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Age dependant effects of rat control on Archey's frog (*Leiopelma archeyi)* at Whareorino, New Zealand

Jennifer M. Germano[1]* , Lucy Bridgman[1] , Helene Thygesen[1] and Amanda Haigh[1]

[1]Department of Conservation, Wellington, New Zealand
*Author for correspondence (Email: jgermano@doc.govt.nz)

Abstract: Predation by introduced mammals is considered a primary threat to New Zealand's native frog populations. Rats are known predators of the terrestrial Archey's frog (*Leiopelma archeyi*), New Zealand's smallest Leiopelmatid frog. During a 12 year study in Whareorino Conservation Area, we investigated effects of sustained rat control on survival, number of independent juveniles per adult, and abundance of Archey's frog. Frogs were monitored following a capture-recapture robust design at four grids, split between a 300-ha 'nontreatment' area and a 300-ha rat control 'treatment' area. Low rat abundances were achieved in the treatment area for much of the study (rat tracking index threshold: < 10%), although, mouse abundances were higher at times there. Adult frog survival rates were greater in treatment (0.74–0.78) compared to nontreatment (0.53–0.55) areas, indicating rat suppression reduces adult frog mortality; however, juvenile and subadult frog survival was lower in treatment (0.03–0.27) than nontreatment areas (0.26–0.61). This may be due to increased vulnerability of smaller frogs to other predators e.g. mice. Population modelling showed ongoing rat suppression has a positive effect on the rate of independent juveniles produced per adult frog and on adult abundance over time, revealing a significant increase in frog abundance in treatment (annual rate of increase, adult frogs: 10.75, 95%; CI [4.62, 17.24]) compared to nontreatment areas where frogs declined (annual rate of decline, adult frogs: −5.73, 95% CI [−10.95, −0.21]). We show that suppressing rat populations is successful for frog population management at Whareorino Conservation Area. However, rat control alone may not be sufficient to recover depleted populations elsewhere or grow newly translocated populations on the mainland. We recommend further work to substantiate the above findings and research to investigate both the impact of mice on native frogs and elucidate age class dependant parameters for Leiopelmatid frogs in mainland and island populations.

Keywords: Archey's frog, landscape scale predator control, *Leiopelma archeyi*, mouse, pest control, rat

Introduction

The devastating effect of introduced mammalian predators on New Zealand's native fauna is well documented (Towns & Daugherty 1994; Clout & Craig 1995; Towns et al. 2001). In particular, negative impacts on bird abundance and diversity are well recognised (King 1984). Significant conservation gains have been made through landscape scale predator control for numerous avian species (Innes et al. 1999; Innes et al. 2010; Whitehead et al. 2010; Robertson et al. 2019). However, the impacts of mammalian predators on other native fauna, including herpetofauna, and our ability to use standard predator control methods to recover their populations, is relatively poorly understood and developed.

The introduced ship rat (*Rattus rattus*) is implicated in the extinction and decline of numerous New Zealand native species. For this reason, control operations to suppress ship rat populations where they occur are a standard conservation practice. Tools include ground-based control using traps or toxic bait in bait stations, or aerial application of 1080 toxin (sodium monofluroacetate). Successful conservation outcomes

following suppression of rats (usually along with other mammalian pests including possums) have been documented in species such as kōkākō and robins (reviewed in Innes et al. 2010). However, the release of mouse populations following rat control has also been recognised (Innes et al. 1995; Ruscoe et al. 2011; Goldwater et al. 2012; Bridgman et al. 2018), and the unintended consequences of increased mouse abundance and activity can undermine conservation outcomes.

New Zealand's endemic amphibians have suffered following introduction of mammalian pests. The extinction of four Leiopelmatid frog species and the reduction in range of the three extant species occurred synchronously with the arrival of humans and the introduction of mammalian predators (Worthy 1987; Towns & Daugherty 1994). Predation by introduced mammals is considered a primary threat to New Zealand's native frog populations on the mainland (Bishop et al. 2013), in particular direct evidence of predation suggests rodents may represent the greatest threat to Leiopelmatid frogs (Egeter et al. 2015). Both Archey's frog (*Leiopelma archeyi*) and Hochstetter's frog (*Leiopelma hochstetteri*) are consumed by ship rats (*Rattus rattus*) with genetic studies suggesting the

impacts of rat predation are greater for the terrestrial Archey's frog than for the semi-aquatic Hochstetter's frog (Thurley & Bell 1994; Egeter et al. 2015; Egeter et al. 2019; Fitzgerald & Campbell 2002).

Several studies have looked at the outcomes of landscape scale predator control for Hochstetter's frog, but results have been mixed (Musset 2005; Nájera–Hillman et al. 2009; Longson et al. 2017; Crossland et al. 2023). Two studies concluded large-scale rat control or eradication had a positive impact on Hochstetter's frog populations; however, these did not control for differences in habitat (Musset 2005; Longson et al. 2017). When habitat differences were considered, Najera-Hillman et al. (2009) found no impact of rat control on Hochstetter's frog populations. More recently, Crossland et al. (2023), found a positive impact of predator control with substantial differences in the level of impact between age classes. In 2006, Hamilton's frog (*Leiopelma hamiltoni*) was released into two areas of the Zealandia mainland sanctuary: a kiwi and mouse-proof enclosure and an area outside of this enclosure which was accessible to both kiwi and mice (Lukis 2009; Karst et al. 2023). While survival was high and recruitment occurred within three years of release inside the mouse and kiwi proof enclosure, the frogs outside the enclosure declined drastically. Predation by kiwi and/or mice was considered the most likely cause of initial decline for the population (Lukis 2009). Despite this, with ongoing mouse control and a supplemental translocation, the Zealandia Hamilton's frog population has continued to survive (Karst et al. 2023). There have been no published studies on the efficacy of predator control for the two terrestrial Leiopelmatid species, Archey's frog and Hamilton's frog.

