# NEW ZEALAND JOURNAL OF ECOLOGY

## RESEARCH

# Post-metamorphic body growth and remarkable longevity in Archey's frog and Hamilton's frog in New Zealand

Ben D. Bell[1]* [iD] and Shirley A. Pledger[2]

[1]Centre for Biodiversity and Restoration Ecology, Victoria University of Wellington, PO Box 600, Wellington 6012, New Zealand
[2]School of Mathematics and Statistics, Victoria University of Wellington, PO Box 600, Wellington 6012, New Zealand
*Author for correspondence (Email: ben.bell@vuw.ac.nz)

**Abstract:** Post-metamorphic body growth and longevity of two archaic terrestrial frogs (Anura: Leiopelmatidae) endemic to New Zealand are described using data from long-term capture-recapture studies and measurements of snout-vent length. Population studies of Hamilton's frog (*Leiopelma hamiltoni*) on Te Pākeka/Maud Island, Marlborough Sounds, have been undertaken since 1976 and Archey's frog (*L. archeyi*) in the Coromandel Ranges since 1982. The expectation-maximisation algorithm was used to fit von Bertalanffy growth curves to the data, providing maximum-likelihood estimation of parameters associated with frog growth. New Zealand endemic frogs take at least 4–7 years to reach breeding maturity in the wild and have maximum life spans of at least 39 years in *L. archeyi* and 45 years in *L. hamiltoni*. Amongst a small sample of 26 Hochstetter's frogs (*L. hochstetteri*) at the Coromandel site, the oldest individual was at least 18 years old.

**Keywords:** age, Archey's frog, body growth, expectation-maximisation algorithm, Hamilton's frog, Hochstetter's frog, longevity, von Bertalanffy model

## Introduction

Little is known about body-size evolution within the most diverse amphibian order, the anurans (Womack & Bell 2020). Here we examine and model changes in size with age and we estimate longevity in two of New Zealand's endemic frogs: Archey's frog (*Leiopelma archeyi*) and Hamilton's frog (*L. hamiltoni*). These archaic and threatened terrestrial frogs (Archaeobatrachia: Leiopelmatidae) are of limited distribution in New Zealand occurring in native forest or along open ridge-tops (Stephenson 1960; Bell 1978; Bishop et al. 2008; Bell & Bishop 2018; Burns et al. 2018). *Leiopelma* species are endotrophic (nutrition from ventral yolk sac, no feeding tadpole stage) and the terrestrial *L. archeyi* and *L. hamiltoni* are exoviviparous (hatchlings complete development on dorsal surface of the male), before dispersing as juvenile frogs from the nest-site after metamorphosis (Bell 1985a, 2011; Altig & Johnston 1989; Thurley & Bell 1994; Bell & Wassersug 2003; King et al. 2009; Bell & Bishop 2018; Cisternas 2019). Growth measurements can begin at this post-metamorphic stage. Both *L. archeyi* and *L. hamiltoni* may live for several decades (Bell 2010; Bell & Pledger 2010, 2011; Bell & Bishop 2018; Bell et al. 2020), with life-spans greater than most frog populations studied in the wild (Duellman & Trueb 1986; Wells 2007). Here we report on long-term capture-recapture data stretching over four decades, so providing a rare opportunity to examine growth over these frogs' many years of life.

## Methods

### Study sites

On Te Pākeka/Maud Island, Marlborough Sounds, capture-recapture studies of *L. hamiltoni* were undertaken at two 12 × 12 m study plots ('Grid 1' and 'Grid 2'; each 144 m$^2$) under native forest in Home Bush over 1983–2021 (Bell 1994; Bell & Pledger 2010), extending two 100 m$^2$ study sites ('A' and 'B') used by Newman (1990) over 1976–1983 (Fig 1a). A further Maud Island study site ('Grid 3') operated over 1984–2021 was in a forested gully above Boat Bay, to which 100 *L. hamiltoni* were translocated from Home Bush over 1984/85, the first successful *Leiopelma* translocation and the first with follow-up monitoring (Bell 1994; Dewhurst 2003; Bell et al. 2004a, 2010; Trewenack et al. 2007; Wren et al. 2023).

In the central Coromandel Ranges a capture-recapture study of *L. archeyi* was carried out over 1982–2021 at a 10 × 10 m ridge-top native forest site ('Grid 4') near Tapu (Fig. 1b; Bell 1994; Bell et al. 2004b). A few (*n* = 26) semi-terrestrial Hochstetter's frogs *Leiopelma hochstetteri* were also caught there, too few to study their growth and longevity in detail.

### Search methods

At each *L. hamiltoni* study site on Maud Island, searches of the ground surface, adjacent tree trunks, branches and foliage were carried over successive nights using headlamps. The frogs are relatively immobile at night, being ambush feeders

**Figure 1.** (a) Night-time sampling site for *Leiopelma hamiltoni* on Maud Island (Grid 1) showing north-east side with raised walkways installed by the Department of Conservation across the 12 × 12 m frog sample areas, October 2021. (Photo: Ben Bell). (b) Jen Germano (foreground), Melanie Williamson and Ken Brown from DOC carefully and systematically searching by day with headlamps for frogs under rocks and other cover on the 10 × 10 m *L. archeyi* study site in the Coromandel Ranges (Grid 4), March 2016. (Photo: Kirst King-Jones).

that habitually sit on, or above, the ground although making some movements overnight (Ramírez 2017). It was relatively easy to catch individuals by hand and almost all frogs seen were captured. Capture sites were marked with reflecting numbered plastic pegs and frogs were secured with a twist-tie in plastic bags bearing the same site numbers (Bell et al. 2004a; Bell & Pledger 2010). At the *L. archeyi* study plot, careful daytime location of frogs was done by progressive searching of potential retreat sites under surface rocks, logs and vegetation, any uplifted sites being gently replaced once searched (Fig. 1b). Additional night searches were made in 1994 and 2012. Sites of capture were marked with numbered plastic pegs, captured frogs then placed in plastic bags, each site-numbered and secured with a twist-tie. Frogs were held in dark bags until they were identified, weighed and measured, and then released at pegged capture sites once the grid had been searched (Bell 1994; Bell et al. 2004b).

**Measurement and individual identification**

For both species, snout-vent length (SVL) was measured with callipers for initial captures of all frogs on each sampling visit (here SVL technically is the mid-dorsal length (Bell 1978) or the snout-urostyle length; see e.g. Gvoždík et al. 2008). Initially new frogs were individually identified by toe-clip marking, with a different toe-clip scheme used at each site (Bell 1994; Bell et al. 2004a,b; Bell & Pledger 2010). On Maud Island, individual *L. hamiltoni* were often difficult to differentiate using their colour pattern, so toe-clipping has continued there to ensure accurate identification of individuals. At Grid 1 & Grid 2 most frogs captured now are already marked. At Grid 3 individual toe-clipping ceased in 2019 after success of the translocation there was clear (Bell 2010; Bell et al. 2010, 2020; Wren et al. 2023). At the *L. archeyi* site (Grid 4) toe-clipping ceased in 2004, after which new individuals were identified by colour pattern using mirror-stage photography (Haigh 2007). Photo-identification was more straightforward for adult frogs than for small frogs, as colour patterns develop with age (BDB, pers. obs.).

**Sex determination**

*Leiopelma archeyi* and *L. hamiltoni* generally cannot be sexed on external morphology, except that females attain greater body size (Bell 1978, 1982; see also Bell & Pledger 2010; Germano et al. 2012). The sex of some females was confirmed by observation of yolky eggs through the abdominal wall, and *L. archeyi* frogs found brooding eggs or hatchlings at the study site could be deemed males (Bell 1985a). No breeding sites of *L. hamiltoni* have been found in the wild; information on the SVL of confirmed adult males coming either from museum specimens (Bell 1978) or from captive breeding (Bell 1985a, 2008; Karst et al. 2023). Individuals of both species frequently had multiple recaptures over many years, increasing the likelihood that their sex was accurately estimated from their SVL. Most *L. archeyi* adults with SVLs > 35 mm and most *L. hamiltoni* adults > 41 mm SVL were regarded as females (Fig. 2; see later discussion). Young frogs could not be sexed, and sexes of some older adults could also not be determined as they could be either mature males or younger females still to attain full size.

