



## REVIEW

## A review of New Zealand native frog translocations: lessons learned and future priorities

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**Abstract:** Translocations are becoming increasingly common although the effectiveness of this conservation tool for amphibians is highly variable. We reviewed ten translocations of *Leiopelma* frogs occurring between 1924 and 2016. Data were gathered on factors which may have influenced translocation outcomes. Results at each location were measured against an established four-step framework for stages of success: survival of individuals, reproduction, population growth, and population viability. Three conservation translocations and two mitigation translocations were considered to have failed, indicated by no or low survival of founders or lack of evidence of reproduction within a reasonable timeframe. Causes of failure include invasive predators at the release site, small founder numbers, homing, and poor habitat quality. The remaining five translocations were considered either successful (meeting all four stages of success), or on the road to success (meeting at least the first two stages of success). Successful translocations included predator control, total release of more than 70 founders, and in some cases adaptive management to address management decisions over time. Our findings emphasise the need for long-term post-release monitoring (> 25 years) to determine translocation success for *K*-selected species. Better, cost-effective, methods for monitoring population growth and population viability are required for *Leiopelma* frogs. Improvements could be made in open access reporting of methods and decision-making, disease risk analysis and stakeholder engagement. Further, improving our knowledge of what makes high quality *Leiopelma* habitat would help to objectively assess potential future translocation sites. Future translocations should consider the impacts of predicted global climate change; assisted migration may be required in the future. Translocations are a risky conservation strategy, so should only be undertaken with good cause, quality planning, and sufficient long-term resources for monitoring and management. Any future translocations for *Leiopelma*, whether motivated by conservation or mitigation, should follow best practice guidelines and use evidence-based decision-making to maximise outcomes.

**Keywords:** conservation, conservation translocation, *Leiopelma*, monitoring, mitigation, reintroduction, translocation success

## Introduction

Translocations have become an increasingly common tool to assist with the restoration of wild populations of threatened species (Seddon et al. 2007; Seddon et al. 2012; Taylor et al. 2017a). Conservation translocations include restoring extirpated populations, expanding a species' historical range, and filling ecological roles (Seddon 2010). The goal is often to establish a new population thereby spreading risk and reducing the likelihood of extinction. Beyond pure conservation motives, translocations are also undertaken to mitigate human-wildlife conflict, primarily to move animals away from a development site in efforts to reduce direct mortality (also known as mitigation translocations or salvage translocations; Germano et al. 2015; Bradley et al. 2020). While the motives may differ, best practice techniques (IUCN/SSC 2013; Linhoff et al. 2021) should be applied in all cases.

Translocation is an important conservation tool in New Zealand (Jones & Merton 2012; Miskelly & Powlesland 2013; Miller et al. 2014; Romijn & Hartley 2016; Jahn et al. 2022). Its success has been due in great part to the fact that the decline of much endemic wildlife has been caused by introduced mammalian species, and because numerous off-shore islands exist which are either predator-free or where eradication efforts are relative straightforward (Armstrong & McLean 1995; Jones & Merton 2012; Parker et al. 2020). Several hundred conservation translocations have been carried out in New Zealand, the majority of which have been for birds (Miskelly & Powlesland 2013) although many herpetofauna and invertebrate translocations have also been performed (Townes & Ferreira 2001; Sherley et al. 2010; Miller et al. 2014; Romijn & Hartley 2016; Townes et al. 2016).

Translocations, for both conservation and mitigation motives, are a high-risk strategy since numerous factors influence whether a species establishes at the release site, including quality of release habitat (Griffith et al. 1989; Osborne & Seddon 2012; Berger-Tal et al. 2020), population and genetic effects of founder number (Fischer & Lindenmayer 2000; Germano & Bishop 2009; Cardoso et al. 2009; Miller et al. 2009; Groombridge et al. 2012; Pacioni et al. 2019), post-release movement (Germano & Bishop 2009; Le Gouar et al. 2012; Bell 2016; McCallen et al. 2018) and stress (Teixeira et al. 2007; Dickens et al. 2010; Parker et al. 2012). The effectiveness of translocations as a conservation tool for herpetofauna has undergone much discussion (Burke 1991; Dodd & Seigel 1991; Reinert 1991; Seigel & Dodd 2002; Trenham & Marsh 2002; Germano & Bishop 2009; Ewen et al. 2014; Miller et al. 2014; Harding et al. 2016). Much of this debate is likely due to the mix of conservation and mitigation translocations of herpetofauna, where mitigation translocations often fail to implement established best practice techniques (Germano et al. 2015; Sullivan et al. 2015; Romijn & Hartley 2016). Further, the misconception that all amphibians are r-selected with fast generation times and large numbers of offspring may have erroneously led to the presumption that they are well-suited to conservation by translocation (Bloxam & Tonge 1995; Tapley et al. 2015). However, reviews have suggested that well-planned translocations can be as successful for herpetofauna as they are for birds and mammals (Germano & Bishop 2009). Translocations have been applied to all extant New Zealand native frog species (Bell et al. 2010; Bishop et al. 2013; Bell & Bishop 2018).

The Leiopelmatidae, an endemic family and the only amphibians native to New Zealand, are high priorities

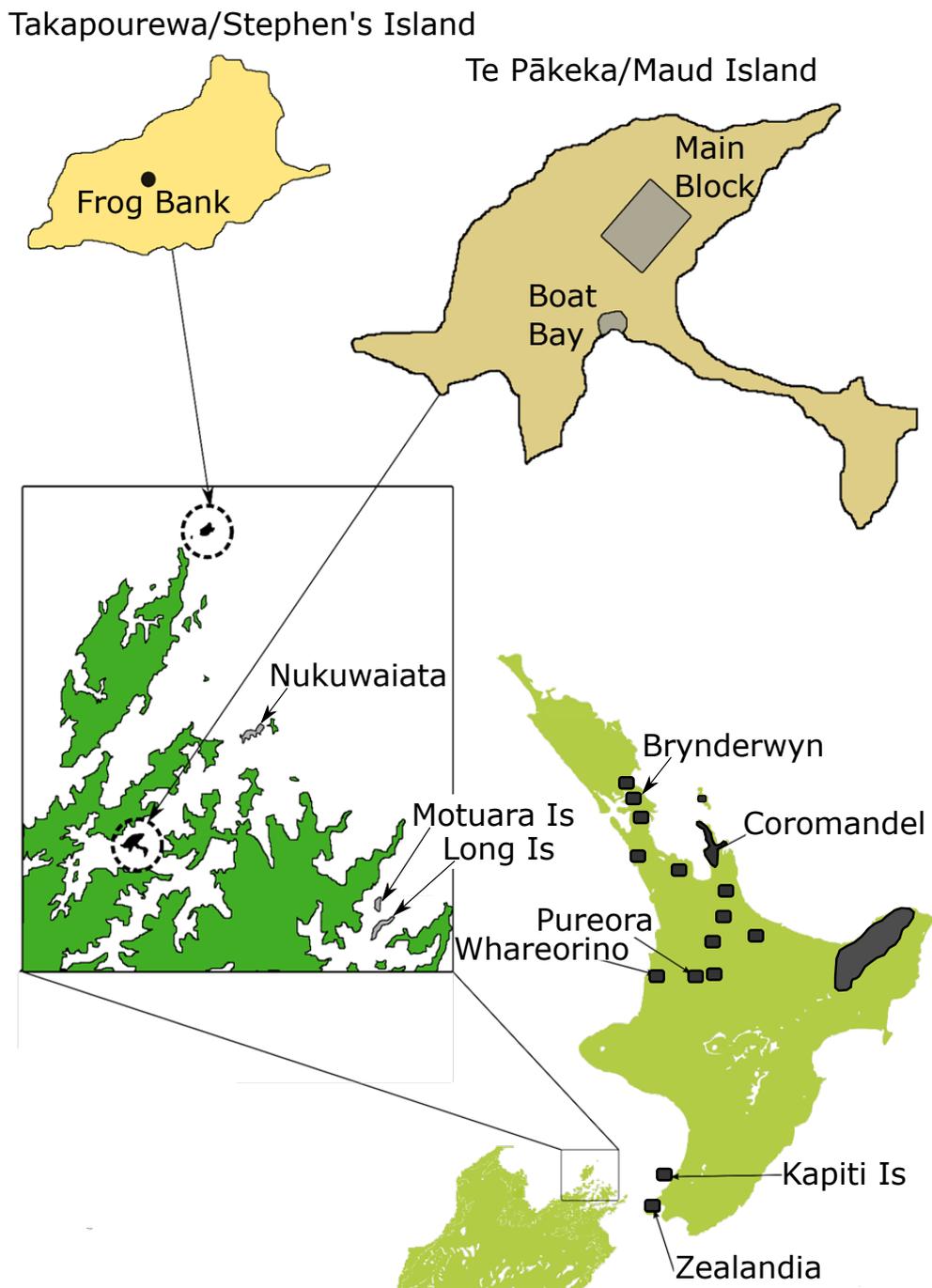
for conservation attention. There are three extant species: Archey's frog (*Leiopelma archeyi*) and Hochstetter's frog (*L. hochstetteri*), both classified as 'At risk – Declining', and Hamilton's frog (*L. hamiltoni*) which is classified as 'Threatened – Nationally Vulnerable' by the New Zealand Threat Classification System (Burns et al. 2018; Easton 2018; Easton et al. 2022).

*Leiopelma* spp. can be split into two groups according to their habitat preferences; *L. hochstetteri* is found closely associated with streams and is the only species in which the endotrophic larvae hatch into water rivulets at the breeding site, while the other two terrestrial species are independent of surface water, found in moist terrestrial sites, and exhibit direct development (Bell 1985a; Bishop et al. 2013; Bell & Bishop 2018). Adults occupy small home-ranges of a few square metres (Bell & Moore 2015; Ramírez 2017). Leiopelmatid frog life history sits towards the *K*-end of the *r-K* continuum (Pianka 1970); they show great longevity, demonstrated by mark-recapture studies that have recaptured many individuals over 40 years of age (Bell & Bishop 2018; Bell & Pledger 2023), and a low fecundity: the largest recorded *L. hochstetteri* clutch being 22 eggs (Bell 1985a).

