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RESEARCH

Cholecalciferol for mouse (*Mus musculus*) control: limited effectiveness and the challenges of tracking tunnels for density monitoring.

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Abstract: In New Zealand, predation on endemic biota by house mice (*Mus musculus*) is a pressing conservation issue. While rodenticides are commonly used, efficacy and bioaccumulation are a concern. Cholecalciferol (vitamin D) offers a reduced risk of bioaccumulation. Our 14-month field study assessed the effectiveness of cholecalciferol-laced bait, which reduced mouse density by up to 59% from peak levels, yet was insufficient for sustained suppression of mice to the low levels required for conservation management. Spatially explicit capture-recapture and footprint tracking revealed that while the block treated with cholecalciferol showed density patterns consistent with suppression, a footprint tracking rate $< 5\%$ was only achievable intermittently. Mouse density peaked in March and was highest in grassland habitat in the block without poison (106 mice ha^{-1}, 95% CI: 87–130), while densities in woody vegetated areas in the same block were lower (57 mice ha^{-1}, 95% CI: 41–80). During peak abundance, mouse densities in the non-poison block were 2.4 × higher than in the poison block. The seasonal variability in both mouse density and footprint tracking rates suggests that seasonality and food availability were the drivers of mouse population dynamics. The relationship between footprint tracking rate and density oscillated through time, with an up to 25-fold variation in mouse density for a given tracking rate. Consequently, we caution wildlife managers that footprint tracking rates may not always serve as a reliable proxy for density and require, context-specific interpretation. Our findings indicate that the success of future mouse toxicant interventions will hinge on both toxicant efficacy and its sensitivity to seasonal climatic and productivity shifts, highlighting the need to better understand the phenological links between mouse density and impacted species.

Key words: biodiversity, conservation, density, footprint tracking, lizard, mice, pest control

Introduction

Predation by house mice (*Mus musculus*), hereafter referred to as mouse/mice, poses a significant threat to vulnerable native and endemic species, making it a key biodiversity conservation concern in Aotearoa | New Zealand (NZ). Arriving in NZ in the 18th century on European ships (Veale et al. 2018), mice quickly become widespread across most mainland ecosystems by exploiting a largely unchallenged niche as a small, agile omnivore. Mice negatively impact NZ's endemic fauna and flora through both competitive and predatory pathways (e.g. Whitaker 1978; Pickard 1984; Newman 1994; Wilson et al. 2006; Wedding 2007; Michelsen-Heath & Gaze 2007; Norbury et al. 2014; Watts et al. 2022; Norbury et al. 2023; Monks et al. 2024). In response to these impacts, conservation authorities in NZ have successfully eradicated mice from 28 offshore islands ranging in size from 2 ha to 2311 ha, through the application of second-generation anticoagulant toxicants, especially brodifacoum (Eason et al. 1996; Eason et al. 2010; Veitch et al. 2019; Murphy & Nathan 2021).

In New Zealand conservation management, toxicants are used to target rodents, including mice, for three distinct purposes: first, eradication from bio-secure offshore islands and fenced sanctuaries (Horn et al. 2019); second, as a vector for toxicants intended to suppress predatory mustelid populations (Innes et al. 2024); and third, to mitigate the direct impacts of rodents on threatened taxa (Hitchmough et al. 2016). Whilst effective tools exist for the first two purposes, we currently lack an effective control tool that can be repeatedly applied for mice for the third purpose.

Brodifacoum is the most widely used toxicant in mouse eradication efforts (Horn et al. 2019; Veitch et al. 2019). Whilst its utility is not in question, brodifacoum's repeated use in mainland ecological settings is more problematic due to bio-accumulation (Spurr et al. 2005). This has led to measures restricting the frequency of brodifacoum use on public conservation lands by the Department of Conservation.

In mainland forests, periodic efforts to poison rodents, including mice, are made over large areas to restore avifauna (Innes et al. 2024). These efforts often use acute-acting poisons, particularly sodium fluoroacetate, commonly known in NZ as 1080 (Eason et al. 2010). Here rats and mustelids rather than

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mice are the target, but mice are impacted by these efforts (Miller & Miller 1995). Mice quickly rebound after these control operations, likely due to an increase in food availability (Murphy 1992; Choquenot & Ruscoe 2000; Gillies 2002; Sweetapple & Nugent 2005; Ruscoe et al. 2011). In addition, the use of 1080 attracts public concern despite it being more humane than brodifacoum and non-bioaccumulating (Eason et al. 2011). While such factors present little issue to eradication efforts on islands, conservation managers currently have no effective control tool for the sustained suppression of mice in mainland habitats. This is particularly a problem for the conservation of endemic reptiles and invertebrates for which no suitable pest free offshore island habitats exist (Hitchmough et al. 2016).

Recent studies suggest that for some lizard populations to recover on mainland NZ, mouse tracking rates, interpreted as an index of abundance, need to be below 5% (Hitchmough et al. 2016; Norbury et al. 2023). Currently, there is mounting concern and evidence that selective predator suppression, such as that undertaken under the Predator Free 2050 initiative, a project to eradicate all rats (*Rattus rattus*, *R. norvegicus*, and *R. exulans*), stoats (*Mustela erminea*), and brush tailed possums (*Trichosurus vulpecula*) from NZ by 2050, can result in mesopredator release of mice to deleterious effect (Bridgman et al. 2018; Linklater & Steer 2018; King 2023; Monks et al. 2024; Samaniego et al. 2024). When conservation management requires reducing the impact of mice on sensitive species to undetectable levels over extended periods, the only currently available tool on the NZ mainland is mammal-proof fencing (e.g. Reardon et al. 2012). However, such fences have proven to leak in every instance thus requiring regular re-eradication or mouse suppression to undetectable levels using traps and toxicants. In many conservation scenarios mammal-proof fencing is not viable due to the location or habitat requirements of the target species. As a result, it is crucial to have an effective, non-bioaccumulating rodenticide that can be used regularly to suppress mouse populations to low levels, both in fenced and unfenced environments.

