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Translocation of Hamilton's frog, *Leiopelma hamiltoni*, to a mainland sanctuary occupied by mice *Mus musculus*

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Abstract: A two-phase translocation of Hamilton's frog (*Leiopelma hamiltoni*) into Zealandia Ecosanctuary Te Māra a Tāne, in Wellington, was the first attempt to restore the species to the mainland. All non-native mammals had been eradicated there, but house mice (*Mus musculus*) re-invaded, providing an opportunity to investigate their impact on *L. hamiltoni*. In Phase I, 60 frogs were translocated into mouse-proof enclosures over 2006–2007. Twelve months into Phase I, 29 surviving frogs were kept in a predator-proof enclosure, and 29 surviving frogs were released into adjacent forest, then monitored over eight months. Survival and recruitment were high in the enclosure, but low in the forest. For Phase II, a further 101 frogs were released in 2012, after a fence had been erected around the release site to exclude little spotted kiwi (*Apteryx owenii*), a potential predator. In Phase II, frog survival and mouse numbers were monitored over nine months, with mouse density being suppressed by annual poisoning operations. On night surveys, 86 of the 101 released frogs were recaptured in the forest, plus four adults from the Phase I release and twelve of their progeny. Overall survival was 0.914 (0.87–0.94 95% CI), but population estimates indicated a negative trend from the second capture period. Negative binomial generalised linear modelling showed temperature was positively correlated with frog emergence ($p < 0.001$). Relative humidity approached significance for frog emergence ($p = 0.0517$), but mouse activity, precipitation during sampling, and precipitation the previous 24 hours did not impact emergence ($p > 0.05$). Surviving adult and young *L. hamiltoni* from Phase I demonstrated some capacity for survival in protected mainland areas with invasive mammal control in place. However, further studies are warranted to better determine their longer-term survival in Zealandia and alongside the threat of mice, as well as of avian predators such as kiwi, and more generally of other invasive mammals.

Keywords: amphibian conservation, Hamilton's frog, house mouse, *Leiopelma hamiltoni*, *Mus musculus*, predation, translocation

Introduction

Hamilton's frog (*Leiopelma hamiltoni*) is one of three extant, endemic frogs of New Zealand (Archaeobatrachia: Leiopelmatidae) and is listed as Threatened – Nationally Vulnerable under the New Zealand Threat Classification System (Burns et al. 2018). The largest of the extant Leiopelmatids, this anuran can reach an age of over 40 years (Bell et al. 2004a; Bell & Pledger 2023). Subfossil remains indicate *L. hamiltoni* was once distributed throughout the lower North and upper South Islands of New Zealand (Worthy 1987). Habitat loss and predation by introduced mammals, particularly rodents, are the most widely accepted reasons for decline or extinction of *Leiopelma* species and these threats have reduced *L. hamiltoni* to two, small natural populations on Takapourewa/Stephens Island and Te Pākeka/Maud Island in the Marlborough Sounds (Worthy 1987; Towns & Daugherty 1994; Bell et al. 2004b; Melzer & Bishop 2010; Newman et al. 2010). Survival of the last two natural populations of *L. hamiltoni* on these islands

has been attributed to the absence of introduced predators (Stephenson 1961; Towns et al. 2001; Bell 2011a) while the two mainland native frog species, Archey's frog (*L. archeyi*) and Hochstetter's frog (*L. hochstetteri*), as well as introduced *Litoria* species, survive sympatrically with a suite of introduced predators (Thurley & Bell 1994; Bell et al. 2004b; Egeter et al. 2011, 2015; Crossland et al. 2023; Germano et al. 2023). Long-term survival of *Leiopelma* species with introduced mammals is not guaranteed (Egeter et al. 2015).

Although there is previous evidence of mice presenting a predatory threat to a range of endemic New Zealand fauna such as eggs of inanga (*Galaxias maculatus*; Baker 2006), McGregor's skink (*Cyclodina macgregori*; Newman 1994; Pickard 1984), and Cook Strait giant wētā (*Deinacrida rugosa*; Newman 1994), there is no conclusive evidence of mice preying on *Leiopelma* species (Egeter et al. 2015). However, in a laboratory setting, mice have ingested the introduced *Litoria raniformis* (Egeter 2014). Assessment of the threat posed by mice is crucial in the conservation management of *Leiopelma*

species, especially as their remaining natural populations are vulnerable to mouse incursions, as seen on Maud Island (Bell & Bishop 2018).

To improve species' viability, there have been five *L. hamiltoni* translocations in the Marlborough Sounds: two of the Stephens Island population and three of the Maud Island population (Wren et al. 2023). The two Stephens Island translocations were in 1992 (Brown 1994) when 12 individuals were translocated 70 m from the source population and from 2004–2006 when 71 individuals were translocated to Nukuwiata Island (Tocher et al. 2006). The first Maud Island translocation was a 1984/85 intra-island translocation ($n = 100$) from the source population in a 16-ha patch of forest (Home Bush), where the population had survived, to a regenerating forest site in Boat Bay (Bell et al. 2004a). The second was a 1997 inter-island translocation ($n = 300$) from Maud Island to Motuara Island in Queen Charlotte Sound (Tocher & Pledger 2005; Bell et al. 2010), supplemented with a further translocation ($n = 300$) from Maud Island in 2014 (Wren et al. 2023). The third was a 2005 translocation ($n = 101$) to Long Island in Queen Charlotte Sound (Germano 2006; Germano et al. 2023).

Reintroduction of native frogs (i.e. Hamilton's frog *L. hamiltoni* and potentially Hochstetter's frog *L. hochstetteri*) has been identified as an integral component of the ecosystem restoration goals of the Karori Sanctuary Trust (2000). This goal is a part of the Trust's broad aim of restoring the 252 ha valley ecosanctuary as closely as possible to a pre-human ecosystem (Campbell-Hunt 2002). Leading up to the Phase I translocation in 2006, the Department of Conservation's native frog recovery group deemed the Maud Island population of *L. hamiltoni* to be the most appropriate native frog source to translocate to the ecosanctuary, given the significantly larger population size than that on Stephens Island.

Located 5 km from central Wellington, the original vegetation of Zealandia Te Māra a Tāne (hereafter 'Zealandia') was cleared through burning and grazing. In 1890 it was progressively retired from farming to protect the city's water catchment. Indigenous vegetation regenerated naturally to form a closed canopy in most areas, but indigenous fauna was severely depleted following habitat loss and introduction of non-native mammals. To allow ecosystem recovery, an 8.6 km predator-proof fence designed to exclude 14 species of non-native mammals was erected around the perimeter of the valley in 1999. An eradication programme commenced in September 1999 using live capture and kill traps, in conjunction with aerial and ground-based application of a second generation anticoagulant, BrodifacoumTM. The valley was declared free of all non-native mammals in 2000.

