.

All rubbish and waste was collected and taken out of Whareorino forest after each field trip.

Capture and handling techniques

When disturbed frogs commonly jump towards the nearest available retreat, and are detected by a searcher. Frogs can be picked up by guiding the fore and index finger under the belly of the frog, from the left or right side of the frog or from the front of the frog. The thumb can then be placed gently on the dorsal surface of the frog and the frog picked up.

The frog should be transferred to a holding container or into the palm of a hand for measurement.

Handlers were advised to be seated whilst they handled frogs so that if a frog was dropped or jumped away from a handler, the frog would not 'fall' too far.

Small frogs, with a snout-vent length (SVL) of less than 20.0 mm were handled in the palm of a hand only, and non-experienced field assistant were generally not permitted to handle frogs smaller than 12 mm SVL.

If a male frog was found brooding a clutch of eggs under a rock, then the rock was replaced, as quickly as possible. Care was taken to put the rock back into the exact position that the rock had been in previously. It was replaced by placing the rock on its side and then very slowly lowering the rock back down. This minimised disturbance to brooding frogs.

Initially frogs were weighed using a 10 gram persola balance while the frogs were held in a 10 cm^2 clear plastic bag. This appeared to cause no stress to the animal, and most individuals remained motionless.

Frogs were generally photographed with their eyes facing away from the camera, because a flash was used and the effect of bright lights on frogs and their eyes is unknown.

Water was collected in 1 litre 'sports drink' bottles, from the stream closest to the study site and taken up to study site where it was used to 'wash' animals, after handling and before they were released. This was done more often during warmer weather, especially if an animal became stressed or dry. The frogs were considered to be stressed if they emitted chirps or made a series of jumps in an attempt to escape from the handler.

Occasionally a frog was required to be contained, while other frogs were being measured. Such a frog was placed in a black container and placed in shade, under a cover till handled further. Each frog was washed with water before being put in the container, and the container was rinsed with water before another frog was placed in it to prevent transmission of any disease.

Frogs were released beside (if rock or log daytime retreat site) or in (if vegetated daytime retreat site) its capture site. Frogs returned to sites under rocks and logs were placed 'snout first' towards their retreat site. Most frogs immediately moved under the retreat site upon release.

Toe clipping

The end of toes were cut with sharp scissors which were dipped in alcohol. The toes were transferred to 1.5 mm eppendorf tubes with 70 % alcohol and stored at 4°C for possible DNA analysis. Toe clipping was conducted by myself and one other experienced handler during the study. Two people were always used, one to hold the frog and cut the toe, the other to record the data, hold the eppendorf and alcohol tubes, and label the eppendorf tube. This ensured that handling time remained within the maximum four minutes approved by the Massey University Ethics Committee.

Captive individuals

L. archeyi raised in captivity from eggs *(Chapter 5)* were minipulated as seldom as possible. Eggs were kept in glass containers and were regularly washed to prevent bacterial infection *(refer Chapter 5)*. Eggs were transported by a stainless steel teaspoon which was washed with distilled water and wiped clean between each transfer. Juvenile and sub-adult frogs were also moved between their glass containers to plates for weighing by using a stainless steel spoon. The frogs were encouraged to jump onto the spoon by gently lifting their head with the rounded edge of the spoon and then gently tapping the rear end of the frog to initiate forward movement. After weighing etc. frogs were washed with distilled water and returned to their containers with the stainless steel spoon. The frogs were not handled by humans.

Survey techniques

During my initial surveys of Whareorino forest and during the continued research in the forest, set survey techniques were followed. These techniques are applicable for in monitoring other native frog populations and have been outlined below. The survey techniques took into account both semi-aquatic and terrestrial frog species and so were designed for use in both habitats. Surveys were conducted as line transects, quadrats or random searches. Three major habitat types were surveyed during this study;

Rock habitat

The areas under rocks were commonly searched as potential daytime retreat sites throughout Whareorino forest. Rock searches were limited to those rocks that could be 'easily' picked up by a searcher, using two hands. Which rocks would be easy to pick up was learnt by experience.

When the underneath of a rock was searched as a potential daytime retreat, it was lifted, with two hands using a straight upwards motion. Rocks were not permitted to be rolled to one side because of the chance of 'squashing' anything underneath.

After the rock was lifted, the searcher would examine the area formally under the rock to observe movement. The length of time that a searcher would wait was dependent upon searcher experience. Searchers new to amphibian field research were required to observe for longer periods (i.e. 3 -5 seconds) than those who were familiar with the techniques because native frogs are cryptic and blend well with their surroundings.

If a frog was found, the frog would be removed and the rock immediately replaced.

If more than one frog were detected then either the rock was temporarily placed to one side till all animals were captured or another researcher (i.e. the data recorder) would undertake the frog capture.

Rocks on soil and leaf litter were most commonly searched during this study, but I also found rocks that were on other rocks or had large air spaces underneath where frogs often eluded capture by rapidly going under the other rocks or jumping into the air space. If this occurred, the rock would be carefully and slowly replaced and no further searching would be undertaken into the next rock layer. This rule prevented the destruction of entire rock piles.

If however a frog escaped under an adjoining rock (i.e. if their were two rocks close together) then a search was conducted under the next rock before the first rock was replaced.

Log (wood) habitat

Retreat sites under logs are often difficult to search in Whareorino forest for several reasons. They were often very decayed and would 'fall apart' when moved. Many logs are also too large to be picked up by searchers. Searching of these sites was limited to small logs with little decay. The logs were picked up, often by two people and placed immediately to one side, if space was available. Otherwise one end of the log would

placed on the ground and held up so that a person could search the retreat site. The log was replaced in the same position as much as possible after the retreat site had been searched.

Vegetation

Rice grass (*Microlaena avenacea*), hook grass (*Uncinia uncinata*) and various ground ferns were commonly searched in Whareorino forest. Searching this habitat was usually undertaken by experienced observers because frogs in this habitat were very small. The grass was parted approximately in half by the searcher first placing each hand back to back, arms extended. The hands were then moved in a downward motion, to a level approximately 10 cm from the base of the grass, at this point the hands parted and thereby divide the grass. When this occurred most frogs would 'fall' or 'jump' to the middle of the plant, or those individuals on the outer leaves would 'fall' or 'jump' into the surrounding leaf litter. The frogs was then detected by their movement.