**Datasets and modelling growth using snout-vent length**

Four datasets from four locations were chosen: three for *L. hamiltoni* on Maud Island (Grid 1, Grid 2, and Grid 3) and one for *L. archeyi* in the Coromandel Ranges (Grid 4). Initially separate analyses were run for each location, with pooling of locations for *L. hamiltoni* for longevity analysis.

For the dataset from each location, growth in SVL was modelled using von Bertalanffy growth curves (von Bertalanffy 1960). The curve for y = expected length (SVL in mm) versus x = age (years) has the equation:

$$y = \mathrm{Asym} - (\mathrm{Asym} - \mathrm{R0})e^{-kx} \qquad (1)$$

with parameters Asym = asymptote, R0 = response (expected SVL) at age 0, and k = instantaneous growth rate at age 0, as specified by Pinheiro & Bates (2000). The derivative $\frac{dy}{dx}$ is k(Asym−y), so the rate of increase is proportional to the shortfall of *y* from Asym, implying that growth slows as the frog SVL nears the asymptote. The asymptote is the expected SVL approached by the individual as growth slows, but actual measurements of SVL have measurement error or variability, so data points may fluctuate above or below the curve.
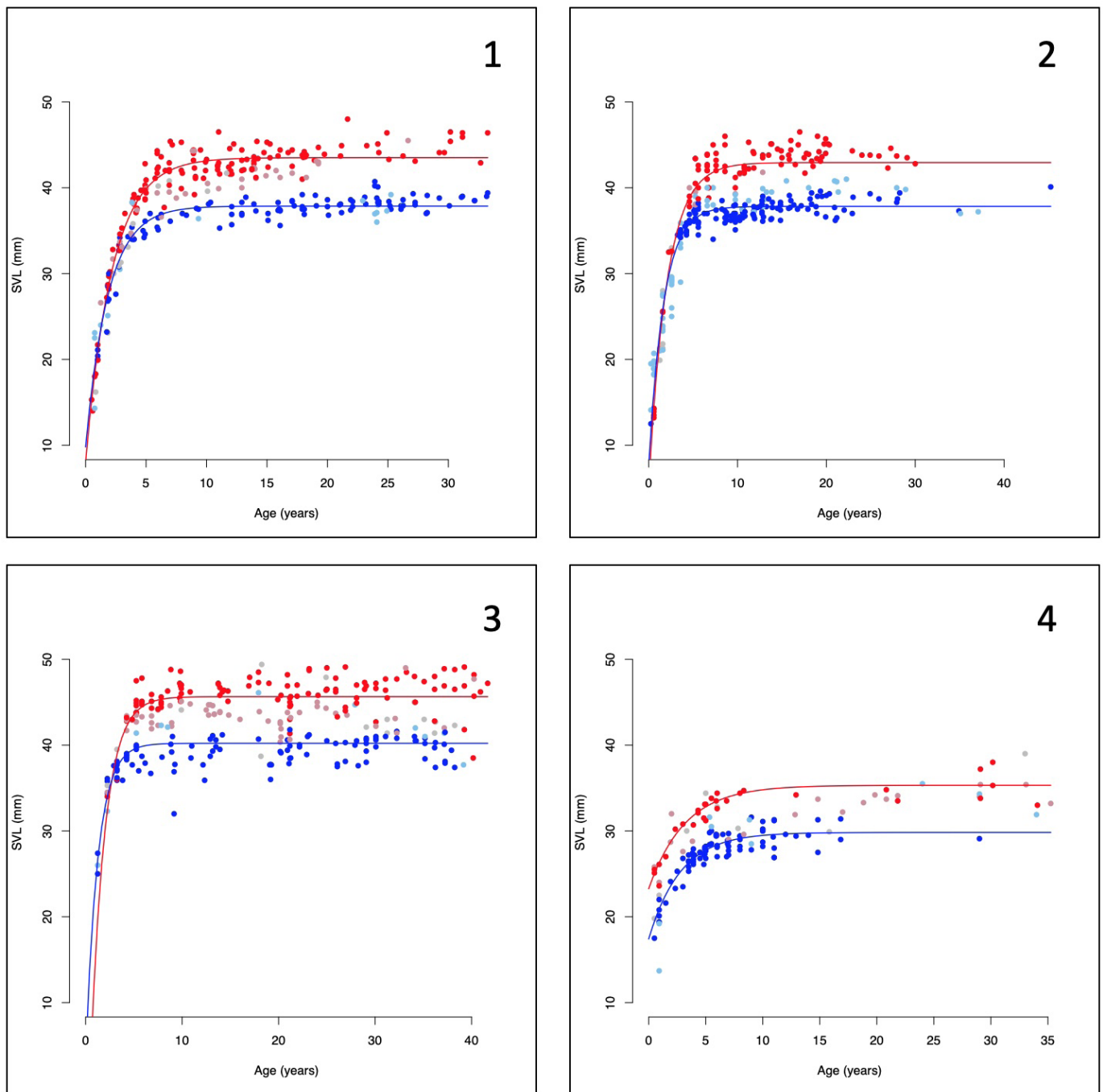
**Figure 2.** Growth curves of SVL resulting from modelling individual recapture data for females (red) and males (blue) at each of the four study sites over the full trapping history of individual frogs. Each point on the plots is a pseudo datapoint not using the observed SVL but the maximum likelihood estimate of the age, as chosen in the generalised expectation maximisation algorithm when estimating age at first capture. The colour used for each point indicates its estimated sex. The colour takes account of the whole history for that individual, although linkages within each ID are not displayed. Points are a strong red or blue if the posterior probability of that individual being female or male respectively is greater than 0.8, a pink or pale blue if the probability is between 0.6 and 0.8, and grey if the probability is between 0.4 and 0.6. (1) Grid 1 *Leiopelma hamiltoni*; (2) Grid 2 *L. hamiltoni*; (3) Grid 3 *L. hamiltoni*; (4) Grid 4 *L. archeyi*.

Fitting each frog with its own growth curve requires more comprehensive data than can be obtained in a capture-recapture study, but the frogs' sexual dimorphism suggests fitting two curves in each population, with a higher asymptote to represent females and a lower to represent males. Other sources of variation about the expected curve could be due to individual variation such as individual differences in rate of growth or ultimate size, or to frog posture or extent of water retention at the time of measurement, or to different people doing the measuring. In this study we assume that all this unmodelled variation combines to give random SVL fluctuation about the curve with variance at age $x$ being $y^2\sigma^2$, where y is the expected SVL at age $x$. This pattern of variance commonly occurs with size measurements where variance increases with the size and the standard deviation is proportional to the current size. In a later study, the variance will be partitioned into two

components, one due to individual frog variation and the other to random unexplained errors (Armstrong & Brooks 2013).

Each frog has an SVL history, a vector of SVL measurements $y$, and the associated time vector of calendar dates $t$ when the measurements were done. Thus, each frog has two pieces of missing information, age at each capture and its sex (Fabens 1965). To find the age vector it is enough to identify the age at first measurement (hereafter 'AFM'). Then ages at later measurements follow since time-spacings between measurements are known. At the $j$th measurement, the age is $x_j = AFM + t_j - t_1$. To determine sex, measurements as an adult are needed. The expectation maximisation algorithm provides maximum likelihood estimates of parameters in a model when these are missing data (Dempster et al. 1977; McLachlan & Krishnan 2008), differing from a fully Bayesian Markov chain Monte Carlo sampling in empirically using the data to start the estimation algorithm rather than assuming a prior probability distribution. The EM algorithm proceeds as follows:

(1) **Step 1**. Initialise by guessing the parameter values for the model, a pair of curves, by inspecting the data. This need not be a very precise guess, as the algorithm will update these estimates using the data.