Since then, several biosecurity breaches have been detected, resulting in rapid and mostly successful follow-up eradications. The house mouse, *Mus musculus*, was the only non-native mammal to have re-established within Zealandia, possibly by exploiting small imperfections in the wire-weave fence mesh (6 × 24 mm), being dropped in by avian fauna, or exploiting fence breaches by fallen branches or trees. It has been possible to eradicate and prevent the re-establishment of most non-native mammals from fenced restoration sites throughout New Zealand, but mice are a notable exception. There are multiple other sites where eradication failed or reinvasion occurred (e.g. Tāwharanui, Maungatautari, and Riccarton Bush). Additionally, mouse abundance typically increases in unfenced conservation areas following rat (*Rattus* spp.) control (Innes et al. 1995; Murphy et al. 1999; Caut et al.

2007). Due to this, Zealandia determined that eradication is not currently feasible and instead continues with routine monitoring and annual control via ground-based application of BrodifacoumTM bait stations.

Mice have previously been considered of secondary importance in areas managed for conservation purposes as mammalian eradication programmes often focus on larger predators such as mustelids (*Mustela* spp.), rats, and possums (*Trichosurus vulpecula*), as they present a greater known predatory threat to many of New Zealand's native species (Department of Conservation 2020). However, there are few conservation sites where mice are the only non-native mammal (Jones & Toft 2006) resulting in a limited understanding of their impact over long periods for all indigenous fauna. The reintroduction of indigenous fauna to Zealandia provided an opportunity to examine the impact of mice on indigenous taxa in the absence of other introduced mammals. Translocation of *L. hamiltoni* into Zealandia presented an opportunity to address a recommendation in a former New Zealand native frog recovery plan that an attempt be made to return extirpated Leiopelmatid frogs to the mainland (Newman 1996). More specifically, the translocation into Zealandia in 2006 and 2012 offered an opportunity to investigate the effects of mice on the survival of a translocated Hamilton's frog population in a location that manages introduced predators (Bishop et al. 2013). The two phase translocation documented in this paper represents the first attempt to return *L. hamiltoni* to the mainland and the first release of *L. hamiltoni* into habitat occupied by house mice.

Methods

Overview

To assess the overall success of the frog translocation in Zealandia, we follow the recommendations of Miller et al. (2014) using four successive time frames: Stage 1, survival and growth of founders; Stage 2, evidence of reproduction; Stage 3, population growth; and Stage 4, viable population. Elsewhere, Wren et al. (2023) have used these criteria to compare the success of all *Leiopelma* translocations that have occurred in New Zealand.

We conducted a preliminary translocation of 60 Maud Island *L. hamiltoni* into Zealandia in 2006 (Phase I) prior to a larger translocation of an additional 101 frogs in 2012 (Phase II). The sequence of releases and related observations is summarised in Table 1. The release site was chosen as an area of the valley with numerous rocks beneath cool, moist, naturally regenerating native forest, and with ground invertebrates appearing similar in composition and quantity to sites elsewhere in the sanctuary. For the first year, Phase I frogs were held in two purpose-built, *in situ* predator-proof enclosures (1.5 × 3.1 × 0.7 m) comprising a treated timber frame and wire weave mesh (3 × 3 mm). Both enclosures were nested in the forest of the lower valley under a closed canopy dominated by kohekohe (*Didymocheton spectabile*), kawakawa (*Macropiper excelsum*), and kōtukutuku (*Fuchsia excorticata*) and filled with logs, rocks, and leaf litter a week before frogs were released. Greywacke rocks were placed around the outside of each enclosure to create a 400 mm buffer zone. Enclosures were located 200 m apart and sufficiently distanced from public access: the first, being on a flat section of forest (E1), and the other on an eastern-facing slope (E2). In 2007, half of the Phase I frogs ($n = 29$) were released into forest

Table 1. A summary of releases, locations, survival, and recruitment of *L. hamiltoni* in Zealandia over 2006–2013.

Period	Date	Enclosure 1		Enclosure 2		Outside Enclosure 2		Comments	
		Released	Confirmed alive	Released	Confirmed alive	Released	Confirmed alive		
Phase I	Feb–Mar 2006	30						Collected from Maud Island in 2004, then kept in captivity, mostly larger (female) size	
	Sep–Oct 2006			30				From Maud Island, mostly smaller (male/smaller female) size	
	Apr 2007		29		29			No breeding but predominantly one sex likely to be in each enclosure	
	Apr 2007			29		29		29 frogs each from two enclosures; mixed to improve likely balance of sexes then frogs released	
	Oct 2007						11	Found outside Enclosure 2	
	Feb–Mar 2008	11 juveniles			27			1	Check of Enclosure 2 - have bred: 13 froglets found, 11 reared to juvenile frog stage; extensive search of OUTSIDE frogs
	Mar 2009	10 juveniles			26				Check of Enclosure 2 - have bred: 10 froglets found and reared to juvenile frog stage
Zealandia, unpub. data	2010	5 juveniles			24			Check of Enclosure 2 - have bred: 5 froglets found and reared to juvenile frog stage	
	Mar 2011	12 juveniles			19			Check of Enclosure 2 - have bred: 12 froglets found and reared to juvenile frog stage; 6 frogs relocated to separate enclosure in Zealandia	
Phase II	Nov 2012							Habitat enhancement (shifted existing rock piles and added additional rocks) and constructed kiwi exclusion fence	
	Dec 2012 Up to Aug 2013					101	102	Released in kiwi exclusion area 90 translocated frogs and 12 progeny found	

habitat occupied by mice immediately adjacent to E2. Habitat adjacent to E2 consisted of a large aggregation of greywacke rocks ($4 \times 2 \times 0.75$ m) assembled prior to release and a further eight smaller piles (2×2 m) located around the main pile at 5 m spacings. The release site emulated Home Bush on Maud Island, having abundant rocks beneath taller closed-canopy forest vegetation (Bell & Bell 1994). A kiwi exclusion fence of hexagonal netting and shade cloth was erected around the release site prior to the release of 101 Phase II frogs in 2012.