Small ground ferns were also searched. These were often collections of sparsely grouped fronds, so only required gentle movements of the fronds to examine the frond bases.

Tree ferns were only searched if they were in transect or quadrats during my study. They were searched by close examination of the crown and often removal or disturbance of the leaf litter and other humus collected in the crown. This was rather destructive, but it was necessary because (Thurley 1996) had found frogs there.

Survey techniques

Line transects

Line transects were used outside the main study area on terrestrial sites only. Neither transect crossed a stream, but this method should be applicable for searching across streams as well.

Line transects were run, through rock habitat, and both rice grass (*Microlaena avenacea*), and hook grass (*Uncinia uncinata*).

Ten meters was considered to be the ideal length for several reasons;

- the average time taken to complete a 10 m transect was 41 minutes (2 people searching and 1 recording), or 75 minutes (1 person searching and 1 recording). Time taken is an important factor as searcher accuracy declines with time.

- the number of refuge sites searched per 10 m transect was consistently high enough to show contrasts with different habitats to show.

- few areas were suitable for more that 10 meters to be searched without there being a change in habitat.

Line transects were conducted by selecting a random point and a random compass direction. A tape measure was then run the length of the transect and everything 0.5 m either side of the tape was searched. Each searcher was equipped with a tape measure to check the distance from the central tape and to measure habitat variables. Searching was conducted till the end of the 10 m transect was reached.

The results from transect searches showed that there was large variation in the number of frogs found per transect. The greatest number of frogs were found in transects with predominantly more vegetation than rocks and the lowest number of frogs were found in transects with the highest number rocks (Figure 7.1). This could be expected in Whareorino forest because *L. archeyi* was the most common frog (*Chapter 2*), and it occurred commonly in vegetation.
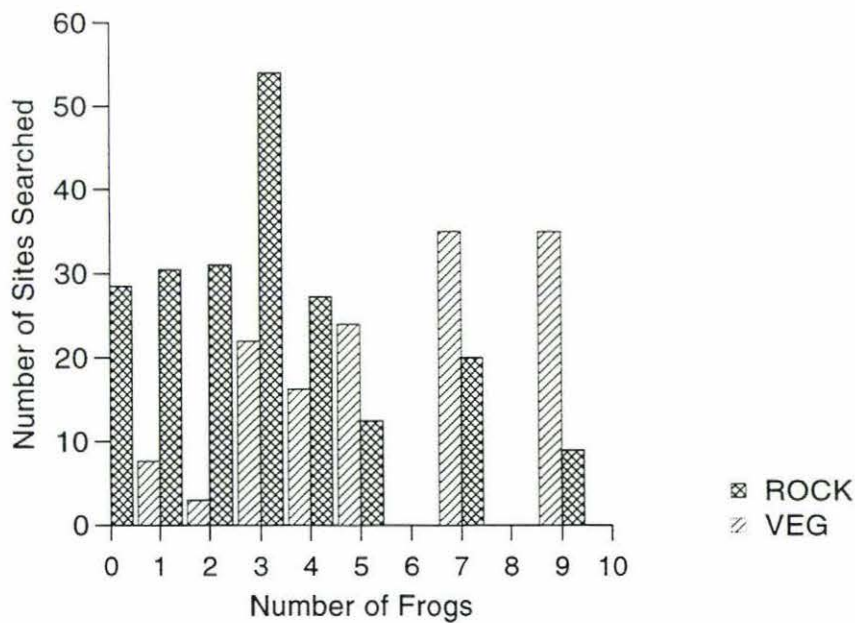
Figure 4.1 The number of vegetative and rocks sites searched per transect in Whareorino forest, in relation to the number of frogs found and their habitat.

I found from habitat surveys in Whareorino forest that different frogs groups are found in different habitats. Both rock and grass habitat, in particular, should be surveyed to account for the differences used by differently aged frogs because I found that a this difference occurs in *L. archeyi* and it may also occur in occur in other terrestrial frog species.

Quadrats

A series of quadrat samples were also conducted in P grid. P grid is divided into 10 m x 10 m plots and quadrat sampling involved randomly placing a series of 5 1 m x 1 m quadrats, within these.

Once in place, each potential daytime retreat site which wholly or partially occurred within the 1 m x 1m quadrat were searched and the micro-habitat details and details of the frogs caught were recorded. This is an intrusive sampling method because it took approximately 2.5 hours to complete 10 1m x 1m quadrats.

The average number of frogs caught per 10 m^2 from quadrat sampling, was higher than the average number caught in line transects. This was probably resulted as twice the number of refuge sites were searched in the quadrat samples (Table 4.1).

Table 7.1 No of sites searched and frogs found during transect and quadrat sampling in Whareorino forest.

	No. of sites and frogs recorded per 10 m^2.		
Sample method	No. of sites	No. of rocks	No. of vegetation sites	No. of frogs
Line transect	41.9	27.5	14.3	2.4
Quadrat sample	83.0	67.0	16.0	4.0

Average number of frogs found recorded per 10m^2 was 0.4 frogs with a range of 0 - 2 frogs per quadrat searched. In comparison line transects yielded 2.4 frog/ 10 m^2 searched. Thus quadrat sampling gave a higher abundance of frogs in Whareorino forest. However such samples took longer to obtain data because a larger number of sites were searched.

I suggest that both sampling methods yield important data. Quadrat sampling, is more thorough and yields a higher number of frogs. Line transects in comparison, can be searched more rapidly, but the searches are less thorough and a lower number of frogs may be recorded. I would suggest, however, that line transects are the ideal sampling method because they cause less disruption and line transects can cover a lot more areas thoroughly. Also a line transect can be set up quicker. Quadrat sampling, requires the grids to be set up first.

Casual searches

Random searches were conducted during the initial surveys of Whareorino forest and later when stream areas within and around P grid were also investigated.