Prior to human settlement, *Leiopelma* frogs ranged over a large portion of New Zealand; *Leiopelma* subfossils have been found from Kaitaia in Northland and as far south as Te Anau in Fiordland (Bell et al. 1985; Worthy 1987; Easton et al. 2018). Significant declines, range contractions and extinctions have been caused by invasive mammals and habitat modification (Bishop et al. 2013; Bell & Bishop 2018). Today the extant leiopelmatid frogs have fragmented ranges and restricted populations (Fig. 1). *Leiopelma hamiltoni* has survived in just two small populations on predator free off-shore islands: Takapourewa/Stephens Island and Te Pākeka/Maud Island (Bell & Pledger 2010; Bishop et al. 2013). *Leiopelma archeyi* is found in two disparate locations: the Coromandel Peninsula and Whareorino Conservation Area (Thurley & Bell 1994). *Leiopelma hochstetteri* is found in fragmented populations across the northern North Island and Aotea/Great Barrier Island. Both *L. archeyi* and *L. hochstetteri* face predation and/or habitat modification threats throughout most of their range (Bell et al. 1985; Bishop et al. 2013; Egeter et al. 2015). There are no known extant *Leiopelma* populations on the mainland South Island.

The reduction of formerly wide-ranging species to small, isolated subpopulations adds further potential pressures since the viability of such populations is often reduced due to factors including low genetic variation (Easton 2018), inbreeding, disrupted social systems, and increased vulnerability to localised catastrophes (e.g. disease outbreaks, predator incursions, fire; Lacy 2000). Additional potential threats have emerged including the chytrid fungus *Batrachochytrium dendrobatidis* (Bd), which may have contributed to significant population declines in *L. archeyi* (Bell et al. 2004a). Habitat destruction also continues to be a threat, especially for *L. hochstetteri* evolutionarily significant units (ESUs) which overlap with human populations and forestry. Further climate change will likely have a negative impact on *Leiopelma* and need to be considered for future conservation management, including identifying appropriate release sites for future translocations (Butt et al. 2021; Jarvie et al. 2021; Germano et al. 2023a).

Conservation management for *Leiopelma* has included invasive species management, forest restoration, captive management, advocacy, disease surveillance, and biosecurity



**Figure 1.** Natural distributions and translocation sites of *Leiopelma* frogs. Translocation source and release sites are labelled. Refer to Table 2 for which sites involved translocation of which species. Adapted from Easton (2018).

protocols to reduce disease transmission (Bishop et al. 2013). However, translocations have become a key tool in combatting the potential disastrous effects of environmental stochasticity especially where populations are limited to small islands or fragmented sites, and providing assurance in the face of an imminent threat e.g. disease (Lacy 2000; Bishop et al. 2013). However, as *K*-selected species, *Leiopelma* life history traits do not easily promote establishment at new sites since population growth is slow.

Where translocations have been implemented for leiopelmatid frogs, in most cases the primary objective has been to establish an additional subpopulation, thus reducing the

extinction risks associated with small, fragmented populations (Bell et al. 2010; Sherley et al. 2010). Other motivations have included disease risk reduction, ecological restoration, and mitigation for habitat destruction caused by human development (Parrish 2004; Beauchamp et al. 2005; Lukis 2009; Sherley et al. 2010; Cisternas 2019). Despite translocations being one of the key tools used for conservation of New Zealand frogs, and having been applied to all species, there has not been a comprehensive review of all *Leiopelma* translocations, with analysis of both techniques and results. The aim of this article is to review all *Leiopelma* translocations, outline the methods used, and assess outcomes. We then discuss factors that led

to success or failure and provide recommendations for future *Leiopelma* translocations.

## Methods

### Terminology

We follow the definitions set out in the IUCN Reintroduction Guidelines (2013), whereby translocations is the overarching term, defined as “the human-mediated movement of living organisms from one area, with release in another” (IUCN/SSC 2013, p. 2). Conservation translocations are those carried out for a specific conservation purpose, rather than mitigation translocations undertaken to reduce mortality from human development. *Leiopelma* frogs have undergone reintroductions (conservation translocation within a species former range) and reinforcements (translocation to sites where the species is still extant), and we also discuss assisted migration (translocation of a species beyond its former range for conservation motives) (Seddon 2010; IUCN/SSC 2013).

### Data collection and analysis

Information was gathered on methods, monitoring, and outcomes for translocations of *L. archeyi*, *L. hamiltoni*, and *L. hochstetteri*. Translocations of all three *Leiopelma* species were included in this review both to increase the number of cases informing our analysis and because with similar life-history and behaviour there is no reason to believe that these species would respond significantly differently to translocation methods. Sources included journal articles, academic theses, grey literature, government reports, and raw data from monitoring collected by the authors and provided by the Department of Conservation. Many co-authors were involved in translocations, so personal experiences often filled knowledge gaps.

Parameters recorded included: taxon, year, translocation type, objective; release site variables (including distance from source, habitat, climate, presence of predators and predator management); pre-release planning (e.g. whether modelling was used, how many releases were planned); founder numbers, age structure, and sex ratio; capture method, time

and conditions in captivity, transport and release methodology; disease screening; post-release monitoring methods; and monitoring data including dispersal, records of reproduction, and recruitment.

There are several cases where two translocations were carried out to the same location, often as part of a planned strategy. As such, throughout this review where we refer to ‘a translocation’ this includes all releases to a single location, unless otherwise specified as individual translocation ‘events’. In the case of the two translocations in the Brynderwyn Hills, while the source population was a single site, releases were to different locations and are considered two different translocations. Due to a low number of cases and variation in methods and reporting, statistical analysis of trends was not possible. As such, descriptive statistics and qualitative assessments are used.

### Assessing success

There is no single definition for translocation success, although it is broadly recognised that those undertaking a translocation are responsible for defining specific objectives prior to release, along with measurable indicators (Armstrong & Seddon 2008; Ewen et al. 2014; Linhoff et al. 2021). Success must be defined in a timeframe appropriate for the life-history of the species in question: species with short generation times that produce large numbers of offspring establish more quickly than long-lived species with low fecundity and long generation times, such as the leiopelmatid frogs.

The goal of this paper was to review the lessons learned and to identify the knowledge gaps for leiopelmatid translocations. Although each translocation had different goals, and project-specific criteria for success (Bell et al. 2010; Cisternas et al. 2021), here we follow the stages of success as developed by Miller et al. (2014), summarised here in Table 1, to be consistent across all cases. This framework standardises the definitions of success and lays out stages along the pathway to a self-sustaining viable population. This model is particularly useful for indicating establishment of *K*-selected species, such as New Zealand frogs, which take considerable time to reach each of the described stages (Miller et al. 2014).

**Table 1.** Framework used for assessing stages of translocation success, adapted from Miller et al. (2014).

Stage	Indicators	Justification
Stage 1: Survival and growth of founders	Recapture of a defined proportion of released individuals; increases in body size, mass, or body condition	Indicates there is habitat and stress is minimal
Stage 2: Evidence of reproduction	Regular detection of animals born in the translocated population	Indicates animals are in breeding condition, can find mates and suitable nesting sites.
Stage 3: Population growth	Capture of more animals than were initially released (including recaptured founders) in a defined monitoring period; evidence of breeding by second generation animals; or measurement of lambda values > 1.0	Indicates population size is increasing; young are surviving and being recruited into the population
Stage 4: Viable population	Consistently high number of individuals caught in each monitoring period (i.e. more than released); immature animals regularly observed; founders comprise a small proportion of captures; or negligible probability of extinction (e.g. from PVA)	Indicates population size is stable and recruitment is successful, but does not preclude recaptures of long-lived founders requires periodic monitoring to confirm.

## Summary of *Leiopelma* translocations

There have been translocations of *Leiopelma* to ten locations, on sixteen occasions between 1924 and 2016, spanning all three species. A summary of key translocation characteristics is provided in Table 2; all data are provided in Appendix S1 in Supplementary Material.

*Leiopelma hamiltoni* is the most translocated species (60% of translocations) because of its high conservation priority being confined to two small island populations. Additionally, until recently these isolated populations were considered two separate species (*Leiopelma hamiltoni* on Takapourewa and *L. pakeka* on Maud Island); they are still managed as genetically distinct populations.

Eight of the ten *Leiopelma* translocations were driven by conservation need with the aim of increasing the number of locations, range or population size, or moving individuals from populations considered to be in immediate danger from disease or mice (Haigh et al. 2011; Bell 2014; Reynolds 2015). The first known translocation of *Leiopelma* was to Kāpiti Island in 1924–1925, the species being described as *L. hochstetteri*, although it was possibly the sympatric *L. archeyi* which had not been described then (Turbott 1942; Bell 1985b). The motivations behind this earliest translocation are unknown, but Kāpiti Island was declared a reserve in 1897 to provide “a preserve for the flora and fauna of New Zealand” (Miskelly 2004) so it is likely that there was a conservation motivation behind this release. Two later translocations of *L. hochstetteri* were mitigation-driven, catalysed by roadworks affecting the source population (Parrish 2004; Beauchamp et al. 2005).

Releases on islands free of invasive predators (either naturally or due to eradication) made up 50% of translocations ( $n = 5$ ); 10% ( $n = 1$ ) were to an island with invasive predators present at the time; and 40% ( $n = 4$ ) were to mainland sites where at least some invasive predators were present, but with differing levels of mammalian predator control. Of the four translocations to mainland sites two were to areas with predator management in place: a fenced sanctuary with only mice present and a site where significant predator control occurs. Native predators were present at all release sites; these included tuatara (*Sphenodon punctatus*), kiwi (*Apteryx* spp.), weka (*Gallirallus australis*), and/or shortfin eels (*Anguilla australis*). However, kiwi and tuatara are excluded with fences at some release sites.