Strict hygiene protocols were adhered to throughout both phases. All frogs from Phase I tested negative for amphibian chytrid fungus *Batrachochytrium dendrobatidis* (Bd) infection prior to initial release and at the beginning and end of each release phase. With the negative results from Phase I, together with chytrid not being detected in the source population on Maud Island (Bell & Pledger 2010; Shaw et al. 2013) and an experimental study suggesting Bd poses a low risk to Leiopelmatids (Ohmer et al. 2013), a sub-sample of 56 frogs from the Phase II cohort were swabbed for Bd and swabs were stored frozen for future analysis. During monitoring of both phases, access to the release site was limited to research personnel, equipment and footwear were treated with biocide (Virkon™) prior to entering the site and frogs were handled using Nitrile examination gloves. Gloves were not changed between handling each frog as the risk of Bd was determined to be low and the frogs were inhabiting the same site.

Data collection

We recorded snout-vent length (hereafter SVL) (mm), left tibia length (mm), weight (g), girth (scale 1–5, 5 being largest), age class (based on SVL) and health (poor, fair, good). As a measure of relative condition, we measured a body condition index (BCI) by log weight / log length (Bell et al. 2004a). We used three methods of identification to determine survival and condition of the frogs. During both phases, we used a capture-photo-recapture programme (Beausoleil et al. 2004; Bradfield 2004; Carafa & Biondi 2004; Mellor et al. 2004; Webster 2004; Germano 2006; Kenyon et al. 2010; Sacchi et al. 2010; Beukema 2011; Hoque et al. 2011) using dorsal, left/right lateral, and frontal photographs. During Phase II, for frogs with indistinguishable markings ($n = 33$), we also used unique toe-clip combinations (Newman 1990), which was done upon initial capture on Maud Island, and eye-vessel patterning (eye venation) as suggested by Bell & Pledger (2010) and Bell (2011b) and validated by Karst (2013).

Phase I Translocation

Collection and liberation

Thirty frogs sourced from a captive colony collected from Maud Island in 2004 and used for a laboratory-based study at the University of Canterbury, New Zealand were released into E1 in February ($n = 22$) and March 2006 ($n = 8$). Frogs had a mean (\pm SE) SVL of 42.5 ± 0.54 mm. A further 30 frogs were collected from Home Bush on Maud Island between 29 September and 3 October 2006 and placed separately into clean plastic containers with damp leaf litter. Frogs were held for a maximum of four nights at controlled temperature and humidity before being transferred to Zealandia and released during daylight hours into enclosure E2. The mean SVL of the latter group was 36.2 ± 0.46 mm due to the deliberate collection of a greater portion of smaller frogs from Maud Island so that the founding population at Zealandia might reflect the bimodal population observed in long-term study

of the wild population (Bell & Pledger 2010).

Both enclosures were searched in April 2007 by carefully removing all substrate; 58 frogs were recaptured (29 in each enclosure). Satisfied that frogs could persist at the site where dispersal, predation and possible competition were controlled, we divided the 58 frogs into two new groups, each with a bimodal SVL distribution and equivalent size-class distributions, as per Tocher et al. (2006), and returned one group ($n = 29$) to enclosure E2 ('INSIDE') and the other group ($n = 29$) was released into immediately adjacent habitat ('OUTSIDE'). The OUTSIDE group became the founding population and comprised four sub-adults (unknown sex), 16 adults (unknown sex), and nine adults (female). All frogs were released during daylight hours to encourage individuals to immediately seek shelter and minimise dispersion of OUTSIDE frogs away from the release site. The OUTSIDE group was not protected from mice or any other potential predator at Zealandia including ruru (*Ninox novaeseelandiae*), tuatara, or little spotted kiwi.

Monitoring Phase I

During April and May 2007, and from September to December 2007 (at least seven nights per month), both INSIDE and OUTSIDE areas were searched starting 60 minutes after sunset. Emerged frogs were captured, measured and photographed before being released at their capture points. For the INSIDE frogs, we systematically searched 1×1 m sections of the enclosure for emerged frogs. For the OUTSIDE group, we moved upslope from the lowest point in the southwest corner, systematically searching a 12×12 m search grid centred on the release site for emerged frogs. Substrate was not disturbed in either area during these searches.

To determine absolute survivorship of the INSIDE frogs, we carefully removed all substrate within E2 during daylight hours on 26 February 2008, finding 27 (93%) frogs alive, all of which were returned to the same enclosure immediately after the search. By way of contrast, only 11 of the OUTSIDE frogs were captured six months after release, with only one OUTSIDE frog captured during extensive night searches conducted 22–27 March 2008 when weather was deemed most conducive to emergence (Cree 1989). During Phase I, adult OUTSIDE frogs increased their BCI significantly more than the INSIDE frogs ($t_{22} = 3.202$, $p = 0.004$; $t_{19} = 2.897$, $p = 0.009$, respectively). Zealandia conducted a census of E2 in 2011, confirming survival of 25 frogs (Zealandia, unpub. data). The INSIDE group, less six that were relocated at the time to a publicly accessible predator-proof enclosure in Zealandia, remain in E2 at the time of publication ($n = 19$) and continue to be detected (Altobelli et al. 2020).

Phase II Translocation

Collection and liberation

Using the same release site as Phase I, in November 2012, we prepared the study site. We slightly shifted and enlarged the site (12.5×15 m) to accommodate a larger cohort. The remaining understorey habitat varied (Figs. 1a,b) and ranged from barren ground to moderate vegetation cover of various ferns and supplejack (*Ripogonum scandens*). Taking advantage of barren ground and walking planks already on site to ensure no potential surviving frogs were underfoot, we relocated the rock piles from Phase I, and with greywacke sourced from within permitted areas in Zealandia, we increased the quantity of rocky habitat to cover approximately 30% of