The advantage to this survey method was that recaptures were possible within the one large study site. However the data on the distribution of frogs within P grid has not been presented in this thesis but the main findings of these surveys are presented below;

- recaptured frogs are often found within 1 or 2 meters of where they were last caught indicating that frogs select retreat sites within the same general area.

- rocks sampled as potential retreat sites, which did not have a frogs underneath, can often be found to have a frog under in a later search.

Random searching therefore was found to be an adequate method of searching a defined areas like P grid and can be a powerful tool when combined with techniques to estimate population sizes.

Key Management Issues

Monitoring

Species abundance and composition at a particular site and at a particular time is estimated by monitoring (Heyer *et.al.* 1994). The same method must be used each time if, changes in species abundance and composition over time are to be assessed.

One of the key issues for the management of mainland native frog populations is that it is not known if native frog populations are increasing or declining. This is the result of a

lack of consistent monitoring of populations. Hence management decisions have had to be made without this knowledge. The frog recovery plan recognised the need to develop suitable monitoring and to implement these in the field, on key populations. I propose that Whareorino forest do warrant regular monitoring for several reasons.

Firstly,, this population contains several unusual and distinct native frog groups including the morphologically larger *L. archeyi* (Thurley and Bell 1994) and the Type A frogs described in this thesis. Secondly, Whareorino forest is the first place that evidence of predation by rats has been found (Thurley and Bell 1994) and I found the dried remains of a frog, thought to be *L. hochstetteri*, by a stream in Whareorino forest, with what appear to be mammalian tooth marks on the legs (Plate 7.1). If this specimen is *L. hochstetteri*, then it is the first evidence of predation upon this frog recorded.

Predation by the introduced frog *Litoria aurea* was also recorded in a previous study (Thurley and Bell 1994), and although I found no introduced frogs during my study careful monitoring and studies should detect if this is a significant problem. Rats (*Rattus* spp.), mustelids and cats (*Felis catus*) were all present in Whareorino forest and all should be regarded as potential frog predators raising concern about the abundance of these potential predators.

Thirdly, introduced mammalian species including goats *Caprus hircus*, deer *Cervus* spp., pigs *Sus scrofa* and possums *Trichosurus vulpecula* occur in Whareorino forest and their browsing and grazing may have an effect upon frog habitat in terms of habitat degradation (Hadden and Westbrooke 1996). Elsewhere such introduced species have been implicated in the decline of both amphibians and reptiles (Murphy 1996). Generally however further habitat disruption, by either human or by introduced mammals should be prevented where possible.

It is impossible to mitigate against the threats of pathogens or other factors which have been implicated with the causes of the global declines in amphibians. Monitoring can only show the effects of any such factor, but it also does not identify the causal agents or prevent their action. Anecdotal records and other evidence should be kept in a central unit so that incidences of deaths attributable to these factors are monitored.

Plate 7.1 Leiopelmatid (*L. hochstetteri*??) remains found in Whareorino forest, 26/12/96.

This study has shown that a mixed frog community occurs in Whareorino forest, consisting of different aged individuals, and individuals from different species occupying different habitats. All are in need some form of protection. Some protection of the habitat is provided by the regular 'cull' of introduced mammals using 1080 baits and controlled hunting by Department of Conservation workers. It should be noted that Whareorino forest is open to the public and the threat of 'collection' by humans is a possibility.

Future scientific studies are required on all frog populations, but such studies should only be carried out, whilst minimising any deleterious effects of the research as frogs are clearly vulnerable species. Further surveys are also needed in other sites an issue which is fully considered in the 'Frog Recovery Plan' (Newman 1996).

Leiopelmatid frogs in Whareorino forest are, as Thurley (1996), found, locally abundant. They and possibly occur beyond the range that both Tertia Thurley and myself searched.

My study of the community structure of these frogs within Whareorino forest has yielded some exciting new results but more questions have possibly been raised than answered. How, for example, similar are the juvenile lifestages of *L. hochstetteri* with those of *L. archeyi*. Also the different frog identified in this study also requires further investigation because this could be a new species.
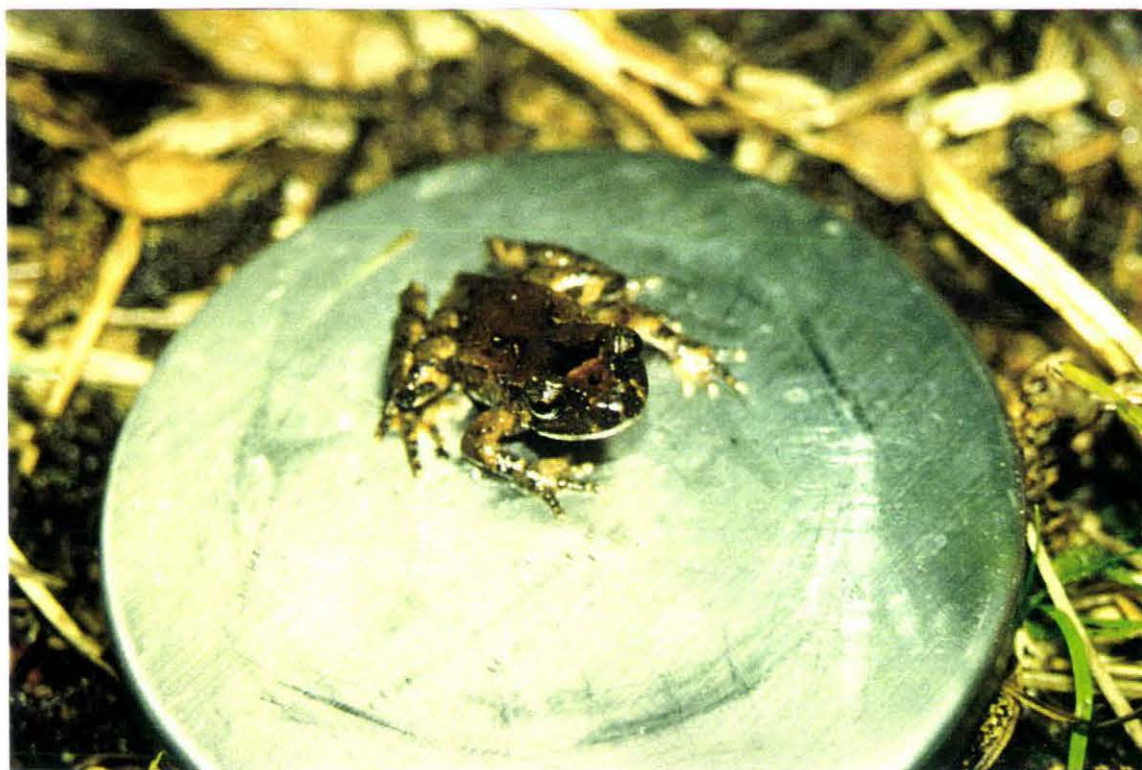
Plate 2.1E: Type A individual, dorsal surface.