## Outcomes

Fifty per cent of translocations, ( $n = 5$ ), meet one or more indicators in the stages of success (Table 3). Of these, three translocations were to predator-free islands (Boat Bay, Motuara Island, and Nukuwaiata), one to a fenced mainland sanctuary (Zealandia) and one to a mainland site with predator control methods implemented specifically for the frogs (Pureora). At all these sites, recaptures of founders showed sufficient quality habitat for survival (Stage 1), and there are regular records of juvenile and subadult recruits, indicating suitability for reproduction (Stage 2). Data from Zealandia and Pureora showed lower incidence of founder recapture and reproduction than at the predator-free island sites and both sites have required a “top up” translocation to aid success (Bell et al. 2004b; Tocher & Pledger 2005; Lukis 2009; Haigh et al. 2011; Karst 2013; Miller et al. 2014; Cisternas 2019; Karst et al. 2023).

At the site of the earliest translocations, Boat Bay, there are also indicators of the third and fourth stages of success—population growth and viable population—after 37 years, new recruits outnumber founders by more than 3:1 (BDB & PD, unpubl. data). On Motuara Island the frog population has expanded to more than 80 metres from the release site and captures frequently included both juveniles and subadults (Tocher & Pledger 2005; Germano 2021). Thus, populations surveyed for more than 20 years since the first release are more likely to show greater progress through the success framework, than those released since 2000.

Releases at the remaining sites do not sufficiently meet the indicators of success. Searches since 1975 on Kāpiti Island failed to detect frogs (Bell 1985b), post-release monitoring failed to detect released individuals at the 2004 Brynderwyn Hills release (Parrish 2004), and at the 2005 Brynderwyn site none of the released frogs was detected more than six days after release (Beauchamp et al. 2005). On both Takapourewa and Long Island a small proportion of individuals did survive at the release site in the long-term—three and  $\geq 10$  founders, respectively—however, these small numbers indicate poor survival at the release site and are unlikely to be self-sufficient without further management. All frogs found on Long Island during the two most recent monitoring sessions, 11–13 years post-release, were in the adult female size category (SW, unpubl. data). While three new individuals have been detected at the Takapourewa release site, and two reached adulthood (EB, unpubl. data), this is an extremely low number of recruits in twenty-four years of monitoring, particularly compared with results at other sites.

A 50% success rate is comparable to or better than similar assessments for other herpetofauna. Dodd and Siegal (1991) found that 19% of herpetofauna translocations were successful, while Germano and Bishop (2008) reported a 41% success rate for herpetofauna globally. Long-term success rates for New Zealand lizards, assessed only for those cases with more than 10 years monitoring data, were 33% (Romijn & Hartley 2016). Our findings are also comparable to success rates for conservation-driven translocations in other fauna (Griffith et al. 1989; Fischer & Lindenmayer 2000; Miskelly & Powlesland 2013).

Griffiths and Pavajeau (2008) found that successful amphibian reintroduction programmes ran for a decade or more before they could be declared a success. All *Leiopelma* translocations began more than a decade ago, with the most recent translocations to Pureora and Zealandia, both beginning in 2006 (Table 2). However, *Leiopelma* are long-lived species, and progress is slow through the stages of success. Even where success is subjectively assessed, decades may be needed before indicators of population viability (the fourth stage of success) are clearly seen, as at Boat Bay and Motuara Island. Monitoring methods may be restricting the ability to assess against some indicators (see below). Romijn and Hartley (2016) reviewed New Zealand lizard translocations (also applying the Miller et al. (2014) stages of success) and found that monitoring of lizards for less than ten years rarely picked up indicators of Stages 3 and 4 in this framework.

Miskelly and Powlesland (2013) report a trend whereby the success of New Zealand bird translocations has improved over time, with just 15.3% success rate in the 1960s rising to 66.6% by the 2000s. While lessons have been learned over time, success was achieved in some of the earliest conservation-motivated frog translocations, e.g. Boat Bay and Motuara Island (Bell et al. 2004b; Tocher & Pledger 2005). The high

**Table 2.** A summary of release site characteristics and processes used in *Leiopelma* translocations. Differences between years at a single release site are separated by a semicolon. \*In some cases translocation type is assumed, because of poor knowledge of precise former range.

Year (s)	Release Location	Site type	Distance from Source	Translocation type	Predators present at time of release	Predator management	Number of founders	Month of release	First evidence of reproduction
<b><i>L. hamiltoni</i> (Te Pākeka ESU): Source Main Block Maud Island</b>									
1984; 1985	Boat Bay, Maud Island	Island	0.5 km	Conservation reintroduction	No invasive predators	Island biosecurity	43; 57	May (both years)	6 years (subadult)
1997; 2014	Motuara Island	Island	33 km	Conservation reintroduction*	No invasive predators, potential risk from kiwi	Island biosecurity, fence excludes kiwi	300; 300	May; June	10 months
2005	Long Island	Island	34 km	Conservation reintroduction*	No invasive predators, potential predation risk from kiwi and weka	Island biosecurity	101	July	Not observed
2006; 2012	Zealandia	Mainland fenced sanctuary	78 km	Conservation reintroduction*	Mice and native predators still present	For a portion of the release, mouse-proof enclosures; fence excludes kiwi and encloses frogs	30+30; 101	February–March + October; December	2 years in enclosure; 5 years outside
<b><i>L. hamiltoni</i> (Takapourewa ESU): Source Frog Bank Takapourewa</b>									
1992	Frog Pit, Takapourewa	Island	70 m	Conservation reintroduction	No invasive predators	Island biosecurity, fence excludes tuatara	12	May	4 years
2004; 2006	Nukuwaiata	Island	25 km	Conservation reintroduction*	No invasive predators	Island biosecurity	40; 31	May (both years)	4 years
<b><i>L. hochstetteri</i>: Source Brynderwyn Hills</b>									
2004	Brynderwyn Hills	Mainland	< 0.5 km	Mitigation (re-enforcement)	Invasive predators present	None	28	October–November	Not observed
2005	Brynderwyn Hills	Mainland	< 0.2 km	Mitigation (re-enforcement)	Invasive predators present	None	25	November	Not observed
<b><i>L. archeyi</i>: Source Whareorino Forest</b>									
2006; 2016	Pureora	Mainland	75 km	Conservation reintroduction*	Invasive predators present	Herbivore exclusion fence, invasive mammals controlled via traps and poison	70; 60	December; October	15 months
<b><i>L. archeyi</i> or <i>L. hochstetteri</i>: Source Coromandel Peninsula</b>									
1924; 1925	Kāpiti Island	Island	c. 450 km	Conservation introduction*	Kiore and rats	-	13; 2	December; March	-

**Table 3.** Current stage of success of all *Leiopelma* translocated populations, assessed against framework in Table 1, adapted from Miller et al. (2014). Note that some assessments are based on unpublished monitoring data. ✓ = stage achieved, ? = some indicators, stage possibly achieved, X = stage not achieved.

Receptor	Stage 1: Survival and growth	Stage 2: Reproduction	Stage 3: Population growth	Stage 4: Viable population	Notes & Key References
Kāpiti Island	-	-	-	-	Limited information so can't be assessed against criteria; Bell (1985b)
Boat Bay, Maud Island	✓	✓	✓	✓	Immature animals regularly observed; recruits outnumber founders more than 3:1; Bell et al. (2004)
Frog Pit, Takapourewa	X	X			Poor anchoring (homing) and very low reproduction at release site; population functionally extinct; Brown (1994); Tocher & Brown (2004)
Motuara Is	✓	✓	?	✓	Immature animals regularly observed; significant population expansion from release site; Tocher & Pledger (2005)
Nukuwaiata	✓	✓	?	?	>80% founders recaptured. Immature animals regularly observed; founders sometimes comprise a small proportion of captures; mark-recapture analysis required; Tocher et al. (2006); Bishop (2005)
Brynderwyn Hills 2004	X				Mitigation-driven translocation. No released frogs were re-captured; experienced issues with monitoring; Parrish (2004)
Brynderwyn Hills 2005	X				Same source population as 2004. Only 1 individual seen more than 3 days post release; Beauchamp et al. (2005)
Long Is	X				11–13 years post release <10% of released frogs captured; no reproduction; injured frog found suggesting predation issues; Germano (2006); Germano et al. (2023c)
Zealandia	✓	✓			Survival and reproduction both in enclosures and free roaming; Lukis (2009); Karst (2013); Karst et al. (2023)
Pureora	✓	✓			Survival and breeding recorded; Haigh et al. (2011); Cisternas (2019); Cisternas et al. (2021)

success rate in early translocations (compared with birds) may have been aided by the low vagility of *Leiopelma* and a better understanding of reintroduction biology by the 1980s, when frog translocations in New Zealand began in earnest. However, unlike birds and lizards, case numbers are too low to establish a true trend over time for native frogs.

Nevertheless, translocations have contributed conservation benefits to *Leiopelma*. In the most recent threat assessments by the New Zealand Department of Conservation, *L. hamiltoni* showed improvement in threat status, changing from Threatened – Nationally Critical to Threatened – Nationally Vulnerable (Burns et al. 2018). Although a taxonomic change combining *L. hamiltoni* and *L. pakeka* was a key driver, this down-listing was also aided by translocations to additional predator-free islands which have increased the number of sub-populations from two to at least five. This demonstrates how co-ordinated and well-planned translocations assist with reducing extinction risk as part of a broader conservation strategy.

## Factors influencing translocation success

### Management of predators at release site

Ensuring that known agents of decline will not be a threat to translocated populations is one of the cornerstones of translocation best practice and is critical for success (IUCN/SSC 2013; Linhoff et al. 2021). Predation by introduced species is known to be a major threat to native frogs (Thurley & Bell 1994; Bishop et al. 2013; Egeter et al. 2015, 2019; Bell & Bishop 2018) and as such is a key factor that needs to be accounted for at release sites.