A potential candidate toxicant is cholecalciferol, more commonly known as vitamin D_3. Cholecalciferol is a natural compound synthesised in skin by the action of sunlight on its precursor, 7-dehydrocholesterol (Eason & Wickstrom 2001). Cholecalciferol is converted to the toxicant 25-hydroxycholecalciferol, mobilising skeletal calcium into the vascular system, causing hypercalcemia and calcification in the cardiovascular, renal, gastrointestinal, pulmonary, and muscular systems (Eason et al. 2000). Death occurs as a result of renal or cardiac failure (Eason & Wickstrom 2001). Cholecalciferol is both an acute (single-feeding) and chronic (multiple-feeding) rodenticide with a time to death similar to those seen in rodents exposed to lethal doses of anticoagulants (typically 3–7 days); however, it differs from other rodenticides in that bait shyness is not associated with its consumption in rodents subjected to diet choice trials that included cholecalciferol baits (Marshall 1984). Importantly, it has a low bioaccumulation risk, as trials suggest there is low residue persistence risk in invertebrates, and toxicity to non-target avian species is also low (Booth et al 2004; Eason et al. 2010; Eason et al. 2020).

Footprint tracking using an array of tunnels with inked tracking cards (hereafter referred to as tracking tunnels) is a mainstay of index monitoring for mice and other small mammals at conservation sites across NZ and is often employed in studies as a proxy index of abundance (Gillies & Willams 2013; Elliot & Kemp 2016; Wilson et al. 2018; Norbury et al. 2023). This is despite there being little correlation between estimates of rodent density and the indices given by the tracking tunnels (Ruscoe et al. 2001; Wilson et al. 2018). Since tracking tunnel indices serve only as an estimate of relative abundance, it would be prudent to also measure absolute abundance and/or density to validate the effectiveness of conservation tools. One approach to estimating absolute density is via spatially explicit capture-recapture (SECR) modelling (Borchers 2012) which has emerged as a key innovation over the last two decades.

Spatially explicit capture-recapture models specifically address the spatial nature of mark-recapture events when deriving estimates of animal density by modelling the spatial relationships between animals and detectors (Efford & Fewster 2013). Spatially explicit capture-recapture mathematically addresses the issue that animals which are near detectors (e.g. traps, camera traps, acoustic recorders) are more likely to be encountered than animals which reside at a distance from the detection devices (Borchers 2012). Consequently, the SECR field methodology relies not only on the detection of identifiable individuals but requires information on the spatial layout of the detection devices and where individuals were detected. Capture probability is then modelled as a function of the probability of being encountered by a detection device (Borchers 2012; Efford & Fewster 2013).

Given the ability of SECR models to provide accurate density estimates by accounting for spatial variation, this study employed a SECR methodology in a 14-month, landscape-scale experiment to evaluate the effectiveness of cholecalciferol bait for sustained mouse suppression. Our primary goal was to determine whether this rodenticide could serve as a sustained control option in environments where mammal-proof fencing or island eradication was impractical. It is important to note the increasingly vexatious distinction between eradication and control of pest populations: eradication entails the removal of all individuals of a target species from a sufficiently biosecure management area according to well established principles (Bomford & O'Brien 1995), whereas effective control suppresses pest populations to densities below impact thresholds (Norbury et al. 2015) for sufficient periods and at adequate frequency to enable threatened species populations to recover. Additionally, our study provided an opportunity to examine how well tracking tunnel indices reflected mouse density.

Methods

Study site

Ōtamahua | Quail Island is an 85 ha island situated within Lyttelton Harbour | Whakaraupō in the South Island of NZ (Fig. 1). The island is composed of Stoddart Basalt and Kaioruru Hawaiite to the north and Allandale Rhyolite to the south (Sewell 1988) and reaches an elevation of 86 m a.s.l. Almost all native vegetation was cleared in the 19th century and the island is now dominated by exotic pasture grasses with several stands of Monterey cypress (*Cupressus macrocarpa*). The island has been subject to an ongoing ecological restoration programme since 1982 by the Ōtamahua | Quail Island Ecological Restoration Trust, which is in the process of replanting 59 ha of native forest. A large suite of introduced animals have been eradicated from the island between 1997 and 2010 and, as yet, there has been no evidence of any re-invasion (Bowie et al. 2011). The species eradicated include