Plate 2.2D: Type A individual, ventral surface.
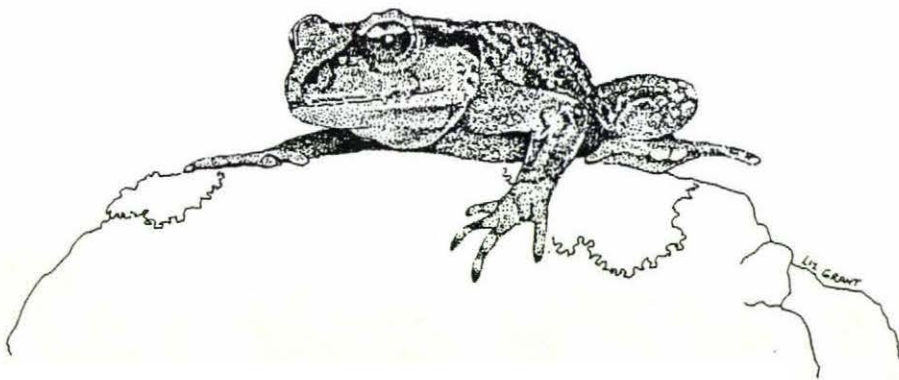
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APPENDICES
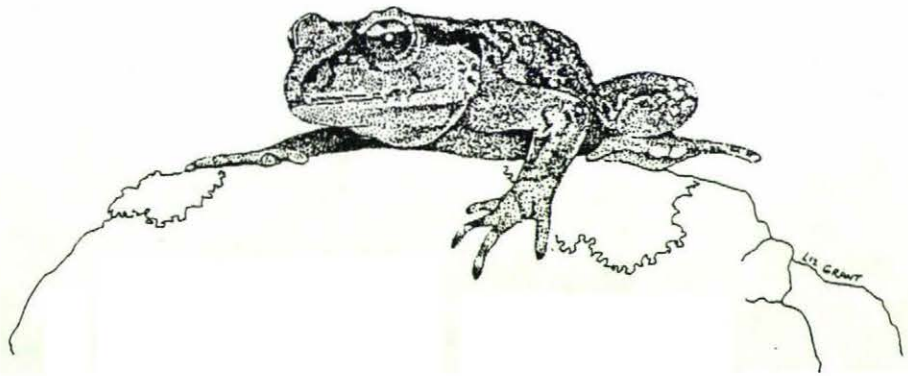
APPENDIX 2.1
THE SEVEN STANDARD MORPHOLOGICAL VARIABLES

FOR FULL DESCRIPTION OF THESE SEE APPENDIX 4.1

1. SNOUT-VENT LENGTH (mm)
2. HEAD WIDTH (mm)
3. REAR SHORT-TOE (EQUIVALENT TO NO. 4, APPENDIX 4.1) (mm)
4. REAR TOE- (EQUIVALENT TO NO. 18, APPENDIX 4.1) (mm)
5. FRONT SHORT-TOE (EQUIVALENT TO NO. 3, APPENDIX 4.1) (mm)
6. FRONT TOE (EQUIVALENT TO NO. 19. APPENDIX 4.1) (mm)
7. WEIGHT (g)

APPENDIX 2.2
STANDARD MORPHOLOGICAL DATA SHEET

SEE APPENDIX 2.1 FOR EXPLANATION OF MORPHOLOGICAL VARIABLES

REF POINT, COMP DEG AND DISTANCE, WERE FOR USE IN P GRID- TO PLOT FROG DISTRIBUTION

TEMPERATURE, WIND AND HUMIDITY READINGS WERE ALSO MEASURED WITH EACH FROG CAUGHT

Frog No.	1996/7 Whareorino Frog Populations Project Karen Eggers	Site No.	Spp. Clipped Y / N	Date: Time:
Temp.	Hum.	Wind	Micro Habitat	SV length	Head	Photo No.
Rear leg (mm)		toe	short-toe	webbing Y / N	Remarks:	light
Front leg (mm)	------	toe	short-toe	ref point	comp deg	distance

Habitat Data sheet:

1996/96 Whareorino frog populations project-- Karen Eggers

Date	Time	ref. pt.	dist.	angle	ground veg		tree veg		log/rock measurements in cm.						colour--green--> brown				frog	photo /
					spp	where in veg	spp	where in veg.	R or L	leng.	wid(1)	wid(2)	depth		100 -75 %	75- 50 %	50- 25 %	25- 0%	Y(No.) /N	film no.