Most *L. hamiltoni* translocations were carried out on islands free of introduced mammals (Table 2). The only mainland release for this species was at the fenced sanctuary Zealandia where the only mammalian predators are mice, which undergo annual predator control with trapping and poison bait. This translocation used adaptive management to specifically test the survival of translocated *L. hamiltoni* in the presence of mice (Karst et al. 2023). The release in Zealandia is a good test case for *L. hamiltoni* co-existence with mice. The

combination of mice and potentially native predators seemed to cause low recapture rates of translocated frogs in the initial release outside small, protected enclosures (Lukis 2009). While better recapture rates were achieved post-2012 when frogs were fenced from native predators but still in the presence of mice, the results are not as positive as we have seen for the same species on predator-free islands and further monitoring is required to establish the current status of this population. Mice have been recorded preying on New Zealand reptiles (Whitaker 1978; Hoare et al. 2007), and their presence reduced post-release survival in a skink translocation (Norbury et al. 2014). In a different fenced mainland sanctuary, Sanctuary Mountain Maungatautari, mice were found to reduce terrestrial invertebrates (Watts et al. 2022). As such, the presence of mice may impact establishment of translocated frog populations by competition for prey, as well as potential predation. Indeed, increased mouse abundance after rat control at Whareorino may have significantly reduced survival rates of both juvenile and subadult *L. archeyi* (Germano et al. 2023b), which would impact the ability of a small, translocated population to establish. Assessment of potential translocation release sites at locations where introduced mammals have been eradicated should include an evaluation of invertebrate prey, to ensure that this key resource has recovered sufficiently from any prior depletion caused by mammalian predation (Gibbs 1990).

Fencing has been used to exclude suspected native predators, notably kiwi at Motuara Island and Zealandia, and tuatara at Takapourewa. The exclusion of kiwi may have helped increase initial survival on Motuara Island; this frog population has now expanded beyond the fence (Tocher & Pledger 2005; Germano 2021). Native predator management at Takapourewa has shown that exclusion of tuatara has significantly increased the remnant *L. hamiltoni* population at this site (Brown 1994; Tocher & Brown 2004; JMG, unpubl. data). Although there is no definitive evidence that native ground-dwelling birds, including weka and kiwi, are a threat to frogs (Beauchamp 1996; Karst 2013), there is anecdotal information that the failure of the Long Island translocation might have been impacted by these species (Germano et al. 2023c). Materials to build a weka and kiwi exclusion fence were taken to the Long Island release site, but the fence was not erected until 2019 after the translocation had likely failed (Germano et al. 2023c). While frogs co-existed with these species in the past, founding a new population with low numbers may require relieving this pressure at least during the establishment phase; erecting a fence is a relatively cost-effective option likely to aid establishment.

Monitoring of predators is key in assessing suitability of mainland sites (Nichols & Armstrong 2012). Measures to reduce predation before and after release can contribute to post-release survival rates and therefore increase chances of population establishment (IUCN/SSC 2013). In Pureora, trapping and poison bait are used to control rats, mustelids, and possums around the *L. archeyi* release site. This population experienced low initial recapture rates compared with those seen for *L. hamiltoni* at island translocation sites, (Haigh et al. 2011) indicating that vital rates may be suppressed compared with mammal-free sites, slowing establishment at Pureora. No predator control measures occurred at the release sites during the translocations of *L. hochstetteri*. Studies investigating the benefits of pest management on this species are inconclusive and further research is required (Mussett 2005; Najera-Hillman et al. 2009a; Longson et al. 2017). Furthermore, for *L. hochstetteri*, shortfin eels and banded kokopu (*Galaxias*

*fasciatus*) may present a significant predation threat (Najera-Hillman et al. 2009b).

It is important to understand the density of predators with which *Leiopelma* can co-exist, particularly for assessing appropriateness of and management for mainland release sites; predation may be a critical factor in determining success at these sites. Establishment is slower at sites with suppressed levels of introduced mammals and even these have required top up translocations (Zealandia and Pureora). Translocations to sites with any level of mammal predation should expect slower population growth, and this should be accounted for in the translocation planning.

### Number of founders

Founding numbers in *Leiopelma* translocations have ranged from 12 (Brown 1994) to 300 (Tocher & Pledger 2005) on any single release occasion (Table 2). Releases with the smallest number of founders were more likely to fail than those with more than 70 individuals released in total. However, larger release number was not a guarantee of success, since 101 individuals failed to establish a population at Long Island.

Maximising the number of potential founders and the genetic diversity of new populations, without jeopardising the source population, will improve chances of success (Tocher et al. 2006; Germano & Bishop 2009; Weiser et al. 2012; Easton et al. 2020). This appears to be verified in *Leiopelma*, where translocations with very small founding numbers (Kāpiti Island and Takapourewa) failed to establish viable populations, and there is no record that the two mitigation translocations in the Brynderwyn Hills augmented populations at the release sites (Table 2). Only at the Takapourewa site has there been evidence of anchoring at the release site (three out of 12 relocated) and breeding (three new individuals recorded) (Brown 1994; Tocher & Brown 2004; JMG, unpubl. data). The small number of anchored frogs and low evidence of recruitment render the population functionally extinct on its own, so this translocation is considered a failure when assessed against the Miller et al. (2014) success framework; however, it was a useful exercise in testing translocation as a tool and the creation of manmade habitat. The decision to translocate just 12 individuals on Takapourewa was justified at the time of release since the source population was very small, estimated at fewer than 200 individuals (Brown 1994), and native frog translocations were experimental at the time warranting caution (Bell et al. 2004b). This outcome may be corrected if the original Takapourewa population can expand its range by 100 m, thereby merging with the small, anchored population.

The smallest translocation on the trajectory to achieving a self-sustaining population is at Nukuwaiata, founded by a two-stage release of 40 initial frogs, followed by 31 individuals two years later (Tocher et al. 2006; Bell et al. 2010). This translocation was guided by a matrix population modelling approach (Tocher et al. 2006). Monitoring at Pureora showed some indicators of success following the release of an initial cohort of 70 frogs, including physical growth and survival of individuals, successful reproduction, and on occasion a large proportion of new recruits among captures (Haigh et al. 2011). However, after four years of monitoring at this site, just 29% of released individuals had been re-sighted and a follow-up translocation was recommended (Haigh et al. 2011). This was implemented in 2016 (Cisternas et al. 2021).

The Motuara Island translocation had the largest number of founders: 300 individuals. Monitoring detected juveniles ten months after release and significant numbers of new recruits

were recorded in the first five years. The additional 300 frogs added to this population in 2014, motivated by a mouse incursion on Maud Island (Bell 2014; Reynolds 2015), was likely not needed to achieve the success observed at this site.

Conservation genetics must be a consideration when deciding on the number of animals for release, and although not explicitly considered in any of the cases in our dataset this was the impetus for the large initial release on Motuara Island. Genetic diversity allows for adaptation of populations to changes in the environment, and for recovery from stochastic events (Jamieson et al. 2008; Jamieson & Lacy 2012). If done poorly, translocations can result in inbreeding depression (i.e. reduced fitness from mating between relatives) and genetic drift (i.e. loss of variation) (Jamieson et al. 2008; Jamieson & Lacy 2012; Keller et al. 2012; Weiser et al. 2016; Taylor et al. 2017b). Both of these effects increase the risk of extinction in small populations and decrease the chances of successful establishment in a translocation (Jamieson et al. 2008; Groombridge et al. 2012; Jamieson & Lacy 2012), although the effects of a bottleneck may take a long time to become apparent in species such as the leiopelmatid frogs with long generation times (Keller et al. 2012; Taylor et al. 2017b). So, while translocations may be beneficial in reducing the impacts of stochastic events in small, fragmented populations, planning for genetic diversity of new populations is critical (Jamieson et al. 2008; Easton 2018; Easton et al. 2020).

Loss of genetic diversity is more likely to occur when source populations are genetically diverse than in those known to be genetically depauperate, since in the former case there is more diversity to lose (Allendorf 1986; Taylor & Jamieson 2008; Miller et al. 2009). *Leiopelma* frogs have already suffered severe range reduction and population fragmentation, which likely caused multiple genetic bottlenecks as the species' population size and range declined in response to habitat loss and predation by introduced species (Easton 2018). This poses a particular risk to *L. hamiltoni*, since relict island populations have often been shown to have genetic variation reduced further than populations of the same species on the mainland (Frankham 1997; Boessenkool et al. 2007; Cardoso et al. 2009). Populations of *Leiopelma* have low genetic diversity compared with other anurans (Green 1994; Clay et al. 2010; Easton 2018).

Modelling can be used to help decision-makers assess likelihood of population establishment with different numbers of potential founders (Armstrong & Reynolds 2012). Tocher et al.'s (2006) model for *L. hamiltoni* showed that populations founded by 20 adults had a higher predicted population growth rate than those founded by 40 adults. However, population size after 30 years was greater in the cases with 40 contributing founders, because the founding population was larger. During translocations the impacts of removing individuals from source populations must also be considered, since small populations of *K*-selected species may take significant time to recover from harvest for translocation (Tocher et al. 2006; Easton et al. 2020). A model that tested nine scenarios for translocation of *L. hamiltoni* from the Takapourewa ESU found that extinction risk of the source population decreased with the removal of 20 rather than 40 adult females (Tocher et al. 2006). Easton et al. (2020) modelled a translocation from the *L. hamiltoni* Maud Island ESU, with the aim of recommending a release number that maximised long-term viability and allelic diversity of both the source and founder populations. Allele retention was best in populations founded by > 150 individuals; however, a harvest of this size led to decline in allele retention in the

source population. Conversely, founder numbers below 120, while having a lower impact on the source population, were more likely to result in loss of alleles and eventual extinction of the translocated population. As such, harvest/release of 130–140 individuals was considered optimal.