Archey's frog, is known from only two, geographically separate locations: Whareorino Conservation Area in the Western King Country and the Coromandel Peninsula (Thurley & Bell 1994; Bell et al. 1998). A third translocated population is establishing in Pureora Forest Park (Cisternas et al. 2021). Found primarily in unmodified podocarp forest 400 m above sea level, Archey's frog is the smallest Leiopelmatid species and listed as At Risk of extinction under the New Zealand Threat Classification System (Burns et al. 2018), Critically Endangered by the IUCN (IUCN SSC Amphibian Specialist Group 2017), and as the most evolutionarily distinct and globally endangered amphibian (Zoological Society of London 2020). The stronghold population of Archey's frog on the Coromandel Peninsula underwent an 88% decline in the late 1990s and has not recovered in over twenty years since the crash was documented (Bell et al. 2004; Bell & Pledger 2015).

In 2003, upon finding direct evidence of rat predation of Archey's frogs, a rat control programme was established at Whareorino Conservation Area (Thurley & Bell 1994; Fitzgerald & Campbell 2002; Thurley 2003). In 2005, a long-term capture-recapture study was set up to monitor the Archey's frog population. In this paper we evaluate the effects of sustained rat control (i.e. continuous suppression of the ship rat population) on the number of independent juveniles produced per adult, survival, and the abundance of Archey's frog in Whareorino Conservation Area and identify options for future predator control research and management to protect Archey's frog populations.

Methods

Study area

The study was undertaken in Whareorino Conservation Area in the Waikato Region of the North Island of Aotearoa/ New Zealand (Fig. 1). The study area comprises of 600 hectares of mixed podocarp forest occupied by Archey's frog and was divided into two c. 300 ha blocks. Continuous ground-based rat control was undertaken starting in August 2003 in the Northern 300 ha block (treatment area), with the Southern 300 ha block left untreated (nontreatment area). Archey's frogs were monitored in both blocks one to two times per year from December 2005. Data presented in this study cover the period August 2003 to December 2015. Other potential predators such as pigs, mustelids and cats were assumed to be similar at both sites and no pig rooting was observed within the grids during the study.

Rat control

Ground-based rat control commenced in the treatment area in August 2003 via a network of bait stations at c. 50 m spacing along lines c. 200 m apart, baited initially for 9 months with Kiwicare No Possums® 1080 long-life gel bait. The anticoagulant Racumin© (Coumatetralyl) was placed throughout the treatment area every two months from May 2004 and later replaced with another anticoagulant D-Block© (Diphacinone). This control was designed to achieve continuous suppression of rats to low densities. During this study, aerial pest control using 1080 was carried out over the treatment half of the study area as part of a much larger (c. 20 000 ha) pest management operation to reduce the density of brushtail possums (*Trichosourus vulpecula*) and rats. This aerial control was undertaken in winter during August 2012.
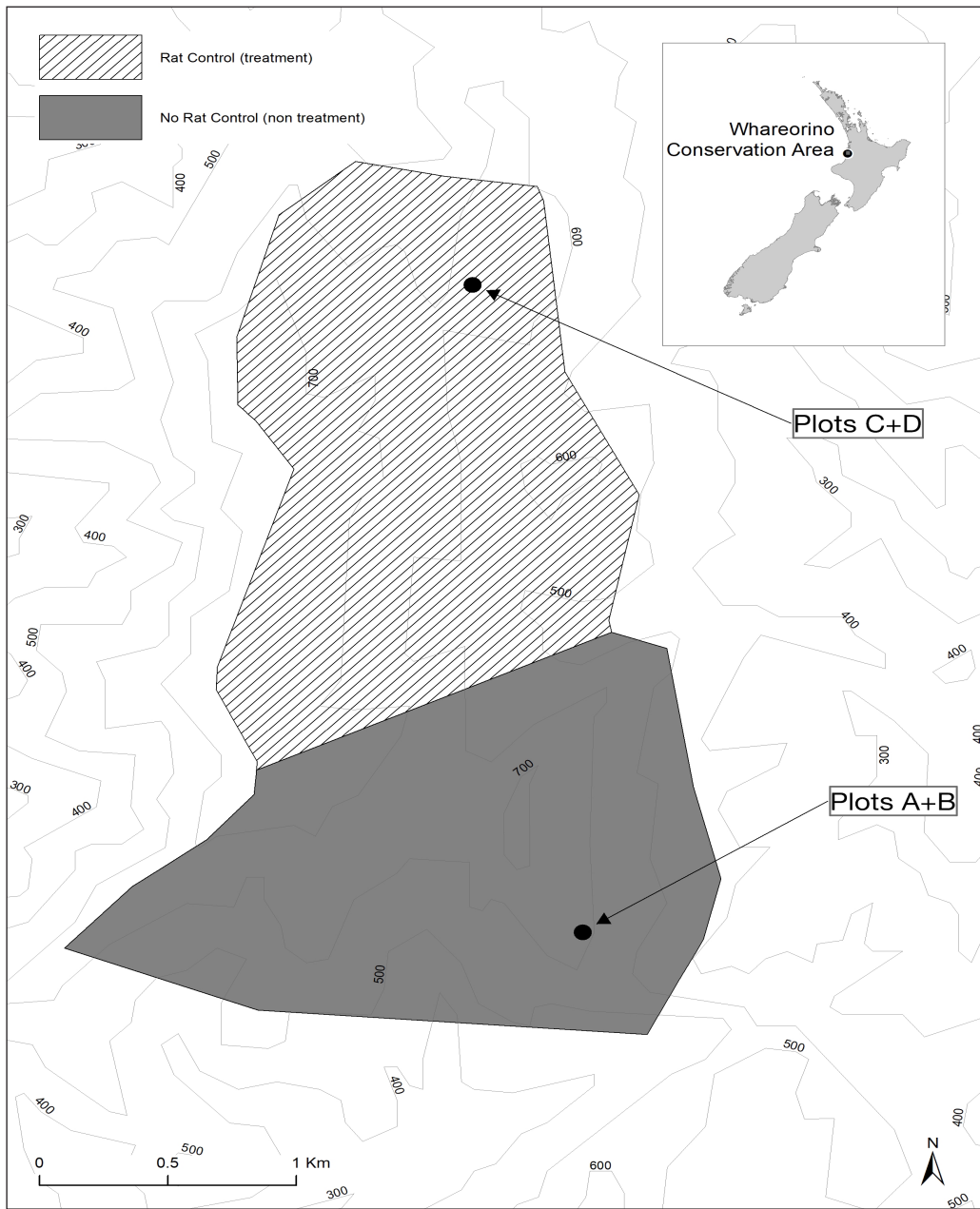
Rodent abundances