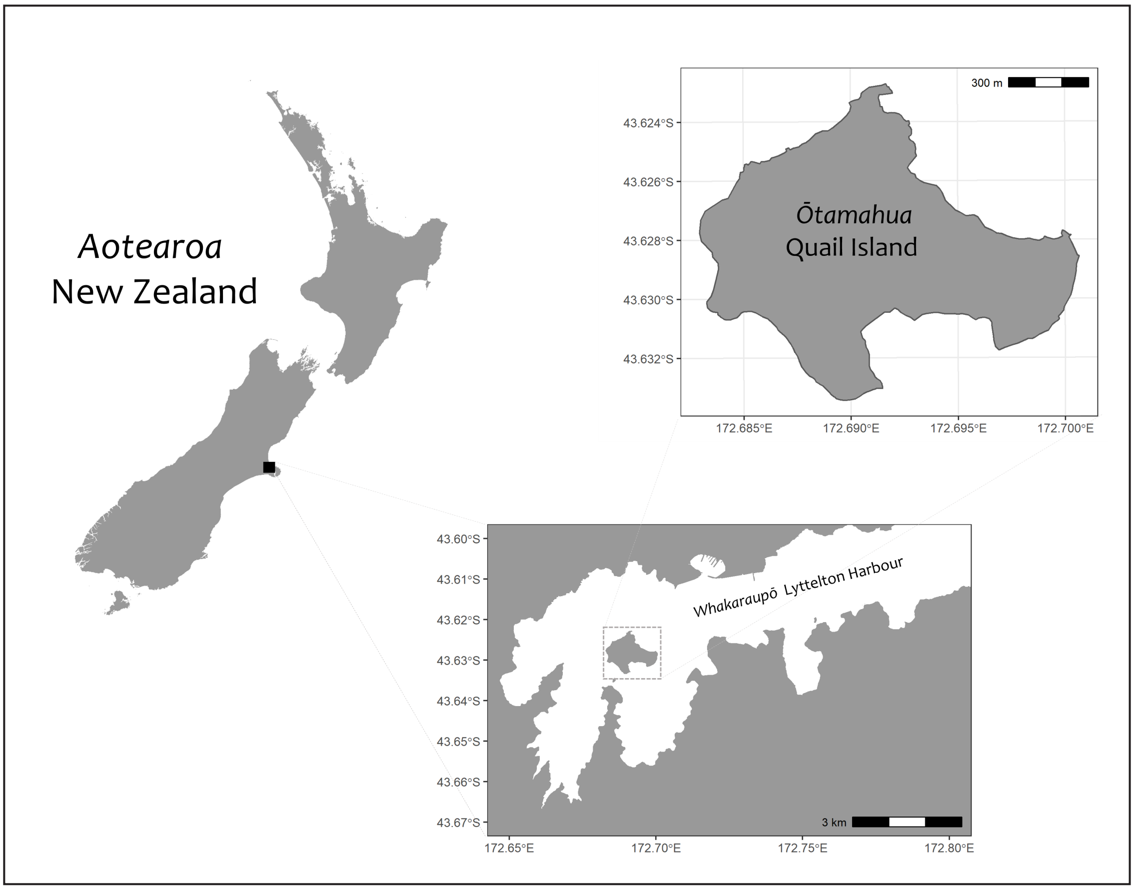

Figure 1. Location of Quail Island relative to Lyttelton Harbour, Canterbury, New Zealand.

rabbits (*Oryctolagus cuniculus*), cats (*Felis catus*), hedgehogs (*Erinaceus europaeus*), mustelids (*Mustela erminea, M. furo*, and *M. nivalis*), possums (*Trichosurus vulpecula*), and rats (*Rattus rattus*, *R. norvegicus*). There have been two attempts to eradicate mice from the island, using brodifacoum bait stations in 2002 and an aerial brodifacoum operation in 2009, but both failed (Bowie et al. 2011). For the purposes of this study, we classified the vegetation in the island as one of two types (Appendix S1 in Supplementary Material): (1) woody vegetation, which includes native restoration plantings, remnant native trees, and stands of *Cupressus macrocarpa*, and (2) grassland, which includes exotic pasture grasses (*Festuca arundinacea*, *Phalaris arundinacea*, *Bromus catharticus*, and *Holcus lanatus*) with patches of *Muehlenbeckia complexa*.

Field methods

To investigate the effectiveness of cholecalciferol as a mouse control tool we targeted two vegetatively comparable areas of c. 19–20 ha for live trap deployment on Ōtamahua | Quail Island, with a minimum of 200 m trapping separation between the two areas. The western block was randomly assigned as the poison treatment, while the eastern block was designated as the non-poison (control) treatment. We refer to these as the poison block and non-poison block, respectively, intentionally retaining the term ‘block’ to emphasise the conflation between treatment and block in the experimental design.

A 15 m × 15 m bait station grid was established across the western block for the deployment of bait (Fig. 2a). Baits were deployed in lockable mouse bait stations (Northpest.co.nz) affixed to wooden boards that were anchored to the ground. Cholecalciferol and its accompanying non-toxic pre-feed were deployed in the form of Feracol paste (Connovation NZ Ltd.) in a formulation containing 4 g kg^{-1} cholecalciferol to bait matrix. The deployment of pre-feed bait occurred only in the treatment block in every month from October 2020 until October 2021, while the poison bait was deployed from November 2020 until October 2021 (i.e. both the western and eastern blocks operated as non-poison controls in the first month of the study). Pre-feed was not provisioned in the non-treatment block due to concerns that without the accompanying toxicant, it would result in an elevation of local carrying capacity that could exaggerate the treatment effect. Two scoops of the pre-feed bait totalling c. 40 g were placed in each bait station in the first week of each month. After a 24–48 hr period the pre-feed bait was replaced with an equivalent amount of toxic bait. The bait stations were cleared, and the process repeated in the first week of the following month. We attempted to calculate the amount of bait consumed by subtracting the weight of the residual bait from the amount deployed, but a lack of facilities to uniformly dehydrate these bait quantities resulted in abandoning the protocol. However, the amount of bait removed from individual bait stations was recorded qualitatively (i.e. none, some, all) from December 2020 onwards.

Given that a SECR approach was used in this study to estimate mouse density, the effect of detector layout (live traps) and other design variables on the precision of density estimates were simulated prior to settling on the detector layout using a SECR design tool (https://www.stats.otago.ac.nz/secrdesignapp/) (Efford & Boulanger 2019). Based on