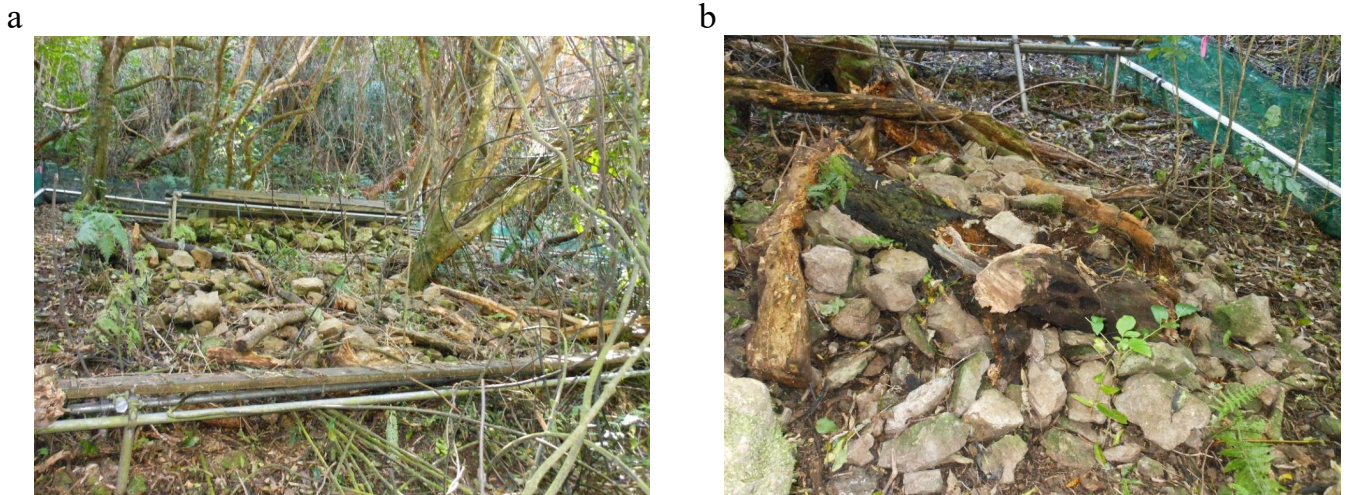


Figure 1. (a) Mid-site Zealandia *Leiopelma* habitat with rocky aggregation and plank walkways to minimise habitat disturbance (Photo: TMK); (b) Lower-site Zealandia *Leiopelma* habitat with rocky aggregation and green kiwi-exclusion fence and white PVC overhang (Photo: TMK).

the site. During this process, care was taken to ensure any surviving OUTSIDE frogs found were captured and held for their protection. One frog (27.8 mm) was found while deconstructing a rock pile from Phase I. It was relocated to the closest rocky habitat on the western side of the enclosure (E2) within the study site. The majority of the rocky habitat was contiguous and concentrated around the enclosure in the western corner of the site, covering approximately 45 square metres, at a depth of approximately 0.5 m. This resulted in an upper aggregation of rocks located in the far western corner of the site, as well as a middle aggregation of rocks on the southwestern side of the site. Additionally, we constructed a separate, lower aggregation of rocks in the eastern corner of the site measuring approximately $3 \times 2 \times 0.5$ m. To remove the potential variable of little spotted kiwi predation, which was not done for Phase I, we erected a kiwi-exclusion fence (hereafter 'exclusion fence') around the perimeter of the study site, including an internal overhang to discourage frogs from dispersing out of the study site (Fig. 1b). All rocks were kept approximately one metre away from the exclusion fence.

From 26 November to 2 December 2012, with care taken not to obtain individuals from established study sites in order to not disrupt population dynamics, we collected 101 *L. hamiltoni* from a wide area within Home Bush on Maud Island. In groups of up to four, frogs were held for a maximum of six nights in clean plastic containers with damp leaf litter. Containers were kept in a temperature and humidity-controlled location. On 2 December 2012, by chaperoned maritime and automotive transport, we transported the frogs to Zealandia for immediate release. Using age classes established for *L. hamiltoni* (Tocher et al. 2006), the translocated cohort consisted of two juveniles, nine sub-adults, 23 adults, all of unknown sex, and 67 adult females. The mean (\pm SE) SVL was 40.3 ± 0.63 mm with a female-biased, non-normal distribution ($p < 0.001$).

Upon arrival at Zealandia, during daylight hours (1720 h) on 2 December 2012, we released the frogs onto the rock aggregations of the study site (31 in upper aggregation, 40 in mid-study site, and 30 in lower aggregation; all of which were at least 4 m away from the Phase I release site) and left them undisturbed for 15 days to allow for acclimation. At release, the site was slightly damp, but it was not raining. With the

one sub-adult found during preparation of the study site, the total number of known frogs was 102.

Monitoring Phase II

We conducted night searches over five consecutive nights approximately every four weeks from 17 December 2012 (period one) through to 2 August 2013 (period nine). Searches commenced approximately 90 minutes after sunset and varied in duration (60–210 min). Cloud cover, moon phase, wind strength, current precipitation, and precipitation in the previous 24 hours were recorded at the start of each search. Wind direction (degrees true north) was obtained from the MetService Kelburn (AWS) (World Meteorological Organisation synoptic number 93437) approximately 7.2 km northeast of Zealandia. Minimum and maximum of both temperature ($^{\circ}$ C) and relative humidity (%) (RH) were recorded by a Digitech hygrometer (model QM7312) throughout the duration of all searches.

Using torches and taking advantage of barren ground and walking planks, systematic searches, including a 2 m buffer zone around the exterior of the exclusion fence were conducted in 1 m transects while manoeuvring uphill to facilitate recapture. Substrate was not disturbed. Following Bell & Pledger (2010), frogs were held in separate, numbered plastic bags and a corresponding number peg was placed at the location found. Emerged frogs captured were measured and photographed before being released at their capture points.

Mouse monitoring

To determine relative abundance of mice in Zealandia during Phase I, we utilised four 1-km index snap-trap lines set for three nights every 2 months during July, September, November 2007, and January 2008. Traps were placed at 25 m intervals along all four lines, baited with peanut butter and oats and covered with an upturned plastic container into which a single 40 mm entry hole had been drilled. All index lines were set and checked during the same week and results expressed as the number of captures per 100 corrected trap nights (C100TN). For each sprung trap, (with or without a mouse) 0.5 days were removed to account for non-availability of sprung traps (Cunningham & Moors 1996).

To investigate mouse activity at the release site during Phase II, we placed ten unbaited tracking tunnels throughout the study site: three tunnels were placed in the upper area of the site under walking planks, four in the middle with three under walking planks and one along the rock aggregation, and three in the lower area with two under walking planks and one in an open area. The tracking tunnels were left open and monitored fortnightly from 3 January to 1 August 2013 for the presence/absence of prints. Additionally, Zealandia continued with their normal bi-monthly predator control programme utilising 3 snap-trap index lines to inform its annual three-week BrodifacoumTM ground-based application. This annual BrodifacoumTM operation occurred in May 2013.

