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RESEARCH

High long-term survival of PIT-tagged pekapeka | lesser short-tailed bats (*Mystacina tuberculata*) through annual pest control operations

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Abstract: Control of introduced mammalian predators is important for the protection of pekapeka | lesser short-tailed bat (*Mystacina tuberculata*) populations, but toxins used to control these predators may also pose a risk to bats when they forage on invertebrates that have consumed toxic bait or if bats directly consume bait. We studied the survival of a population of lesser short-tailed bats at Pikiariki, Pureora Forest Park, between 2012 and 2024, over which time conservation managers varied the methods and timing of toxin application for rat control to reduce secondary poisoning risk to bats. Reducing the duration of rat control operations and timing them to occur prior to the bat breeding season successfully reduced exposure of the bats to toxins. Although rat control operations effectively reduced relative rat abundance in the short term, there was no relationship between duration of rat control operations and annual mean rat tracking rates (the mean tracking rate for each year). Neither annual mean rat tracking rates nor the amount of time toxin was present in bait stations explained very much variation in bat survival from year to year. With an overall mean rat tracking rate across all years of 27 %, mean annual survival of the adult female lesser short-tailed bat population across all years was high (0.86), resulting in growth of the population. More frequent rat tracking data could be collected to test whether relative rat abundance at specific times of the year can be used to set a more precise operational target for rat control to further benefit bats. We recommend continuing to monitor the bat population as well as the relative abundance of rats and other introduced mammalian predators to improve the understanding of factors influencing bat survival. While an overall mean rat tracking rate of 27 % may allow this lesser short-tailed bat population to grow, other, more vulnerable, forest species requiring lower residual relative rat abundance targets should be considered in future management plans.

Key words: anticoagulant rodenticides, predator control, *Rattus rattus*, toxin, tracking tunnels

Introduction

New Zealand has two extant pekapeka | bat species, the lesser short-tailed bat (*Mystacina tuberculata*) and the long-tailed bat (*Chalinolobus tuberculatus*). Both species are susceptible to predation by introduced mammals. Cats (*Felis catus*) have been documented preying upon both species (Daniel & Williams 1984; Borkin et al. 2022), including a feral cat responsible for the death of at least 102 lesser short-tailed bats found beneath a roost tree in Rangataua, central North Island (Scrimgeour et al. 2012). A stoat (*Mustela erminea*) was filmed removing several lesser short-tailed bats from a roost in Whirinaki Forest, central North Island (Sarah Wills, DOC Murupara, pers. comm.), and brushtail possums (*Trichosurus vulpecula*) were observed attempting to reach into roosts containing young long-tailed bats on 50% of monitored nights in South Canterbury (O'Donnell & Borkin 2021). An irruption of ship rats (*Rattus rattus*) was linked to the disappearance of lesser short-tailed bats and greater short-tailed bats (*Mystacina robusta*) from Big South Cape Island (Daniel & Williams 1984). Ship rats have also been recorded in lesser short-tailed bat maternity roosts in Northland (Daniel & Williams 1984) and entering singing roosts in Pureora Forest (Parsons & Toth 2021). However, there is no direct evidence of rat predation on New Zealand bats.

Management to protect ecosystem values, including both bat and bird populations, aims to control these pests, and evidence is building that bat populations benefit from this management. Survival of both long-tailed bats and lesser short-tailed bats was higher in years of rat control compared to those with unmanaged ship rat and stoat irruptions in the Eglinton Valley, Fiordland (Pryde et al. 2005; O'Donnell et al. 2011; O'Donnell et al. 2017).

Pest control operations typically use toxins (e.g.

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rodenticides) and/or traps to reduce pest abundance (Innes et al. 2024a). While these operations are generally beneficial (Binny et al. 2021), lesser short-tailed bats may be at risk from ingesting toxins either directly or secondarily (through feeding on invertebrates which have ingested bait) because they forage beneath the forest canopy and on the forest floor. This risk was highlighted at Pikiariki within Pureora Forest Park, west of Taupo (central North Island); in 2009 over 100 lesser short-tailed bats were killed by exposure to the anticoagulant rodenticide diphacinone, distributed as RatAbate® (Connovation Ltd., Auckland) 0.005% cereal paste in biodegradable plastic bags stapled to trees along bait station lines (Dennis & Gartrell 2015). In contrast, a three-month rat control operation using diphacinone had zero to negligible effect on survival of lesser short-tailed bats between October 2013 and April 2014 (the bat breeding season) when the toxin was delivered in cereal pellets (Pestoff Rat Bait 50D, 0.05g kg^{-1}, Animal Control Products Ltd., Whanganui, New Zealand) placed in bait stations (Philproof Pest Control Products, Hamilton, New Zealand). However, diphacinone residues were detected in communal guano deposits, indicating sub-lethal exposure (Dennis 2019). The long-term effects of such exposure remain unknown. In response to the ongoing risk of toxin exposure, the Department of Conservation (DOC) changed the toxin to pindone (a less potent and less persistent anticoagulant rodenticide; Fisher et al. 2003), further reduced the duration of toxin availability in bait stations at Pikiariki, and timed operations to avoid the months when bat activity was highest and pups and juveniles were present.

The lesser short-tailed bat population in Pikiariki has been monitored since 2012. DOC has also monitored relative rat abundance and documented all pest control operations over this period. This paper builds on the lesser short-tailed bat survival and toxin exposure work by Dennis (2019), by investigating the effect of changing the toxin to pindone and reducing the duration of rat control operations at Pikiariki on (a) relative rat abundance, (b) exposure of the lesser short-tailed bat population to toxins, and (c) annual survival rates of the lesser short-tailed bat population. Exposure to toxins can supress rat populations, but uncontrolled or poorly controlled rat populations may have a negative effect on lesser short-tailed bat survival, and exposure to toxins may have a negative effect on lesser short-tailed bat survival. Depending on the strength of these relationships, pest control operations that use toxins to reduce rat populations may have a neutral, net positive, or net negative effect on the Pikiariki lesser short-tailed bat population. The net effect may depend on the type of toxin used, its presentation, and how long it is present in the environment.

While both ship rats and brown rats (*Rattus norvegicus*) occur in Pureora Forest Park, this paper is concerned with ship rats because they are the predominant rat species in this forest (Innes et al. 2001) and are a more agile climber (King & Forsyth 2021), hence are a greater threat to New Zealand's tree-roosting bats.