(2) **Step 2: The E Step**. Use the current model parameters to obtain a probability distribution and expected value for the missing data. This together with the actual data forms the completed data.

(3) **Step 3: The M Step**. Use the current completed data to refit the model (update the parameters estimates). Find the log likelihood under the completed data (LLc).

(4) **Step 4**. Repeat Steps 2 and 3 until the sequence of updated LLc converges. The final update of the current parameters provides maximum likelihood estimates of the parameters of the two fitted curves. A simple adjustment converts LLc to LLint, a marginal log likelihood integrated over all possible choices of completions of the data. LLint is used for overall model comparisons such as likelihood ratio tests, analysis of deviance and Akaike information criterion (AIC) values.

For the frog analyses, on each grid full details and a worked example using R (R Core Team, 2020) are available on the second author's home page; see Data and code availability. For the dataset from each location, successive SVLs of each identified individual frog were categorised into five classes based on the extent of SVL information on their SVL at first capture: Class A: SVLs from 1st calendar year (see Bell (2011) for *L. hamiltoni*); Class B: SVLs from estimated 2nd calendar year; Class C: SVLs from estimated 3rd calendar year; Class D: SVLs from estimated 4th calendar year or later that showed successive increases in SVL (i.e. later stages of growth but accurate age estimate not possible); Class E: SVL from older (mature adult) frogs that showed no growth across successive captures so were not included in the growth analysis but may be included in estimated longevity calculations.
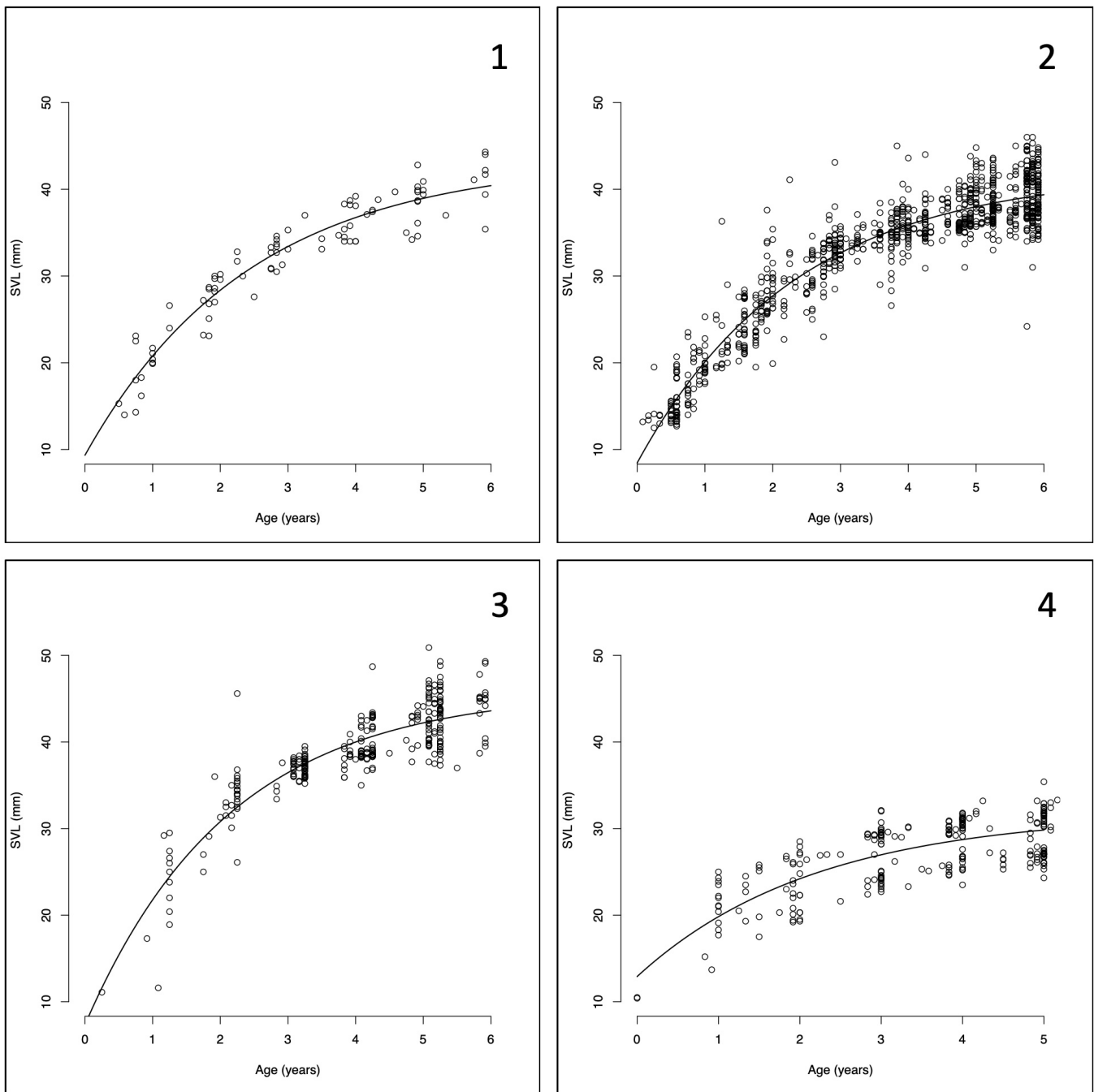
## Results

### Growth analysis

Growth curves resulting from modelling individual recapture data for each of the study sites over the full trapping history of individual frogs are illustrated in Fig. 2. To provide more detail over the initial growth period, growth up to year 6 is illustrated in Fig. 3. The smaller SVL asymptote reached in the *L. archeyi* population (Grid 4) is clearly evident (Figs. 2, 3; Table 1). For *L. hamiltoni* on Maud Island, the ultimate SVL reached (the asymptote) was distinctly greater in the lower-density population (Grid 3) derived from the 1984/85 translocation to Boat Bay (Figs. 2, 3; Table 1).

The three study grids were compared to find if adequate fits to the data could be obtained by pooling data over different grids. Comparison of residual deviance over three proposed groupings of the data showed that modelling Grid 1, Grid 2, and Grid 3 separately ([(1)(2)(3)]; Figs. 1 & 2) gave a much better fit than combining Home Bush Grids 1 and 2, with Grid 3 remaining separate [(12)(3)]. This, in turn was better than combining all grids [(123)]. Since there were many data, all separations into more groups had p values < 0.0001, but in splitting [(1)(2)(3)] the split [(12)(3)] gave a lower average deviance residual than [(1)(23)] or [(13)(2)]. This occurred in both female and male groups. The asymptote estimates from combining two groups was between separate asymptotes, with a weighting towards the larger data set. For example, for females, asymptotes for Grids 1 and Grid 2 were 43.503 and 42.932 respectively, with the combined group [(12)] having value 43.041. Similarly, males' asymptotes went from 37.864 and 37.829 to 37.841 when Grids 1 and 2 were grouped.