R= rock
L = log

retreat frog

APPENDIX 4.1

COMPLEX BODY MORPHOLOGY ---- THE MEASUREMENTS

1. Snout-vent length, from tip of snout to vent (SVL).
2. Head width from right shoulder to left shoulder, perpendicular to snout-vent length (HD).
3. The length of the right radio-ulna to the tip of third toe (RRST).
4. The length of the right astragalus and calcaneum to the tip of fourth toe (RFST).
5. Length of the right femur (FEM*).
6. Length of the left tibio-fibula (TIBF*).
7. Length of the left fourth toe, from 1st meta-tarsal joint to the tip of the toe (rear foot) (R4T*).
8. Length of the left fifth toe, from 1st meta-tarsal joint to the tip of the toe (rear foot) (R5T*).
9. Length of the left humerus (HUM*).
10. Length of the left 4th toe, from 1st meta-tarsal joint to the tip of the toe (front foot) (F4T*)
11. Length of the front 3rd toe, from 1st meta-tarsal joint to the tip of the toe (front foot) (F3T*)
12. Width of the gap between the closest anterior points of the eyes (ANTE).
13. Width of the gap between the closest posterior points of the eyes (POTE).
14. Width of radio-ulna, closest to joint with humerus, but perpendicular to line of radio-ulna (RADU).
15. Distance from humerus/shoulder joint to the tip of the snout on right side, (SNT*)
16. Length of the left femur (FEM*).
17. Length of the right tibio-fibula (TIBF*).
18. Length of the right fourth toe from the 1st meta-tarsal joint to tip of the toe (rear foot) (R4T*).
19. Right side, third toe length, from the 1st meta-tarsal joint to tip of the toe (front foot) (F3T*).
20. Length of the right humerus (HUM*).
21. Distance from humerus/shoulder joint to the tip of the snout on left side (SNT*).

----

*Measurements averaged for analysis

Complex body morphology

Date	Time	SPP	R FEM	L FEM	R TIBF	L TIBF	RF4T LR5T	RF3T LR4T	LF3T RR4T	RF4T RR5T	R HUM	L HUM	AN TE	POTE	R SNT	LSNT

Recorder Intials

APPENDIX 4.3
RAW MORPHOLOGICAL DATA FOR WHAREORINO FROGS

DATA SUPPLIED FOR THE PURPOSES OF EXAMINATION ONLY.

APPENDIX 4.4

POOLED WITHIN CANONICAL STRUCTURE FOR MORPHOLOGICAL VARIATION IN LEIOPELMATID FROGS FROM WHAREORINO FOREST.

Variable	CAN1	CAN2
SVL	0.494731	-0.241474
HD	0.492493	-0.397301
RRST	0.508943	-0.184658
RFST	0.522256	-0.107247
TIBF	0.439162	-0.188746
FEM	0.472716	-0.182049
POTE	0.491338	-0.190567
ANTE	0.579508	-0.256872
SNT	0.586667	-0.174145
RADU	0.239829	-0.349936
R5T	0.475613	0.016379
F4T	0.494582	-0.000800
F3T	0.512523	-0.001368
R4T	0.524291	0.042501

APPENDIX 4.5

POOLED WITHIN-CLASS STANDARDISED CO-EFFICIENTS FOR CANONICAL

DISCRIMINANT ANALYSIS

Variable	CAN1	CAN2
SVL	-1.274966786	-1.491919249
HD	-1.129574823	0.911273500
RRST	0.683974344	1.262318168
RFST	0.785808679	0.563256946
TIBF	-1.060982926	-1.195674181
FEM	0.752651632	0.064462233
POTE	0.041370575	-0.386517232
ANTE	-0.684006256	0.952853061
SNT	-0.270608233	1.2994415165
RADU	-0.300949783	-1.397627442
R5T	-1.082197530	0.416303598
F4T	0.986355412	-0.1346224990
F3T	0.142406401	0.263430681
R4T	2.097325148	-0.397730182

Analysis of Tail Reduction in Metamorphosing *L. archeyi*
Computer program run on Sas for Windows Version 6.1

```
options ls=78 ps=63 nodate;

data baby ;
  input par temp days ;
cards ;
1 15 19
1 15 21
1 15 21
1 11 17
1 11 21
1 11 20
2 15 33
2 11 34
2 15 28
;
run;

title 'unbalanced RBD : Baby10mm data' ;

proc format ;
  value temp 15='high' 11='low' ;
run;

proc glm data=baby;
  class par temp ;
  model days = par temp par*temp / ss3 ;
  means par temp par*temp / tukey lines ;
  lsmeans par temp par*temp /pdiff stderr;
run;
```

_____

Program was repeated for data at the 4mm length and 2mm length

Input variables:
par = Parent (ie Brooding Male)
temp = incubation temperature
days = number of days since hatching

Analysis of Weight Change in Developing *L. archeyi*
Computer program run on Sas for Windows Version 6.1

```
options ls=78 ps=63 nodate;


data wei;
   input par temp days;
cards ;
1 15 0.1085
1 15 0.1155
1 15 0.1110
1 11 0.1029
1 11 0.1060
1 11 0.1071
2 15 0.1181
2 11 0.0958
2 15 0.1056
;
run;

title 'Unbalanced data: weight 30 days';

proc format ;
   value temp 15='high' 11='low';
run;

proc glm data=wei;
   class par temp;
   model days = par temp par*temp / ss3;
   means par temp par*temp / tukey lines;
   lsmeans par temp par*temp / pdiff stderr;
run;
```

Program was repeated for data at 60 days, 90 days and 120 days.

Input variables:
par = Parent (ie Brooding Male)
temp = incubation temperature
days = number of days since hatching

Analysis of Snout-vent Length Change in Developing *L. archeyi*
Computer program run on Sas for Windows Version 6.1

```
options ls=78 ps=63 nodate;


data svl;
   input par temp days;
cards ;
1 15
1 15
1 15
1 11
1 11
1 11
2 15
2 11
2 15
;
run;

title 'Unbalanced data: snout-vent length 30 days';

proc format ;
   value temp 15='high' 11='low';
run;

proc glm data=svl;
   class par temp;
   model days = par temp par*temp / ss3;
   means par temp par*temp / tukey lines;
   lsmeans par temp par*temp / pdiff stderr;
run;
```

───

Program was repeated for data at 60 days, 90 days and 120 days.