Methods

Study area

The Pikiariki pest control area (38°26′ S, 175°39′ E) borders Pureora Village, approximately 45 km north-west of Taupo. It covers 900 ha of the c. 80 000 ha Pureora Forest Park in the central North Island and comprises c. 750 ha of podocarp-hardwood dominated native forest (including an Ecological Area) and c. 135 ha of Douglas fir (*Psuedotsuga menziesii*) with native understory (Fig. 1). The terrain is relatively flat, with a temperate and moist climate (temperature range = −5.6 °C–30 °C, mean temperature = 11.1°C, average annual rainfall = 1539 mm; data from Earth Sciences New Zealand). The Pikiariki pest control area is bordered by exotic forestry, farmland, and a regenerating native corridor which connects Pikiariki to the large (c. 50 000 ha) portion of Pureora Forest Park in the south. Waipapa (South and North) pest control areas, also within Pureora Forest Park, are 1.5 km to the north of Pikiariki across farmland (Fig. 1).

Lesser short-tailed bats

There are three sub-species of lesser short-tailed bat; the northern lesser short-tailed bat (*M. t. aupourica*), the central lesser short-tailed bat (*M. t. rhyacobia*), and the southern lesser short-tailed bat (*M. t. tuberculata*). Our subject, the central lesser short-tailed bat, is ranked under the New Zealand Threat Classification System as "At risk – declining" (O'Donnell et al. 2023). Lesser short-tailed bats are a forest obligate species, whose foraging behaviour includes feeding on the forest floor. They roost in tree cavities, often communally in large numbers, with peak numbers during the summer through to early autumn when annual breeding occurs (Parsons & Toth 2021).

Lesser short-tailed bats may be vulnerable to rat predation year-round because in colder temperatures at any time of year they enter bouts of torpor (Czenze et al. 2017), with lowered body temperatures that reduce reaction times; in the summer, bat pups, that cannot fly or are still learning, are likely to be more vulnerable to predators. Ship rats have been observed preying on the pups of flightless Egyptian fruit bats (Chen et al. 2025).

All known lesser short-tailed bat roosts at Pureora Forest Park are within the Pikiariki pest control area (DOC Pureroa, unpubl. data; Fig. 1), which is also where the home ranges of 17 of the 18 bats radio-tracked by Toth et al. (2015) occurred. However, lesser short-tailed bats have been recorded regularly flying to Waipapa (Toth et al. 2015; Bennett 2019).

Pest control

Productive, temperate, podocarp-hardwood forests that occur within Pureora Forest Park have high abundances of mammalian predators year-round, and high potential for rat numbers to increase rapidly after control operations (Innes et al. 2001, 2024b). Added to this, the Pikiariki pest control area is vulnerable to rapid reinvasion because it is relatively small, with a high edge to area ratio. Pikiariki has received pest control almost annually since 1995 (DOC Pureora, unpubl. data) because of its high ecological values. This control aims to maintain low possum numbers and reduce rat numbers through the bird breeding season (September–March), with the assumption that this will also benefit bats.

The Pikiariki pest control area comprises a grid of Philproof bait stations. During the study period (2011/12–2023/24), bait station spacing was initially 50 × 150 m (2011–2014) and, in subsequent years, 100 × 100 m (over c. 825 ha) or 100 × 75 m (over c. 75 ha). Bait stations were filled in late winter/spring with anticoagulant rodenticides (either diphacinone or pindone). Five shorter duration operations (2015 and 2017–2020) used one fill of pre-feed (a non-toxic version of the bait) and one fill of toxic bait in the bait stations prior to the bat breeding season, while four medium- to long-

