



RESEARCH

Responses at the source and release site following an inter-island translocation of *Leiopelma hamiltoni*

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Abstract: The use of translocations for conservation management has increased in frequency over recent decades. Though many early translocations were carried out as one-off management exercises, the need to test release strategies and gain knowledge in order to improve future reintroductions has been recognised. This study examined both the movements and survival of 101 *Leiopelma hamiltoni* (Anura: Leiopelmatidae) translocated to Long Island, New Zealand, and the response of the source population on Te Pākeka/Maud Island to the removal of a discrete subset of frogs. An experimental approach was taken to test whether familiarity would improve anchoring to the site and discourage homing and dispersal post translocation. Frogs translocated with their neighbours did not stay with those individuals and those that were released in a random pattern did not move towards their former Maud Island neighbours. While initial movements were significantly oriented to the bearing of Maud Island, after several months this had changed to indicate that the frogs moved in a downhill direction. Capture-recapture abundance estimates suggest a decline in the population of translocated frogs during the 46 months post-release and follow up surveys 10–13 years post-release confirm that this translocation failed. Capture-recapture abundance estimates suggest that the 240 m² grid emptied of frogs (i.e. the source population) took one year to return to pre-translocation densities. There is little doubt that translocations will continue to be an important tool for the conservation management of leiopelmatid frogs in New Zealand and for amphibians worldwide. However, a commitment to post-release monitoring, use of methods that allow for causes of failure to be assessed, and testing release strategies is imperative to informing methods and improving the success rates of future translocations.

Keywords: familiarity, *Leiopelma*, movement, neighbour, recolonisation, reintroduction, source population, translocation

Introduction

The success of translocations as a management tool for endangered herpetofauna has been a highly debated topic (Burke 1991; Dodd & Seigel 1991; Seigel & Dodd 2002; Trenham & Marsh 2002; Germano & Bishop 2009; Miller et al. 2014; Germano et al. 2015; Sullivan et al. 2015; Harding et al. 2016). Despite this, translocations have continued and are often necessary for the survival of threatened herpetofauna. This is especially true in New Zealand where introduced mammalian predators are present throughout the mainland, leading to the decline of numerous species. New Zealand's endemic amphibian fauna include five extinct and three extant leiopelmatid frogs, the latter of which are all threatened with extinction (Burns et al. 2018; Easton et al. 2021). Management of these species has faced many difficulties, but availability of offshore islands and sanctuaries free from invasive mammalian predators have made translocations a viable conservation option for at least one of the three extant species. Including the

release reported here, there have been nine translocations of leiopelmatid frogs with varying levels of success (Bell 1985, 2010; Lukis 2009; Bell et al. 2010; Beauchamp et al. 2013; Cisternas et al. 2021; Wren et al. 2023).

The use of translocations for management and mitigation has increased over the past decade (Seddon et al. 2007; Miller et al. 2014). As these techniques become more commonplace, it is no longer feasible to treat each case as an isolated trial. To improve the effectiveness of translocations for herpetofauna, techniques being used and the responses of the animals being translocated need to be rigorously tested. This can be done in an experimental framework such as described here or in the translocation of frogs to Zealandia (Lukis 2009), or within a structured and active adapted management framework used overseas and recommended by the 2007 Amphibian Conservation Action Plan (Griffiths et al. 2007; Canessa et al. 2019).

Leiopelma hamiltoni, Hamilton's frog, is a small terrestrial sedentary frog species, with home ranges of 0.5–25 m²

(Webster 2004; Bell 2010). Although relatively abundant, prior to recent translocations *L. hamiltoni* was restricted to a 15 ha patch of remnant forest on Te Pākeka/Maud Island, Pelorus Sound, and a 300 m² rock pile near the summit of Takapourewa/Stephens Island (Newman 1990; Tocher & Brown 2004). Maud Island lies less than 1 km from mainland New Zealand, a traversable distance for predatory flightless birds (weka, *Gallirallus australis*) and invasive predators such as stoats (*Mustela erminea*) and rats (*Rattus spp.*) (Clout & Russell 2006; Gaze & Cash 2007). These islands are also vulnerable to fire, particularly in summer. To offset the risk of having only two range restricted populations, the Department of Conservation (DOC) prioritised the translocation of *L. hamiltoni* to other predator-free islands in the Marlborough Sounds (Bishop et al. 2013).

There have been six translocations of *L. hamiltoni* with two intra-island and four inter-island releases (Wren et al. 2023). These have had varying levels of success. Homing and dispersal from a release site is one of the main reasons for failure of herpetofauna translocations globally (Germano & Bishop 2009). In at least one intra-island *L. hamiltoni* translocation, homing was also an issue with at least two of twelve translocated frogs returning to their capture location (Tocher & Brown 2004). Additionally in this same release, seven of the twelve frogs potentially moved away from the release site and were not recorded for more than 19 months after release (M. Tocher, pers. comm.).