Input variables:
par = Parent (ie Brooding Male)
temp = incubation temperature
days = number of days since hatching

Analysis of Tail Reduction in Metamorphosing *L. archeyi*
Raw Data (Cards)

For tail length = 4mm

Parent	Temperature	Days
1	15	33
1	15	33
1	15	33
1	11	34
1	11	37
1	11	41
2	15	46
2	11	58
2	15	40

For tail length = 4mm

Parent	Temperature	Days
1	15	37
1	15	36
1	15	37
1	11	43
1	11	41
1	11	44
2	15	50
2	11	65
2	15	45

Analysis of Weight & Snout-vent Length Change in
Developing *L. archeyi*
Raw Data (Cards)

Weight
For days after hatching = 60 days

Snout-vent Length
For days after hatching = 60 days

Parent	Temperature	Weight	Parent	Temperature	SVL
1	15	0.1121	1	15	9.3
1	15	0.0958	1	15	9.63
1	15	0.1145	1	15	8.93
1	11	0.1051	1	11	8.73
1	11	0.1065	1	11	9.2
1	11	0.1007	1	11	8.93
2	15	0.1244	2	15	9.5
2	11	0.1068	2	11	8.9
2	15	0.1370	2	15	8.9

For days after hatching = 90 days

Parent	Temperture	Weight	Parent	Temperture	SVL
1	15	0.1070	1	15	9.03
1	15	0.1004	1	15	8.47
1	15	0.1054	1	15	8.48
1	11	0.1014	1	11	8.52
1	11	0.1041	1	11	8.68
1	11	0.0965	1	11	8.81
2	15	0.1269	2	15	9.5
2	11	0.1047	2	11	9.22
2	15	0.1172	2	15	9.58

For days after hatching = 120 days

Parent	Temperature	Weight	Parent	Temperture	SVL
1	15	0.1000	1	15	8.54
1	15	0.0764	1	15	8.06
1	11	0.0831	1	11	8.83
1	11	0.1041	1	11	8.81
1	11	0.1037	1	11	8.50
2	15	0.1237	2	15	8.98
2	11	0.0988	2	11	9.35
2	15	0.1059	2	15	

Individual Number 3 died at day ninty-seven

Snout-vent Length Change in Developing *L. archeyi*
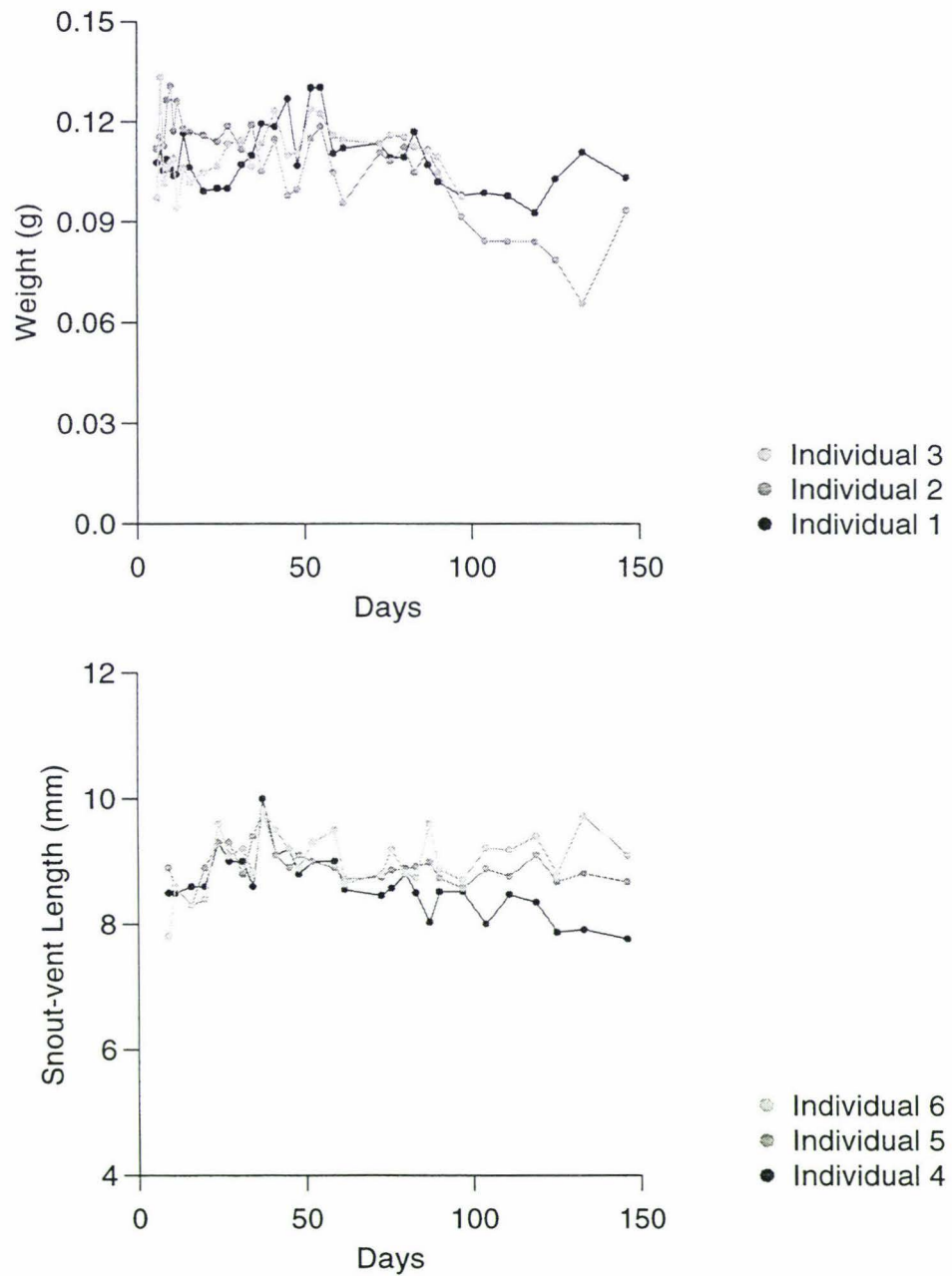
Figure ???? Change in snout-vent length during early development in captive *L. archeyi*
A: Individuals 1, 2, & 3; B: Individuals 4, 5, & 6.
Number 3 died after 96 days in captivity