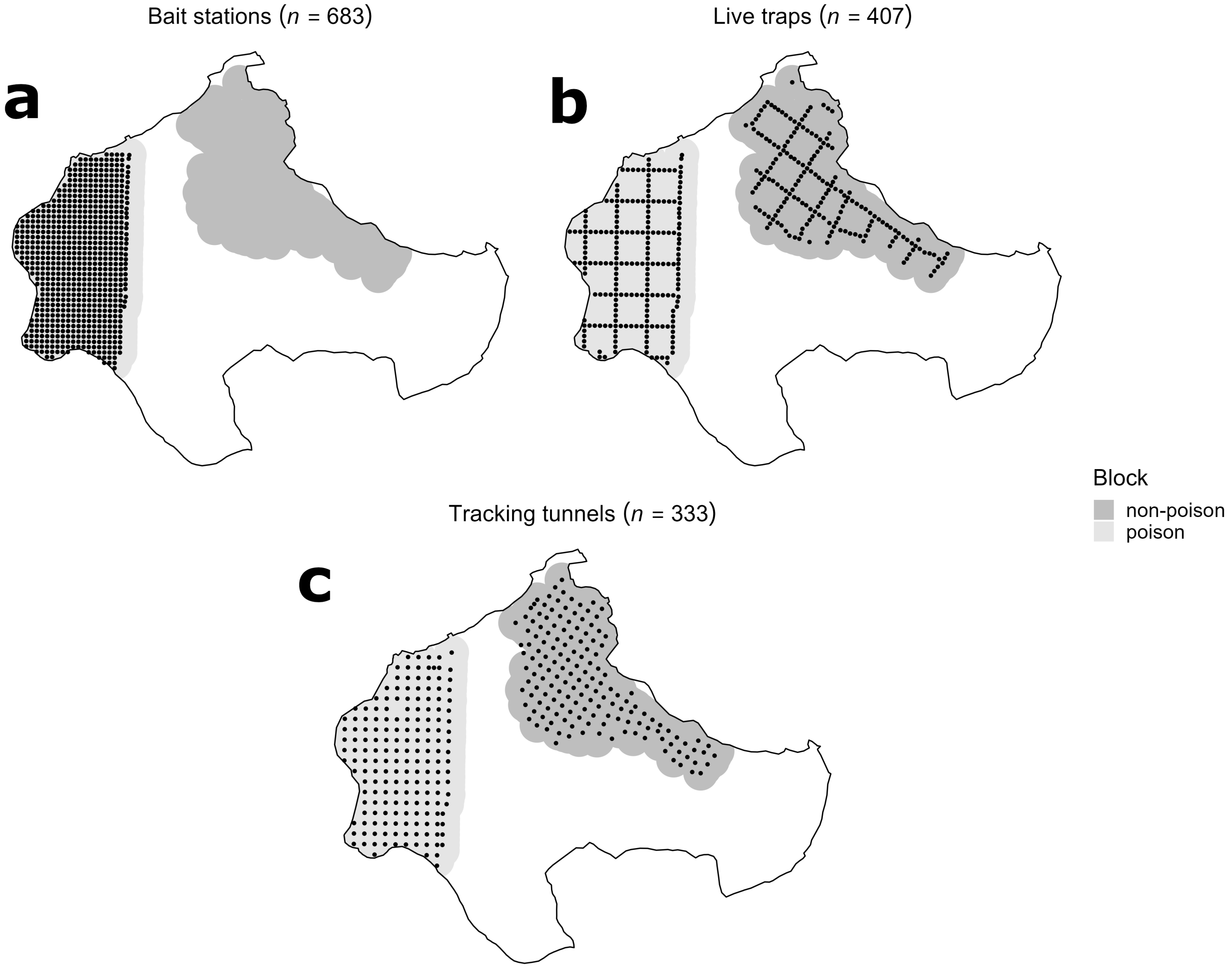

Figure 2. The monitoring arrays and poison deployment across Quail Island. Key: a) bait stations deployed at 15 m spacing, b) live traps at 15 m spacing on a lattice at 90 m spacing, c) tracking tunnels deployed at 30 m spacing.

these considerations a lacework design consisting of a criss-crossed trap layout with lines forming an equally spaced square grid was settled upon, where traps were spaced at 15 m along lines that were 90 m apart (Fig. 2b). Lacework configurations reduce the risk that home ranges will align systematically with the trap array, which can result in biased density estimates (Efford 2019). Physical obstacles present in the field led to minor discrepancies from the planned configuration. Applying a 100 m buffer around the live traps (the eventual area of SECR integration) and censoring the area by the island perimeter allowed us to estimate the effective area of the western (poison) block to be 22.6 ha and the eastern (non-poison) block to be 26.7 ha. The live trap arrays were run for 4–5 consecutive nights simultaneously in both poison and non-poison blocks.

Tracking tunnels and mouse capture sessions occurred simultaneously in poison and non-poison blocks. Tracking tunnels and cards (www.gotchatraps.co.nz) were deployed across both areas using a 30 m × 30 m grid on the first Monday or Tuesday of each month (Fig. 2c). Tunnels were activated for a single night using a smooth peanut butter lure (Pic's Peanut Butter Ltd.) and ran during the prefeed baiting period. Tracking card data were collected from November 2020 onwards. The purpose of the tracking tunnels was to employ a method, independent of SECR, to (1) assess the impact of cholecalciferol, and (2) to understand whether the presence-absence tracking tunnel data itself was a reasonable proxy of density, which is often assumed but not proven.

Capture-recapture was conducted every month using 185 live capture traps in the non-poison block and 222 traps in the poison block area. Traps consisted of both Longworth small mammal traps and Lifetrap small mammal traps (www.nhbs.com) (Fig. 2b). The Lifetrap is an updated version of the Longworth trap and near identical in material construction and dimensions but differs in colour, with the Longworth traps being bare aluminium while the Lifetraps were coated in green paint. For the purposes of this study, we have assumed that the two trap models were sufficiently similar that they introduced no bias into the study design. Additionally, the traps were deployed randomly with equal proportions in both poison and non-poison blocks. In the interests of animal welfare, traps were provisioned with food (commercial rodent food), moisture (carrot), and dry bedding (polyester fibre). Traps were opened at dusk to avoid non-target captures such as skinks (*Oligosoma maccanni* and *O. polychroma*). Due to the risks of mice suffering from hyperthermia, traps were checked shortly before sunrise to ensure all were serviced and closed before in-trap temperatures increased to levels that could impact mouse wellbeing. Captured mice were emptied into a bucket and subsequently handled while restrained within a soft plastic mesh that did not restrict breathing (Fig. 3). Each mouse was tagged on first capture with a numbered ear tag (small animal ear tag: www.nationalband.com), sexed, and weighed. Monitoring was conducted on the first week of every month from October 2020 until November 2021. Monitoring dates were only shifted to avoid heavy rainfall events. Data were recorded and safeguarded in the field using the Kobotoolbox app (www.kobotoolbox.org). The dominant vegetation type (either grassland or woody vegetation) was recorded at each trapping location as a potential covariate.

Analytical methods

All data were analysed using the program R version 4.3.1 (R Core Team 2023). Functionality required for the SECR was obtained via the "secr" package (Efford 2020). Additional functionality for core components of the wider analysis came from the "sf" package (Pebesma 2018) for spatial transformations, the "DHARMa" package (Hartig 2021) for model diagnostics, the "AICcmodavg" package (Mazerolle 2020) for model selection, the "tidyverse" package (Wickham et al. 2019) for data wrangling, and "pracma" (Borchers 2023) for analysis of autocorrelation.