Additional strategies of widespread collection to maximise the genetic diversity of founder populations have been implemented in *Leiopelma* translocations to Boat Bay (Bell et al. 2004b), Motuara Island (Tocher & Pledger 2005), and Pureora (AH, unpubl. data; Cisternas et al. 2021). Adding subadults to the release, as on Nukuwaiata, has also been suggested to reduce the bottleneck effect without increasing impact on the source population (Tocher et al. 2006; Bell et al. 2010). Furthermore, if translocations are suspected, or found, to have caused a bottleneck, supplementary translocations which increase genetic diversity can rectify this issue. This strategy was implemented in the case of *L. archeyi* at Pureora (Cisternas et al. 2021). However, care must be taken to ensure this is done as early as possible for new founders to have a greater impact on the overall population (Ramstad et al. 2013; Robertson et al. 2019).

### Habitat quality at release site

An appropriate release site is one of the major factors that will likely influence translocation success (Griffith et al. 1989; Osborne & Seddon 2012; IUCN/SSC 2013; Berger-Tal et al. 2020; Linhoff et al. 2021). Poor habitat was the most reported cause of amphibian translocation failure in one global review (Germano & Bishop 2009). *Leiopelma* show high site fidelity over the long-term, remaining in the same home ranges over repeated surveys (Bell & Moore 2015; Ramírez 2017) so it is important to maximise habitat quality within the home range of each translocated frog. While most leiopelmatid translocations assessed several sites prior to release, few detailed reports on habitat assessment were written making review of this planning aspect difficult (Bell 1995; Department of Conservation 2006). An assessment of temperature and humidity using dataloggers was the most reported type of habitat assessment (Appendix S1). Additional qualitative factors reported in relation to habitat at release sites for the terrestrial species include native forest canopy, understorey vegetation, and, for *L. hamiltoni*, the presence of rock piles on the forest floor (Bell et al. 2004b; Tocher & Pledger 2005; Department of Conservation 2006; Cisternas 2019; Karst et al. 2023). In the mitigation translocations for *L. hochstetteri*, frogs were released at nearby stream sites known to be inhabited by this species (Parrish 2004; Beauchamp et al. 2005; Beauchamp et al. 2010).

Improvements could be made in habitat assessments, increasing objectivity and use of quantitative tools to reduce risk of failure in any future translocations. However, the debate over the definition of habitat (Hall et al. 1997; Gaillard et al. 2010; Stadtmann & Seddon 2020) does not help guide decision-makers in how to appropriately assess potential release sites. Stadtmann and Seddon (2020) define habitat, in the context of translocations, as “a species-specific set of resources and environmental conditions that enable a population to persist and reproduce”. It is important to remember that habitat is a dynamic concept, which changes for a single species across space and time (Osborne & Seddon 2012; Stadtmann & Seddon 2020). As such, habitat is either present or absent at a given site at a particular time and may vary in quality from low to high, over time and space. It is not always possible to use former range or current presence or absence as a proxy

for high quality habitat and consideration must be given to likely future changes to ensure longevity at the new site (for a full discussion, see Osborne & Seddon 2012).

All species of leiopelmatid frog currently occupy very small areas when compared with their former ranges (Bishop et al. 2013; Bell & Bishop 2018). It is difficult to assess habitat for relict species since their current distribution may not represent high quality habitat. For example, *L. hamiltoni* survived only in rock tumbles on Maud Island and Takapourewa (Newman et al. 1978; Newman 1990). On Maud Island, this was the only site that retained substantial forest cover as it was not cleared for farming due to unsuitable rocky ground (Germano 2006). On Takapourewa the rock pile offered the only refuge from introduced cats and desiccation when the whole island was denuded of forest (Bell 1985b; Tocher et al. 2006). For *L. hamiltoni*, the presence of rock piles has been considered a necessary habitat characteristic at release sites (Bell et al. 2004b; Tocher & Pledger 2005; Germano 2006; Lukis 2009; Karst 2013; Bell 2014; Karst et al. 2023) but other retreats or vegetation may be suitable for this species too. In fact, monitoring at Long Island found most frogs in an area beyond the release site rock pile where there were smaller rocks and substantial leaf litter (SW & LE pers. obs.), potentially a humid and favourable environment. Depth of leaf litter was also found to be a key microhabitat indicator of *L. archeyi* presence (Hotham 2019).

Quantitative habitat assessment was carried out for a proposed translocation of *L. hochstetteri* to Orokonui Ecosanctuary, a fenced mainland sanctuary near Dunedin (Easton et al. 2016). The authors modelled resource use in pine plantations and native forest where the species was present, then assessed the proposed release site using these results. Cisternas (2019) conducted a post-translocation assessment of the source and release site habitats for the *L. archeyi* translocation to Pureora, noting a higher incidence of epiphytic vegetation on trunks at the source site, possibly indicating a difference in ambient humidity. Refinement of our understanding of what makes good quality microhabitats (Easton et al. 2016; Cisternas 2019; Hotham 2019) can be used to improve quantitative analysis of site selection for future translocations.

Trewenack et al. (2007) argued the case for using modelling in planning, optimising and interpreting translocations based on the *L. hamiltoni* study at Boat Bay. Species distribution modelling can also be a useful tool when assessing habitat quality at potential release sites, although in the case of *Leiopelma* the limited relict ranges may not provide sufficient information to apply this technique (Fouquet et al. 2010; Germano et al. 2023a). Nevertheless, models have been successfully developed with limited information (Porter et al. 2006; Lentini et al. 2018), and models may be critical in predicting suitability of sites in the face of a changing climate (see latter section; Germano et al. 2023a). However, while modelling may be useful, a simple list of resources required, along with the acceptable range of environmental conditions may be sufficient to highlight gaps in knowledge and provide some objectivity to site selection (Stadtmann & Seddon 2020). More physiological research is required to establish temperature and humidity preferences and limits, which have only been studied in a limited capacity for *L. hochstetteri* (Easton 2015) and *L. archeyi* (Cree 1989).

Significant habitat modification took place prior to *L. hamiltoni* release at two sites. At Takapourewa, aside from island-wide planting for forest regeneration, rock piles were

created, the release site was seeded with invertebrates, and at the time of release additional water was added to each release point to ensure high humidity (Brown 1994). At Zealandia, rocks, logs, and leaf litter were added to the enclosures and, later, rock piles were created and extended prior to releases of frogs outside of the enclosures (Lukis 2009; Karst 2013; Karst et al. 2023). Invertebrate prey were added to frog enclosures at Zealandia to ensure ongoing availability of food (Lukis 2009). At Pureora a fence was erected, and later extended, to exclude herbivores such as deer and goats from the release area (Cisternas 2019). The structural variety of vegetation has subsequently increased within the fence, providing additional release sites and likely increasing humidity, thus improving habitat quality at this site (Cisternas 2019; Easton 2020a). When assessing potential release sites, it is important to consider that habitat may need to be modified or restored, and then managed to maintain its suitability in the long-term (Osborne & Seddon 2012). The greater the need for ongoing habitat management, however, the greater the cost of implementing a translocation to a site.

### Post-release dispersal and long-term movement

Post-release movement—homing and dispersal from release areas—is one of the commonly reported causes of translocation failure (Berger-Tal et al. 2020), including for herpetofauna (Germano & Bishop 2009). Short-term relatively long-distance dispersal of individuals after translocation means they do not contribute to the founding population, demographically or genetically (Le Gouar et al. 2012). Dispersing individuals may also experience increased mortality if they move beyond protected or high-quality habitat (Roe et al. 2010). Individual frogs seem to differ in time taken to establish a home range at a new site, indicated by a wide range of distances moved by individuals recorded in the year post-release; median distances travelled in the first year were significantly further (up to 4.5 times) than those seen in source populations (Karst 2013; Germano et al. 2023c). Animals often show an exploratory phase post-release as home-ranges are established, where distances moved are greater than is typical in source populations (Le Gouar et al. 2012; Berger-Tal & Saltz 2014). Individual *L. hamiltoni* from the second translocation cohort at Boat Bay dispersed further on average (8.0 m) than the first cohort (4.8 m) when released at the same point, presumably travelling beyond the already established home ranges to find vacant habitat (Bell et al. 2004b; Trewenack et al. 2007). Trewenack et al. (2007) modelled dispersal and settling of translocated *L. hamiltoni* after release at Boat Bay, Maud Island, noting that identification of an appropriate model and parameter values after the first or second translocation could aid future translocations in several ways; for example: (1) predicting the size of the area required to translocate a given number of animals, or (2) knowing approximately what size area should be searched in capture-recapture experiments – searching too large an area may be costly, while observations may be missed if too small an area is searched (Trewenack et al. 2007).

As with many translocations, several cases showed a short period of high loss of individuals after release, likely due to a mixture of post-release mortality and/or dispersal from the release site, e.g. *L. hamiltoni* on Motuara Island (Tocher & Pledger 2005), *L. archeyi* at Pureora (Cisternas 2019), and *L. hochstetteri* at the Brynderwyn Hills (Parrish 2004). Thus, dispersal may reduce effective founder population size. Recaptures at all sites in the first year showed dispersal into the wider release area (Brown 1994; Bell et al. 2004b; Tocher

& Pledger 2005; Germano 2006). At two sites (Motuara Island and Pureora) monitoring areas were expanded to account for dispersal (Tocher & Pledger 2005; Cisternas 2019).

Familiarity between released individuals reduces dispersal in some species (Le Gouar et al. 2012; Shier & Swaisgood 2012; Moseby et al. 2020), but not always (Armstrong 1995; Armstrong & Craig 1995; Mitchell et al. 2021), and has been shown to increase survival and reproductive success (Shier 2006; Shier & Swaisgood 2012). *Leiopelma* share retreat sites in the wild (Ramírez 2017; Cisternas et al. 2023). They are attracted to the scent of neighbouring conspecifics with this effect waning with increasing distance between home-ranges (Waldman & Bishop 2004; Waldman 2016). Furthermore, clear associations between individual *L. hamiltoni* were seen in a social network analysis (Lamb et al. 2021) and extend over years in an outdoor captive environment (Altobelli et al. 2020). Despite this, releasing frogs with their neighbours on Long Island had no impact on anchoring frogs, and no long-term effect on movement or survival (Germano 2006).