**Table 1.** Parameter estimates generated by the expectation maximisation algorithm for missing data (Sex and AFM, age at first measurement), followed by fitting the two curves using non-linear mixed effects in R (Pinheiro & Bates 2000, R Core Team 2020). Estimates of asymptotes, standard deviations, R0 and k are tentative, as they were built using only data from individuals with at least four captures. Estimates of R0 in Grid 3 and Grid 4 were not available (NA) due to a failure of convergence, probably caused by too few individuals with four or more SVL measurements. The average numbers of SVL measurements per individual were 6.6, 6.7, 4.4 and 2.8 for Grids 1–4 respectively.

| Grid | 1 | | 2 | | 3 | | 4 | |
| Species | *L. hamiltoni* | *L. hamiltoni* | *L. hamiltoni* | *L. hamiltoni* | *L. hamiltoni* | *L. hamiltoni* | *L. archeyi* | *L. archeyi* |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Time period | 1978–2021 | | 1976–2021 | | 1984–2021 | | 1982–2021 | |
| No. frogs | 44 | | 544 | | 217 | | 250 | |
| No. measurements | 291 | | 3635 | | 960 | | 710 | |
| Sex | Female | Male | Female | Male | Female | Male | Female | Male |
| Asymptote | 43.5 | 37.86 | 42.93 | 37.83 | 45.64 | 40.21 | 35.32 | 29.83 |
| S.D. of asymptote | 1.07 | 0.5 | 1.12 | 0.96 | 1.31 | 0.92 | 1.12 | 0.37 |
| R0 | 8.04 | 9.8 | 5.29 | 7.69 | NA | NA | NA | NA |
| k | 0.46 | 0.54 | 0.48 | 0.59 | 0.67 | 0.79 | 0.31 | 0.36 |

**Figure 3.** Growth curves of SVL resulting from modelling individual recapture data for each of the study sites during the *initial growth phase* of individual frogs shown in Fig. 2. (1) Grid 1 *Leiopelma hamiltoni*; (2) Grid 2 *L. hamiltoni*; (3) Grid 3 *L. hamiltoni*; (4) Grid 4 *L. archeyi*.

## Longevity

For determining longevity, our focus was on older frogs, so we arbitrarily chose to illustrate just those individuals reaching > 20 years of age (Figs. 4, 5).

For *L. hamiltoni* we present minimal attained ages (interval between first and last capture) and estimated ages (known minimal age plus estimated age at first capture) based on MLE modelling (Fig. 4). Many *L. hamiltoni*, of both sexes, had > 20 years of capture, the longest interval (to date) being for a male with 39 years between its first and last capture (Fig. 4a). Allowing for growth time before first capture, the oldest *L. hamiltoni* female reached an estimated age of 45 years,

oldest males reached 42 years, and many frogs of either sex reached estimated ages of 24 years or more (Fig. 4b).

At the Coromandel site, the interval between first and last capture reached at least 30 years in eight *L. archeyi*: 3 females to 30 years; 1 female to 31 years; 1 female to 32 years; 1 female and a possible male to 33 years; and 1 female to 34 years. The oldest *L. archeyi*, a female, reached an estimated age of 39 years, with estimated ages of 20 or more years of age in 17 frogs, mostly females (Fig. 5). Coromandel populations of *L. archeyi* experienced major declines over 1996–2001, with relatively more smaller frogs, which included males, disappearing then (Bell et al. 2004b).
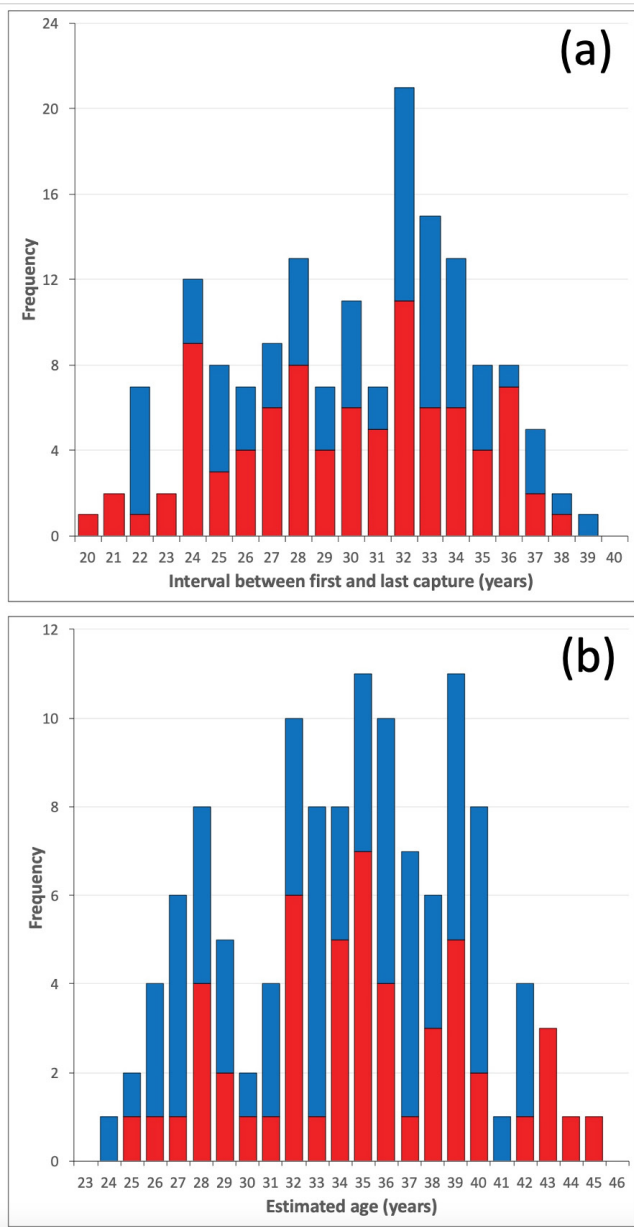
**Figure 4.** (a) Intervals between first and last capture of female (red) and male (blue) *Leiopelma hamiltoni* on Maud Island for individuals known to reach at least 20 years; (b) Estimated ages of these older *L. hamiltoni* based on MLE modelling.
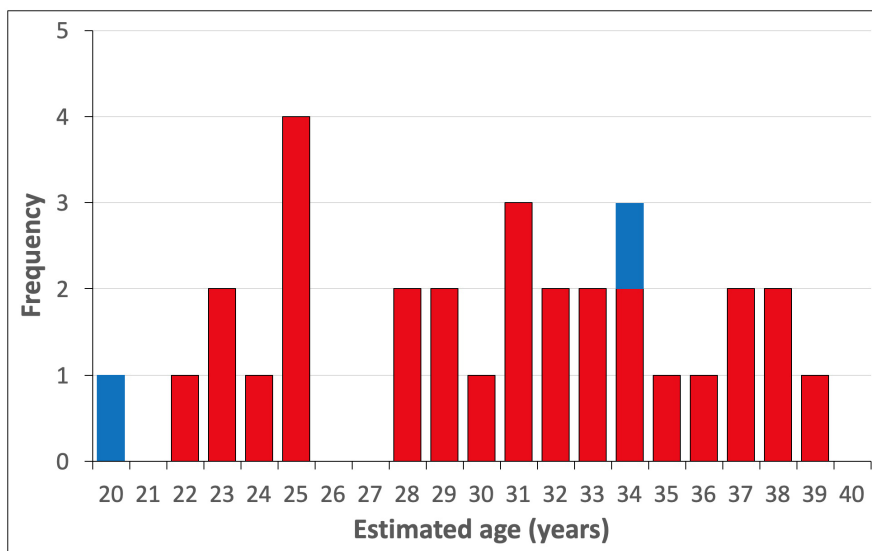


**Figure 5.** The estimated ages of older female (red) and male (blue) *Leiopelma archeyi* known to reach 20 or more years at the Coromandel study site. The estimated age of each frog is the interval between first and last capture plus its estimated age at first capture based on MLE modelling.

Only 26 individual *L. hochstetteri* were taken at the ridge-top Coromandel site, so were not included in MLE growth analyses. Amongst the few caught, the interval between first and last capture reached 9, 12, and 14 years in three frogs, all females, and their estimated ages were at least 12, 17, and 18 years. *L. hochstetteri* has not been studied long enough to obtain higher longevity values in its preferred creek-side habitats, although some mark-recapture and sampling studies have been undertaken (Tessier et al. 1991; Slaven 1992; Whitaker & Alspach 1999; Crossland et al. 2005; Chris G. Longson†, EcoQuest Education Foundation, pers. comm.).