To estimate density via SECR, for each of the 14 monitoring sessions (months), we tested a suite of four candidate models representing competing hypotheses. The four models were: a null model (~1), a block effect (~block), a vegetation effect (~vegetation), and an additive effect of block and vegetation (~block + vegetation). The detection function, which describes the decline in detection probability with distance from the centre of a home-range (Efford 2022), was modelled using a hazard rate function (based on preliminary model selection and observation of convergence issues). The area of spatial integration was determined by adding a 100 m buffer to the extent of the blocks and then masking it so its spatial extent could not exceed the seaward boundaries of the island. For each session we used an information theoretic approach to determine the most parsimonious model using Akaike's Information Criterion small sample size adjustment (AICc, which converges to AIC at high sample sizes) and ranked the models by their model likelihood (sensu Burnham & Anderson 2002). Model averaging was then used to estimate the density for each monitoring occasion disaggregated by block and vegetation type when appropriate.

Figure 3. Mouse restrained in soft plastic mesh for tagging and sampling.

As we were interested in the naïve predictive power of footprint tracking rates as a proxy of density, we compared the former against the equivalent density estimates using general linear regression in combination with a model selection approach using AICc (via the "AICcmodavg" package) on a set of five candidate models. Model diagnostics were examined using the "DHARMa" package. A log-log transformation was applied to ensure normality of residuals was obtained. From this, 95% prediction intervals were formulated to better understand the inherent variability associated with trying to predict mouse density from footprint tracking rates. To assess for the presence of a persistent temporal trend in the ratio of footprint tracking to density (i.e. the observed footprint tracking rate divided by the model averaged density estimate) we disaggregated the data by block and vegetation type and created a time series for each treatment-vegetation combination. We then calculated the rescaled range Hurst exponent for each time series (Hurst 1951; Weron 2002; Borchers 2023). The Hurst exponent provides a method for determining the presence of temporal autocorrelation, which measures the degree to which observations at one point in time are related to observations at previous or subsequent time points. A Hurst exponent > 0.5 indicates a positive autocorrelation (MacIntosh et al. 2013). The presence of temporal autocorrelation would suggest that future data points are influenced by past values, indicating some form of dependence over time.

Results

A total of 2766 individual mice were captured at least once over the course of the study, with 1064 mice being recaptured on more than one occasion. Model selection conducted using SECR revealed the most parsimonious model varied through time, with the *~block* and *~block + vegetation* models being the top-ranked model for six occasions each, while the *~1* and *~vegetation* models were only top-ranked for one month each (Fig. 4). Model averaging indicated that mouse density was generally higher in the non-poison than poison block, and in grassland areas compared to woody vegetation (Fig. 4). Mouse densities were largely indistinguishable in terms of block for the first four months following the deployment of poison (Fig. 4). Mouse density peaked in March for all vegetation and block types, with mean density being c. 2.4 × higher in the non-poison than the poison area during that period. The exception was the grassland poison block where the peak was a month earlier. Over the entire monitoring period, mean mouse

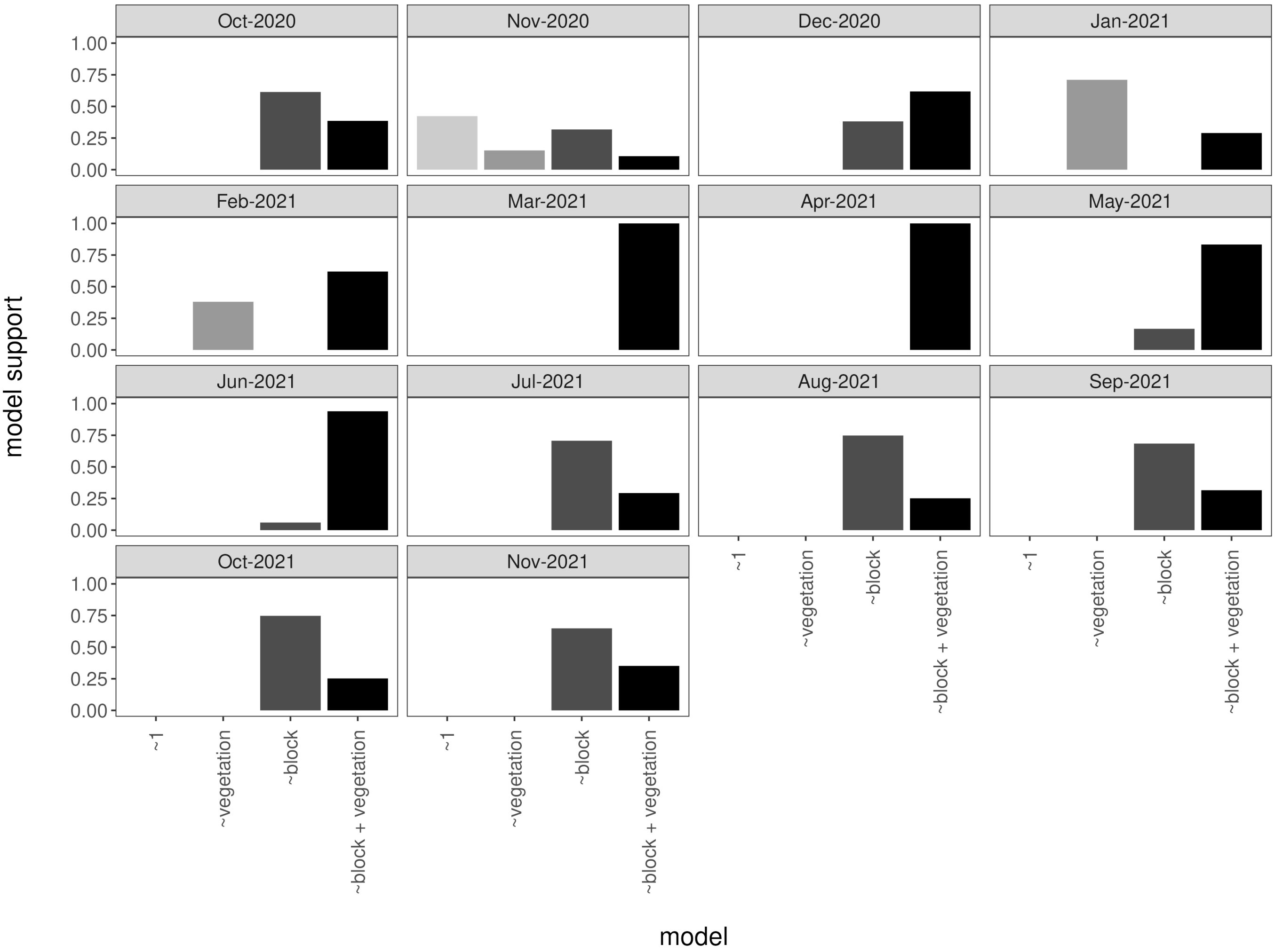

Figure 4. Support for different models (based on AICc model weight) varied with monitoring occasion.