Two frogs on Takapourewa were recaptured back at the source population three and seven years after release; the time of movement in the second case is unknown due to there being six years between captures at the release and source (Tocher & Brown 2004). This case, along with initial movements towards the source population seen at Long Island (Germano 2006) and Zealandia (Karst 2013), indicate that the potential for homing needs to be considered. Homing instincts are known to reduce with increasing distance from the source population for many species (Rogers 1986; Van Vuren et al. 1997; Le Gouar et al. 2012; Hinderle et al. 2015). As such, translocations to sites less than 500 m from the source population are not recommended.

As populations establish and the core release site reaches carrying capacity, new recruits will disperse to find unoccupied habitat. The time for core populations to stabilise at the release site may vary with founder size, occurring within six months at Motuara Island but taking six to eight years with fewer founders at Boat Bay (Bell et al. 2004b; Tocher & Pledger 2005). Systematic searches measuring extent of population dispersal are rarely reported for *Leiopelma* populations. A trial of occupancy monitoring on Motuara Island attempted to find the extent of the population range with individuals found over 70–80 m from the release site in two directions surveyed, likely a conservative measure of population spread given the dry weather and limited number of search plots used (Germano 2021).

### Release strategy

Different release strategies included translocations conducted in a one- or two-step process, or multi-step using adaptive management (Appendix S1). In two cases where a two-stage release was planned, both were implemented because of uncertainty: initially about the effectiveness of translocation as a technique suitable for *Leiopelma* (Boat Bay), and secondly regarding the effect of harvest on a very small founder population (Bell 1994; Bell et al. 2004b; Tocher et al. 2006). Both cases resulted in successful translocations. A multi-step adaptive management approach was applied at Zealandia, an appropriate strategy for the first case of attempted translocation of *L. hamiltoni* to a mainland site. This progressed first with soft-release enclosures, then an experimental release of half the individuals outside enclosures, followed by an additional release combined with habitat management aimed at improving survival and population establishment (Lukis 2009; Karst 2013; Karst et al. 2023). While not initially planned, the

second release of *L. archeyi* at the Pureora site in 2016 was undertaken because of low recapture rates, but was strategically used to increase genetic diversity and to correct a female bias (Haigh et al. 2011; Cisternas et al. 2021). Motuara Island was the only site that showed indicators of success from a single release (Tocher & Pledger 2005), but here a second release was undertaken as an emergency transfer when mice were detected on Maud Island (Bell 2014; Reynolds 2015).

The effectiveness of augmentation, or follow-up translocations, has been questioned as the purpose is not always clear (Armstrong & Ewen 2001). Conducting translocations in a two-step process appears to be an effective method for *Leiopelma* translocations and documentation of decision-making was good (Bell et al. 2004a; Tocher et al. 2006; Bell 2014; Cisternas et al. 2021; Karst et al. 2023). In most cases second releases were implemented using an adaptive management approach, allowing for the suitability of a site to be tested, management to be refined, and for the impact on source populations to be minimised. Motuara Island was the only case where success was seen with a single release occasion, however, the high founding group number here, compared with other sites, likely contributed to signs of establishment being detected in a short period of time. Several augmentations undertaken were not explicitly planned from the outset, rather they were implemented as adaptive management. Willingness to continually assess whether management needs to change in response to ongoing results is critical in ensuring long-term success at release sites. It is also important to have an exit strategy or contingency plan prior to release if the translocation outcome is not ideal (Germano et al. 2023d).

The month of release varied although releases occasions were most commonly conducted in late-autumn and winter (May–July;  $n = 8$ ), with fewer releases in spring (October–November;  $n = 3$ ) and summer (December–March,  $n = 5$ ). Success was seen in translocations carried out across all seasons. Most releases occurred during the cooler seasons to provide time for frogs to establish before the additional stress of warmer, drier summer weather and to avoid disruption of breeding. Releases at Zealandia and Pureora were carried out during summer, which may have contributed to slower establishment at these sites.

The physical process of translocating animals causes stress. Chronic stress caused by poor technique can result in several effects linked to failure e.g. altered immune response, suppression of reproduction, reduced predator response, and altered behaviour (for a full discussion see Dickens et al. 2010; Parker et al. 2012). Stress can also lead to mortality (Teixeira et al. 2007). As such, all steps should be taken to minimise stress during handling and transport.

### Disease

Disease is a key consideration during translocations, where potential risks include the introduction of disease to a new site, infection of translocated individuals at the release site, and post-release stress causing parasites or other organisms to become pathogenic (Cunningham 1996; Ewen et al. 2012a; Sainsbury et al. 2012; IUCN/SSC 2013; Linhoff et al. 2021). This is of particular importance for amphibians, where the chytrid fungi *Batrachochytrium dendrobatidis* (Bd) and *Batrachochytrium salamandrivorans* (Bsal) have caused population declines and species extinctions globally (Berger et al. 1998; Daszak et al. 2003; Stuart et al. 2004; Stuart 2012; Martel et al. 2013; Stegen et al. 2017).

Frogs in New Zealand have tested positive for Bd (Shaw

et al. 2013; Eda 2022; Eda et al. 2023). While disease has been implicated as a contributing factor in the crash of the Coromandel Archey's frog population (Bell et al. 2004a), there is debate about the extent of Bd resilience in *Leiopelma* (Bishop et al. 2009; Shaw et al. 2010; Moreno et al. 2011; Ohmer et al. 2013). Nevertheless, the discovery of Bd in the Whareorino *L. archeyi* population instigated an emergency translocation to Pureora, (Department of Conservation 2006; Haigh et al. 2011; Cisternas et al. 2021). The best practice of disease management for *Leiopelma* was seen in this Pureora translocation; here disease management was critical as the translocation purpose was to create a Bd free population (Department of Conservation 2006; Haigh et al. 2011; Cisternas et al. 2021). Frogs spent three and six months at Hamilton and Auckland Zoo respectively, where they were quarantined and disease screening took place (Haigh et al. 2011; Cisternas 2019). Unfortunately, these precautions have not resulted in the Pureora population remaining Bd-free (Cisternas et al. 2021), although population establishment is still progressing.

Pre-release disease screening was not carried out in the majority of *Leiopelma* translocations. However, most of these were for *L. hamiltoni*, a species whose restriction to islands with high biosecurity protocols meant that at the time of translocation, disease risk was considered low. A more recent study resulted in weak Bd positive tests on Maud Island (Eda 2022; Eda et al. 2023), so screening may become increasingly important in the future. Disease risk analysis and pre-release screening could be improved for *Leiopelma* translocations; biosecurity measure at some sites (notably islands) are well designed to limit the introduction of disease.

#### Founding group structure: sex, age class, and density

Sex-identification in *Leiopelma* is not easily achieved; adult females can be distinguished by their larger size, but identification of adult male *L. archeyi* and *L. hamiltoni* is only possible where long-term data has established their snout-vent length has stabilised within the male size range or by hormone assay (Germano et al. 2011, 2012; Bell & Pledger 2023). Although requiring experience, the sex of adult *L. hochstetteri* may be evident from the thickness of their forelimbs, those of males being more muscular (Bell 1978). Sex identification of sub-adults is not possible in the field. The female bias seen in most translocation events may be a result of the larger female size making them more likely to be detected during collection for release. Given males are known to exhibit parental care in *L. archeyi* and *L. hamiltoni* (Bell 1985a), caution must also be taken to avoid collection for translocations at times when males exhibit low emergence due to guarding of egg-clusters, which may also lead to a female sex bias in collection.

The bias towards females in some founder populations does not appear to have impacted the ability of populations to establish (Table 3). However, reproduction and rates of population growth, may be limited in female biased populations by the number of males available to care for egg clusters. The augmentation translocation of *L. archeyi* to Pureora in 2016 was designed to address this imbalance by releasing more individuals in the male size class through a combination of hormone assay sex identification of quarantined animals and release of smaller individuals (Cisternas 2019; Cisternas et al. 2021). However, in all other translocations the individuals did not spend sufficient time in captivity and/or hormonal assay techniques were not yet available (Appendix S1).

Most founding populations comprised a majority adults (Table 2). Even in the case of Nukuwaiata, where modelling

recommended a 50:50 release of adults:subadults (Tocher et al. 2006), the actual release was adult-biased (JMG, unpubl. data). Releases utilising a high proportion of adults likely assisted with establishing populations, as reproduction and recruitment can occur earlier assuming suitable breeding conditions are met. However, including a significant proportion of subadults in the founding population may help reduce the impact on the source, by limiting the number of reproductive animals removed and therefore maintaining its potential to recover from the loss. Adding subadult frogs to a cohort of adults also increases the number of potential founders at the release site thereby improving chance of success (Tocher et al. 2006). Furthermore, there is evidence that subadults are more likely to remain at the release site (Tocher & Brown 2004). As such, any future translocations should consider the benefits of including subadults in the founding cohort; modelling may help assess whether this strategy is suitable (Tocher et al. 2006; Armstrong & Reynolds 2012).

Release density of frogs varied between events, ranging from less than one frog  $m^{-2}$  (Cisternas 2019) to as high as 75 frogs  $m^{-2}$  (Bell 2014). There is a balance between releasing frogs at too low a density, which might reduce chances of individuals breeding and thus cause population and genetic effects, and too high a density, which likely increases post-release stress as frogs compete for refuges and establish home-ranges. Releasing frogs at a high density in Zealandia may have increased initial dispersal for these reasons (Lukis 2009). Aiming for a release density similar to that found in natural populations is likely the most balanced approach (Tocher et al. 2005).