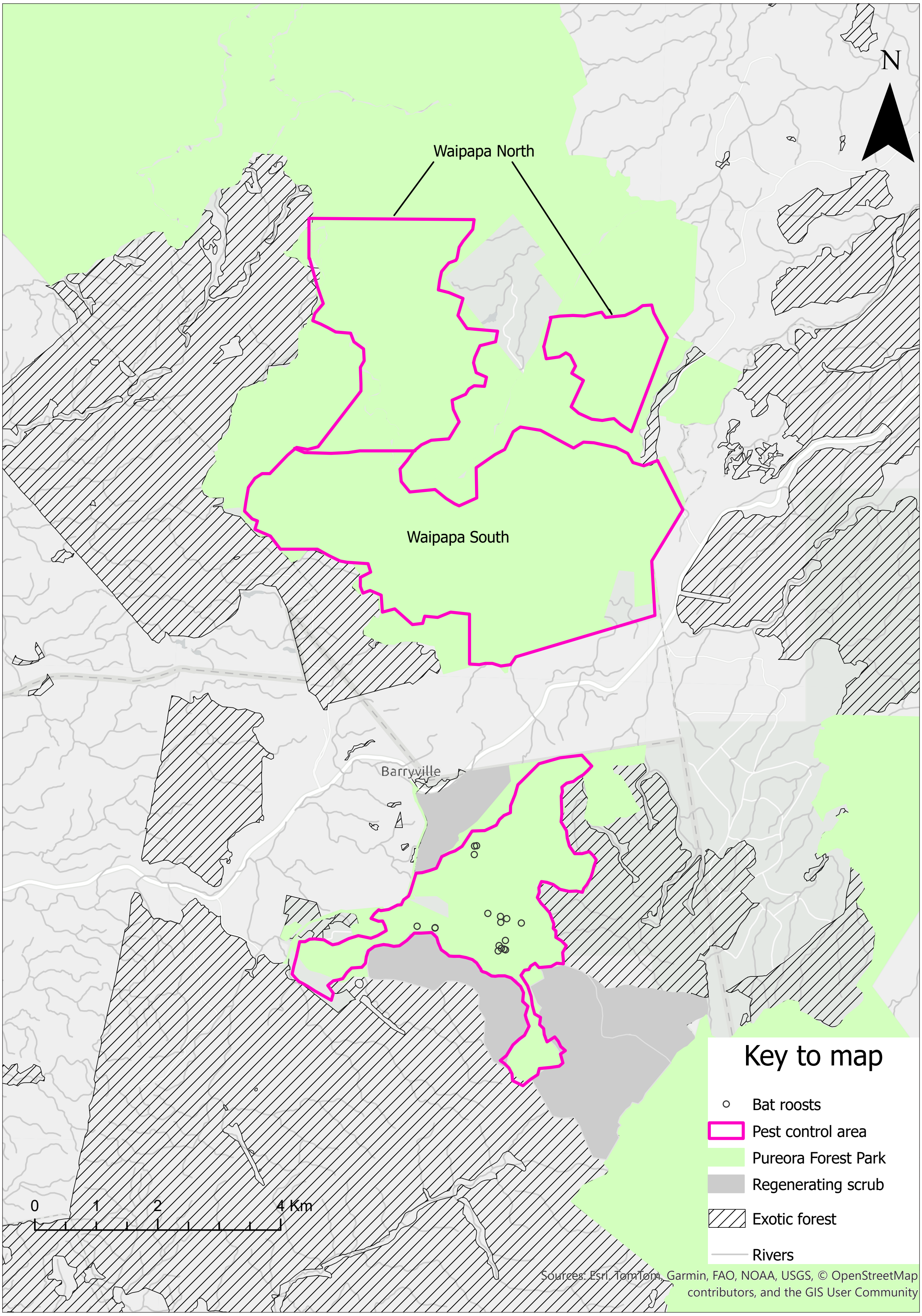

Figure 1. Location of the study site and known lesser short-tailed bat roosts at Pikiariki within Pureora Forest Park, central North Island, New Zealand, and the pest control areas at Pikiariki, Waipapa South, and Waipapa North.

duration operations (2011/12–2014/15) used multiple fills of toxic bait to provide bait to rats continuously through the bat breeding season. Winter applications of aerially sown 1080 pellets (pre-fed, 0.15% 1080 Pellets RS5 Orillion sown at 1.5 kg ha^{-1}) were substituted for ground-based anticoagulant rodenticide control in 2016 (to target possums) and 2022 (to target possums and rats), and no pest control was applied in 2021 and 2023 (Table 1).

Tracking tunnels were used to provide indices of relative rat abundance as described by Gillies and Williams (2013). Abundance was generally measured at least four times a year until 2020, when measurement was reduced to two or three times a year. To investigate the relationship between relative rat abundance and annual survival of adult and juvenile female bats, mean tracking tunnel results at Pikiariki between the previous and current bat breeding seasons (i.e. from February in the previous year to the current February when bats were recaptured) were used. This metric was used because bats may be vulnerable to predation throughout the year within roosts and at foraging areas, given that rat numbers are naturally high throughout the year in the local forest type (Innes et al. 2001; Walker et al. 2019).

Although Pikiariki was the focus of the project, bats are known to travel to Waipapa South pest control area (Toth et al 2015; Bennett 2019; TT pers. obs.) and it is possible that they also travel to Waipapa North pest control area (Fig. 1), so the timing of pest control operations at these areas was also taken into consideration in the analysis and interpretation of results. Stoat trapping at Pikiariki began in 2014, but trapping effort was not consistent and the stoat population was not monitored, therefore the potential relationship between stoat abundance and bat survival is not modelled in this study.

We modelled relative rat abundance (in %) in relation to site (Pikiariki, Waipapa South, or Waipapa North), toxin availability (duration in days per year scaled from 0–1), and a random effect of year using the package "glmmTMB" (Brooks et al. 2007). Binomial models are usually fitted to presence-absence tracking data (e.g. Whitau et al. 2023) but this was over-dispersed (DHARMa zero-inflation test ratio was 80.3, $p < 0.01$; Hartig 2022), so we used a beta-binomial model, which also had lower AICc (924 compared to 1029 for binomial). Model effects were summarised with the package "sjPlot" (Lüdecke 2024).

Guano and carcass collection for pindone residue testing

Following the method of Dennis (2019), we collected guano from the base of roost trees during the spring, summer, and autumn months between 2012 and 2019 when bats were present at known communal roosts. Collection was performed during all pest control operations, except for the 2016 and 2022 aerial 1080 operations because these occurred during winter months when the bats do not frequently use known communal roosts (TT pers. obs.).

Searches for dead bats beneath communal roosts were not systematic. However, when dead bats were encountered at roosts during guano collection, when catching bats, or when downloading data loggers, they were sent to Wildbase Pathology, Massey University, for necropsy, and liver or maggots from the carcasses were sent to Landcare Research/ Manaaki Whenua, Lincoln, for toxin residue testing.

Bat survivorship

A total of 2316 bats were marked with Passive Integrated Transponder (PIT) tags between 2012 and 2024, with 60 individuals tagged in the first year and c. 200 each year thereafter. Tag insertion and data capture followed the method described in Edmonds et al. (2017).

In January and February 2013, bats were caught at roosts to identify PIT tagged individuals using hand-held scanners (Allflex Compact Reader, Biomark HPR Lite Reader, or Biomark HPR Plus Handheld PIT Tag Reader) (Toth 2016). From November 2013, radio-frequency identification antennae and loggers were installed at six communal roost entrances to identify PIT tag numbers of individual bats leaving or entering roosts, and at a seventh, newly discovered roost in March 2014 (Dennis 2019). Logger data used in this study was collected between January and March each year.

We estimated annual survival of adult and juvenile female bats using the mark-recapture data with Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992) extended to include multi-state recaptures that allowed the transition from juvenile to

Table 1. Pest control methods and timing of operations at Pikiariki, Pureora Forest Park, between 2011 and 2023. Pesticides used were: pindone pellets (Pindone Pellets, Key Industries Ltd., 0.5g kg^{-1}); diphacinone pellets (Pestoff Rat Bait 50D, Animal Control Products Ltd., 0.05g kg^{-1}); and 1080 pellets (0.15% 1080 pellets RS5, Animal Control Products Ltd., 1.5g kg^{-1}).