Data Analysis

We analysed our data via capture-recapture analysis for an open population using a Jolly-Seber model (Pledger et al. 2010). The model provided survival (Φ) and capture probabilities (p) as well as population estimates (\hat{N}) for each period. The data included 44 secondary capture occasions and nine primary capture periods. Parameters for the Jolly-Seber model were: n_j = number of individuals captured at time j
 \hat{N}_j = population size at time j , including individuals underground, at period K
 Φ_j = survival rate from trip j to trip $j+1$ ($j = 1, 2, \dots, K-1$)
 p_j = probability of capture at time j

Population estimates were calculated by:

$$\hat{N}_j = n_j / p_j \tag{1}$$

The Jolly-Seber model with the lowest Akaike information criterion (AIC) had survival (Φ) held constant over time, time-dependent probability of capture (p) and population estimation for each period (\hat{N}_j) with a linear trend beginning at the second period ($\Phi(\cdot)p(t)\hat{N}_j(l)$ from period two) (Table 2).

We used the Shapiro-Wilk test to test for normality, and non-parametric tests where data were not normally distributed. Mean values are presented with \pm standard error of the mean. The negative binomial generalised linear model was used to determine correlation of covariates and total number of frogs emerged. The significance level was set at $p = 0.05$ with 95% confidence interval (CI).

BCI was used as a measure of relative condition (Bell et al. 2004a). The short duration of study did not warrant continuous monitoring of individual SVL; therefore, SVL obtained during the collection on Maud Island was used for

all BCI calculations. Mean weights per period were used to calculate individual BCI and the Kruskal-Wallis test was used to compare the change in BCI per period.

Minimum number alive (MNA) was calculated by the summation of the number of individuals caught at time t and the number of individuals present, but not caught at time t , which were recaptured at a later stage (Krebs 1966).

Results

Mouse Trapping: Phase I

Mouse captures peaked on all four index lines in July 2007 with a mean (\pm SE) of 23.1 ± 5.9 captures per 100 corrected trap nights (C100TN). In September 2007, captures declined to zero captures per C100TN on two of the four lines following Zealandia’s annual control operation in July 2007 (mean (\pm SE) of 1.4 ± 0.0 captures per C100TN across four lines). Captures then increased to a mean (\pm SE) of 2.7 ± 3.8 and 5.4 ± 3.3 captures per C100TN in November 2007 and January 2008 respectively across the four index lines.

Mouse Activity: Phase II

The tracking tunnels did not show mouse activity until 4 weeks after the start of monitoring, on 31 January 2013, whereafter activity increased as the mouse activity reached its peak from 9 May through to 6 June 2013 with a tracking rate of 90 % (May–June). Peak relative abundance was recorded in July during Phase I (2007) while peak tracking activity occurred in May–June during Phase II (2013). The difference in timing may be due to annual variation in climate and availability of food resources or may just reflect the different methods employed during each phase to estimate relative abundance. Peak mouse activity of Phase II corresponds with May peak mouse abundance indicated by Zealandia’s 2013 index snap trap line data (Zealandia, unpub. data). Following Zealandia’s annual ground-based application of BrodifacoumTM in late May 2013, activity in tracking tunnels reduced to 20% tracking rate during June monitoring. No activity was observed in the tunnels for the remainder of the study.

As Zealandia’s index snap trap line data were not available at the time of our analysis, the relationship with mouse density was not able to be determined. Acknowledging limitations, tracking rates were used as an approximate index of relative abundance during Phase II (Gillies & Williams 2013). Analysis of these rates did not show mouse activity to be significantly related to frog emergence ($p > 0.05$).

The National Institute of Water and Atmospheric Research (NIWA) reported decreased rainfall prior to the start of this study in October 2013. By February and March 2013 (third and fourth capture periods), rainfall was at its lowest, resulting in a declared drought on 15 March 2013 (National Institute of Water and Atmospheric Research 2013). This lack of rainfall was substantiated by the MetService (Kelburn) report of monthly total rainfall (Table 3).

Despite drought conditions, analysis did not show the amount of precipitation in the previous 24 hours, nor precipitation during monitoring as significant ($p > 0.05$) in relation to frog emergence. Mean temperature showed a positive correlation ($p < 0.001$) with overall frog emergence. Mean RH approached significance ($p = 0.0517$) showing a potential positive trend with overall emergence.

Table 2. Jolly-Seber candidate models selection table with AIC values. (.) indicates constant over time, (p) is capture probability, (t) is time dependent, \hat{N}_j is population size at time j , (l) is linear trend.

Model	AIC	Δ AIC	$\hat{N}p$
$\Phi(\cdot)p(t)\hat{N}_j(l)$ from period two	380.85	0	13
$\Phi(\cdot)p(t)$	389.32	8.47	18
$\Phi(\cdot)p(t)\hat{N}_j(\cdot)$ from period two	390.79	9.74	12
$\Phi(t)p(t)$	396.98	16.13	24
$\Phi(\cdot)p(t)\hat{N}_j(\cdot)$	407.63	26.78	11
$\Phi(t)p(\cdot)$	428.68	47.83	18
$\Phi(\cdot)p(\cdot)$	433.37	52.52	11

Table 3. Mean monthly rainfall for the duration of the study. Source: MetService, Kelburn.

Month	Mean rainfall (mm)	± 1SE
December 2012	2.26	0.708
January 2013	2.85	1.251
February 2013	2.36	1.782
March 2013	2.92	1.968
April 2013	2.89	1.093
May 2013	4.57	1.971
June 2013	8.41	3.239
July 2013	3.26	1.288

Frog Monitoring: Phase I OUTSIDE + Phase II

The number of recaptures for individual frogs ranged from 13 (one frog), down to zero (15 frogs) over the nine months of Phase II monitoring. Eighty-six of the 101 Phase II frogs were recaptured at least once during the monitoring, as well as four OUTSIDE frogs from Phase I (13.8% of the original 29 released) including one not seen since its release in February 2006. A further 12 frogs (including the one that was found while preparing the site) were found during this study; none of which could be identified as either Phase I or Phase II cohorts. Using the age classes established by Tocher et al. (2006), these 12 frogs consisted of one adult female and 11 sub-adults. One of the Phase I OUTSIDE adults and three of the unidentifiable frogs were found outside the exclusion fence and were returned to the centre of the site once all data processing was complete. To assess overall survival, all 101 frogs from the Phase II translocation, as well as the four found from Phase I and the 12 unidentifiable frogs found during Phase II monitoring ($n_{tot} = 117$) were used in survival estimates. Overall survival was high during Phase II monitoring (0.914; 0.87/0.94 CI).