## Discussion

In a review on age determination in amphibians and reptiles, Halliday and Verrell (1988) concluded that only two methods, skeletochronology and mark-recapture, were reliable. Our studies of *L. archeyi* and *L. hamiltoni* did indeed find that mark-recapture was an effective method for estimation of growth and longevity. With up to 45 years of research, we accumulated some of the world's longest-run data on wild frog populations, providing rare opportunities to study individual growth over several decades. We revealed remarkable longevity of up to at least 39 years in *L. archeyi* and 45 years in *L. hamiltoni*, while we also found an increased growth response to reduced densities in a translocated *L. hamiltoni* population and following a population decline in *L. archeyi* (Bell et al. 2004a,b, 2020).

### Growth

One step in the expectation maximisation algorithm formalised a procedure already used for juvenile *L. hamiltoni* by Bell (2011), categorising frogs here into five classes based on the extent of information about age provided by SVL. Class A and B frogs were first caught in their first two years respectively, and given that there was an annual pulse of emerging post-metamorphic young *L. hamiltoni* in February, a small frog caught in, say, October could, on the basis of its SVL measurement, be classed as being 8 months or 20 months or > 32 months old at first capture. Although only about five or six possible annually spaced AFMs need to be tried, the age at the first measurement (AFM) can be found to the nearest month, because of the pulse of juvenile frogs each year. *Leiopelma archeyi* juveniles emerged earlier than *L. hamiltoni*, generally from late December–January onwards (BDB, unpubl. data).

The EM method used all information from frogs which were caught and measured at least twice. In estimating AFM, each frog had all its juvenile measurements used, rather than just the measurement at first capture. This meant a first measurement which might be off the curve was not too influential in determining how it best fitted to the curves. The best information about AFM comes from captures when the frog is small, while the best information about sex comes from mature frogs which have essentially stopped growing. While the AFM and sex missing data were estimated using all data where the individual had at least two measurements, the actual curve-fitting (Figs. 2, 3; Table 1) was based only on individuals with at least four measurements, as required for the non-linear mixed effects procedure.

We have not given detailed results such as AIC values, likelihood ratio tests or components of variance due to individual effects. Such comparisons were done for *L. hamiltoni* in 2011 using non-linear mixed effects analyses (Bell & Pledger 2011) but employing data from very few individuals: only those

which were in Class A or Class B and also had at least four SVL measurements. We now have many more data, but there remains a problem that we still have a substantial proportion of individuals caught fewer than four times, especially at Grid 3 (Boat Bay) and at Grid 4 (Tapu), with average numbers of measurements only 4.4 and 2.8 respectively. Pinheiro and Bates (2000; Section 6.4) provide an option for data which they label "sparse", having many individuals but few observations per individual. Their suggestion is to use the positive-definite diagonal option for the variance-covariance structure within individuals. However, this analysis would not make full use of covariance information available from individuals which actually do have enough data. Our analysis shows that wrapping a finite mixture around a regular nonlinear mixed effect analysis works, giving maximum likelihood estimates for the parameters in von Bertalanffy curves and useful posterior probabilities for interpretation of results. However, we wish to improve modelling by including partial information from animals with fewer than four length measurements, while still retaining variance/covariance information from longer histories.

A fuller analysis of these data will involve continued use of finite mixtures but a switch to the incremental version of the von Bertalanffy curve (Fabens 1965) with the re-parameterisation proposed by Armstrong and Brooks (2013) to substitute k/Asym for k. We plan to build and evaluate a likelihood-based procedure which fully uses data from each individual measured at least twice, and to assess relative amounts of information provided by each individual. The total variance will be split into a component due to individual differences and a residual random component. Supplementary data where sex is actually known, e.g. observation of eggs through the abdominal wall, can be used after analysis to evaluate the accuracy of our data-based approach.

While there is no information on age and SVL at first breeding in the wild, captive reared F1 *L. archeyi* at Auckland Zoo metamorphosed in December 2013 and laid eggs in October 2017, aged three years 10 months, their F2 offspring subsequently metamorphosing in Dec 2017. By February 2017, aged three years two months, the F1 male had grown to 34 mm SVL and the F1 female to 35 mm SVL (Richard Gibson, Auckland Zoo, pers. comm.). While this demonstrates breeding maturity can occur in captive *L. archeyi* at four years of age, in the wild population at Tapu the rate of increase in SVL with age was less, as were sizes attained, so breeding maturity is likely to take longer there, up to at least seven years (Figs. 2, 3).

The conditions for growth of Maud Island *L. hamiltoni* at Grid 1 and Grid 2 in Home Bush were relatively stable over the time that growth measurements were taken, so that growth from the juvenile stage to reaching growth curve asymptotes for both sexes were distinct, females clearly reaching a larger size than males (Fig. 2; Table 1). At Boat Bay (Grid 3), however, the translocated population benefitted from intraspecific competitive release presumably with higher per capita food availability, developing better body condition (heavier per unit length) than frogs in the source population around Home Bush (Bell et al. 2004a). This resulted in growth to a greater size (SVL) in both sexes (Fig. 3; Table 1). Again, for *L. archeyi* in Coromandel (Grid 4), a major population decline over 1994–1996 resulted in differential survival of more females (Bell et al. 2004b), coupled with competitive release of survivors over subsequent years, with numbers much reduced and not returning to former levels (Bishop et al. 2008; Bell & Pledger 2015; Bell & Bishop 2018). This

influenced growth rates and body size, both sexes tending to grow larger than previously.

**Longevity**

A species' longevity relates to its lifespan, the period of life from birth until death (Bonsall 2006), being directly linked to reproduction and survival, both key attributes of fitness. Despite this, large-scale comparative studies quantifying implications of longevity for the ecology and life history of ectotherms are scarce (Scharf et al. 2015; Stark & Meiri 2018, 2021; Womack & Bell 2020). For amphibians, larger species living in colder environments experience slower growth and metabolic rates, reducing intrinsic drivers of mortality and increasing longevity (Stark & Meiri 2018, 2021). Marked phenotypic plasticity is evident in amphibians (Wells 2007) and identifying selective pressures that induced longevity in Leiopelmatid frogs is clearly speculative, for today we can only witness outcomes of past evolution. New Zealand's isolation, coupled with a temperate oceanic environment lacking predatory mammals (but with some avian predators), is likely to have induced evolutionary traits favouring a long-life (Scharf et al. 2015; Stark & Meiri 2018; Galván & Møller 2018).

Examining drivers of amphibian longevity, Stark and Meiri (2018) concluded that larger amphibians living in colder environments probably experience slower growth and metabolic rates, reducing intrinsic drivers of mortality and increasing longevity. While they initially hypothesised that species that reduce extrinsic mortality pressures via chemical protection and nocturnality have greater longevity, the analysis was later corrected (Stark & Meiri 2021), the authors then finding that this relationship was no longer significant. However, this correction revealed only minor differences in overall results (Stark & Meiri 2021). The extant New Zealand *Leiopelma* species broadly fit these predictions, but are relatively small with maximum snout-vent lengths of 38–50 mm, whereas most extinct species were larger (Worthy 1987a,b; Easton et al. 2018, 2021). All extant species appear distasteful to potential predators (Bell 1985b), with granular glands concentrated on the dorsum and sides of *L. archeyi* and *L. hamiltoni*, but more diffuse over the body surface in *L. hochstetteri* (Green 1988).