Several mammalian and avian studies have investigated the impact of translocating familiar individuals together to improve post-release survival and establishment. The results have been mixed, with increases in anchoring, reproduction and/or survival for some species (Shier 2006; Shier & Swaisgood 2012) and no impact for others (Armstrong 1995; Armstrong & Craig 1995; Anstee & Armstrong 2001; Franks et al. 2020; Mitchell et al. 2021). As *L. hamiltoni* are attracted to the scents of neighbouring individuals (Lee & Waldman 2002; Waldman & Bishop 2004), it was hypothesised that translocation with neighbours might increase survival and anchoring to the release site, thereby reducing the dispersal/homing instincts for Leiopelmatid frogs. Furthermore, during translocations it is necessary to consider the potential negative impacts of removing individuals from a source population (IUCN/SSC 2013). Removal of individuals for translocation may cause changes to population size, density and demographics at the source population, as well as genetic and behavioural effects (Tocher et al. 2006; Bain & French 2009; Pacioni et al. 2019; Hogg et al. 2020; Mitchell et al. 2021).

The aims of this study were to look at the outcome and movements of *L. hamiltoni* in both the newly translocated Long Island population and the source population on Maud Island following removal of c. 100 frogs. Our goals were to: (1) determine whether the translocation to Long Island was a success in the short-term (up to eight months post release) and long-term (two to thirteen years post release), (2) determine whether release with familiar individuals would alter the movements or survival of frogs following translocation, and (3) measure how long it would take this sedentary species to recolonise a source plot emptied of frogs for translocation.

Methods

Study sites

The source population for the translocation came from a 12 ×

20 m plot in the old growth forest remnant on Te Pākeka/Maud Island, Pelorus Sound, New Zealand (Fig. 1). The plot was located on the lower slopes, approximately 100 m above sea level on the eastern side of the remnant forest. Large rock piles cover the forest floor, creating the preferred microhabitat of *L. hamiltoni*. Potential predators at the source include morepork (*Ninox novaeseelandiae*), kōtare/kingfisher (*Todiramphus sanctus*), and weka (although weka numbers are controlled on Maud Island for the benefit of other native species).

The release site for translocated frogs was a 10 × 12 m area on the western side of Long Island, Queen Charlotte Sound, New Zealand (Fig. 1). This site is steep with boulder piles resembling those on the Maud Island and a large area of suitable rocky habitat extending directly uphill of the release location. It is in a gully that allows for high moisture levels. Potential predators at this site include morepork, kōtare/kingfisher, weka, and little spotted kiwi (*Apteryx owenii*). A boardwalk was constructed prior to release on Long Island to allow for monitoring with minimal environmental disturbance.

Collection of frogs from the source population on Te Pākeka/Maud Island

Between 27 and 30 June 2005, 98 frogs were collected from the source plot on Maud Island. Attempts were made to remove all the frogs from this plot. As these frogs are nocturnal, searches for emergent frogs were conducted at night. During the day, rocks or any other obstacle that could act as a retreat site,

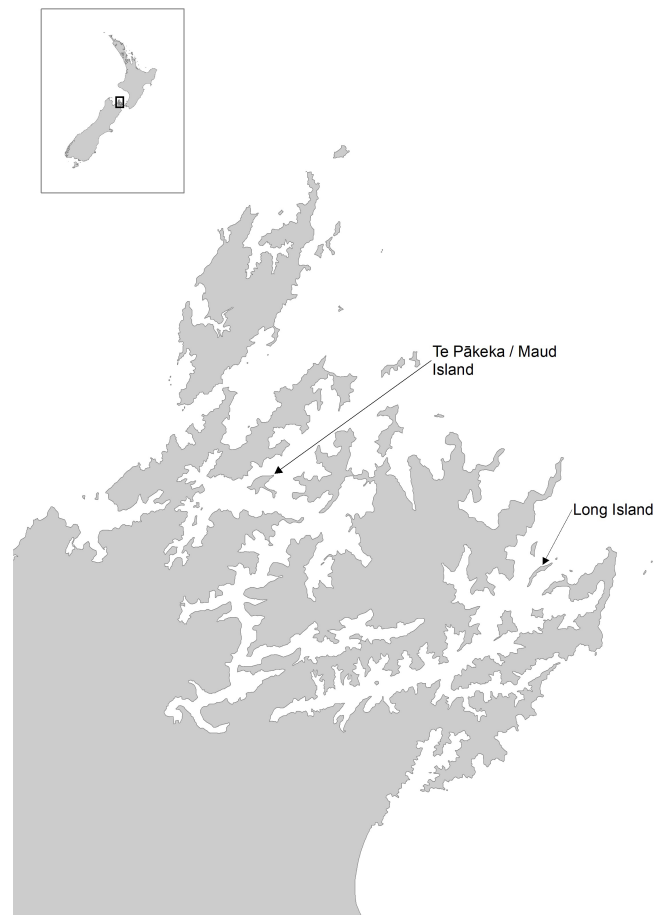


Figure 1. Te Pākeka/Maud Island and Long Island in the Marlborough Sounds, New Zealand.

were shifted until soil and roots were encountered to capture as many individuals as possible, including those who had not emerged, and to fully empty the plot. All rocks were returned to their original positions where possible. An additional three frogs were found elsewhere on the island and translocated along with the 98 frogs. The original location of each frog was mapped to determine the spatial distribution within the source plot and to indicate proximity to neighbouring frogs.