Year	Bait used	Period of operation	Duration	During breeding season
2011/12	Diphacinone	16 August 2011–23 April 2012	251 days (long)	Yes
2012/13	Diphacinone	2 August 2012–2 May 2013	273 days (long)	Yes
2013/14	Diphacinone	25 November 2013–21 February 2014	88 days (medium)	Yes
2014/15	Pindone	21 August 2014–14 April 2015	236 days (long)	Yes
2015	Pindone	24 August–16 October	53 days (short)	No
2016	Aerial 1080	1 July	-	No
2017	Pindone	4 September–12 October	38 days (short)	No
2018	Pindone	27 August–3 October	37 days (short)	No
2019	Pindone	2 September–30 September	28 days (short)	No
2020	Pindone	2 September–28 September	26 days (short)	No
2021	No pest control		-	-
2022	Aerial 1080	31 August	-	No
2023	No pest control			

adult bats. Analysis was performed in R 4.4.2. (R Core Team 2021) using RMark (Laake 2013) as an interface to Program MARK (White & Burnham 1999). Any bat that was not sexed at the time of capture and any bat that was known to lose its tag (determined through the discovery of the tag beneath a roost tree) was excluded from the analysis. Bats that were of unknown age when first captured and tagged were excluded from the analysis for that year but included as adults if recaptured in subsequent years. The variables investigated were the length of time (in days) that diphacinone or pindone was present in bait stations, occurrence of an aerial 1080 operation and the effect a year later, and relative rat abundance at Pikiariki. We investigated all possible combinations of these variables and used time (year) and age (juvenile or adult) as the fully parameterised global model and compared models based on Akaike Information Criterion (AIC). The best model is the one with the lowest AIC. Models that have a difference (Δ AIC) of less than two have substantial support. Models with Δ AIC of 4–7 have less support, and models with Δ AIC greater than 10 have essentially no support (Burnham & Anderson 2002).

Population viability analysis

A population viability analysis was calculated to look at the effect of estimated adult and juvenile survival rates on the long-term viability of the lesser short-tailed bat population, following the method of Pryde et al. (2005). The proportion of females breeding in their first, second, third, and subsequent years is unknown for lesser short-tailed bats because there have not been enough repeat captures of individual bats of known age to estimate this metric. We used estimates of these parameters from a long-tailed bat population in the Eglinton valley, Fiordland, and assumed an equal sex ratio for juveniles (O'Donnell 2002). These parameters were entered into an age-classified population matrix (Leslie Matrix) to calculate the intrinsic growth rate of the population (Caswell 2001).

Population estimate

The Schnabel method (Schnabel 1938) was used to estimate the abundance of lesser short-tailed bats in the Pikiariki population in 2024. Fur clipping was used to mark individuals and the ratio of marked to unmarked captures was used to estimate the adult population size.

Results

Pest numbers

Rat tracking rates were lowest soon after toxic baits were deployed. They increased once the baits were removed, or during longer operations where bait stations were regularly refilled to keep bait continuously available (Fig. 2). There was

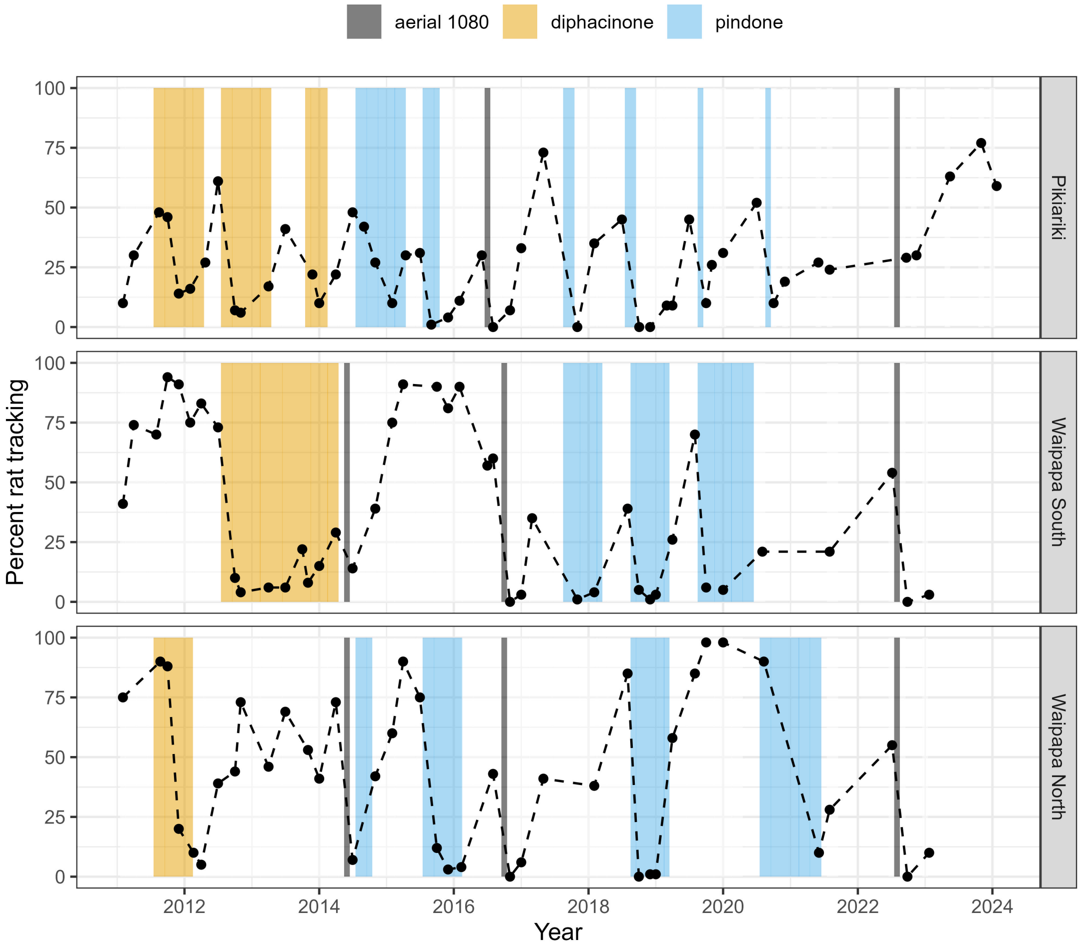

Figure 2. Pest control operation (toxin type and availability in bait stations) and relative rat abundance (percentage of tunnels tracked) in three pest control areas of Pureora Forest Park, New Zealand, from 2011 to 2024. Coloured bars show toxic bait availability by month. Dashed lines show the rat tracking index.