## Future Considerations

### Climate change

Translocation planning needs to account for the long-term suitability of a location under realistic predicted climate scenarios (Schwartz & Martin 2013; Butt et al. 2021). Indeed, the effects of climate change are already being experienced by leiopelmatid frogs; fifty years of records show increasing summer temperatures and soil moisture deficit at *L. hamiltoni* sites in the Marlborough Sounds (Germano et al. 2023a). The ability of native frogs to adapt to climatic changes has not been assessed but they may be vulnerable due to known traits, including specific microhabitat requirements, limited ability to disperse, and *K*-selected life history traits lengthening the time required to adapt to changing conditions (Germano et al. 2023a). Therefore, climatic changes may result in reduced viability or potentially extinction of subpopulations or ESUs.

Translocations are likely to become a key management tool in assuring survival of *Leiopelma* in the face of a changing climate, particularly in the case of ESUs or sub-populations where dispersal beyond the current site is not possible, e.g. off-shore islands, and isolated habitats on the mainland. Here it will be necessary to assist dispersal, via translocations, to sites with predicted future climatic conditions within the suitable range for the species in question. This may include assisted migration (Seddon 2010; Chauvenet et al. 2013; Hällfors et al. 2017) outside the species' historic range, but where environmental conditions are predicted to be within acceptable limits in the future, and to sites where the species may have naturally settled had their distribution not been so drastically altered or isolated by human intervention.

In the long-term, translocations to large areas of contiguous habitat on the mainland may be the optimum strategy to allow populations to self-disperse to suitable sites in response to a changing climate (e.g. altitudinal migration). However, this strategy relies on establishing large populations in the presence of introduced predators, albeit where management can reduce the impact of these predators. This is a challenge for a *K*-selected species and is yet to be demonstrated via translocation of *Leiopelma* frogs.

### Cultural and social aspects

Exercising Māori tikanga (i.e. customs and correct procedures) when performing translocations in New Zealand can enhance mana (authority and prestige) for iwi and build relationships among everyone involved (Lyver et al. 2019). It also allows hapu and iwi to exercise their role as kaitikai (guardians). Consultation with iwi was conducted before all of the frog translocations reported here (with the exception of the early release on Kāpiti Island for which details are not known), though this aspect was often not detailed in reporting. In most cases, iwi representatives assisted in the collection and/or release of frogs. In the translocation of *L. archeyi* frogs to Pureora forest, iwi were actively engaged during all project stages working with other practitioners and stakeholders from the collection of frogs to the post-release monitoring (Cisternas et al. 2019).

When undertaking a translocation project it must be recognised that different stakeholders may have different objectives for engaging with the project, e.g. scientists might focus on ecological restoration or long-term species survival, while tangata whenua may see their involvement as an expression of kaitiakitanga, place-based customary responsibilities and practices of Māori whose genealogical history connects them to land, based on principles of reciprocity and the desire to maintain these relationships for future generations (McAllister et al. 2019). A local community member may simply appreciate the joy of knowing a species is nearby (Cisternas 2019; Cisternas et al. 2019; Parker et al. 2020). These objectives are not mutually exclusive, but it is important to understand this element of conducting a successful translocation at the outset and know that it can be achieved by meaningful stakeholder engagement (Parker et al. 2020).

In the case of New Zealand, collaboration with tangata whenua can reveal Māori customs and concepts relevant to conservation, such as the intrinsic understanding that humans are a part of nature, kaitiakitanga, and specifically native frogs as taonga (treasures) (Cisternas 2019). Cisternas et al. (2019) outline a framework for future partnerships, based on the philosophy of building relationships, exchange of knowledge, and incorporation of all voices. Social and cultural aspects will become increasingly important in the context of translocations, as releases become more common at sites that are closer and more accessible to a wider range of stakeholders e.g. mainland sites and sanctuaries versus islands where access is limited.

### Post-release monitoring

Several different types of monitoring are involved with translocations (Nichols & Armstrong 2012). In the case of New Zealand frogs, these may include monitoring of the source population for potential impacts of removing individuals, monitoring climatic variables at potential release sites prior to making the decision to translocate, and monitoring of predator levels before and after a translocation has taken place to ensure these are within acceptable levels. However,

in this section we focus on post-release monitoring of the focal species, a critical step in assessing progress, and in informing management decisions to aid success.

The duration of post-release monitoring for conservation-driven native frog translocations was notable with monitoring ongoing at all sites, spanning 37 years at Boat Bay, and over 30 years at Takapourewa. This is rare longevity for population monitoring on a global scale, especially among amphibians. Input from statisticians at a relatively early stage allowed techniques to be altered to maximise results, particularly in some of the earlier translocations (Pledger 1998; Tocher & Pledger 2005). In some cases, monitoring was initially conducted frequently but as it became clear the population was establishing time between monitoring trips was increased (e.g. Motuara Island, Nukuwaiata).

Most translocated *Leiopelma* populations have been monitored using mark-recapture, identifying individual frogs either by unique toe clip codes or via photo ID. To date, mark-recapture has provided valuable information, contributing to our understanding of natural history, population biology, ecology, and reintroduction biology for these species. For example, we have obtained estimates for survival of released individuals (Bell et al. 2004b; Tocher & Pledger 2005; Tocher et al. 2006; Bell & Pledger 2023), learned that competitive release increases body condition and reduces time to maturity in founder populations (Bell et al. 2004b; Tocher & Pledger 2005; Bell & Pledger 2023), increased our knowledge on post-release dispersal (Brown 1994; Tocher & Pledger 2005; Germano 2006; Lukis 2009; Karst 2013; Cisternas 2019; Karst et al. 2023) and found that homing is likely in adults when released over shorter distances (Tocher & Brown 2004).

These valuable data have allowed us to assess all populations against the first two stages of success (Table 3). However, this review has highlighted some important points related to post-release monitoring, notably in relation to assessing the third and fourth stages of success. In most cases, the mark-recapture surveys have been conducted on a grid immediately surrounding the release site, to facilitate repeated documentation of individuals and capture sites. But due to a combination of the species life-history and behaviour, the pattern seen in several of the case studies examined here is for settlement of most of the founding cohort at or near to the release site, while any additional release cohorts, or new recruits find home ranges in currently unoccupied habitat increasingly distant from the release site (Bell et al. 2004b; Tocher & Pledger 2005; Treweek et al. 2007). As such, when monitoring focusses on demographic patterns in the area immediately surrounding the release site, Stage 3 in translocation success (population growth) may not be recorded as home ranges of new recruits are primarily established beyond the monitoring grid. Additionally, monitoring a fixed area may miss animals that disperse beyond this space, as was highlighted when some individuals were found beyond the monitoring grid in a wider search at Pureora (Quinnell 2017; Cisternas 2019). Further, our data indicate cases where the number of released individuals is greater than the carrying capacity of the area monitored, the pattern seen may show initial population reduction (from dispersal and mortality) followed by levelling of the population at the presumed carrying capacity, as seen on Motuara Island (Tocher & Pledger 2005) but not necessarily yet at Boat Bay (Bell et al. 2004b; BDB, unpubl. data). The challenge in detecting Stage 3 is evident in Table 3, where for populations at Motuara Island, and possibly Nukuwaiata, evidence of Stage 4 has been detected before monitoring has

shown robust proof of population growth.

As adult *Leiopelma* are relatively sedentary, often captured repeatedly in a localised area, it will potentially take the lifespan of these frogs (over 40 years) for some indicators of Stage 4, e.g. founders make up a small proportion of captures, to be detected using mark-recapture in a restricted release-site plot. At the oldest successful translocation of 100 frogs at Boat Bay it was not until 2005, more than 20 years after the first release, that the population was first estimated to exceed 200 individuals (BDB & PD, unpubl. data). As such, a commitment for long-term monitoring is required from the outset. Difficulty in monitoring outcomes is exacerbated by the cryptic nature of *Leiopelma* and the inconsistency in emergence dependent on weather conditions (Newman et al. 1978; Cree 1989). This may result in several years between encounters of an individual; one individual frog at Maud Island evaded capture for more than 20 years, despite annual monitoring (Bell & Pledger 2010).

Data for the last two monitoring trips (2015 and 2016) at Nukuwaiata show markedly different results; in 2015 monitoring recorded 47 individuals of which 17 individuals (36%) were from the founding release group, 5 individuals (11%) were adult recruits, and 25 individuals (53%) were juveniles or subadults (< 35mm). Conversely, in the 2016 monitoring session there were 38 individuals recorded, 29 of which were from the founding group (76%), 5 individuals (13%) were adult recruits, and 4 individuals (11%) were juveniles or subadults. In this case, a different conclusion regarding progress in establishment of the population may have been reached based on the varying results for proportion of captures made up by original release frogs. However, this is likely a combined effect of the cryptic nature of the species, wetter weather conditions during monitoring in 2015 more favourable to smaller individuals, and potentially experience of survey personnel. This emphasises the need for data analysis that accounts for such covariates.

Identification of individuals is necessary for the mark-recapture techniques currently employed. Photo ID has proven useful in *L. archeyi* population studies (e.g. Bradfield 2004; Cisternas et al. 2022), however there is a degree of error with this technique since pattern markings may change over time in some individuals (Easton 2020b, 2021; SW pers. obs.). In the other two *Leiopelma* species, identification of some individuals is not possible, since a significant proportion—up to a third—have no distinct markings (Germano 2006). Further, different recorders may identify different features on the same frogs (Parrish 2004) meaning this technique could be prone to inaccuracy if a consistent system of assessing markings is not applied by all personnel conducting monitoring sessions. Toe clipping has been successfully employed at several sites. Even though this has been shown not to impact survival (Bell & Pledger 2010) it has raised both ethical and cultural concerns and is increasingly not used, while microchipping remains impractical for all but the largest frogs owing to the relative sizes of young frogs and transponders. As such, we currently have no ideal method to identify individuals in the short, medium, or long-term.