density was highest in non-poisoned grassland (25.4 ha^{-1}), and lowest in the poisoned woody vegetation (7.3 ha^{-1}), with mouse densities in non-poisoned woody vegetation (15.1 ha^{-1}) and poisoned grassland (13.0 ha^{-1}) being somewhat similar. The hazard-rate detection function varied with monitoring occasion, with detectability reducing with increasing population size (Appendix S2). Notably, SECR density estimates describe no effect of the cholecalciferol bait on mouse density for the first four months of the poison treatment. Thereafter, mice were present in consistently but varying lower densities in the poison block compared to the non-poison block (Fig. 5).

Footprint tracking initially showed a similar pattern to that of density over the first eight months, increasing to a peak in March, with more mouse footprints being detected in the non-poison block than in the poison block, and fewer detections in wooded areas than in grassland (Fig. 6). While the tracking tunnel activity recorded in the final six months in the poison block mirrored the pattern recorded by density, in the non-poison block footprint tracking rates rapidly increased, resembling levels like those seen at the population peak in March.

Model selection (Table 1) supported a naïve linear relationship between log-transformed footprint tracking rates and log-transformed mouse density as the top-ranked model (Table 1), with a moderate correlation (adjusted $r^2 = 0.55$). However, support for the top-ranked model was not unanimous (AICc weight = 0.43), with other models including vegetation and block effects having moderate support (AICc weight = 0.11–0.31). The 95% prediction interval around the top-ranked model demonstrated that on average a 25-fold variation in mouse density could be expected for any given footprint rate (Fig. 7). However, the relationship between footprint tracking and density fluctuated non-randomly throughout the study (Fig. 8). A subsequent analysis of the Hurst exponents (relating to the temporal relationship between footprint tracking and density), disaggregated by block and vegetation, suggested that there was evidence for a temporal autocorrelation (i.e. interdependence between consecutive observations) in the non-poisoned grassland (H = 0.68), non-poisoned woody vegetation (H = 0.67), and poisoned grassland (H = 0.63). Evidence of temporal autocorrelation was equivocal for the poisoned woody vegetation (H = 0.50).

There was no indication, at any point in the study, that the consumption of bait was limited by its availability on any more than a local scale. At least 50% of bait stations appeared to have a full complement of bait at the end of every monthly baiting period, with only four months recording a small proportion of bait stations emptied of bait (< 5%) (Fig. 9). The highest rate of bait clearance was recorded in November 2021 when 4.1% of recorded bait stations were assessed as being empty.

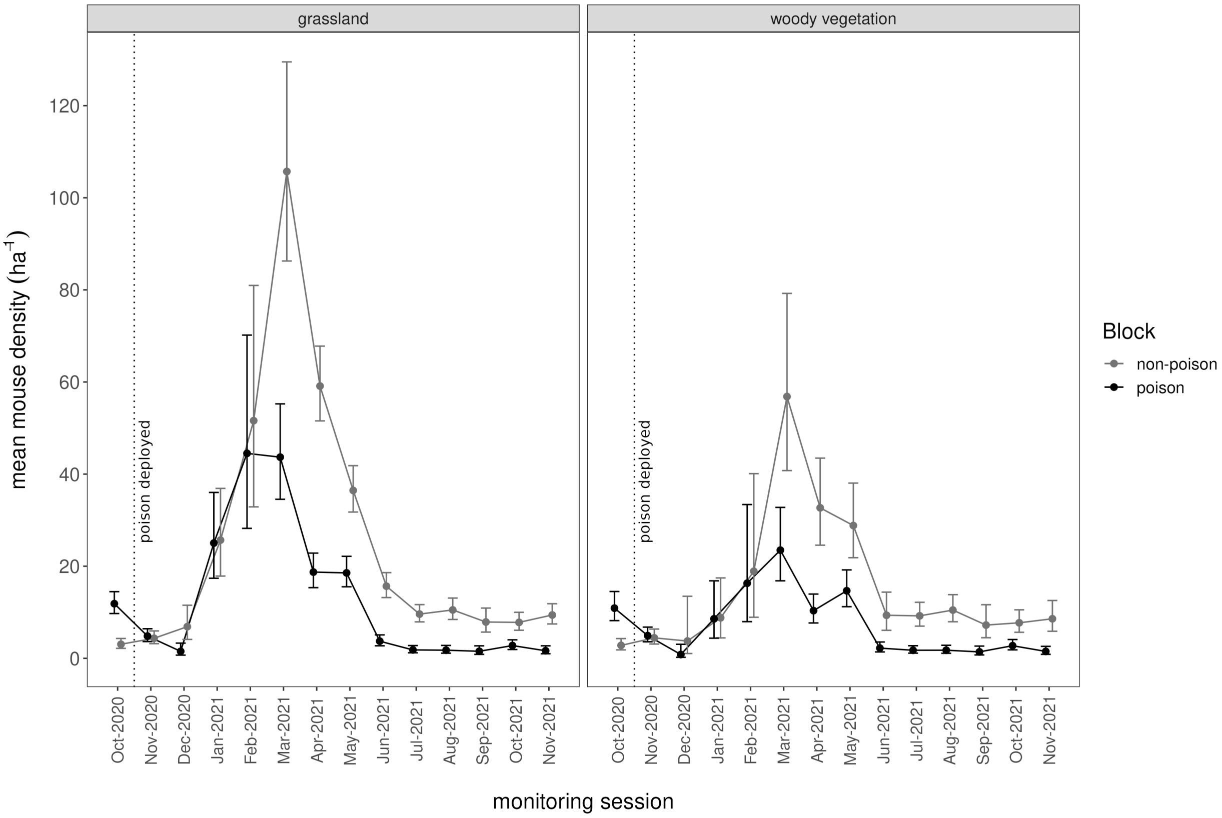

Figure 5. Mean density estimated for mice in poison and non-poison blocks from model averaging disaggregated by vegetation type and block (shown with 95 % confidence intervals).