While stressing growth and longevity in this paper, we recognise that longevity represents the upper end of ages attained by the study species. In *L. hamiltoni*, for example, Bell and Pledger (2010) found that at Grid 1 and Grid 2, overall mean survival rates (± SE) of frogs were 0.84 (± 0.04) and 0.83 (± 0.04) respectively, which translate into average life expectancies of 6.3 and 5.8 years respectively. At Boat Bay (Grid 3), to which 100 frogs were translocated, they were at much lower density with a high mean annual survival rate (0.97 ± 0.01), indicating a higher average life expectancy of 33.3 years (Bell et al. 2004a).

Understanding growth and longevity variation between amphibian species has conservation implications since long-lived species with slow growth and maturity may be more vulnerable to habitat change and disturbance, and to changes in climate, because they have lower annual reproductive output and are less able to compensate for increased mortality (Purvis et al. 2000; Bell et al. 2004b; Froglife 2020). High mortality of *L. archeyi* did occur in Coromandel over 1996–2001 (Bell et al. 2004b), numbers remaining lower since (Bell & Pledger 2015; Bell 2020).

More widely, amongst urodele amphibians, salamanders may reach 12–15 years, others over 20 years (Wells 2007;

Reinke et al. 2022). Voituron et al. (2011) predicted a maximum lifespan of over 100 years and an average adult lifespan of 68.5 years for the olm (*Proteus anguinus*) a blind aquatic cave-dwelling urodele from Europe. In captivity, giant salamanders (*Andrias davidianus* and *A. japonicus*) can live for more than 60 years, while the size of some individuals of North American hellbender (*Cryptobranchus alleganiensis*) suggests they may live for 30 years in the wild (Taber et al. 1975; Petranka 1998; Browne et al. 2013).

In frogs, *Leiopelma* species (Archaeobatrachia: Leiopelmatidae) from New Zealand share a basal position with two species of tailed frogs *Ascaphus* (Archaeobatrachia: Ascaphidae) from North America, the (*Ascaphus* + *Leiopelma*) clade representing the sister-group of all other living anurans (Roelants & Bossuyt 2005). In *Ascaphus truei* aquatic larvae take 1–4 years to metamorphose and juveniles are sexually mature after 1–4 years (Bull & Carter 1996; Wallace & Diller 1998). *Ascaphus montanus* does not reach sexual maturity until 7–8 years of age and has a relatively long life-span of up to 15–20 years (Green 2003). Interestingly, there is also evidence of long-term social relationships in *L. hamiltoni*: conspecific associations between two females occurred over an eight-year interval at Zealandia Ecosanctuary, Wellington (Altobelli et al. 2020).

In other frogs, species protected from predators by toxic skin secretions, like yellow-bellied toads *Bombina variegata,* are recorded as living as long as 20 years in the wild, but smaller species tend to have shorter life spans (c. 3–5 years; Lehtinen & MacDonald 2011). For example, in more temperate regions, spring peepers (*Pseudacris crucifer*) survive to an estimated 4–5 years (Lykens & Forester 1987; Zimmitti 1999), while some tropical frogs are known to live for only 1–2 years (Galatti 1992; Kluge 1981; Ramirez et al. 1998). In the Neotropical frog *Rana vaillanti* from Mexico, average life expectancy was estimated to be only eight months (Ramirez et al. 1998). One temperate frog species thought to have a very short life span is Blanchard's cricket frog (*Acris crepitans blanchardi*; Lehtinen & MacDonald 2011; McCallum et al. 2011). Autumn breeding populations in Texas consisted almost entirely of known young of the year (Pyburn 1958) and Bayless (1969) found evidence of fast growth rates, so metamorphs could probably grow to reproductive maturity and breed within the same year that they metamorphosed. Reinke et al. (2022) reported for anurans a longevity range of 1.7–18.2 years (average ± SE = 8.17 ± 0.62 years). Overseas examples serve to remind us of just how remarkable longevity of up to 45 years that we describe for *Leiopelma* species might be. We hope that our findings might spur others to investigate frog longevity over the longer-term elsewhere in the world, as we have done in New Zealand.

## Acknowledgements

**Figure 6.** The late Phil Bishop recording frog measurements during a sampling visit to the Coromandel site (Grid 4) in April 2013, while his larger-than-life 'Archey's frog' looks on. Kevin Carter (DOC) holds a *Leiopelma archeyi* in a numbered plastic bag. (Photo: Tanya Karst).

## Additional Information and Declarations

**Author contributions:** BDB contributed to the conception and design of field research, organising and participating in sampling trips, and assembling long-term datasets that form the basis of this paper. SAP made a substantial statistical contribution by developing and adapting models to analyse these data, leading to figures that describe ageing patterns. Both authors contributed to figures describing longevity and to writing and editing this paper. Both authors approved the initial and final submissions of this paper.

## References

Altig R, Johnston GF 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. Herpetological Monographs 3: 81–109.

Altobelli JT, Cornwell TM, Lamar SK, Bell BD, Bishop PJ 2020. *Leiopelma hamiltoni* (Hamilton's Frog). Conspecific associations observed across eight years. Natural history notes. Herpetological Review 51: 819–821.

Armstrong DP, Brooks RJ 2013. Application of hierarchical biphasic growth models to long-term data for snapping turtles. Ecological Modelling 250: 119–125.

Bayless LE 1969. Post-metamorphic growth in *Acris crepitans*. The American Naturalist 81: 590–591.

Bell BD 1978. Observations on the ecology and reproduction of the New Zealand native frogs Herpetologica 34: 340–54.

Bell BD 1982. The amphibian fauna of New Zealand. In: Newman DG ed. New Zealand Herpetology. New Zealand Wildlife Service Occasional Publications 2. Wellington, New Zealand Wildlife Service. Pp. 27–89.

Bell BD 1985a. Development and parental care in the endemic New Zealand frogs. In: Grigg G, Shine R, Ehmann H eds. The biology of Australasian frogs and reptiles. Chipping Norton, Surrey Beatty and Sons. Pp. 269–278.

Bell BD 1985b. Conservation status of the endemic New Zealand frogs. In: Grigg G, Shine R, Ehmann H eds. The biology of Australasian frogs and reptiles. Chipping Norton, Surrey Beatty and Sons. Pp. 449–458.

Bell BD 1994. A review of the status of New Zealand *Leiopelma* species (Anura: Leiopelmatidae), including a summary of demographic studies in Coromandel and on Maud Island. New Zealand Journal of Zoology 21: 341–349.

Bell BD 2008. The discovery of Maud Island frogs *Leiopelma pakeka* breeding in Karori Wildlife Sanctuary and the rearing of their young. Centre for Biodiversity & Restoration Ecology Report: 2008 (1). Wellington, Victoria University of Wellington. 21 p.

Bell BD 2010. The threatened Leiopelmatid frogs of New Zealand: Natural history integrates with conservation. Herpetological Conservation and Biology 5: 515–528.

Bell BD 2011. Breeding phenology of *Leiopelma pakeka*: a threatened frog never found breeding in the wild. Herpetological Review 42: 29–32.

Bell B 2020. Archey's frog – an evolutionarily distinct and long-lived terrestrial frog at risk in New Zealand. Symposium: Recovering amphibian & reptile species from the brink of extinction: Developing best practice guidelines. Book of abstracts, 9th World Congress of Herpetology, 5–10 January 2020, Dunedin, New Zealand.

Bell BD, Pledger SA 2010. How has the remnant population of the threatened frog *Leiopelma pakeka* (Anura: Leiopelmatidae) fared on Maud Island, New Zealand, over the past 25 years? Austral Ecology 35: 241–256.

Bell BD, Pledger SA 2011. Growth rates of the New Zealand leiopelmatid frogs – how fast do these frogs grow and how informative are the data? New Zealand Journal of Zoology 38: 269–270.

Bell BD, Wassersug RJ 2003. Anatomical features of *Leiopelma* embryos and larvae: Implications for Anuran evolution. Journal of Morphology 256: 160–170.