On capture, each frog was placed in a numbered plastic container with a damp paper towel. Frogs were weighed with an electronic balance (Ohaus Scout Pro), measured for snout-vent length (SVL) using callipers, and photographed to enable individual identification. Frogs were stored in plastic containers in polystyrene boxes where the temperature was kept between 10–16°C for 1–5 days until their release on Long Island.

On the first rainy night following the removal, the plot was checked to ensure that all frogs had been cleared. Only three frogs were found within the plot and four in the surrounding area suggesting that most resident frogs had been removed from the plot. The source plot was then divided into eight 6 × 5 m quadrats to enable easy comparison of the spacing and density of original resident frogs to those that recolonised the site.

Translocation release on Long Island

On 1–2 July 2005, frogs that were collected from the source population were released on Long Island. The release site was divided into 30 2 × 2 m squares. Groups of frogs (2–10 individuals per group; mean = 4) were released at the centre of each square. To test the impact of familiarity on fidelity to the release site, the frogs were separated into two experimental groups: one was released with neighbours (animals found 0.0–1.0 m of one another) from the source population and the second was randomly assigned a square. Groups most often contained male and female size classes; individuals of neighbour groups were determined by proximity at the source site. The random group ($n = 53$) was distributed across the northeast side of the grid in squares that were chosen randomly by a computer. The non-random group ($n = 48$) was distributed throughout the southwest half of the grid. For this subset of frogs, frogs were released keeping neighbouring groups collected from Maud Island together.

Translocated population monitoring

Following the translocation four monitoring trips were carried out at Long Island in 2–8 July 2005, 24 February–2 March 2006, 24–26 September 2007, and 27 April–4 May 2009. All emerged frogs were caught by hand, measured for SVL, weighed, photographed, and returned to their point of capture. Individual frogs were identified from photographs using long-term natural markings on the skin and scars. Encounter histories were determined for each frog released for each of the monitoring periods. The release site was also surveyed on 8–12 October 2015, 25–31 July 2016 and 20–26 September 2018, however photographs were not collected of all individuals and some frogs remained unidentified; therefore these visits could not be used in the capture-recapture analysis.

Movements following translocation

Twenty-five randomly selected frogs were tracked on the night of release using non-toxic fluorescent powder (Radiant Color Ltd., R-105 Series). This method provides detailed paths with little effect on the animal (Eggert 2002; Rittenhouse et al. 2006; Ramirez et al. 2017). Each frog was placed in a Petri

dish containing the powder and given a slight shake to stick the powder to their feet. The Petri dish was opened and left on a rock so that the frogs could move when they were ready. The frogs were left for 30 minutes after which their movements were tracked with a UV light. If a frog was still on the ground surface, another 30 minutes was allowed before checking the tracks. Paths were followed until the frogs disappeared under rocks or the powder track dissipated. The detailed path taken by each frog was mapped and all distances and bearings were measured. In addition, straight-line distances and bearings from the release point to the finish location were measured.

Longer-term movements were monitored at the Long Island release site between 3–8 July 2005 (one-week post-translocation) and 24 February–2 March 2006 (8 months post-translocation). During each monitoring trip, nocturnal searches for emergent frogs were carried out at the release site and a roughly 10 m surrounding area. Frog locations were marked with a numbered peg and mapped the following day. The distance and compass bearing from each individual's original release site was determined. Frogs that moved less than 1 m were excluded from the analysis of bearings, as this often centred on the same rock and was not considered a directional movement.

Monitoring recolonisation at the source site

The original 12 × 20 m source plot on Maud Island was surveyed for recolonising frogs four times throughout the year following removal. Visual searches were carried out for 2–4 person-hours per night for 5–6 nights during the following periods: 17 October–8 November 2005, 3–15 December 2005, 16–25 January 2006, and 8–13 June 2006. Recolonising frogs were measured (SVL and weight) and photographed for individual identification. Locations were marked with a numbered peg and mapped the following day.

Data analyses

Population Monitoring

Photographic capture-recapture data were analysed using the Cormack-Jolly-Seber model (CJS) in program MARK (v7.1). The CJS model is an open population model allowing for births, deaths and migration (Lebreton et al. 1992) and was used to estimate survival (ϕ) and capture probabilities (p). Four models were considered for the population of frogs translocated to the Long Island plot (Table 1) and for the population that recolonised the source plot on Maud Island.