Indices of rat and mouse relative abundance were measured for one night approximately every three months throughout the year, using four lines of ten inked footprint tracking tunnels baited with peanut butter c. 50 m apart in the treatment area (Gillies & Williams 2013). Three lines in the nontreatment area were monitored for one night every three to six months for comparison with rat and mouse abundances in the treatment area.

To ensure representative coverage of both the treatment and nontreatment areas, tunnel lines were placed c. 200 m apart and run from randomly chosen points and bearings perpendicular to the central ridgeline through the study area. The management threshold set for continuous suppression of rats within the treatment area was a mean rat tracking index of < 10%. This was based on knowledge, at the time, of rodent suppression for bird conservation in similar North Island forests (Innes et al. 1999) and therefore considered an achievable threshold that should provide protection to the frog population. A threshold tracking index was not set for mice.

Frog monitoring

Within each of the 300 ha rat control treatment and nontreatment blocks, two 10 × 10 m frog monitoring grids were established from a set of 4–5 'candidate' grids in each block. Grids A and B were in the nontreatment area, and grids C and D in the rat control treatment area. Candidate grids were set up from randomly chosen points and bearings taken from a fixed location in each block. From these, grids A to D were chosen

Figure 1. The location of Whareorino Conservation Area.

so that habitat, altitude and microclimate were as similar as possible and frog abundance sufficient, at least 8–10 frogs per night in preliminary surveys, for capture-recapture surveys. Each grid was divided into five lanes, each two metres wide.

Frog monitoring surveys were designed to facilitate analysis using the robust design (Pollock 1982; Kendall 2011) at each of the four grids. From November 2005–May 2013, two monitoring sessions were completed annually per grid in November/December and February/March, each comprising four consecutive nights of capture-recapture surveys. The exception to this was 2011, where the November/December survey was missed. From November 2013 to December 2015, one monitoring session took place each year in November/ December. Monitoring was carried out over a four-week period, one week per grid, during the summer months when conditions were best suited for finding emergent frogs. i.e.

humid, warm nights (Cree 1989; Webster et al. 2003). Starting one hour after sunset, each grid was systematically searched by a consistent number of searchers for emergent frogs once during each search night.

Each frog was captured and placed in a plastic bag; the microhabitat (e.g. under fern; on log) and location within the grid to the nearest centimeter were recorded. Frogs were photographed using a specially designed mirror box which allowed one image to capture four views of each frog simultaneously (Wallace 2004; Haigh et al. 2007). Unique patterned skin markings were later used to identify individual frogs for capture-recapture analysis (Bradfield 2004). Frogs were then weighed and measured (snout-vent-length) before being released at the exact capture location. To reduce the risk of disease transmission new nitrile gloves were used when handling each frog.

Table 1. Parameters incorporated into a set of open robust design multi-strata models to analyse Archey's frog capture-recapture data from four monitoring grids at Whareorino Conservation Area. S is the survival rate, Psi is the between stratum transition rate, p is the capture probability, pent is the probability of entering the study area, Phi is the probability of remaining in the study area. Stratum refers to whether frogs were classed as adult, subadult or juvenile when they were captured.

S	Psi	p	pent	Phi
time	time	time	time	time
stratum	stratum	stratum		
grid		stratum+time		
stratum+time				
stratum+grid				
stratum*grid				
stratum*grid+time				

Analysis

Rodent abundance

We calculated rat and mouse tracking indices as a proxy for abundance (Gillies & Williams 2013). We calculated the mean percentage (± standard error) of tunnels per line containing rat and mouse tracks in each of the treatment and nontreatment areas during each quarterly rodent monitoring session. We graphed rat and mouse tracking indices to evaluate population trends and the effectiveness of rat control in the treatment area.

Frog population dynamics

We categorised frogs as juvenile, subadult or adult according to their snout vent length at each capture. We classed frogs that were ≤ 14 mm as juvenile; frogs that were 14–25 mm as subadult and frogs that were ≥ 25 mm as adult (Thurley & Bell 1994; Bell et al. 1998).