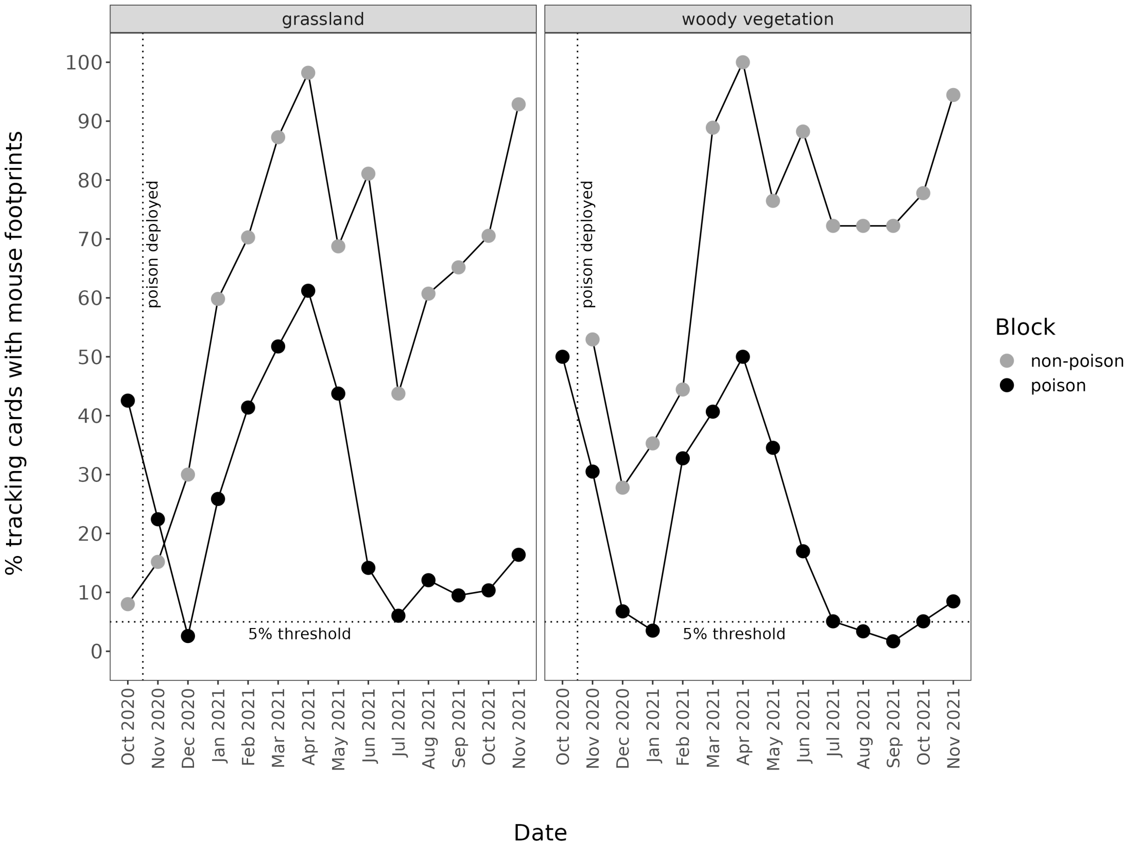

Figure 6. Monthly fluctuation in percentage of tracking cards showing an index of proportional mouse presence across vegetation types.

Table 1. Model selection table for the relationship between density and footprint tracking rate. Models ranked by AICc (AIC with a small sample correction). Key: K = number of parameters, AICc = AIC with a small sample correction, Δ AICc = difference in AICc value between the model and the top-ranked model, AICcWt = model weight (likelihood), Log-likelihood = measure of goodness-of-fit.

Model name	K	AICc	Δ AICc	AICcWt	Log-likelihood
log(density) ~ log(tracking)	3	131.95	0	0.43	−62.74
log(density) ~ log(tracking) + vegetation	4	132.60	0.65	0.31	−61.89
log(density) ~ log(tracking) + block	4	134.05	2.1	0.15	−62.62
log(density) ~ log(tracking) + block + vegetation	5	134.76	2.81	0.11	−61.76
log(density) ~ 1	2	173.54	41.58	0	−84.65