Due to uncertainty in model selection, we used model averaged parameter estimates according to model weight. Akaike's Information Criteria (AIC) was used to select the most appropriate model (Burnham & Anderson 2007). Abundance estimates (N_j) were obtained using:

$$N_j = n_j / p_j \quad (1)$$

where n_j is the number of captured individuals and p_j is the estimated capture probability in period j (Seber 1982). Log-normal 95% confidence intervals (Burnham et al. 1987) give a lower limit of $N_L = N/r$, and an upper limit of $N_U = Nr$. For 95% confidence intervals, r is calculated as:

$$r = \exp \left[1.96 \sqrt{\ln (1 + CV(N^2))} \right] \quad (2)$$

Movement Analysis

Statistical analysis of movement was done in JMP (version

Table 1. Model selection table for Cormack-Jolly-Seber capture-recapture analysis at the release site.

Model	AICc	Delta AIC	AIC weight	Model likelihood	Parameters	Deviance
$\phi(\cdot)p(t)$	386.56	0.00	0.62	1.00	5	8.67
$\phi(\cdot)p(\cdot)$	389.06	2.51	0.18	0.29	2	17.47
$\phi(t)p(t)^*$	389.56	3.01	0.14	0.22	7	7.36
$\phi(t)p(\cdot)$	390.95	4.40	0.10	0.11	5	13.07

*One parameter inestimable

5.0.1a, SAS Institute Inc.) for distance travelled and Oriana (version 2.0, Kovach Computing Services) for directional movement. Body condition indices were calculated as: log weight/log SVL (Dewhurst 2003). Two tailed t -tests were used to compare the sizes and body conditions of frogs invading the plot with original residents and the distances travelled by randomly and non-randomly placed frogs on Long Island. An ANOVA was used to compare the body condition of frogs between capture periods. Chi-square tests were used to compare the proportions of recolonising and original frogs in each Maud Island quadrat each session.

For post-translocation movement data, Rayleigh's test for uniformity was used to determine whether frog path bearings were uniformly distributed (Zar 1999). Due to the departure from a von Mises distribution, the non-parametric Mardia-Watson-Wheeler test was used to determine differences between treatment groups (Zar 1999). Circular-linear correlation coefficients were used to look at correlations between bearings taken and path straightness and distance. Significance levels were set at $\alpha = 0.05$.

Results

Population monitoring of translocated frogs

Since the release of frogs ($n = 101$) on Long Island in June 2005, capture-recapture abundance estimates suggest a population decline (Fig. 2). On the first sampling occasion (a week post-translocation), there were 32 captures of 31 individuals; on the second trip (eight months post-release) 47 captures of 33

frogs; during the third sampling period (> 2 years post-release) 9 captures of 8 individuals and on the final trip (> 4 years post-release) 13 captures of 11 individuals. Additional surveys not included in the capture-recapture model gave the following results: zero captures in Oct 2015 (ten years post-release), ten captures of eight individuals in July 2016 (11 years post-release) and three captures of three individuals in September 2018 (13 years post-release). No new recruits were found at any point. While some individuals captured in 2016 and 2018 were not identified, their large SVL (all > 43.5 mm) means it is highly unlikely that these individuals were previously unrecorded recruits (Bell & Pledger 2023).

There was a low resighting rate during the first monitoring trip which resulted in large confidence intervals surrounding the abundance estimate (Fig. 2). Precision improved with successive surveys and the abundance estimates in the third and fourth monitoring periods show a population decline as confidence intervals do not overlap with those during the first monitoring period (Fig. 2). Of the CJS models (Table 1), $\phi(\cdot)p(t)$, had the most support suggesting that survival was constant and that capture probability varied over the monitoring periods. The most parsimonious CJS model has a survival estimate of 0.737, but because of model uncertainty average survival estimates were between 0.685 and 0.751 (Table 2).

During the September 2007 trip, one frog was caught with severe head injuries which included a portion of its jaw missing and an injured eye (Fig. 3). Although the cause is not known, this is consistent with injuries likely to occur due to a predation event. Injuries have been seen in the Stephens Island/Takapourewa and Maud Island populations, so this may also be due to rock movement or other natural causes.