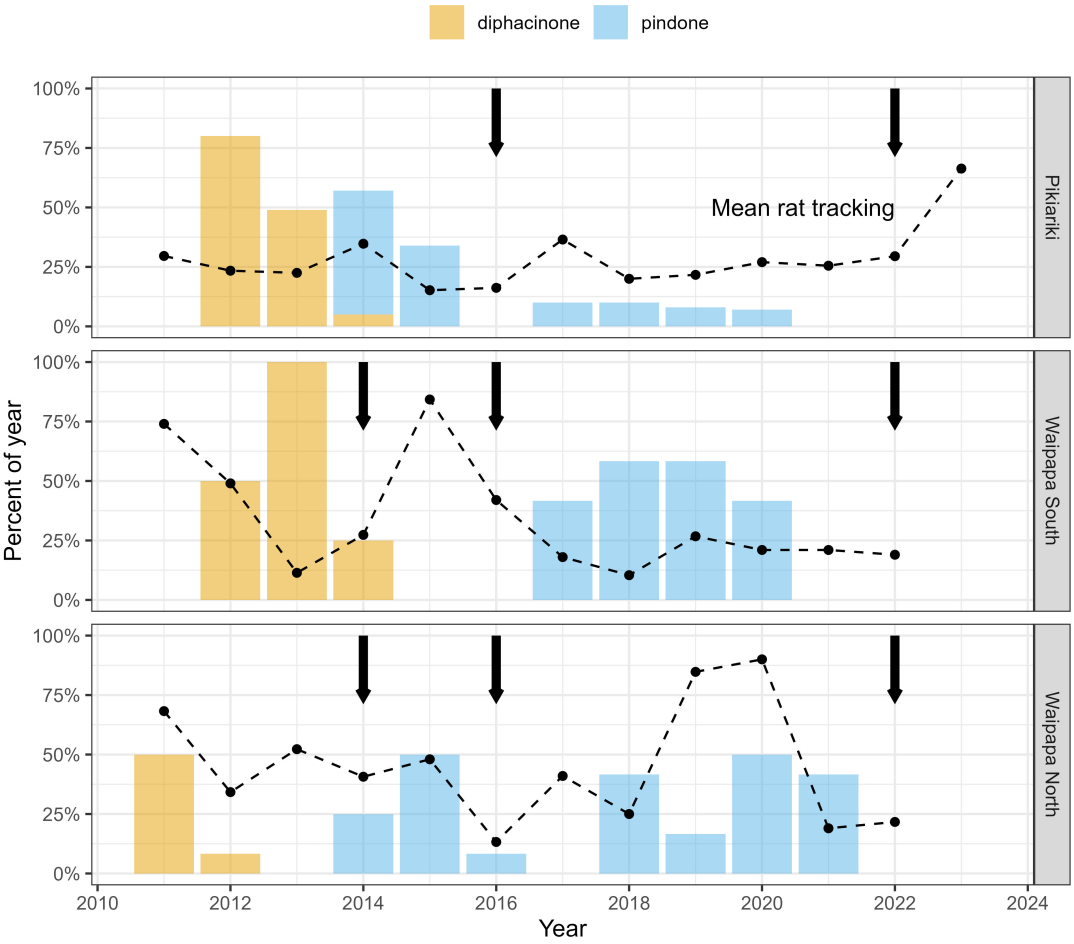

Figure 3. Period of toxin use (percentage of each 12-month period that diphacinone [orange] or pindone [blue] was deployed in bait stations) and annual mean relative rat abundance (percentage of tracking tunnels with rat prints) in three pest control areas of Pureora Forest Park, New Zealand. Black arrows show when aerial 1080 was applied. Dashed lines show the rat tracking index.

a significant positive effect of the number of days since toxic baits were last deployed on rat tracking rates (for Pikiariki in spring, odds ratio 1.127, pr(>|z|) < 0.001, full results are in Appendices S1–S3 of Supplementary Material).

Annual mean rat tracking rates, calculated as the mean of all measures from the previous February to the February when bats were recaptured, varied over time and across the three pest control areas (Figs. 1 & 3). In Pikiariki, the focal area of this project, annual mean rat tracking rates between 2011 and 2024 ranged from 14 to 66%, but were below 30% for all years except 2017, 2022, and 2023 in Pikiariki (Fig. 3). The overall mean of the annual mean rat tracking rates in Pikiariki across the duration of the study was 27% . Over all sites, application of aerial 1080 had a negative effect on rat tracking rates, reducing the predicted annual mean from 27% to 17% (p = 0.011). Availability of pindone and diphacinone also had negative, but not significant, effects (odds ratio = 0.30 and 0.52 for pindone and diphacinone, respectively; all p > 0.1; Appendices S4–S5).

Toxin residue in guano and dead bats

Changing the toxin from diphacinone in 2013/14 to pindone in 2014/15, with both operations delivered across the bat breeding season at Pikiariki, did not result in fewer detections of toxin residues in guano samples. However, the incidence of toxin residues in guano was reduced by reducing the length and timing of the pest control operations. Toxin residues were detected in guano during ten of the 12 months sampled in the longer operations of 2012/13 and 2014/15 (Dennis 2019). The medium duration operation conducted during the breeding season (2013/14) showed residues in five of the six months tested (Dennis 2019). In contrast, the shorter operations outside of the breeding season (2015/16, 2017/18, and 2018/19) showed residues in two of the 20 months tested. A similar pattern was observed in dead bats: seven of eight bats (or maggots within them) tested during the longer operations (2012/13 and 2014/15) and the operation during the breeding season (2013/14) contained toxin residues, whereas only two from seven dead bats tested during the short operations outside of the breeding season (2015/16, 2017/18 and 2018/19) contained residues (Appendix S6).

During the period when diphacinone was used, four dead pups and one juvenile were recovered, two of which were in a suitable condition for necropsy. Neither had obvious haemorrhages that would be consistent with anticoagulant poisoning, although one had diphacinone residues in its liver, and residues were also detected in maggots from another bat (Dennis 2019). During the period when pindone was used, six of 33 bat carcasses and two moribund bats recovered were in suitable condition for necropsy. Only one of these (found after a shorter duration pindone operation) showed signs consistent with anticoagulant poisoning, with intramuscular and pulmonary haemorrhaging. No pindone residues were detected in its liver, but since the half-life of pindone is short (Fisher et al. (2003) estimated that the hepatic elimination rate in laboratory rats (*R. norvegicus*) was two days) this does not eliminate pindone poisoning as a cause of death.