Capture-recapture models

We analysed capture-recapture data using the open robust design multi-strata (ORDMS) models (Kendall & Nichols 1995; Kendall 2011) available in Program Mark (White & Burnham 1999). These models allow for temporary emigration which is appropriate for New Zealand frogs which may hide underground and be unavailable for an entire monitoring session of several nights (Bell & Pledger 2010).

ORDMS models include the following parameters which were incorporated into a set of models with predictor variables as described in Table 1:
• Survival: S
• transition rate between stratum (i.e. age class): Psi
• capture probability: p
• the probability of entering the study area: pent
• the probability of remaining in the study area: Phi

With 8 different parameterisations of S, 3 for Psi, 4 for p, 2 for pent and 2 for Phi (Table 1), in total $8 \times 3 \times 4 \times 2 \times 2 = 384$ different models were fitted. We ranked models according to Akaike Information Criteria (AIC) to determine the combination of parameters and predictor variables that best fit the data.

Post-hoc analyses of frog abundance and independent juveniles produced per adult

We used the derived estimates of population size, N, from the ORDMS model that best fit the data to calculate the rate of producing independent juveniles per adult frogs as N for new juvenile frogs at time t divided by N for adults at time $t - 1$. Independent juveniles are considered as post-metamorphic juveniles that are independent following a period of parental care. We took only the estimates from the more regular November/December capture sessions to avoid any confounding between seasonal effects and year on frog abundance, particularly for juvenile frogs. We used linear mixed effects models to determine whether juvenile recruitment rates differed for grids C and D receiving the rat control treatment compared to nontreatment area grids A and B. We included time as a random effect to account for potential fluctuations in production of independent juveniles per adult over time that were unrelated to suppression of the rat population. We also included a grid 'factor loading' variable, coded as −1 and +1 for the two grids in the same treatment group, to account for potential inherent variation in juvenile production rates due to differences in frog abundance on grids, unrelated to rat control.

To evaluate whether there was any effect of the rat control treatment on frog population size we again took the derived estimates of juvenile, subadult and adult N, from the ORDMS model that best fit the data using the estimates from the more regular November/December capture sessions. We log transformed the N estimates and used linear regression models to determine whether abundance of frogs in each age stratum varied depending on the application of the rat control treatment. We included time as a continuous predictor variable and we included an interaction term between the rat control variable and time. We also used a grid 'factor loading' variable to account for potential inherent variation in frog population size on grids, unrelated to rat control.

All capture-recapture models were carried out using Program Mark (White & Burnham 1999) version 9.0 called through RMark (Laake 2013) in R 4.1.2 (R Core Team 2021). Linear mixed effects models were carried out in R 4.1.2 using the lme4 package (Bates et al. 2015).

Results

Rat control and rat and mouse abundance

Between 2003 and 2015, 60 rat and mouse tracking tunnel monitoring sessions were completed in the treatment area and 34 in the non-treatment area. The mean tracking rate for rats in the treatment area dropped from a pre-control level of 62.5% (± 9.5 se) to 0 % (± 0) within two to four weeks of first bait application in August 2003 compared to a mean tracking rate of 86.7% (± 6.7) in the nontreatment area (Fig. 2). In the treatment area, the mean rat tracking index was maintained at or below the 10% threshold for most of the study period (i.e. for 76.7 % of all tracking tunnel monitoring sessions). By comparison, mean rat tracking rates ranged from 27.3% (± 3.9) to 93.3% (± 6.7) in the nontreatment area throughout the study period (Fig. 2).

Mean mouse tracking rates stayed at or below 10% in the nontreatment area throughout the study period. By comparison, in the treatment area, mean mouse tracking was 5% (± 5) before rat control started and then fluctuated between zero and 37.5% (± 7.5) and was above 10% for 12/60 (20%) of all tracking tunnel monitoring sessions (Fig. 2).

Frog monitoring

Eighteen monitoring sessions took place on each grid from November 2005 to December 2015, totalling 72 sampling nights per grid. A combined total of 6426 frog captures were recorded and 2569 individual frogs identified across the four monitoring Grids A to D (Table 2).

Capture-recapture models

The ORDMS model that best fit the frog capture-recapture data was:

$$S(\sim Grid * stratum + time)Psi(\sim stratum)pent(\sim time)$$
$$Phi(\sim time)p(\sim stratum + time) \qquad (1)$$

We rejected all other models because AIC differed by more than two from the best model.

Survival of frogs varied according to the grid they were captured on and stratum (adult, subadult or juvenile) and there was an interaction between these two variables. Survival

Table 2. Number of Archey's frogs captured, and individual frogs identified from eighteen monitoring sessions at four grids, November 2005 to December 2015, Whareorino Conservation Area. Grids A and B were in an area with no rat control. Grids C and D were in an area where a rat control treatment was applied.