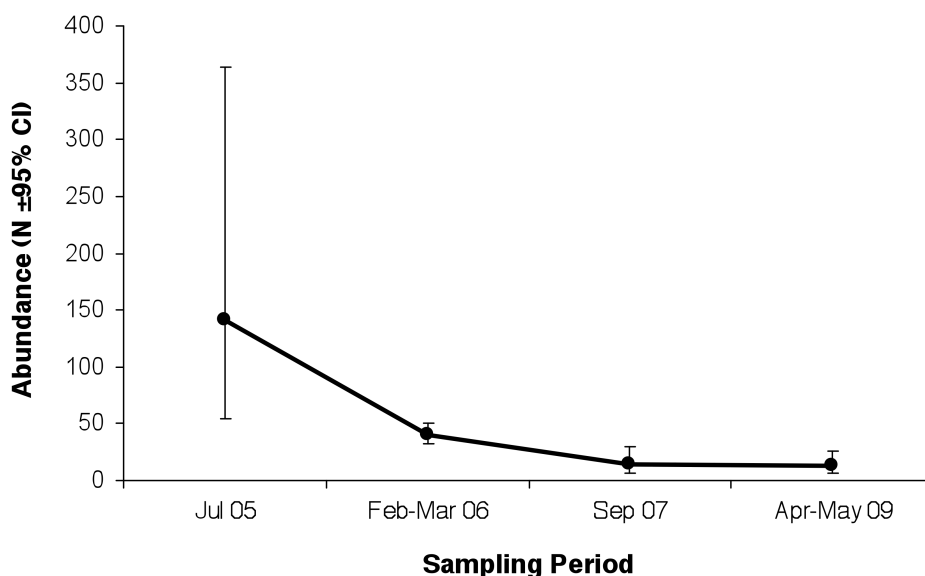


Figure 2. Cormack-Jolly-Seber estimate of abundance for *Leiopelma hamiltoni* on Long Island after translocation in June 2005, with 95% confidence intervals.

Table 2. Parameter estimates for survival (φ) and capture (p) of released individuals after model averaging for four different sampling periods of *Leiopelma hamiltoni* translocated to Long Island.

Sampling period	Parameter	Survival estimate	95% CIs	Parameter	Capture estimate	95% CIs
July 2005	φ_1	0.685	0.579–0.987	p_1	0.314	0.231–0.411
February–March 2006	φ_2	0.745	0.347–0.941	p_2	0.382	0.240–0.547
September 2007	φ_3	0.714	0.365–0.915	p_3	0.206	0.063–0.497
April–May 2009	φ_4	0.751	0.365–0.941	p_4	0.343	0.052–0.832

**Figure 3.** Photograph of a translocated frog showing severe injuries to the face, including damage to the eye and a missing portion of the top jaw, possibly due to a predation attempt.**Movements of translocated frogs immediately after release**

The compass bearings travelled by frogs on Long Island on the night of release were not randomly distributed ($n = 25$, $z = 5.451$, $p = 0.003$). The mean bearing travelled was 309.3° ($SE = 16.3^\circ$). The direction of movement was not correlated with the total distance moved ($r = 0.105$, $p = 0.784$) nor with straight-line distances moved ($r = 0.147$, $p = 0.62$). However, bearings were significantly correlated with the path straightness indices ($r = 0.615$, $p < 0.001$).

Frogs released with unfamiliar individuals travelled significantly further in terms of total distance moved than

frogs released with their neighbours ($t = -2.24$, d.f. = 12, $p = 0.045$). When analysing the straight-line distances moved, there was a non-significant difference in distance travelled between randomly and non-randomly placed frogs ($t = -2.00$, d.f. = 13, $p = 0.066$).

Movements of translocated frogs one week and eight months post-release

During the week following the release on Long Island, the distances moved ranged from 17 cm to 1171 cm from the point of release with a mean of 297.1 cm ($SE = 48.2$, $n = 31$).

The mean bearing travelled was 232.8° (SE = 16.8, $n = 25$), and the bearings were not randomly distributed ($z = 5.159$, $p = 0.005$). The direction of travel was significantly correlated with distance moved, with frogs that moved in a southerly direction moving furthest ($r = 0.381$, $p = 0.04$).

Eight months after the translocation to Long Island, the distance moved from initial release sites varied from 28 cm to 1552 cm with a median of 429.3 cm and a mean of 502 cm (SE = 62.6, $n = 33$). The bearings between the release site and point of capture were not uniformly distributed ($z = 4.948$, $p = 0.006$) and the mean was 169.2° (SE = 17.4, $n = 30$). The direction of travel was not correlated with distance moved ($r = 0.293$, $p = 0.097$).

There was no significant difference in the distance moved by randomly and non-randomly placed individuals either one week following translocation ($t = 0.28$, d.f. = 27, $p = 0.784$) or eight months post translocation ($t = -1.18$, d.f. = 30, $p = 0.249$). There was also no significant difference in the bearings taken by randomly placed and non-randomly placed individuals ($w = 0.812$, $p = 0.666$) immediately following release. Spatial patterns on Long Island eight months following translocation did not resemble those originally found on Maud Island. Groups that were relocated with neighbours did not stay with those individuals. Similarly, those that were released in a random pattern did not search out or move towards their Maud Island neighbours.

Recolonisation of the emptied source plot

Ninety-eight live resident frogs were removed from the 240 m² plot in June 2005. The frogs were found both on the surface (12.2%) and under rocks (87.8%). Measurements for depth below the surface were taken for 16 of the frogs found under rocks. These ranged from 10 to 80 cm below the surface, with a median of 35 cm. Of the 98 resident frogs removed from the plot, 90 (91.8%) were adults and 8 (8.2%) were subadults.