Residues of diphacinone or pindone were found twice in guano and three times in dead bats, despite bait having been removed from bait stations at Pikiariki at the time of sampling and carcass recovery. In these cases, bait was present in, or recently removed from, Waipapa South and/or North. Also, in 2020, when the dead bat (of the six necropsied in this study) that showed clinical signs consistent with anticoagulant poisoning was found, there was no bait deployed in Pikiariki, but pindone was present in Waipapa South (Appendix S6).

Survival and recapture modelling

We made a total of 4820 captures of 1299 PIT-tagged adult and juvenile female bats between 2012 and 2023. No new bats were tagged in 2022 due to COVID-19 restrictions on field work. The recapture rate was above 60% for all years (Appendix S7).

Estimated annual survival rates of adult females were high (range = 0.77–0.93, mean 0.86, n = 12 years) and even in the years with the highest rat tracking rates at Pikiariki bat survival was not particularly low (Fig. 4).

In the best-ranked model wi (AIC) = 90%, the probability of survival varied with age and year as interactive terms (Appendix S8). There was much less support for Model 2 (Δ AIC = 4.42, wi = 9.88%) where the effect between age and year was additive. The other three top models (3–5), that all included duration of pindone availability and an interaction between annual mean rat tracking rate and the year after an aerial 1080 operation, had a combined weighting of only 1% and a Δ AIC of greater than 21, indicating there was very little support for these models compared with Model 1. Model 23 (global model) is used as a reference. Survival estimates from the top-ranked model, which included the interaction between year and age (Model 1 in Appendix S8), was therefore used to estimate mean annual survival.

Population viability analysis

The mean annual survival rate of female lesser short-tailed bats was 0.86 for adults and 0.56 for juveniles. Assuming the proportion of adults breeding in each year was similar to that of the Eglinton valley long-tailed bat population, the four-age class Leslie matrix produced a finite population growth rate (lambda λ) of 1.04, indicating a population growing at a rate of 4% per year (Fig. 5).

Population size estimate

The adult population size was estimated using 1066 capture events over nine capture sessions between 22 January and 1 February 2024, resulting in 1328 adults (95% CI 1169–1538). The recapture rate for individual sessions ranged from 3% to 48% (Appendix S9). This 2024 population estimate compares with a closed mark-recapture population estimate made in November 2013 of 777 adults (95% CI 618–1021) (Dennis 2019).

If the estimated population growth rate of 1.04 is applied to the baseline estimate of 777 adults, the projected population estimate at the start of the 2023/24 breeding season is 1208. This is lower than the Schnabel population estimate of 1328 (1169–1538) However, the Schnabel estimate does fall within the confidence intervals of the projected population size (Fig. 5).

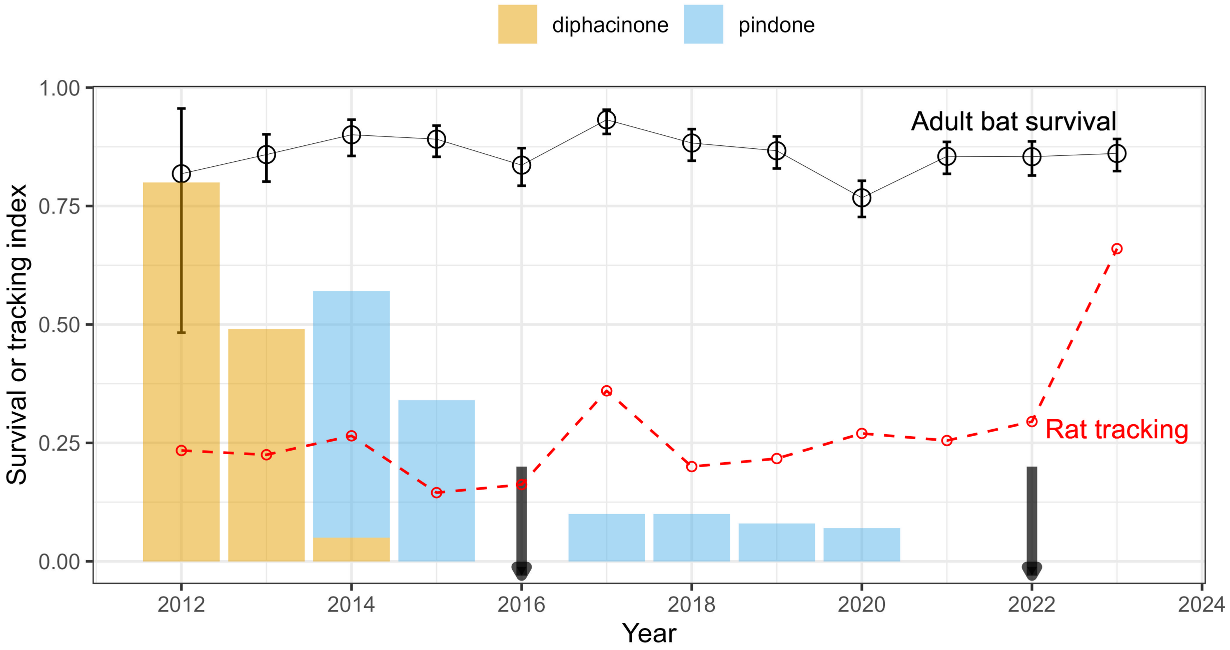

Figure 4. Annual survival estimates for adult female lesser short-tailed bats (*Mystacina tuberculata*) (2012–2024) at Pikiariki, Pureora Forest Park, with 95% confidence intervals. The year refers to the survival period between annual breeding seasons, for example 2020 refers to survival between February 2020 and February 2021. Coloured bars show the proportion of each 12-month period that toxin was deployed in bait stations in Pikiariki. Black arrows show 1080 operations in Pikiariki. Red circles show annual mean rat tracking rates in Pikiariki from February to February. The scale on the y axis relates to rat tracking index, annual bat survival, and the proportion of each 12-month period that toxin was deployed.