Weight Change in Developing *L. archeyi*
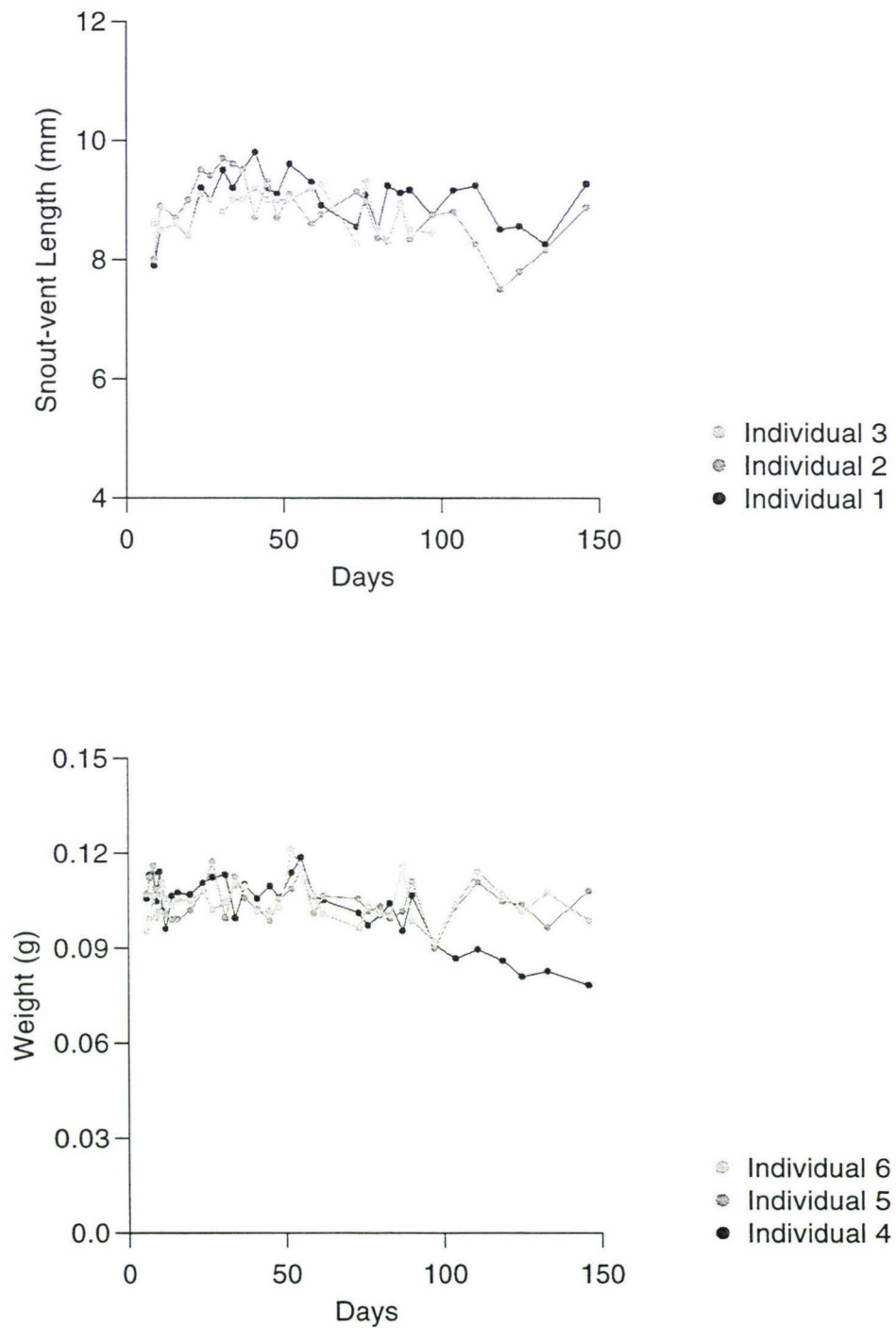
Figure ???? Change in weight during early development in captive *L. archeyi*
A: Individuals 1, 2, & 3; **B**: Individuals 4, 5, & 6.
Number 3 died after 96 days in captivity

Toad Ringer Solution

To make 0.9 % solution;

Sodium Chloride		6.5g / litre
Calcium Chloride	2.4 % solution	5ml / litre
Potassium Chloride	4.2 % solution	3ml / litre
Sodium Hydrocarbonate	5 % solution	2ml / litre
Sodium Hydrophosphate	5 % solution	0.2ml / litre
Glucose Solid		1g / litre

Mix all together and emerse tadpole

Recommendations: keep solutions chilled & fresh
change regularly

Appendix 6.1

Pitfall trap sample sheet (Invertebrate record sheet)

Sample No:		Total no. of ind.
Set No:		Total no. of spp.
Date:		Ref. spp taken from this sample
Date Sorted:		
ID:	Number:	Sizes (mm)

APPENDIX 6.2

COLEOPTERA
- STAPHYLINIDAE
- SCARABIDAE
- CARABIDAE
- CURCULIONIDAE
- MELANDRYIDAE
- HYDRAENIDAE
- HYDROPHILIDAE
- TENEBRIONIDAE
- EUCINEMIDAE
- CHYSOMELIDAE
- NOSODENDRIDAE
- EROTYLIDAE
- LEIODIDAE (CHOLEVINAE)

ACARI
PSEUDOSCORPIONES
ARANEAE
OPILIONES
ISOPODA
AMPHIPODA
COLLEMBOLA
ENTOMOBRYIDEA
DIPLOPODA
CHILOPODA
PARAPHANTIDAE
ATHORACOPHORIDAE

DIPTERA
- SPHAEROCERIDAE
- SCIARIDAE
- PSYCHODIDAE
- CHIRONOMIDAE
- CECIDOMYIIDAE
- MYCETOPHILIDAE
- TIPULIDAE
- MUSCIDAE
- TRICHOCERIDAE
- PHORIDAE

HYMENOPTERA
- FORMICIDAE
- DIAPRIIDAE
- PLATYGASTRIDAE
- MEGASPILIDAE
- ENCYRTIDAE
- MYMARIDAE
- SCELIONIDAE - TELEASINAE
- BRACONIDAE

HEMIPTERA
- NABIDAE
- DELPHACIDAE
- CERATOCOMBIDAE
- APHIDIDAE
- COCCOIDEA
- CICADELLIDAE
- LYGAEIDAE
- ARADIDAE

Stomach and Rectal Content Analysis-- Frog No. (Blank Sheet)