During the year following the removal of resident frogs there were 163 capture events for 90 recolonising frogs. Of these 90 individuals, 80 (88.9%) were adults and 10 (11.1%) were subadults. There was no significant difference in SVLs between the resident and recolonising frogs ($t = -1.092$, d.f. = 186, $p = 0.277$), though resident frogs were significantly heavier ($t = -1.984$, d.f. = 184, $p = 0.049$). When divided into age classes, the SVL did not differ significantly for recolonising and resident subadults ($t = 1.763$, d.f. = 16, $p = 0.097$) nor weight ($t = 1.445$, d.f. = 16, $p = 0.168$). However, when looking solely at adults, the recolonising frogs were both significantly smaller in SVL ($t = -1.996$, d.f. = 168, $p = 0.048$) and weight ($t = -2.589$, d.f. = 166, $p = 0.011$) than resident frogs.

The resident frogs showed a bimodal distribution in SVL with two peaks that likely represents the sexual size dimorphism of the species (females are larger than males). The recolonising frogs did not show the same bimodal distribution and were missing many of the larger female frogs.

There were no significant differences between the body conditions of resident and recolonising subadults ($t = 1.875$, d.f. = 16, $p = 0.0791$). However, recolonising adults had significantly lower body condition than resident adults ($t = -2.251$, d.f. = 166, $p = 0.0257$).

The number of captures differed between monitoring periods with 15 captures in October 2005, 62 in December 2005, 49 in January 2006, and 38 in June 2006. When analysing measurements of recolonising frogs by monitoring period, there were no significant differences in SVL ($F = 1.8160$, d.f. = 3, $p = 0.1503$) or weight ($F = 0.4232$, d.f. = 3, $p = 0.7368$).

When comparing the relative percentage of recolonising individuals found in each quadrat to the original resident frogs (i.e. source population), there were significant differences between the original spatial distribution and the monitoring periods in October ($\chi^2 = 17.3$, d.f. = 7, $p < 0.05$), December ($\chi^2 = 28.2$, d.f. = 7, $p < 0.05$), and January ($\chi^2 = 30.3$, d.f. = 7, $p < 0.05$). However, by June 2006 there was no significant difference between the relative percentage of recolonising frogs in each quadrat and the original spatial distribution of resident frogs ($\chi^2 = 7.1$, d.f. = 7, $p > 0.10$).

Ninety individuals were captured in the plot over the year following the removal of frogs for translocation. Based on the capture-recapture data, the most parsimonious Cormack-Jolly-Seber model determined by the lowest AIC_c was one that assumed constant survival rate and time-dependent capture probability (Table 3).

Based on the chosen model, population estimates were determined for the last three sampling periods. The population estimates are as follows: 66 (SE = 0.145, 95% CI = 49–124) for December 2005, 118 (SE = 0.070, 95% CI = 83–182) for January 2006, and 161 (SE = 0.048, 95% CI = 106–258) for January 2006. These estimates indicate that frog abundance increased within the plot during the year, and that consequently the densities of frogs grew from 28 frogs 100 m⁻² to 67 frogs 100 m⁻².

Discussion

Population monitoring of translocated frogs

The survival rate estimate was relatively low for the frogs translocated to Long Island (0.74 for model specific survival or 0.69–0.75 for model averaged survival). An intra-island translocation of the same species to Boat Bay, Maud Island showed a low survival rate (0.64) for individual frogs immediately post-translocation which increased to 0.97 in subsequent years (Bell et al. 2004). Another *L. hamiltoni* translocation to Motuara Island showed a very low survival rate immediately following release (0.07) followed by an increase to a rate similar to Boat Bay (0.99) (Tocher & Pledger 2005). The survival rate in this study was similar to the initial Boat Bay survival rate, but unlike the Boat Bay and Motuara translocations, the survival rates of frogs on Long Island failed to increase, perhaps suggesting that habitat and environmental conditions were not favourable. No recruitment of *L. hamiltoni* was observed on Long Island in surveys over a 13-year period.

Frogs may have dispersed away from the study site, but even searches greater than 20 m outside the grid failed to locate many individuals. For example, combined results from surveys in 2016 and 2018 found a total of just 10 individuals, none further than 10 m from the release area boundary, despite

Table 3. Cormack-Jolly-Seber models used to estimate abundance from the mark-recapture data from the recolonisation plot on Te Pākeka/Maud Island.

Model	AIC _c	Delta AIC _c	Parameters
$\phi(\cdot)p(t)$	155.53	0.0	4
$\phi(t)p(\cdot)$	157.76	2.23	5
$\phi(t)p(\cdot)$	158.52	2.99	4
$\phi(\cdot)p(\cdot)$	159.71	4.18	2

thorough searches over a wider area. Most frogs found during these two sessions were clustered 1–5 m north-east of the release site, easily visible from the monitoring grid. During the Boat Bay translocation, most frogs stayed close to the release site; the first cohort settled an average of 4.8 m from the release site and the second cohort an average of 8 m (Bell et al. 2004). Though frogs may have travelled outside our search radius on Long Island, it is unlikely the cause of decline. Overall, due to the low survival rate and the lack of reproduction, this translocation was deemed a failure.