Population size estimation (\hat{N}) (Fig. 2) showed a negative regression (slope = -4.69, -6.70/-2.68 CI), which follows the initial trend in population estimates from the Boat Bay and Motuara Island translocations (Bell et al. 2004a; Tocher & Pledger 2005). The MNA also indicated a decline in population over the nine months of monitoring. This conservative method is the worst-case scenario and the estimate of the last period of capture (July–August 2013) represents unique individuals recaptured during that period only.

Condition

Changes in mean BCI over the duration of the study were found to be significant ($p < 0.001$) and showed there was a substantial increase in BCI of the initial 101 frogs captured on Maud Island (0.472 ± 0.016), to the sub-sample of 45 frogs captured in January 2013 at Zealandia. Thereafter, the BCI per month dropped and fluctuated slightly (Fig. 3).

We found three frogs from the Phase II translocation with physical injuries and/or abnormalities. Upon initial recapture, one was found with an injured rear right foot and appeared to be otherwise in good health during each of its subsequent captures ($n = 3$). The second, on its fifth recapture, was found with a yellow, subcutaneous mass approximately 5.2 mm in diameter, over the right pectoralis. The frog was active, and the mass did not seem to restrict the normal range of motion of the limb. A fine needle aspirate was performed by Dr. Danielle Sijbranda, Doctor of Veterinary Medicine at Wellington Zoo and was diagnosed as a lipoma. The frog was returned to the study site and subsequently recaptured, appearing with the lipoma and still otherwise in good health. A third frog, on its fourth and final capture, was found with an inflamed mandibular joint. There were no additional obvious injuries; the frog was active and appeared to be in good condition.

On 7 May 2013, we found a dead frog in the northeast quadrant of the study site. Upon initial discovery, the frog appeared to be in an intermediate state of decomposition

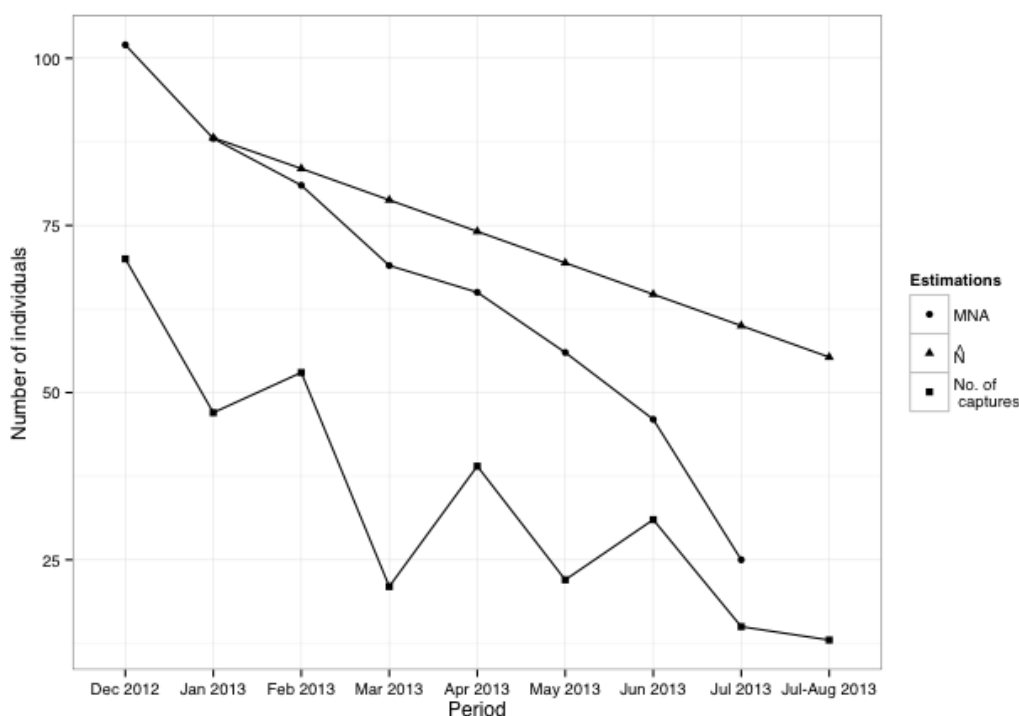


Figure 2. The number of captures, minimum number alive (MNA) and estimated population size (\hat{N}) at Zealandia over successive capture periods, December 2012 and July–August 2013. Probability of recapture (p_i) is needed to accurately estimate the population estimate (\hat{N}_i) therefore (\hat{N}_i) (depicted \hat{N} as in Fig. 2) is not an accurate calculation for the last period of the monitoring. Additionally, with no successive captures after period 9 (July–August 2013), MNA for period 9 could not be calculated.