Grid	Captures	Individuals
A	707	212
B	1178	451
C	2193	961
D	2348	945
Total	6426	2569
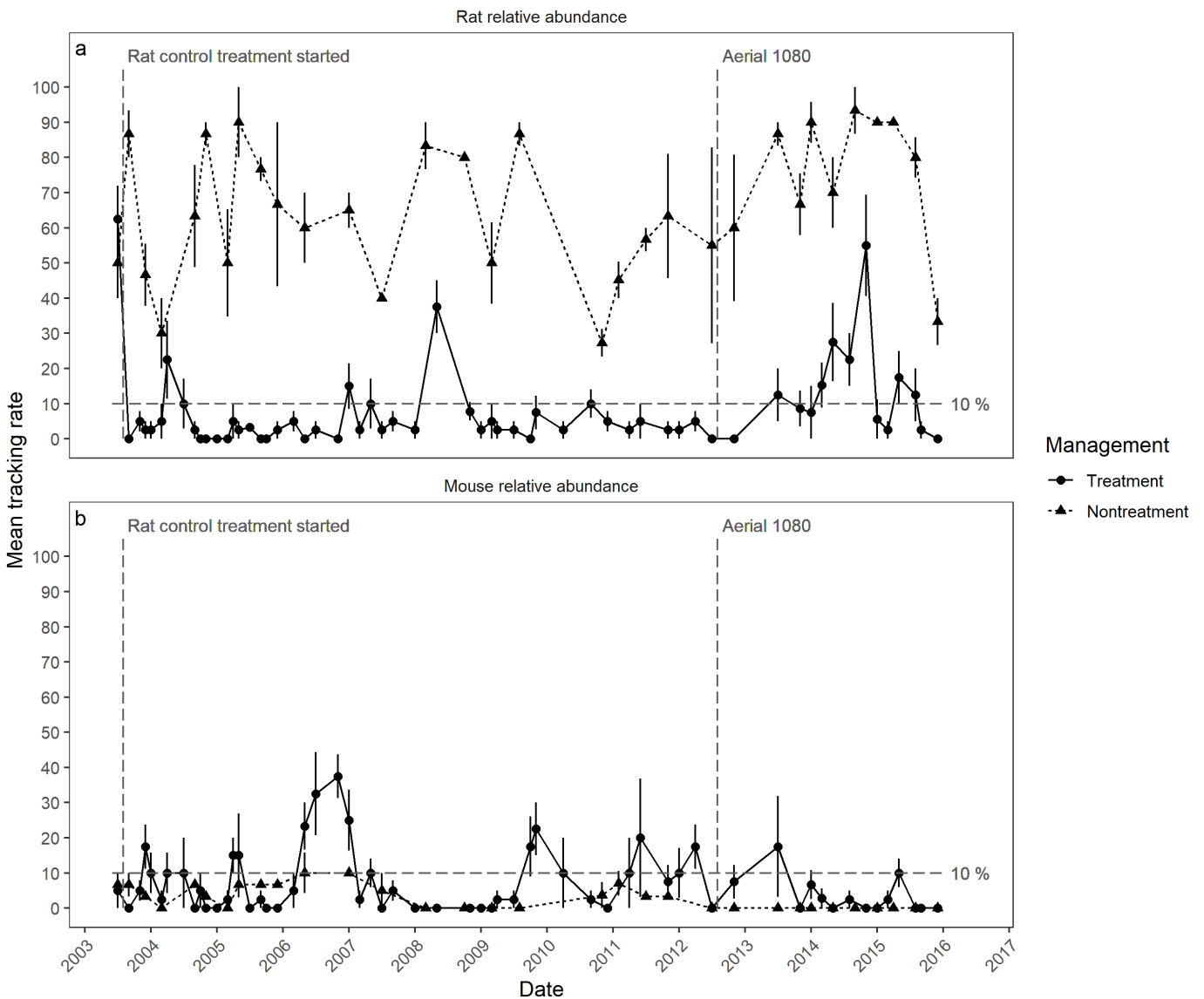
Figure 2. Mean tracking rates for (a) rats and (b) mice in the rat control treatment and non-treatment management areas at Whareorino Conservation Area. Data are the mean percentage of rodent monitoring tunnels with rat or mouse footprints recorded in them. Error bars are ± standard error.

Table 3. Annual survival rates for juvenile, subadult and adult frogs on four independent monitoring grids estimated using an open robust design multi-strata capture-recapture model. Grids A and B were in an area with no rat control. Grids C and D were in an area where a rat control treatment was applied. Figures in parenthesis are 95% confidence intervals.

| Grid | Survival estimate | | |
	Adult	Subadult	Juvenile
A	0.50 (0.37, 0.64)	0.48 (0.33, 0.63)	0.58 (0.18, 0.98)
B	0.49 (0.35, 0.63)	0.39 (0.26, 0.51)	0.25 (0.08, 0.41)
C	0.70 (0.59, 0.81)	0.24 (0.14, 0.33)	0.14 (0.07, 0.18)
D	0.74 (0.64, 0.85)	0.25 (0.15, 0.34)	0.04 (0.01, 0.08)

Table 4. Output from post-hoc linear models performed on the derived estimates of N for adult, subadult and juvenile frogs captured on four monitoring grids (A, B, C, D) extracted from open robust design multi-strata mark-recapture models. Variables included were rat control treatment vs. no rat control and time. A grid factor loading variable was included to account for potential inherent variation in frog populations on grids, unrelated to rat control.

|	Estimate	Std. Error	T value	P value
Adult frogs				
(Intercept)	3.347	0.196	17.047	$<2.000 \times 10^{-16}$***
Time	−0.059	0.029	−2.032	0.050
Rat Control Treatment	−0.024	0.278	−0.088	0.930
Grid Factor Loading	−0.173	0.139	−1.245	0.222
Time:Rat Control Treatment	0.161	0.041	3.922	0.000***
Time:Grid Factor Loading	0.026	0.021	1.287	0.207
Subadult frogs				
(Intercept)	3.581	0.307	11.675	1.920×10^{-13}***
Time	−0.111	0.045	−2.445	0.020*
Rat Control Treatment	0.130	0.434	0.3	0.766
Grid Factor Loading	0.061	0.217	0.279	0.782
Time:Rat Control Treatment	0.173	0.064	2.691	0.011*
Time:Grid Factor Loading	0.037	0.032	1.154	0.257
Juvenile frogs				
(Intercept)	1.904	0.411	4.637	5.060×10^{-5}***
Time	−0.023	0.061	−0.376	0.709
Rat Control Treatment	0.813	0.581	1.4	0.171
Grid Factor Loading	0.030	0.290	0.104	0.918
Time:Rat Control Treatment	0.158	0.086	1.84	0.075
Time:Grid Factor Loading	0.014	0.043	0.326	0.746

of adult frogs was higher on grids C and D, where the rat control treatment was in place, compared to grids A and B in the nontreatment area; however, survival of subadult and juvenile frogs was lower on treatment grids C and D than on non-treatment grids A and B (Table 3). Survival of frogs also varied over time.