Date Sorted :

Family Group	Size -mm ($\pm$ 0.5 mm)	Number
Stomach Content Analysis		
Rectal Content Analysis		

Stomach and Rectal Content Analysis-- Frog No. 10

Date Sorted : 16.12.97

Family Group	Size -mm (± 0.5 mm)	Notes
Stomach Contents		
Diplopoda	12.0 mm	
Diplopoda	5.0 mm	
Amphipoda	11.0 mm	
Amphipoda	10.0 mm	
Amphipoda	10.0 mm	
Coloepteran	4.0 mm	Chrysomelidae
Coleopteran	3.0 mm	Curculionidae
Coleopteran	**	prosternum
Acari	1 mm	leg
Araneae	**	chelicera
Vegetation -	fern spores	
	frond & leaf segments	
	Rectal Contents	
Coleoptera	4.0 mm	elytra, pronotum, ventrites
Diptera	2.0 mm	Trichoceridae- wings
Hymenoptera	**	ovipositor-3.0 mm
Diptera	**	Metasternum (2 of)
Coleoptera	**	Polyphaga (3 of)

Stomach and Rectal Content Analysis-- Frog No. 11

Date Sorted : 16.12.97

Family Group	Size -mm (± 0.5 mm)	Notes
Stomach Contents		
Amphipoda	10.0 mm	
Coleoptera	6. 0 mm	
Orthopteran		thorax segment
Wood	7.0 mm	
Rectal Contents		
Diplopoda		
Amphipoda	13.0 mm	
Insect larvae	2.0 mm	
Aranea	2.0 mm	carapace & chelicera
Acari	2.0 mm	
Acari	1.0 mm	
Vegetation	fern spores	

Stomach and Rectal Content Analysis-- Frog No. 39

Date Sorted : 17.12.97

Family Group	Size -mm (± 0.5 mm)	Number
Stomach Contents		
Acari	1.0 mm	
Acari	1.0 mm	
Acari	1.0 mm	
Acari	1.0 mm	
Acari	1.0 mm	
Acari	1.0 mm	
Acari	1.0 mm	
Acari	1.0 mm	
Insect larvae	2.0 mm	
Araneae	2.0 mm	
Collembola	3.0 mm	
Rectal Contents		

Stomach and Rectal Content Analysis-- Frog No. 135

Date Sorted : 17.12.96

Family Group	Size -mm (± 0.5 mm)	Number
Stomach Contents		
Collembola	2.0 mm	
Collembola	1.0 mm	
Coleoptera	2.0 mm	Staphylinidae
Rectal Contents		
Hemiptera	2.0 mm	Lygaeidae-lygaeoidae

Stomach and Rectal Content Analysis-- Frog No. 12

Date Sorted : 16.12.97

Family Group	Size -mm (± 0.5 mm)	Notes
	Stomach Content Analysis	
Insect larvae	4.0 mm	
Insect larvae	3.0 mm	
Amphipoda	7.0 mm	
Coleoptera	4.0 mm	Tenebrionoidea or Melandryidae
	Rectal Content Analysis	
Acari	1.0 mm	
Acari	1.0 mm	
Formicidae	3.0 mm	
Araneae	2.0 mm	
Coleopteran	3.0 mm	Head
Vegetation	fern spores	
	leaf segments	

Stomach and Rectal Content Analysis-- Frog No. 133

Date Sorted : 16.12.97

Family Group	Size -mm (± 0.5 mm)	Notes
	Stomach Content Analysis	
Collembola	2.0 mm	
Collembola	2.0 mm	
Collembola	2.0 mm	
Collembola	2.0 mm	
Collembola	2.0 mm	
Collembola	2.0 mm	
Collembola	2.0 mm	
Collembola	2.0 mm	
Collembola	2.0 mm	
Collembola	1.0 mm	
Collembola	1.0 mm	
Collembola	1.0 mm	
Acari	2.0 mm	
Acari	1.0 mm	
Araenae	2.0 mm	
Araenae	3.0 mm	
Isopoda	5.0 mm	
Insect larvae	5.0 mm	
Insect larvae	3.0 mm	
Insect larvae	3.0 mm	
Insect larvae	3.0 mm	
Insect larvae	7.0 mm	
Diptera	10.0 mm	Tipulidae- Bryachyteris
Diptera	2.0 mm	Sphaeroceridae
Diptera	1.0 mm	Psychodidae
Diptera????	5.0 mm	Schicophoran head
Hymenoptera	2.0 mm	Diapriidae
	Rectal contents	
Insect larvae	2.0 mm	
Insect larvae	1.0 mm	
Insect larvae	1.0 mm	
Psueodscorpione	2.0 mm	
Psuedoscorpione	3.0 mm	

Stomach and Rectal Content Analysis-- Frog No. 136

Date Sorted : 17.12.97

Family Group	Size -mm (± 0.5 mm)	Notes
	Stomach Content Analysis	
Insect larvae	1.0 mm	
Insect larvae	6.0 mm	
Acari	1.0 mm	
Acari	1.0 mm	
	Rectal Content Analysis	
Acari	0.5 mm	
Acari	1.0 mm	
Vegetation	fern spores	

Stomach and Rectal Content Analysis-- Frog No. 134

Date Sorted : 17.12.97

Family Group	Size -mm (± 0.5 mm)	Notes
Stomach Content Analysis		
Amphipoda	4.0 mm	
Acari	1.0 mm	
Collembola	1.0 mm	
Insect larvae	5.0 mm	
Rectal Content Analysis		
Acari	1.0 mm	
Acari	1.0 mm	
Microsnail	1.0 mm	
Insect larvae	2.0 mm	
Insect larvae	2.0 mm	
Collembola	1.0 mm	
Collembola	1.0 mm	
Collembola	1.0 mm	
Pseudoscorpione	1.0 mm	
Coleoptera	3.0 mm	
Vegetation	fern spores	

APPENDIX 6.5

DATA SUPPLIED FOR THE PURPOSES OF EXAMINATION ONLY.