Establishing the cause of translocation failure

The success or failure of a translocation is dependent on a myriad of factors. It is often impossible to confirm exactly why a translocation failed, especially over a decade following release. Rigorous investigations of factors intrinsic to the frogs (e.g. animal behaviour, individual health) and extrinsic ecological measurements of habitat quality, microclimate and predation pressure alongside future releases may help to elucidate the causes of failure. It is also possible that several factors could work synergistically to cause a translocation to fail, which taken on their own may not have the same consequences.

Although difficult to confirm with certainty, this translocation may have declined due to poor habitat at the release site. Although suitable rocky habitat existed at and uphill of the translocation release site, the shortage of understory ferns and seedlings and the exposure to wind may have made the location prone to desiccation.

Some translocation sites (e.g. Boat Bay and Motuara) have high quantities of rocky habitat similar to that found on Maud Island. Others, such as Long Island and Nukuwaiata, are much patchier as far as the availability of rock tumbles. At sites such as Zealandia, rocky habitat was enhanced to support newly translocated frogs (Karst et al. 2023). While it may not be entirely essential, when available in abundance, this unique resource may increase translocation success rates through the provision of key microclimate variables such as increased humidity and added protection from predators. In the later surveys (2016 and 2018) captured frogs were clustered in a location just beyond the release grid, where rocks, and therefore the gaps between the rocks, were smaller (an estimated 90% of rocks < 30 cm vs 30% on the release grid) and there was a higher amount of leaf litter (an estimated 80% of the ground with leaf litter coverage vs 15% on the release grid) mostly in the form of tree fern fronds (SW, unpubl. data). The smaller rock gaps and high presence of leaf litter likely provided more humid refugia than on the release grid.

Predatory birds (kiwi and weka) were observed at the Long Island release site and an injured frog was found inside the grid which suggests that predation may have contributed to the translocation failure. Although Leiopelmatid frogs are known to exhibit anti-predator behaviour (Green 1988) and have also evaded predation by captive weka (Beauchamp 1996), the poor habitat at the release site could have reduced the effectiveness of antipredator behaviours. Even moderate predation levels could have large impacts on a small, translocated population such as this.

During the successful Motuara translocation of *L. hamiltoni* (Tocher & Pledger 2005), a kiwi-proof fence was constructed around the release site to aid population establishment by reducing predation pressure. Predation by kiwi and/or mice has also been implicated as the cause of decline for the initial release of *L. hamiltoni* in the Zealandia Wildlife Sanctuary (Lukis 2009). In the case of the Zealandia translocation,

survival was high and breeding occurred within two years for frogs that were released into predator-proof enclosures (Bell 2008); frogs released outside of the enclosure declined to zero over 12 months (Lukis 2009). A later supplemental release of frogs to Zealandia inside the kiwi proof fence has shown initial signs of success (Karst et al. 2023). A fence was erected retrospectively around the small remaining translocated frog population on Long Island in 2019.

Post release movements and the impacts of familiarity

Many anuran species have strong homing tendencies following translocation (Oldham 1967; McVey et al. 1981; Matthews 2003; Germano & Bishop 2009; Arcila-Pérez et al. 2020; Shaykevich et al. 2021). This was previously seen in *L. hamiltoni* during a short distance intra-island translocation on Takapourewa/Stephens Island where two frogs travelled more than 70 m to their original capture location after being moved (Tocher & Brown 2004) and a further seven frogs were not recorded at the release site beyond 19 months post-release (M. Tocher, pers. comm.), so either moved from the release site or suffered post-release mortality. Dispersal from release site and homing are the top reasons for translocation failure for herpetofauna (Germano & Bishop 2009). Translocation with familiar individuals has previously been used successfully as a tool to improve survival and anchor animals to a site in other taxonomic groups (Shier 2006; Shier & Swaisgood 2012).

During this translocation to Long Island, the immediate movements of *L. hamiltoni* were typically short distances to nearby retreats, mostly less than 1 m from the release point. Direction of travel was significantly oriented to 309°, similar to the northwest bearing of Maud Island from Long Island (320°); however, this was not maintained in the long-term.

During the week following release, frog movements were significantly oriented with a mean of 233° and after 8 months post-translocation, this changed to 169°. Longer-term this trend meant that *L. hamiltoni* moved downhill from the release site potentially towards increased moisture levels. Downhill movements were also observed in Leiopelmatid translocations at Boat Bay (Dewhurst 2003) and Pukeokahu (Cisternas et al. 2022). At Boat Bay, this was attributed to better habitat below the release point (Dewhurst 2003). In this translocation, however, assumed better habitat of dense rock piles was located uphill of the release site with less cover downhill. *Leiopelma hamiltoni* may simply tend to move downhill along a slope following translocation. This tendency to move down-slope or downstream after being displaced has been noted for other amphibians (Oldham 1967; Muths et al. 2001) and should be considered in planning future translocations.