Bell BD, Pledger S 2015. Archey's frog, *Leiopelma archeyi* in the Coromandel Ranges – how has it fared since its population crash over 1996-2001? In: Nelson NJ, Keall SN eds. Recent developments in New Zealand herpetofauna research; Abstracts of papers presented at the 15th and 16th biennial conferences of the Society for Research on Amphibians and Reptiles in New Zealand; 2015 Conference abstracts. DOC Research & Development Series 347. Wellington, Department of Conservation. 11 p.

Bell BD, Bishop PJ 2018. Status of decline and conservation of frogs in New Zealand In: Status of conservation and decline of amphibians: Australia, New Zealand, and Pacific Islands. Amphibian Biology 11: 185–199.

Bell BD, Pledger S, Dewhurst P 2004a. The fate of a population of the endemic frog *Leiopelma pakeka* (Anura: Leiopelmatidae) translocated to restored habitat on Maud Island, New Zealand. New Zealand Journal of Zoology 31: 123–131.

Bell BD, Carver S, Mitchell NJ, Pledger S 2004b. The recent decline of a New Zealand endemic: how and why did populations of Archey's frog *Leiopelma archeyi* crash over 1996–2001? Biological Conservation 120: 189–199.

Bell BD, Bishop PJ, Germano JM 2010. Lessons learned from a series of translocations of the archaic Hamilton's frog and Maud Island frog in central New Zealand. In: Soorae PS ed. Global re-introduction perspectives: additional case-studies from around the globe. IUCN/SSC Re-introduction specialist group. Abu Dhabi, IUCN.SSN. Pp. 81–87.

Bell BD, Cree A, Hare KM 2018. Remarkable longevity in New Zealand's terrestrial herpetofauna. Combined meeting of the Australian Society of Herpetologists and the Society for Research on Amphibians and Reptiles in New Zealand, Kindilan, Queensland, 2018, Abstracts. Pp. 21.

Bell B, Dewhurst P, Moore J, Pledger S 2020. Highlights of long-term studies of endemic New Zealand frogs (Anura: Leiopelmatidae) over several decades. Abstracts of 9th World Congress of Herpetology, 5–10 January 2020, Dunedin, New Zealand.

Bishop PJ, Germano JM, Bell BD 2008. Leiopelmatid frogs: the world's most archaic frogs. In: Stuart SN, Hoffmann M, Chanson JS, Cox NA, Berridge RJ, Ramani P, Young BE eds. Threatened amphibians of the world. Lynx Edicions (in association with IUCN-The World Conservation Union, Conservation International and NatuServe). Pp. 71–72.

Bonsall MB 2006. Longevity and ageing: appraising the evolutionary consequences of growing old. Philosophical Transactions of the Royal Society London B 361: 119–135.

Browne RK, Li H, Wang Z, Okada S, Hime P, McMillan A, Wu M, Diaz R, McGinnity D, Briggler JT 2013. The giant salamanders (Cryptobranchidae): Part B. Biogeography, ecology and reproduction. Amphibian and Reptile Conservation 5: 30–50.

Bull E L, Carter BE 1996. Tailed frogs: Distribution, ecology, and association with timber harvest in Northeastern Oregon. United States Forest Service Research Paper 497: 1–12.

Burns RJ, Bell BD, Haigh A, Bishop P, Easton L, Wren S,

Germano J, Hitchmough RA, Rolfe JR, Makan T 2018. Conservation status of New Zealand amphibians 2017. New Zealand Threat Classification Series 25. Wellington, Department of Conservation. 7 p.

Cisternas TJ 2019. Translocation management of *Leiopelma archeyi* (Amphibia, Anura: Leiopelmatidae) in the King country. Unpublished PhD thesis, University of Otago, Dunedin, New Zealand.

Crossland MR, MacKenzie DI, Holzapfel SA 2005. Assessment of site-occupancy modeling as a technique to monitor Hochstetter's frog (*Leiopelma hochstetteri*) populations. Department of Conservation Research and Development Series 218. Wellington, Department of Conservation. 23 p.

Dempster AP, Laird NM, Rubin DB 1977. Maximum likelihood from incomplete data via the EM algorithm. Journal of the Royal Statistical Society Series B 39: 1–38.

Dewhurst P 2003. Survival of a translocated population of the Maud Island frog (*Leiopelma pakeka*) and morphometric comparisons with the source population. Unpublished MConSc thesis, Victoria University of Wellington, Wellington, New Zealand.

Duellman WE, Trueb L 1986. Biology of Amphibians. New York, Mc Graw-Hill. 670 p.

Easton LJ, Rawlence NJ, Worthy TH, Tennyson AJD, Scofield RP, Easton CJ, Bell BD, Whigham PA, Dickinson KJM, Bishop PJ 2018. Testing species limits of New Zealand's leiopelmatid frogs through morphometric analyses. Zoological Journal of the Linnean Society 183: 431–444.

Easton LJ, Tennyson AQJD, Rawlence NJ 2021. A new species of *Leiopelma* frog (Amphibia Leiopelmatidae) from the late Pliocene of New Zealand. New Zealand Journal of Zoology 49(3): 215–224.

Fabens AJ 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29: 265–289.

Galatti U 1992. Population biology of the frog *Leptodactylus pentadactylus* in a central Amazonian rainforest. Journal of Herpetology 26: 23–31.

Galván I, Møller AP 2018. Dispersal capacity explains the evolution of lifespan variability. Ecology and Evolution 8: 4949–4957.

Germano JM, Molinia FC, Bishop PJ, Bell BD, Cree A 2012. Urinary hormone metabolites identify sex and imply unexpected winter breeding in an endangered, subterranean-nesting frog. General and Comparative Endocrinology 175: 464–472.

Gvoždík V, Moravec J, Kratochvil L 2008. Geographic morphological variation in parapatric Western Palearctic tree frogs, *Hyla arborea* and *Hyla savignyi*: Are related species similarly affected by climatic conditions? *Biological Journal of the Linnean Society* 95(3): 539–556.

Green DM 1988. Antipredator behaviour and skin glands in the New Zealand native frogs, genus *Leiopelma*. New Zealand Journal of Zoology 15: 39–45.

Green DM 2003. Rocky Mountain tailed frog, *Ascaphus montanus*. In: Hutchins M, Duellman WE, Schlager N eds. Grzimek's animal life encyclopedia, Volume 6, Amphibians. 2nd edn. Michigan, Gale Group. Pp. 80–81.

Haigh AJM 2007. Frog photographic mirror stage: instructions & information. Hamilton, Department of Conservation. 6 p.

Halliday TR, Verrell PA 1988. Body size and age in amphibians and reptiles. Journal of Herpetology 22: 253–265.

Karst T, Lukis K, Bell BD 2023. Translocation of Hamilton's frog *Leiopelma hamiltoni,* to a mainland sanctuary occupied by mice *Mus musculus*. New Zealand Journal of Ecology 47(2): A11.

King CM, Roberts CD, Bell BD, Fordyce RE, Nicoll RS, Worthy TH, Paulin CD, Hitchmough RA, Keyes IW, Baker, AN, Stewart AL, Hiller N, McDowall BM, Holdaway RN, McPhee RP, Schwarzhans WW, Tennyson AJD, Rust S, McCadie I 2009. Phylum chordata: lancelets, fishes, amphibians, reptiles, birds, and mammals. In: Gordon DP ed. The New Zealand inventory of biodiversity. Volume one; Kingdom Animalia; Radiata, Lophotrochozoa, Deuterostomia. Christchurch, Canterbury University Press. P p. 431–551.

Kluge AG 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest building gladiator frog. Miscellaneous Publications, Museum of Zoology, University of Michigan: 160:1–170.

Lehtinen RM, MacDonald MC 2011. Live fast, die young? A six-year field study of longevity and survivorship in Blanchard's cricket frog (*Acris crepitans blanchari*). Herpetological Review 42: 504–507.