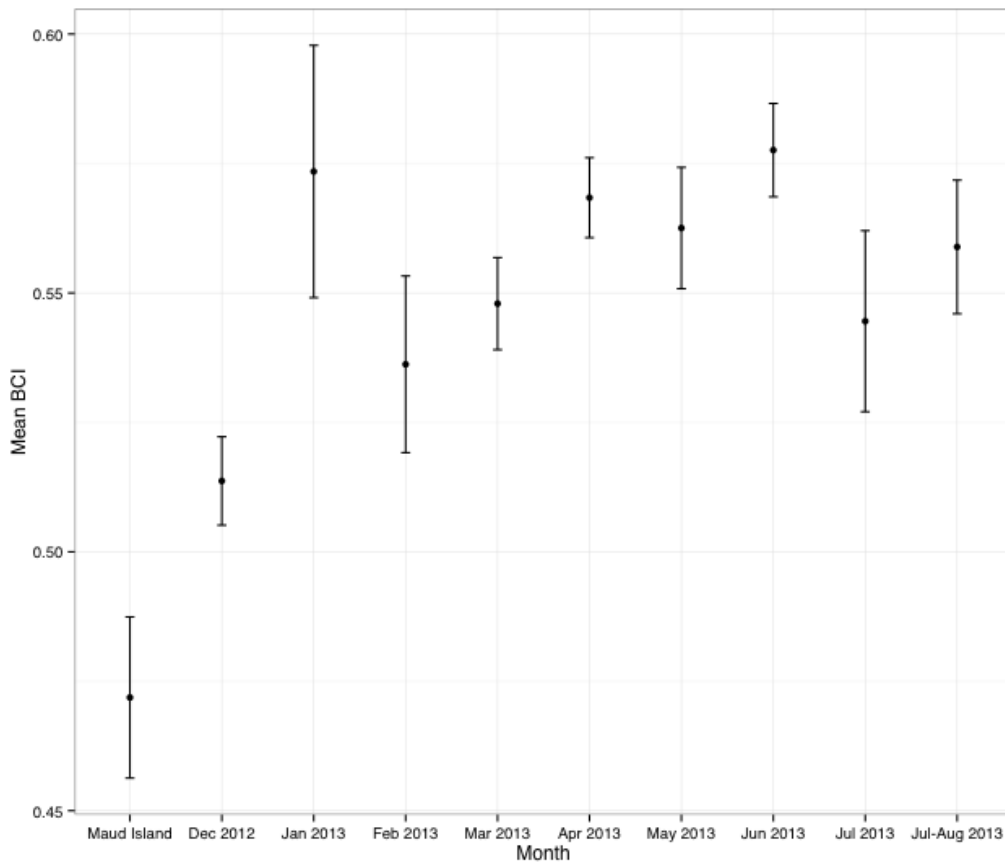


Figure 3. Mean body condition index ($BCI \pm 1$ SE) of frogs caught between December 2012 and July 2013 at Zealandia compared to BCI of frogs caught at Maud Island.

covered with what appeared to be small white larvae. A post-mortem examination indicated that the frog had been dead for approximately 3–4 days prior to its discovery and did not appear to have any damage (i.e. bite marks or signs of being crushed). The frog did not appear to be toe-clipped, and the stage of decay made it impossible to identify it by skin markings, so its identity remains unknown.

Breeding in the predator-proof enclosures

Although this study focused on frogs living outside the enclosures, as reported by Bell (2008), during Phase I we recorded amplexus inside enclosure E2, on 16 December 2008, and two discrete clusters of froglets inside this enclosure on 26 February 2008. Both clusters were located on soil under approximately 70 cm of rocks and in small, separate hollows (depth = 20 mm) under a medium-sized rock (300 mm²). An apparent male frog (SVL = 38.3 mm) was found on top of the first cluster of four froglets and moved off when disturbed. A fifth froglet was later found near this cluster and was assumed to have also belonged to this cluster. Another apparent male (also SVL = 38.3 mm) was found on the second cluster of eight froglets and remained in place until prompted. At the time of their discovery, all froglets were at a similar stage of development with visible yolk sacs, limbs, and long tails (Lukis 2009). Because of the disturbance to their habitat, and to negate possible risks of cannibalism occurring within the enclosure, froglets were immediately removed from the enclosure and transferred onto moist paper in 10 cm glass Petri dishes (one cluster per dish) at the time of capture. They were then taken to Victoria University, Wellington where they were held in incubators until metamorphic processes were complete; for

husbandry and development see Bell (2008). Twelve juvenile frogs were released back into a separate predator-proof enclosure in Zealandia 2008. A second cohort of 13 juveniles were recorded and removed from the original enclosure (E1) in March 2009 and incubated in similar conditions before being released into a segregated area of the second enclosure.

During Phase II monitoring, E2 was also searched for emerged frogs. Eighteen of 19 adults released into the enclosure following the previous census were confirmed alive (94.7%), and a number of froglets were observed. The juvenile count during searches varied from one to 15. Two froglets emerged 6 May 2013 measured approximately 11.52 mm and 12.85 mm SVL, respectively, suggesting success of the most recent breeding cycle at that time (Bell 2011a).

Discussion

Seddon et al. (2007) recommended that those contemplating a reintroduction determine a priori its specific goals, overall ecological purpose, and any inherent technical and biological limitations, and that evaluation processes incorporate both experimental and modelling approaches. The specific aim of the Zealandia frog translocation was to return the Maud Island frog to a mainland site relatively free of predators, apart from the house mouse which had re-invaded there (Lukis & Bell 2007; Lukis 2009; Bell et al. 2010; Karst 2013). The initial release of 30 *L. hamiltoni* was a conservation management move in response to their availability at relatively short notice from stock previously held for research in captivity (Bell et al. 2010), so only limited experimental and modelling

approaches were incorporated at that stage. Rather, the study built on that initial phase by supplementary translocations directly from the source population on Maud Island in 2006 ($n = 30$) and 2012 ($n = 101$). Both these study phases involved population modelling and experimental comparison of groups of translocated frogs inside Zealandia, including comparison of survival and recruitment inside and outside the predator-proof enclosures, and released frogs inside and outside the kiwi-exclusion fence. Were this study now at the planning stage, we envisage greater incorporation of experimental and modelling approaches following those recommended in the reintroduction biology literature (Seddon 1999, 2010; Seddon et al. 2007, 2012; Armstrong & Seddon 2008; Taylor et al. 2017; Linhoff et al. 2021).

This translocation of *L. hamiltoni* to Zealandia as part of efforts to restore the site's original biota presented a unique opportunity to investigate the suitability of habitat also occupied by house mice. Continued high survival and successful recruitment within the predator-proof enclosure showed mouse-free habitat at Zealandia to be suitable for *L. hamiltoni*. Outside of the enclosure we found that mice, when managed, did not appear to substantially reduce short-term survivability of *L. hamiltoni*, with survival estimates (0.91) in Phase II over the 9 months of monitoring post-release, which approached the initial survival estimates of the successful Boat Bay (0.97) and Motuara Island (0.99) translocations (Bell et al. 2004a; Tocher & Pledger 2005). Limitations at the time of analysis inhibited a clearer understanding of survival. Further studies are needed to ascertain the cause of decline in population estimates, especially given the steep decline detected at Zealandia, as well as to determine long-term survivability outside of E2. The impact of mice on different size cohorts might reveal increased vulnerabilities of age or sex classes that could affect translocation success, for instance larger individuals may have less of an opportunity to seek refuge within the habitat to evade predation. On the other hand, smaller frogs may be more vulnerable to mice due to their size.

There was a 5-year interval between Phase I and II translocations. With slow growth and three to four-year maturation (Bell 1978; Bell & Pledger 2023), one generation of progeny could have reached adulthood during this time. Twelve unidentifiable frogs found during Phase II are likely progeny from Phase I and suggests breeding took place and positive recruitment. Progeny were of at least two separate age classes (one adult female, 11 sub-adults) suggesting more than one successful breeding season. Following criteria given by Miller et al. (2014), our findings suggest that the Phase I translocation might have been at least a partial success in that we have seen evidence of positive recruitment over a period greater than the maturation cycle of *Leiopelma*. However, without supplementation from the Phase II translocation, the longevity of the very small founding population ($n = 29$) remains questionable (Germano & Bishop 2009). After the Phase II supplementation of 101 frogs, we did record improved survival and growth of founders and evidence of reproduction, so both Stage 1 and Stage 2 of the success criteria advocated by Miller et al. (2014) have been achieved in Zealandia. Whether population growth and population viability are achieved (Stages 3 & 4) will require further research and more time to assess, as these are long-lived frogs (Bell & Pledger 2023).