On the night of release, randomly released frogs moved significantly further than frogs released with neighbours. *Leiopelma hamiltoni* may be more willing to share retreat sites with known individuals immediately after translocation; however, over longer timeframes, there was no difference in distance travelled or the direction taken by frogs released in either group. The frogs failed to retain or regroup into their original spatial patterns from Maud Island. Familiarity appears to have no long-term impact on the frogs following translocation. Similar results have been found for translocated saddlebacks (*Philesturnus rufusater*; Armstrong & Craig 1995), robins (*Petroica longipes*; Armstrong 1995), hihi (*Notiomystis cincta*; Franks et al. 2020) and western pebble-mound mice (*Pseudomys chapmani*; Anstee & Armstrong 2001), none of which were affected by release with familiar individuals.

Recolonisation of the source site

Despite the sedentary nature and small home ranges of *L. hamiltoni*, the emptied source plot was recolonised within a year to pre-translocation levels and with a similar density and spatial distribution to the original frog population. This suggests that if animals are removed from a healthy population, the vacant habitat will be quickly filled. Connectivity is one of the key factors in site colonisation (Falaschi et al. 2021). The fact that the emptied plot was highly connected to the wider population on all four sides likely increased the speed of recolonisation.

For mammals, two processes of recolonisation have been identified for cleared areas (Ji et al. 2004). Firstly, animals surrounding the area may expand their home range to fill empty niches that have reduced competition for food and cover. The second mechanism is recolonisation by natal dispersal (Ji et al. 2004) where offspring of the animals in the surrounding area move into the vacant habitat. For amphibians, the migration of breeding adults as well as juvenile dispersal and colonisation is well documented (Semlitsch 2008). *Leiopelma hamiltoni* is a relatively sedentary species that does not migrate. In the emptied plot on Maud Island, the proportion of juvenile and adult frogs remained roughly the same in the original resident population and the population of recolonisers. This suggests that natal dispersal was not the driving factor in recolonisation and that it is more likely that surrounding frogs simply increased their home ranges to fill empty niches.

In this study, recolonising adult frogs were significantly smaller in size and had significantly lower body condition than the resident frogs which were removed for translocation. It is possible that if the frog habitat on Maud Island is nearing capacity, a subset of less fit and less competitive frogs may move out to look for empty niches elsewhere. Differences in weather and food availability between years can however not be discounted as a potential reason for differences in body condition between resident and recolonising frogs.

Conclusion

Translocations make up a vital part of conservation work carried out to preserve New Zealand's endemic fauna including leiopelmatid frogs. Unfortunately, in this case, the translocation of frogs from Maud Island to Long Island failed to produce a self-sustaining population. It is important to review the outcomes of translocations, particularly those that fail, so that improvements can be made in the future.

This study was set up to test the impacts of animal behaviour on translocation of Leiopelmatid frogs, in particular homing and attraction to neighbours via chemical communication. It was likely that factors beyond the focus of this study led to the failure of this release. In retrospect, knowledge about wider ecological factors such as habitat quality, microclimate, and native predators would have been useful to determine why this translocation failed. These factors should be considered and measured appropriately for future releases. Perhaps just as importantly, the results of such monitoring must be included in progress reports that are shared with technical experts and decision makers to inform future action. Additionally, as even low to moderate levels of predation can be detrimental to a small release cohort, future releases could consider establishing lower order species prior to the release of higher order predators when using translocations to restore an ecosystem.

Alternatively, a predator-proof fence could be erected around the initial release site so that translocated frogs (or any species lower in the food chain), can establish a stable base population prior to exposure to predation.

Future Leiopelmatid translocations should consider the tendency of frogs to disperse downhill from the release site. Familiarity with neighbouring frogs does not appear to be a factor in post release movement or survival. Despite their sedentary nature, if *L. hamiltoni* are removed from a stable high density source population, frogs are easily and quickly able to recolonise vacant habitat. This ability to readily invade emptied habitat may also have implications for future restoration work where increasing the available habitat may be a low-risk tool for expanding other *Leiopelma* populations that are currently constrained by available space.

Translocations will undoubtedly continue to be an important tool for the conservation management of leiopelmatid frogs in New Zealand and for amphibians worldwide. The simple release of animals into the wild however, does not guarantee success. Rigorous testing of reintroduction strategies is only carried out in a small percentage of translocation and reintroduction studies (Seddon et al. 2007). Robust, well-documented techniques and long-term monitoring will continue to be important as the field of reintroduction biology progresses. It is critical that translocations are approached with forethought, planning, and a commitment to post-release monitoring. By scientifically testing reintroduction strategies, we can gain valuable information to perfect these techniques and increase our probability of success in the future.

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Data availability: There are no publicly available data or code associated with this article.

Author contributions: JG conceptualised the project, and JG, PB, and SW undertook the fieldwork. JG and TW undertook

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