Lykens DV, Forester DC 1987. Age structure in the spring peeper: so males advertise longevity? Herpetologica 43: 216–233.

McCallum ML, Brooks C, Mason R, Trauth SE 2011. Growth, reproduction, and life span in Blanchard's cricket frog (*Acris blanchardi*) with notes on the growth of the Northern Cricket Frog (*Acris crepitans*). Herpetology Notes 4: 25–35.

McLachlan GJ, Krishnan T 2008. The EM algorithm and extensions. 2nd edn. Hoboken, John Wiley & Sons, Inc. 400 p.

Newman DG 1990. Activity, dispersion, and population densities of Hamilton's Frog *Leiopelma hamiltoni* on Maud and Stephens Islands, New Zealand. Herpetologica 46: 319–330.

Petranka JW 1998. Salamanders of the United States and Canada. Washington DC, Smithsonian Institution Press. 587 p.

Pinheiro JC, Bates DM 2000. Mixed effects models in S and S-PLUS. New York, Springer-Verlag. 544 p.

Purvis A, Gittleman JL, Cowlishaw G, Mace GM 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society, London B 267: 1947–1952.

Pyburn WF 1958. Size and local movements of a population of cricket frogs (*Acris crepitans*). Texas Journal of Science 10: 325–342.

R Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramirez J, Vogt RC, Villarreal-Benitez J 1998. Population biology of a neotropical frog (*Rana vaillanti*). Journal of Herpetology 32: 338–334.

Ramírez PA 2017. Behavioural patterns of two native *Leiopelma* frogs and implications for their conservation. Unpublished PhD thesis, Victoria University of Wellington, Wellington, New Zealand.

Reinke BA, Cayuela H, Janzen FJ, Lemaitre J-F, Gaillard J-M, Lawing AM, Iverson JB, Christiansen DG, Martínez-Solano I, Sánchez-Montes G, Gutiérrez-Rodríguez J, Rose FL, Nelson N, Keall S, Crivelli AJ, Nazirides T, Grimm-Seyfarth A, Henle K, Mori E, Guiller G, Homan R, Olivier A, Muths E, Hossack BR, Bonnet X, Pilliod DS, Lettink M, Whitaker T, Schmidt BR, Gardner MG, Cheylan M, Poitevin F, Golubović A, Tomović L, Arsovski D, Griffiths RA, Arntzen JW, Baron J, Le Galliard J, Tully

T, Luiselli L, Capula M, Rugiero L, McCaffery R, Eby LA, Briggs-Gonzalez V, Mazzotti F, Pearson D, Lambert BA, Green DM, Jreidini N, Angelini C, Pyke G, Thirion J, Joly P, Léna J, Tucker AD, Limpus C, Priol P, Besnard A, Bernard P, Stanford K, King R, Garwood J, Bosch J, Souza FL, Bertoluci J, Famelli S, Grossenbacher K, Lenzi O, Matthews K, Boitaud S, Olson DH, Jessop TS, Gillespie GR, Clobert J, Richard M, Valenzuela-Sánchez A, Fellers GM, Kleeman PM, Halstead BJ, Campbell EH, Byrne PG, Frétey T, Le Garff B, Levionnois P, Maerz JC, Pichenot J, Olgun K, Üzüm N, Avcı A, Miaud C, Elmberg J, Brown GP, Shine R, Bendik NF, O'Donnell L, Davis CL, Lannoo MJ, Stiles RM, Cox RM, Reedy AM, Warner DA, Bonnaire E, Grayson K, Ramos-Targarona R, Baskale E, Muñoz D, Measey J, de Villiers FA, Selman W, Ronget V, Bronikowski AM, Miller DAW 2022. Diverse aging rates in ecothermic tetrapods provide insights for the evolution of aging and longevity. Science 376: 1459–1466.

Roelants K, Bossuyt F 2005. Archaeobatrachian paraphyly and Pangean diversification of crown-group frogs. Systematic Biology 54: 111–126.

Scharf I, Feldman A, Novosolov , Pincheira-Donoso D, Das I, Böhm M, Uetz P, Torres-Carvajal O, Bauer A, Roll U, Meiri S 2015. Late bloomers and baby boomers: ecological drivers of longevity in squamates and the tuatara. Global Ecology & Biogeography 24: 396–405.

Slaven DC 1992. *Leiopelma hochstetteri*: a study of migratory thresholds and conservation status. Unpublished MSc thesis, University of Auckland, Auckland, New Zealand.

Stark G, Meiri S 2018. Cold and dark captivity: Drivers of amphibian longevity. Global Ecology and Biogeography 27: 1384–1397.

Stark G, Meiri S 2021. Corrigendun: Cold and dark captivity: Drivers of amphibian longevity. Global Ecology and Biogeography 30: 2513.

Stephenson EM 1960. New Zealand native frogs. Tuatara 8: 99–106.

Taber CA, Wilkinson RF Jr, Topping MS 1975. Age and growth of hellbenders in the Niangua River, Missouri. Copeia 1975: 633–639.

Tessier C, Slaven D, Green DM 1991. Population density and daily movement patterns of Hochstetter's frogs, *Leiopelma hochstetteri,* in a New Zealand mountain stream. Journal of Herpetology 25: 213–214.

Thurley T, Bell BD 1994. Habitat distribution and predation on a western population of terrestrial *Leiopelma* (Anura:Leiopelmatidae) in the northern King Country, New Zealand. New Zealand Journal of Zoology 21: 431–436.

Trewenack AJ, Landman KA, Bell BD 2007. Dispersal and settling of translocated populations: a general study and a New Zealand amphibian case study. Journal of Mathematical Biology 55: 575–604.

Voituron Y, de Fraipont M, Issartel J, Guillaume O, Clobert J 2011. Extreme lifespan of the human fish (*Proteus anguinus*): a challenge for ageing mechanisms. Biology Letters 7: 105–107.

von Bertalanffy L 1960. Principles and theory of growth. In: Nowinski WW ed. Fundamental aspects of normal and malignant growth. Amsterdam, Elsevier. Pp. 137–259.

Wallace RL, Diller LV 1998. Length of the larval cycle of *Ascaphus truei* in coastal streams of the redwood region, northern California. Journal of Herpetology 32: 404–409.

Wells KD 2007. The ecology and behavior of amphibians. Chicago, The University of Chicago Press. 1148 p.

Whitaker AH, Alspach PA 1999. Monitoring of Hochstetter's frog (*Leiopelma hochstetteri*) populations near Golden Cross Mine, Waitekauri Valley, Coromandel. Science for Conservation 130. Wellington, Department for Conservation. 36 p.

Womack MC, Bell RC 2020. Two-hundred million years of anuran body-size evolution in relation to geography, ecology and life history. Journal of Evolutionary Biology 33: 1417–1432.

Worthy TH 1987a. Osteology of *Leiopelma* (Amphibia, Leiopelmatidae) and descriptions of three new subfossil *Leiopelma* species. Journal of the Royal Society of New Zealand 17: 201–251.

Worthy TH 1987b. Palaeoecological information concerning members of the frog genus *Leiopelma*: Leiopelmatidae in New Zealand. Journal of the Royal Society of New Zealand 17: 409–420.

Wren S, Bishop PJ, Beauchamp AJ, Bell BD, Bell EA, Cisternas J, Dewhurst P, Easton L, Gibson R, Haigh A, Tocher M, Germano JM 2023. A review of New Zealand: native frog translocations: lessons learned and future priorities. New Zealand Journal of Ecology: 47(2): A12.

Zimmitti SJ 1999. Individual variation in morphological, physiological, and biochemical features associated with calling in spring peepers (*Pseudacris crucifer*). Physiological and Biochemical Zoology 72: 666–676.