While this study found no direct evidence of predation by mice, a more thorough examination of palatability of different *L. hamiltoni* development stages is warranted. It has been suggested that Leiopelmatid frogs have unpleasant skin

secretions that may deter mammalian predators (Green 1988). To date, rats are the only rodent for which there is conclusive evidence of predation on native frogs (Thurley & Bell 1994; Egeter 2014; Egeter et al. 2011, 2015). There is compelling evidence that mice have negatively impacted other fauna (Baker 2006; Newman 1994) and it is possible that a small level of predation of the most vulnerable stage (e.g. eggs and/or hatchlings) would eventually have a detrimental effect on demographics of the translocated frog population. Future analysis of adult and juvenile survival rates in the presence of mice would be useful to compare to other Leiopelmatid studies of frogs under various predator control regimes (Crossland et al. 2023; Germano et al. 2023).

The reduced recapture events and the declining population estimate seen towards the end of Phase II is similar to observations made following previous *L. hamiltoni* translocations to mice free habitat (Bell et al. 2004a; Tocher & Pledger 2005). Reduced population estimates, MNA, and number of captures are of short duration and do not necessarily indicate an accurate representation of survival of the population over a longer period of time. High recaptures in the beginning of the study may have been due to greater activity because of unfamiliarity of new habitat and non-established retreat sites. Once the frogs became more familiar with their environment and established retreat sites, emergence time and therefore probability of capture may have decreased. Declining recaptures were not thought to be due to capture-shyness (Bell & Pledger 2005; 2010) because the probability of capture held constant over time in the Jolly-Seber analysis. Other factors to consider include skill in finding cryptic frogs in a heterogeneous terrain, frog mortality, misaligned search and emergence timing, and dispersion from the study site.

A study on the smaller *L. archeyi* (Cree 1989) and studies on separate populations of *L. hamiltoni* on Stephen's Island and on Maud Island (Newman 1990), found moisture-related factors (i.e. precipitation and RH) to have a significant effect on frog emergence and therefore capture rates. Precipitation and relative humidity were not found to be significant in this study (albeit RH approached significance). A drought declared in March 2013 may have impacted smaller individuals as they are more susceptible to cutaneous water loss due to surface area to volume ratios. Peak months for the drought in Wellington were February and March (National Institute of Water and Atmospheric Research 2013) with only mean monthly rainfall of 2.36 ± 1.78 mm and 2.92 ± 1.97 mm, respectively. There were only 21 recaptures during March (the smallest being a frog with a SVL of 35.8 mm), flanked by 53 in February and 39 in April. It is possible that rainfall could have had more of a significant effect on emergence, but with rainfall only occurring on five out of 44 capture occasions, perhaps there were too few rainy nights to show a statistical significance. Frogs captured during the drought were active and did not show signs of obvious desiccation.

This study supports the findings from Newman (1990) where emergence of *L. hamiltoni* adults on Maud Island was significantly correlated with temperature. Newman credited the dense Maud Island vegetation as protection against drought conditions, whereas on Stephen's Island the 'frog bank' then lacked forest protection, leaving it more exposed to the elements. The Zealandia release site habitat was protected by an intact forest canopy but did not have a well-developed understorey. However, its locality within the valley is sheltered from early morning sun with rocks covering approximately 30% of the 187.5 m² site, providing retreat sites, facilitating

soil moisture retention and mitigating dehydration risks.

The mean BCI of Phase II frogs at the conclusion of this study was higher than the mean BCI recorded at the time of capture on Maud Island, similar to the increase in BCI observed following a previous translocation (Bell et al. 2004a). The increase may be due to variation in water balance (e.g. increased cutaneous water retention; Bell et al. 2004a), particularly as collection on Maud Island occurred during a dry week. However, there was also likely a release of resource competition from habitat that was possibly at carrying capacity (Tocher & Pledger 2005; Bell & Pledger 2010). Caution does need to be taken when interpreting BCI. Snout vent length upon initial capture was used for all calculations, and growth of and/or muscle tension variation during SVL measurement may also be contributing factors for the increase in BCI. This said, the fluctuation of BCI from period four in February until the end of the study compares to the mean BCI of the founding population at Boat Bay 20 years post translocation (Bell et al. 2004a), suggesting the frogs at Zealandia were generally in good condition during the 9 months of monitoring.

Mice did not appear to have a detrimental impact on BCI through competition but further work is required to understand this dynamic, particularly where mice are not managed to the degree they are at Zealandia. While mice have been found to alter the composition, relative abundance, and size distributions of invertebrate fauna (Angel et al. 2009; Watts et al. 2022), and there is a likely overlap of diets: *L. hamiltoni*: Acari, Coleoptera, Diptera, Hymenoptera and Araneae (Kane 1980); and *M. musculus*: Araneae, Lepidoptera, Coleoptera and Diptera (Miller & Webb 2001; Ochoa 2004). However, competition between house mice and *L. hamiltoni* was not apparent during this study.

Further understanding about the relationship between *L. hamiltoni* and mice is needed to determine the relative abundance of mice required to sustain the long-term survival and condition of translocated individuals. Consideration also needs to be given to how the required relative abundance of mice is best achieved. During both phases of this study, Zealandia deployed Brodifacoum™ annually to ground-based bait stations located every 25 m throughout the sanctuary. Invertebrates (*L. hamiltoni* prey) may ingest Brodifacoum™ bait; however, invertebrate bioaccumulation is not understood (Fisher 2009). And, while primary or secondary poisoning of amphibians has not been recorded to date (Hoare & Hare 2006), further work is required to discern whether Brodifacoum™ has a possible negative impact on the long-term translocation success of *L. hamiltoni*.

We recommend this study be taken into consideration for future studies and adaptive management of *L. hamiltoni* in Zealandia, especially given the 500-year goal of the sanctuary where wildlife roam free.

Dedication

This article is dedicated to Phillip J Bishop. His passion, dedication, and inquisitiveness for our amphibian taonga was truly inspirational. The contributions he made to amphibian conservation are in our view, unparalleled.

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Author contributions: BB provided supervision of this research and conceptualised the idea for this paper. Phase 1 investigation was undertaken by KL and Phase 2 completed by TK. TK conducted the formal analysis and provided the original draft of this manuscript. All authors contributed to the review and editing.

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