The transition rates for frogs changing strata varied according to the stratum from which they were transitioning. The annual rate for juvenile frogs transitioning to subadult frogs was 0.92, 95% CI [0.84, 0.96]. The annual rate for subadult frogs transitioning to adult frogs was 0.13, 95% CI [0.11, 0.15]. The parameters Phi and pent (the probabilities of entering and remaining in the study area, respectively) varied according to time. The probability of capture, p, was influenced by stratum and time. Capture probability for adult frogs ranged from 0.20, 95% CI [0.18, 0.22] to 0.27, 95% CI [0.24, 0.30]. Similarly capture probability for juvenile frogs ranged from 0.19, 95% CI [0.17, 0.23] to 0.26, 95% CI [0.22, 0.30], whilst subadult capture probability tended to be higher and ranged from 0.31 95% CI [0.28, 0.33] to 0.39, 95% CI [0.36, 0.43].

Frog abundance and independent juveniles per adult
The rat control treatment had a significant positive effect on the rate of producing independent juveniles per adult (t = 3.663, p = 0.001). The model predicted a rate of 0.24 in the absence of rat control and 0.7 in the presence of rat control.

Post-hoc linear models performed on the derived estimates of N for the frog populations on each grid showed that rat control had a positive effect on frog abundance over time. This effect was significant for adult and subadult frogs (Table 4). For adult frogs, in the absence of rat control, there was a −5.73, 95% CI [−10.95, −0.21] annual decline in abundance. For subadult and juvenile frogs this annual decline rate was −10.50, 95% CI [−15.46, −5.26] and −2.26, 95% CI [−7.67, 3.47], respectively. In the presence of rat control, frog populations increased with annual rates of 10.75, 95% CI [4.62, 17.24]; 6.36, 95% CI [0.48, 12.60] and 14.48, 95% CI [8.14, 21.19] for adult, subadult and juvenile frogs, respectively (Fig. 3).
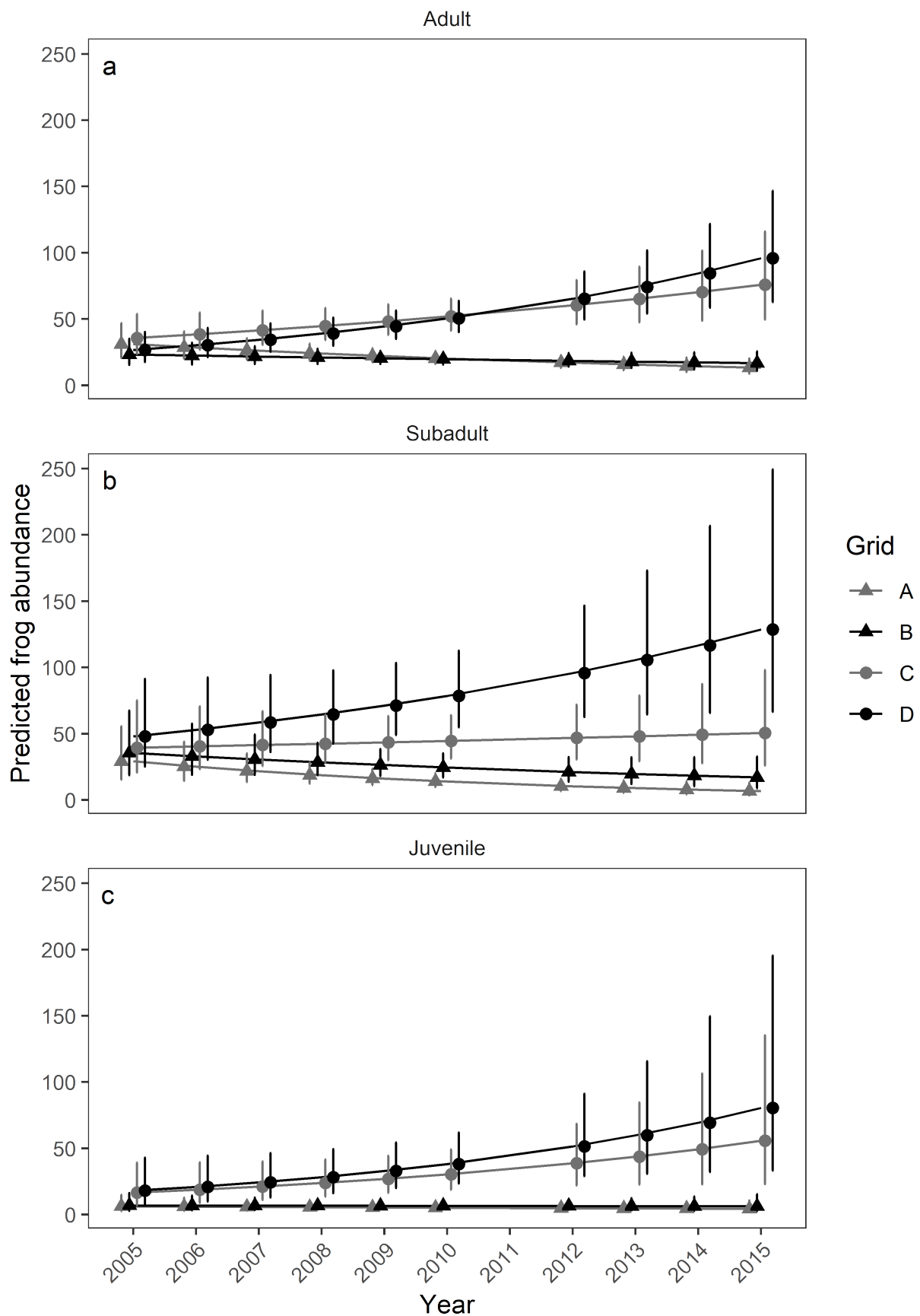
Figure 3. Abundance (N) of (a) adult, (b) subadult and (c) juvenile frogs predicted from post-hoc linear models performed on the derived estimates of N extracted from open robust design multi-strata mark-recapture models. Error bars are 95% confidence intervals. Frogs were captured on four independent monitoring grids. Grids A and B were within a nontreatment area where no rat control took place. Grids C and D were within an area where rats were controlled. Linear models showed a significant increase in adult and subadult abundance over time on grids C and D in the rat control area compared with grids A and B outside of the rat control area.