While the Miller et al. (2014) framework proved useful in assessing stages of success for native frog translocations, some indicators were rarely or never seen in post-release monitoring for *Leiopelma* using current methods. For example, at Stages 3 and 4 indicators include “capture of more animals than were initially released, in a defined monitoring period”, but with the cryptic nature of these species this is rarely achieved even when conditions are favourable; during annual monitoring

at Boat Bay over 37 years there is only one occasion where more than 100 individual frogs have been captured in a single monitoring trip. Another indicator for Stage 3, “breeding by second generation animals”, may take a long time to confirm given breeding is rarely observed; indeed no *L. hamiltoni* breeding has yet been seen in the wild. As a result, parentage cannot be attributed to a specific individual using technologies applied to date, and inferences using generation times will take decades.

In practice, different monitoring methods may be required to detect indicators of Stages 3 and 4 more quickly after translocation. A site occupancy method has been recommended for population monitoring of non-translocated *L. hochstetteri* (Crossland et al. 2005). This technique may have application for translocations and may be useful for the other species, particularly to assess the latter stages of population establishment. Trials of the site occupancy method (MacKenzie et al. 2017) have been undertaken for *L. archeyi* (Haigh et al. 2021) and *L. hamiltoni* (Germano 2021). Detection at both sites was highest after rain, so surveys coinciding with wet weather should be able to achieve more robust results with fewer survey repeats (Germano 2021; Haigh et al. 2021). Occupancy may prove a useful technique for translocations, particularly in assessing population dispersal during the latter stages of establishment. Alternatively, Cisternas et al. (2023) applied spatially explicit capture-recapture (SECR) to data from the Pureora site to assess population density at the release site and recommended that a replication of the monitoring grid would improve the reliability of demographic information for the population.

However, for all species, the cryptic nature of these frogs makes all monitoring challenging. Karst (2013) found that a frog had been missed during a census of a small enclosure at Zealandia, so even when material within a defined enclosure was removed these cryptic frogs can remain undetected. Long periods of non-detection are not uncommon for individuals, including a case of more than 20 years between re-captures (Bell & Pledger 2010). Monitoring is most effective when weather conditions are favourable, encouraging emergence, and thus detection probabilities, to be high (Cree 1989; Newman 1990). As such, timing monitoring trips to coincide with forecast rain, while not always logistically possible, will assist in improving results. Timing should also avoid seasons when male emergence may be low due to parental care (Cisternas 2019). Regardless, methods need to account for imperfect detection of individuals among sampling, as widely recommended in the literature for demographic monitoring of amphibian populations (Heyer et al. 1994; Schmidt et al. 2002; Mazerolle et al. 2007; Bailey & Nichols 2010).

Translocations have often been criticised for a lack of post-release monitoring, despite the fact that monitoring outcomes is necessary to assess success (IUCN/SSC 2013; Linhoff et al. 2021). However, the long-term monitoring at most *Leiopelma* translocation sites has been remarkable; but, with competing demands for conservation funding monitoring should be strategic, gathering the information necessary to answer key questions for assessing success (Ewen & Armstrong 2007; Nichols & Armstrong 2012). Cost-efficiency is even more critical when dealing with species such as the leiopelmatid frogs, which take a long time to establish populations. With limited funding, monitoring for translocations needs to be sufficient to answer questions relevant to assessing population establishment to inform conservation managers, or to answer specific research questions. Moving to less frequent monitoring

may be acceptable after the early stages of success have been confirmed (survival and reproduction), and where we are more confident of success based on our knowledge of what makes a high-quality release site. Further, it may be necessary to move to a different monitoring method as the stages of establishment are achieved. This approach, while answering the question of translocation success, may not, however, be appropriate where broader research questions are being asked, e.g. the long-term population monitoring work of Ben Bell and colleagues at several *Leiopelma* sites (Bell & Pledger 2010), although the emphasis for *L. hamiltoni* at Boat Bay has now changed, with toe-clipping no longer used (Bell & Pledger 2023).

### Can we establish the causes of success or failure?

Given the range of variables that differ between *Leiopelma* translocations, it is difficult to draw direct comparisons and definitively establish causes of success or failure in each case. However, predator management at release sites seems to be a key factor. This is no surprise, since introduced predators are a major threat to these species (Bishop et al. 2013; Bell & Bishop 2018; Egeter et al. 2019). Most successful translocations for *L. hamiltoni* (Boat Bay, Motuara Island, and Nukuwaiata) have involved releases on predator-free islands with high biosecurity controls. In Zealandia the test for whether this species can establish in the presence of mice with management measures, is looking positive (Karst et al. 2023), but it remains to be seen the extent to which this population can grow under the predation and competitive pressures that mice likely present. Data from Pureora show that a population of *L. archeyi* can likely be established at a site with ongoing management of some introduced mammals, both predators and herbivores (Cisternas 2019; Cisternas et al. 2023), although population growth seems to be slower than at sites where invasive predators are absent.

Founding cohort number also seems to play a role in determining success, given that all cases that show indicators of success (Boat Bay, Motuara Island, Nukuwaiata, Zealandia and Pureora) were founded with more than 70 individuals. This is in line with modelling (Tocher et al. 2006; Easton et al. 2020) and wider translocation theory (Armstrong & Seddon 2008; Ewen et al. 2012b).

Taking an adaptive management approach, altering management protocols to answer specific questions and respond to new data may also assist with population establishment in *Leiopelma* (Canessa et al. 2019). This type of approach has managed risk while testing specific questions at Zealandia (Karst et al. 2023) and was used to respond to low capture rates and modify monitoring protocols at Pureora (Smale 2006; Haigh et al. 2011; Quinnell 2017; Cisternas 2019; Cisternas et al. 2023).

The first translocation of either *L. hochstetteri* or *L. archeyi* to Kāapiti Island failed. However, with a small founding group, presence of introduced mammalian predators, and release at the start of summer it is not surprising that this attempt was not a success. The intra-island translocation on Takapourewa likely failed due to a combination of small founder numbers and proximity to the source resulting in homing of some individuals. However, the decision to conduct this as a trial with just 12 frogs was justified given the small size of the source population and that there had only been one clear conservation-led translocation at that time.

One unexpected result is the failure of *L. hamiltoni* to establish at the Long Island site. A population had already been successfully established at a similar site on neighbouring Motuara Island (Tocher & Pledger 2005) and the founding cohort (101 individuals), while smaller than on Motuara Island, had already proven large enough to establish a population at Boat Bay (Bell et al. 2004b). Habitat surveys in 2018, while providing limited information post-release, indicated mostly minor differences between the sites, although percentage of bare rock was a notable exception. One major difference was native predator management at the release site, with Motuara Island having a kiwi-proof fence but this measure was not taken on Long Island, so predation by weka or kiwi cannot be ruled out as contributing to failure at this site (Germano et al. 2023c). However, poor habitat quality may also have been a contributing factor (Germano et al. 2023c).

We currently have little evidence to support translocations as a tool for providing long-term benefit to *L. hochstetteri*; however, more positive outcomes may be seen if best practice methods were implemented for this species (IUCN/SSC 2013; Linhoff et al. 2021). Mitigation translocations carried out for this species had small founding populations, which were only monitored for a few weeks after release, with unknown long-term survival of relocated individuals (Parrish 2004; Beauchamp et al. 2005). Further, these are the only cases where a release was carried out where there was a resident population of the same species, and the effects of introducing new individuals to sites with an established population are unknown. If a site is at or near carrying capacity, there is a risk that introducing additional individuals will result in mortality or dispersal of either the released frogs, or some of the resident population, thus providing no net gain to the population or species (Germano et al. 2015; Sullivan et al. 2015). Evidence from mitigation translocations for New Zealand lizards indicates that success rates are lower, IUCN best practice is not often followed, and the long-term monitoring necessary to assess success is rarely carried out in line with these global trends for mitigations regardless of taxa (Germano & Bishop 2009; Germano et al. 2015; Sullivan et al. 2015; Romijn & Hartley 2016; Lennon 2019; Bradley et al. 2020).

While it is possible to establish populations of *L. hamiltoni* and *L. archeyi* through translocation, managers need to broadly consider the likely benefits of undertaking translocations versus the potential costs. Translocations are relatively high-risk and require significant resources, both up front (e.g. habitat modification, predator control) and long-term (e.g. monitoring and adaptive management). In some cases it may be more effective to prioritise management of current stronghold sites for better outcomes with lower risk. As such, translocations need to be considered as one option among a suite of conservation management techniques. Results, both successes and failures (Miller et al. 2014), should continue to be reported for both existing and future translocation sites to assist with future decision-making. Lessons from conservation translocation of *Leiopelma* indicate that translocations with larger founding cohorts (more than 70 individuals), to sites without a resident population, and that are free of mammalian predators are more likely to succeed. Finally, we recommend that the translocation-related goals in the Native Frog Recovery Plan (Bishop et al. 2013), when next reviewed, be re-visited and updated in line with findings from this review.

*Leiopelma* translocations have performed at, or above, the expected level of success based on reviews of translocations for other taxonomic groups in New Zealand and abroad, with a

success rate of fifty per cent. While much effort has gone into intensive monitoring of released populations, current methods may not be providing good value for money after survival of individuals and reproduction have been recorded. Additional methods may need to be applied to monitor the latter stages of translocation success: population growth and reaching a viable population. With varied methods applied across translocations to date it is difficult to conclude which factors have most influenced translocation success for *Leiopelma*; however, predator management, founding numbers and habitat quality appear to be potentially significant in determining outcomes. Beyond this, there are several steps during a translocation where measures can be taken to increase chances of success. Good planning, site assessment, and involvement of stakeholders, particularly tangata whenua, prior to any decisions being made will assist in assessing whether translocations are an appropriate tool given the objectives and high-risk nature of this intervention. Both conservation-driven and mitigation-driven translocations should follow established best practice guidelines. Consideration should be given to the long-term predicted suitability of any future release sites, which may need to involve assisted migration to allow for the effects of climate change.

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## Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

### Appendix S1. Spreadsheet of reviewed translocations.

The New Zealand Journal of Ecology provides supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed and copy-edited but any issues relating to this information (other than missing files) should be addressed to the authors.