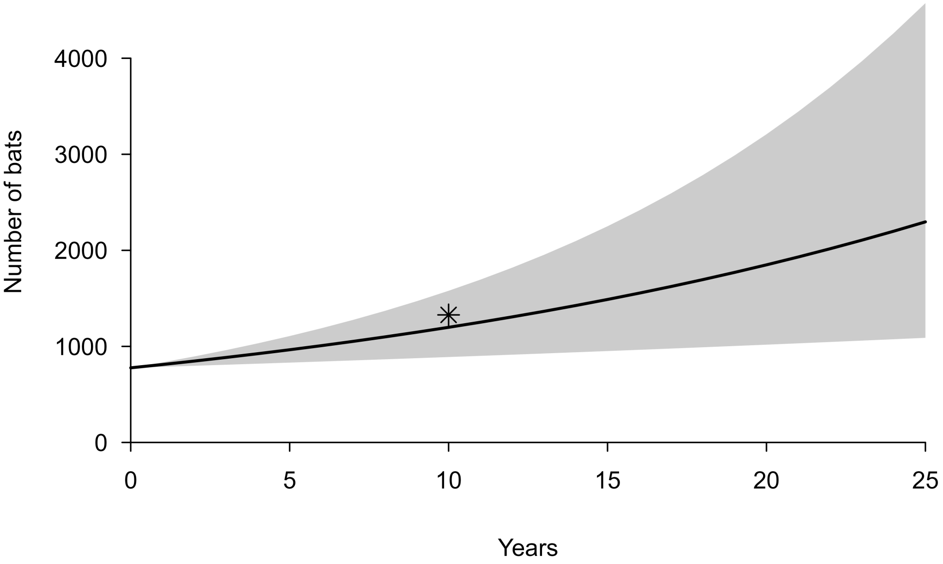

Figure 5. Projected growth of the lesser short-tailed bat population at Pikiariki, Pureora Forest Park, using a starting population of 777 adults (estimated population size in November 2013; Dennis 2019) and annual growth rate of 1.04, estimated using mean annual survival rate over a 10-year period. The * refers to the 2023/24 Schnabel population estimate calculated 10 years after the baseline estimate. The shaded areas represent the 95% confidence intervals.

Discussion

Introduced mammalian predators drive the decline of many native fauna species; therefore, pest control operations are a core conservation activity in New Zealand (Binny et al. 2021; Innes et al. 2024a, 2024b). However, the risk of operational by-kill must be carefully assessed to ensure that operations lead to positive population trends for native species. In Pikiariki, conservation managers have had to try to balance the requirement to maximise rat suppression and minimise non-target impact on lesser short-tailed bats.

Toxins are an effective rat control tool, and relative rat abundance was low in the months immediately after toxic bait deployment at the three pest control areas in Pureora Forest Park. However, tracking tunnel data showed relative rat abundance can recover rapidly after toxic baits are removed, supporting observations made by Innes et al. (1995), and that rapid re-invasion is likely at Pikiariki given its relatively small area and large boundary (Griffiths & Barron 2016; Carpenter et al. 2023). After initial knock-down, rats recovered to some extent during the longer duration pest control operations despite bait being available. This recovery may be because bait becomes less palatable as it ages, or alternative preferred foods may become available, thereby limiting the uptake of toxic bait and reducing its effectiveness in sustained control of rat populations (Gillies et al. 2003). Sustained use of one bait type and toxin for many years may also contribute to toxin operations becoming less effective over time due to behavioural and physiological resistance, bait shyness, and aversion (Clapperton 2006). There is also evidence of potential resistance to anticoagulant rodenticides in New Zealand ship rats (Sran et al. 2023). The periodic use of acute toxins such as 1080 is therefore important to help minimise these issues.

Annual mean relative rat abundance, used as a measure because bats may be vulnerable to rat predation year-round, was not related to the proportion of months in the year that anticoagulant toxic baits were available. Nevertheless, annual mean relative rat abundance was lower in years with aerial 1080 operations, as expected because broad-scale application of aerial 1080 is more effective than anticoagulant toxins at reducing rat abundance to very low levels immediately following application (Innes et al. 2024a). Our study however was not designed to compare effectiveness of toxic baits on rat abundance and conclusions are limited by inclusion of before-and after measurements in the annual mean rat tracking rates, and low replication of sites and operations. Furthermore, low frequency of rat monitoring in some years is unlikely to capture any seasonal variation of abundance.

Reducing the duration of toxic bait operations effectively decreased but did not eliminate the incidence of detected exposure of the bats to toxins. The finding of toxin residues in guano and dead bats despite bait having been removed from bait stations at Pikiariki is consistent with the finding of Dennis (2019), who also recorded toxin residues in guano and in maggots collected from a dead juvenile in 2014 when diphacinone was absent from Pikiariki but present in Waipapa North. These results are unsurprising since some bats forage at Waipapa where toxic baits are also used (Toth 2015; Bennett 2019; TT pers. obs.). Another possible source of toxin availability after bait removal from Pikiariki is bait persisting outside of bait stations (e.g. in rat caches). Prolonged persistence in invertebrates appears unlikely, but not impossible, given Fisher et al. (2007) concluded that Wellington tree weta (*Hemideina crassidens*) would probably excrete diphacinone within a period of days following exposure. Bait deployment on private farmland between Pikiariki and Waipapa South could be a toxin source, though it is unknown whether any bait was present during the study period. No toxin residues were detected in guano during the 2017/18 and 2018/19 austral summers when bait was present for at least five months in Waipapa South after it was removed from bait stations in Pikiariki. The reason for this is unknown, but further suggests, along with the finding of Toth et al. (2015), that Pikiariki is an important foraging area for this population.

Dennis (2019) concluded that while a 3-month operation using cereal pellets containing diphacinone in bait stations had zero to negligible effect on short-term (6-month) bat survival, sub-lethal exposure of bats was of concern. Our study extends these findings and indicates that there has been growth of the lesser short-tailed bat population despite exposure to diphacinone and pindone and possible associated sub-lethal effects. However, sub-lethal effects of chronic exposure to anticoagulants have been detected in other mammal species e.g. altered gene expression resulting in decreased fitness in bobcats (*Lynx rufus*) (Fraser et al. 2018) and reduced reproductive rates in merino sheep (*Ovis aries*) (Robinson et al. 2005), and any such impacts on the bat population would not have been detected by this study. We recommend continuing to minimise the use of anticoagulants at Pikiariki while recognising that sustained pest control is necessary for protecting this and other vulnerable species. Continuing Waipapa rat control operations through the summer months (after ceasing toxin operations in Pikiariki before the bat breeding season) appears to be an effective strategy to decrease (but not eliminate) exposure of bats to toxins, while decreasing rat numbers during the kōkako breeding season sufficiently for this rat sensitive species to increase at Waipapa (Innes et al. 1999; DOC Pureora, unpubl. data).