Discussion

Rodent population dynamics

The nontreatment tracking data show that the Whareorino Conservation Area has high natural levels of rats usually tracking in the 50–90% range and rarely falling below 30%. This is similar to what Walker et al. (2019) characterised as a warm "ratty" forest. Predator management tools used in this study (e.g. ground baiting, aerial 1080) were successful in suppressing the ship rat population and kept tracking numbers below the 10% threshold for most of the study period.

Rats supress mouse populations through intraguild predation (Bridgman et al. 2013; Bridgman et al. 2018). Due to this interaction effect, mouse abundance and activity can increase following ship rat control (Innes et al. 1995; Ruscoe et al. 2011; Goldwater et al. 2012; Bridgman et al. 2018; Walker et al. 2019). In the nontreatment area with high rat abundance, mean mouse tracking rates never rose above 10%; however, in the treatment area where rat numbers were suppressed, mean mouse tracking rates rose above 10% in five of the study years.

Frog population dynamics

Survival

We found that survival rates for adult frogs on grids within the rat control area were greater than for adult frogs in the nontreatment area. This indicates that suppression of the rat population removes a source of increased mortality for adult frogs. A number of introduced mammalian species are known predators of native and introduced frogs in New Zealand including ship rats, stoats, pigs, cats and ferrets (Egeter et al. 2015). Ship rats in particular have been the focus of most reports of native frog predation (Thurley & Bell 1994; Egeter et al. 2019; Fitzgerald & Campbell 2002), and other studies on predator control (Musset 2005; Nájera–Hillman et al. 2009; Longson et al. 2017; Crossland et al. 2023). The mechanism by which rats impact adult Archey's frog survival is likely to be through predation.

Despite this, it has been noted that there is a paucity of evidence of direct predation on *Leiopelma* spp. (Egeter et al. 2015). Egeter (2014) concluded that traditional methods of identification of prey in small mammal stomach and faecal contents would be of limited use for identifying frog bones and that caution is required when using forensic pathology to determine the predator species responsible for the death of a frog. However, in laboratory trials he did find that both mice and ship rats consumed introduced southern bell frogs (*Litoria raniformis*) of a similar size to adult Archey's frogs, though they required motivation and did not consume frogs as readily as Norway rats (Egeter 2014). Frogs may not be a primary prey of rats, but rats may consume them during times of alternative food shortage. Studies have also shown that even if direct predation events are rare, disturbance, from predators, particularly ubiquitous ones, can impact prey fitness (Creel & Christianson 2008).

Whilst adult frog survival was higher when rats were controlled, juvenile and subadult frog survival was lower. We see two potential explanations for this finding: (1) higher survival (and abundance) of adult frogs creates more intraspecific competition for resources with resulting impacts on survival of subadult and juvenile frogs; (2) the release of house mice following rat control resulted in a new pressure which disproportionally impacted smaller frogs. Little is known about intraspecific competition and density-related

population dynamics of New Zealand native frogs to support or oppose explanation (1). In support of explanation (2), whilst there is no direct evidence of wild mouse predation on Leiopelmatid frogs (Egeter et al. 2015), in laboratory trials mice consumed southern bell frogs and the translocation of Hamilton's frog to Zealandia suggests that mice may be an issue in the absence of other mammals (Lukis 2009; Egeter 2014; Karst et al. 2023). It is not inconceivable that smaller frogs would be disproportionately preyed upon by mice as a small predator capable of accessing small refuges used by juvenile and subadult frogs. For example, white-footed mice (*Peromyscus leucupus*) selectively prey upon eggs of a small size and are limited by the gape of their mouth (DeGraaf & Maier 1996).

Information from other islands in the Southern Ocean suggest that the range and severity of mouse predation is greatly increased in the absence of other introduced mammals (Angel et al. 2009). Recent studies in New Zealand have also begun to show the serious impacts of mice on lizards and invertebrates, especially in the absence of other predators (Hoare et al. 2007; Norbury et al. 2014; Watts et al. 2022; Norbury et al. 2023). While this study did not show definitive impacts of mice, the lower survival of juvenile and subadult frogs in rat-suppressed sites indicates the need for further investigation. This is especially true as the large reduction in survival of juveniles and subadults occurred with just a moderate increase in mouse tracking rates following rat control. Growing efforts across the country of rat, stoat and possum control through initiatives such as Predator Free 2050, may have detrimental impacts on some taxonomic groups, such as herpetofauna and invertebrates if mice are not also controlled. It is critical that predator control programmes fit the biodiversity values that they aim to protect and the outcomes sought.