We found limited evidence for a relationship between annual mean relative rat abundance at Pikiariki and annual bat survival, and survival rates were high despite rat indices over the bat breeding season regularly exceeding 15% and, in one year, a winter rat tracking rate of 73%. This may suggest that lesser short-tailed bats at Pikiariki are less affected by rat predation than other vulnerable species (e.g. long-tailed bats; Pryde 2005). In addition, annual mean relative rat abundance was not closely related to the proportion of months in the year that bait was available, partly due to the short-lived effect of toxins in supressing rat numbers, and it is likely that more frequent and regular measures of relative rat abundance during the year would clarify the relationship between relative rat abundance and bat survival.

The lack of a clear relationship between high relative rat abundance and reduced bat survival was unexpected, because other short-tailed bat populations have been significantly affected by rats. The colonisation and subsequent irruption of ship rats on Big South Cape Island in 1963 caused the extinction of resident lesser and greater short-tailed bats (Daniel & Williams 1984; Bell et al. 2016), and low survival of lesser short-tailed bats in Eglinton Valley was highly correlated with rat irruptions (O'Donnell et al. 2011). Until recently, a key difference between Eglinton Valley and Pureora Forest Park has been that the beech forests of the Eglinton are subject to rat irruptions and subsequent population crashes following beech seed masting events, with rats at low abundance in the years between mast events (King & Moller 1997). In contrast, the podocarp-hardwood forests at Pureora Forest Park have continuously high rat abundance every year (Innes et al. 2001). However, as noted by Elliot and Kemp (2016), the relationship between rats and some beech forests has recently changed. Since 2014, some rodent populations have recovered quickly after 1080 operations in beech forests. This has happened in the Eglinton, and relative rat abundance is now higher between beech masts than it used to be (tracking rates up to 17%). Despite this, survival of the lesser short-tailed bat population in Eglinton has continued to be high (DOC Te Anau, unpubl. data). Podocarp-hardwood forests are more diverse than beech forests (Allen et al. 2013) and so would provide rats with more dietary choices if lesser short-tailed bats are not a preferred food. There may be some other characteristics of the habitat at Pureora which improve survival odds, including the potential influence of other predators on this population.

Our population viability analysis predicts an increasing bat population under the current management regime (a regime which minimises bat exposure to toxins while supressing rat populations), providing the effectiveness of rat control under this regime does not decrease. A limitation of this prediction is that reproductive parameters for this population are unknown and were therefore based on long-tailed bat monitoring data from the Eglinton Valley. These may be different for lesser short-tailed bats at Pureora Forest Park. We recommend research into reproductive parameters of lesser short-tailed bats so that more accurate estimates can be made in the future.

This study suggests that, for the lesser short-tailed bat population at Pureora Forest Park, a suitable operational target for rat control is to achieve an annual mean rat tracking index below 27% and reduce rat populations as much as possible in October before the bat breeding season starts. However, because our results are based on limited data, particularly for years with less than four rat monitoring events, we suggest more monitoring is needed to confirm this target. Vulnerability of the bat population to rat predation is likely to vary seasonally in ways that are not yet understood e.g. bats may be more vulnerable during winter as they roost alone more frequently compared to summer when communal roosting is more common. Conversely, they could be more vulnerable in summer when there are many non-volant young present. Moreover, while this regime may be sufficient to protect the lesser short-tailed bat population, it is possible that lower rat densities will be required to sustain other vulnerable species in this forest such as toutouwai | North Island robins (*Petroica longipes*) and pekapeka | long-tailed bats. In the Eglinton Valley, long-tailed bat populations recovered when rat indices were reduced to < 5% (O'Donnell et al. 2017) and rat indices over 30% during the bat breeding season correlated with annual bat survival which would predict a declining population (< 79%) (Pryde et al. 2005). This is also true for long-tailed bats at Whirinaki Forest (DOC Murupara, unpubl. data). Armstrong et al. (2006) suggested rat tracking rates < 20% were required for a translocated population of North Island robin to grow, and Binny et al. (2021) suggest that rat indices should be below 15% for positive general biodiversity benefits, with benefits to birds increasing as indices approach 0%. If conservation managers trial alternative pest control methods to achieve lower rat indices for longer periods, we recommend considering non-toxic methods of pest control in Pikiariki to further reduce the potential for lethal or sub-lethal poisoning of lesser short-tailed bats. Traps are an alternative, though these also have potential to kill bats so should be assessed to ensure minimal risk to bats before use. One study at Pikiariki using video monitoring of Goodnature Ltd. A24™ self- resetting traps using A24 pre-feed paste (chocolate) found no interaction of lesser short-tailed bats with the traps, indicating that they may be safe to use (Bridgman et al. 2025).

There are many factors that may impact lesser short-tailed bat survival. To understand these, it is important that conservation managers continue to regularly monitor the bat population and likely factors influencing survival, including other potential predators (stoats, cats, and possums) both within Pikiariki and across the wider area, and explore potential relationships between these and bat survival. Such outcome monitoring will inform bat management both at Pureora Forest Park and elsewhere to ensure non-target impacts are minimal and do not impact the viability of bat populations.

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Supplementary material

Additional supporting information may be found in the online version of this article.

Appendix S1. Description of models of the effect of management on relative rat abundance.

Appendix S2. Potential predictor variables for models of relative rat abundance at time of survey.

Appendix S3. Results of the model of relative rat abundance at time of survey.

Appendix S4. Potential explanatory variables for models of annual average rat tracking.

Appendix S5. Results of the model of annual average rat tracking.

Appendix S6. Anticoagulant toxin regime and toxin residue test results for guano and dead bats, during years guano collected from Pikiariki was tested, from August 2012 to May 2016 and August 2017 to May 2020.

Appendix S7. Summary of captured and logged PIT-tagged female lesser short-tailed bats, between January and March each year from 2011 to 2024.

Appendix S8. All models that were run as part of the analysis to describe apparent survival in adult and juvenile female lesser short-tailed bats, 2012–2024.

Appendix S9. Session capture numbers for Schnabel population estimate 2024.