A study of predator control impacts on Hochstetter's frogs showed a substantial difference in the impacts of predator control on the various age classes of frogs (Crossland et al. 2023). While mice were not in high abundance at this site, along with the results of this study, it does suggest that age classes differences should be explicitly considered in future Leiopelmatid monitoring (Crossland et al. 2023).

Independent juveniles per adult

We found that breeding productivity, expressed as the ratio of independent juvenile frogs in the population per adult, was higher in the rat control area compared to nontreatment. This measure incorporates fertilisation, parental care, hatching, rearing, and survival to the stage where the juvenile frog is detected in a survey. Given that survival of small frogs was negatively impacted by the rat control treatment, we infer that the positive impact of rat control on the appearance of independent juveniles is most likely to be linked to vulnerability (and associated lower survival) of adult frogs along with their offspring during the stage of male parental care of eggs and hatchings. This may be similar to some New Zealand bird species which are also most vulnerable to mammalian predators on the nest (Remeš et al. 2012). It may also lead to differential survival by sex as male Archey's frogs provide parental care; however, we were unable to test this due to the fact that terrestrial Leiopelma are monomorphic and cannot be sexed in the field (Germano et al. 2012).

Abundance

We found that despite negative impacts of rat control on subadult and juvenile survival rates, the benefits of higher adult survival

and improved rates of producing independent juveniles led to increasing abundance of frogs in the rat control area over time, compared to a population decline in the nontreatment area. This shows that the rat control programme is having the desired frog population recovery outcome. The terrestrial Leiopelmatid frogs are known to live for over 40 years (Bell & Pledger 2023), have clutch sizes of only 1–19 eggs and exhibit male parental care (Bell 2010). Like many New Zealand species, this suggests that they are a prime example of K-selected life history traits. Like other long-lived, K-selected species (King & Moors 1979; Robertson et al. 2011; Whiterod et al. 2018), adult survival of Leiopelmatid frogs is a key driver in the maintenance of populations.

Implications for Leiopelmatid conservation and recommendations for the future

Several studies have looked at the population dynamics of Leiopelmatid frogs (Bell et al. 2004; Tocher & Pledger 2005; Bell & Pledger 2010). However, most of these focused on adult survivorship or overall survivorship, which can be strongly influenced by adult frog parameters given that juveniles make up a smaller proportion of the population. In that regard, this study provides insight into how to recover native frog populations, through our examination of age-specific population dynamics in the presence and absence of rat control. The results of Crossland et al. (2023) also suggest that responses to management may differ based on age class. Comparison of population dynamics under various management regimes can help to identify critical factors that are necessary for the conservation of a species (Robertson et al. 2011).

Our results show that suppressing rat populations to tracking rates below 10% is proving successful for frog population management at Whareorino Conservation Area and supports the now completed expansion of rat control into the 300 ha nontreatment area. In this current study, the urgency under which rat control was commenced in 2003 precluded collection of baseline population data. We therefore recommend continuing annual frog monitoring for comparison of population dynamics before and after rat control (BACI design) now that pre-treatment baseline data are available. Thereafter, monitoring effort could be scaled back to track management outcomes and detect any unforeseen population declines.

While the results of this study suggest that rat control may be adequate to maintain or slowly grow a large population such as the Whareorino Archey's frog population, we caution against generalising these results to other situations for two main reasons. Firstly, our study has no replication, which would more robustly support transfer of our findings. We recommend studying how other frog populations respond to rodent control. Secondly, rat control on its own may not be sufficient to recover depleted populations or to grow newly translocated Leiopelmatid populations on the mainland. Unfortunately, K-selected species are usually slow to recover from declines and may even have impaired recovery if population declines are rapid and large or if threats are not abated (Hutchings 2015; Whiterod et al. 2018). The stronghold population for Archey's frogs in Coromandel saw a loss of 88% from 1996 to 2001 (Bell et al. 2004) and has yet to recover from this crash more than 20 years later (Bell & Pledger 2015). Mainland translocations to sites with predators (e.g. Pureora, Zealandia outside the mouse proof enclosure) have not been as successful as those to predator-free offshore islands or within a mouse proof enclosure (Wren et al. 2023). This study has focused on a particular forest type and the results may not be representative of other habitats with different productivity cycles or stochastic events such as beech masting. This may also be the case if efforts are needed to grow significant numbers of frogs to mitigate, compensate or offset for losses to populations where decision makers allow land-use activities or industrial development that kill frogs. Managers will have to find ways to influence multiple factors (e.g. survival of various age classes, recruitment) if they are doing so at sites with mammalian predators. They also need to strongly consider that little is known about the impacts of mice on native frogs and that rat control does lead to a release of mouse populations, which may in turn have detrimental impacts on frogs.

Further research is needed to investigate the impact of mice on Leiopelmatid frogs. Whether this is done by direct experimental removal of rats and mice, monitoring of life history parameters for frog populations that co-exist with mice, and/or analysis of existing frog population data sets where mouse incursions have occurred on predator-free islands, all would add to our knowledge about the level of risk that mice pose to frog conservation and inform future conservation management programmes. Additionally, elucidating age class dependant parameters for Leiopelmatid frogs in both mainland (i.e. in the presence of predators) and island populations would allow for the modelling of population dynamics under various management regimes and may help determine what recovery is feasible and over what timeframes.

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Additional Information and Declarations

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