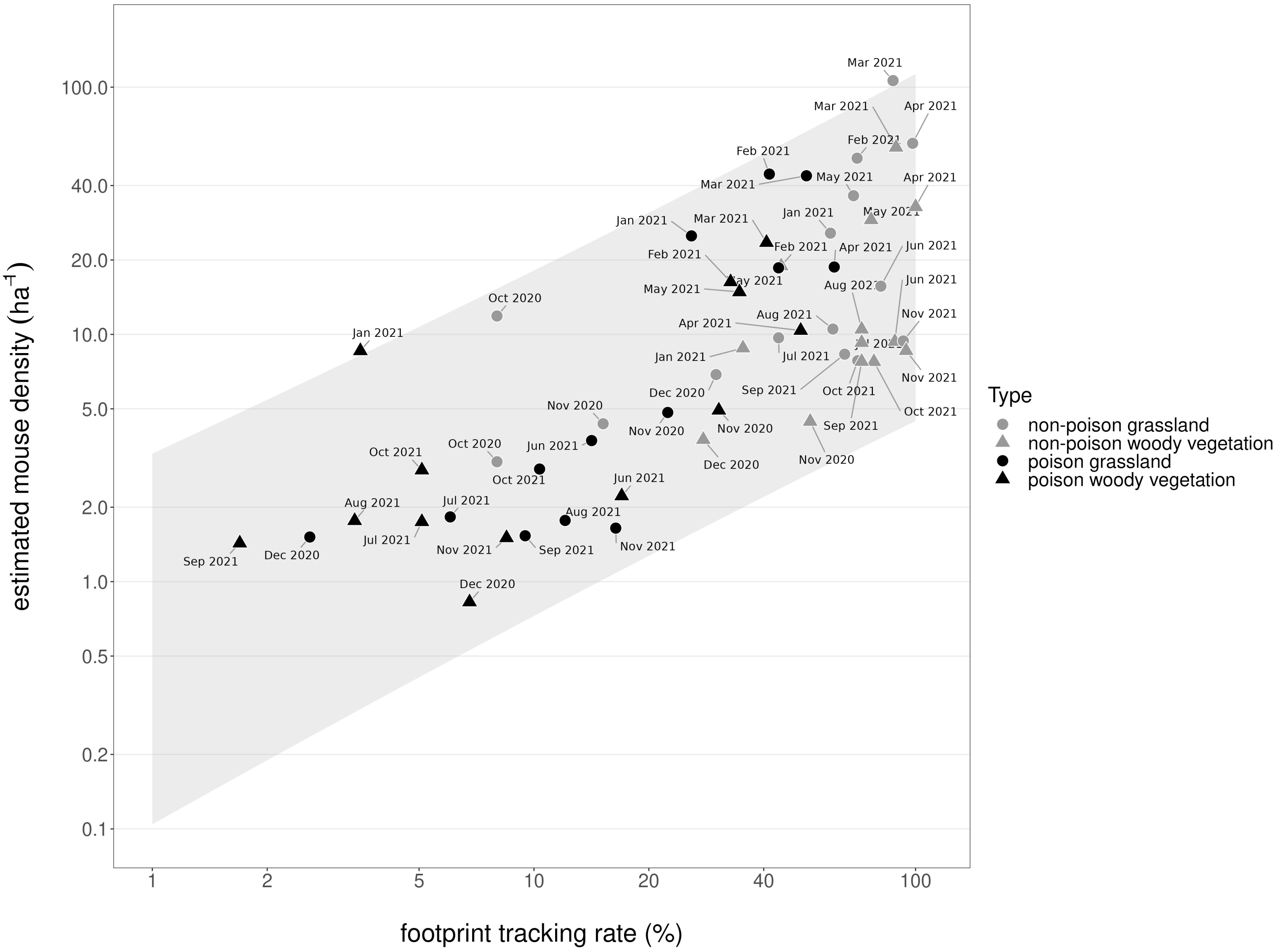

Figure 7. The naïve relationship between the overall footprint tracking rate and mouse density (log-log scale) shown with ± 95% prediction intervals.

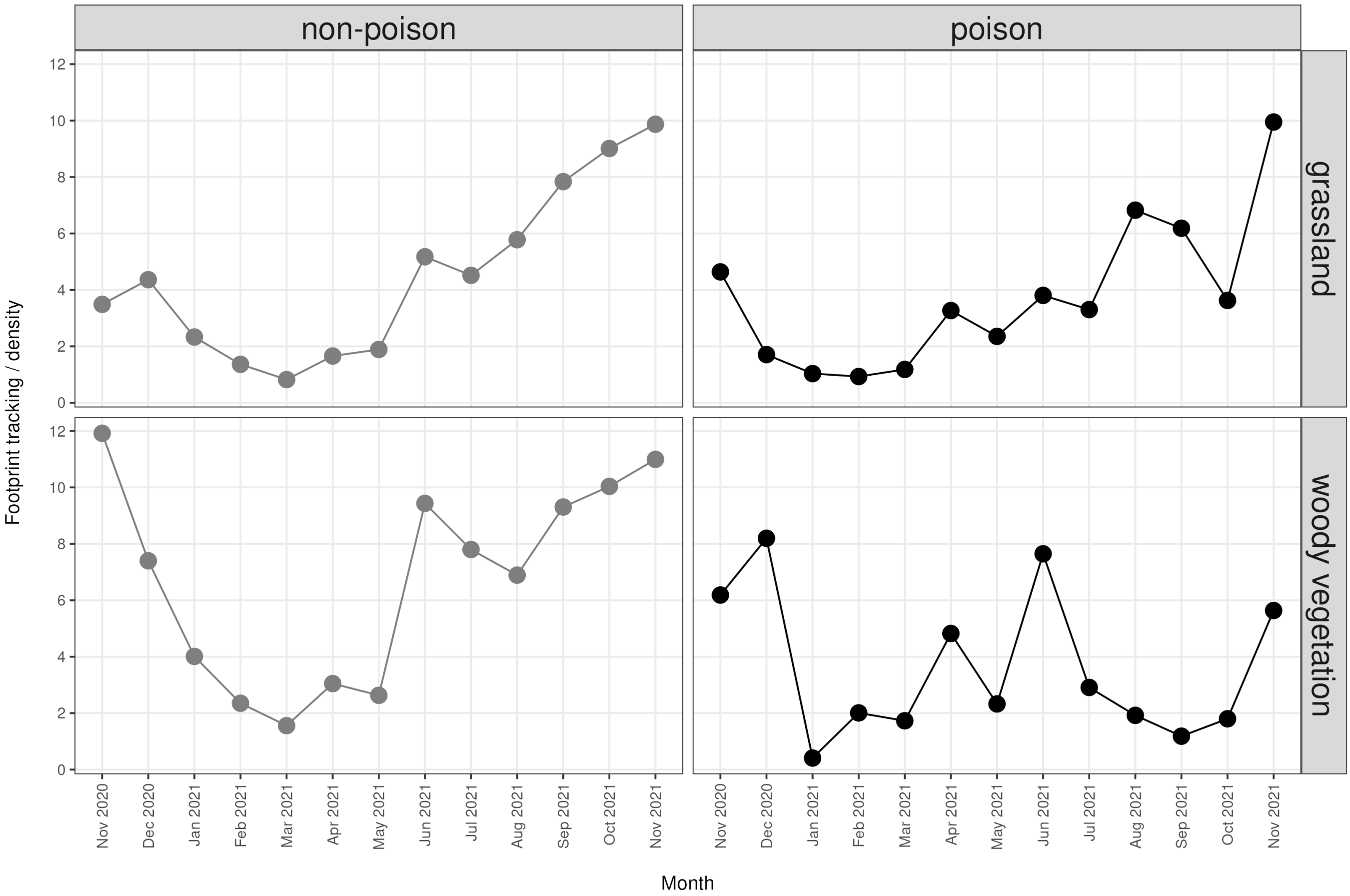

Figure 8. The monthly fluctuation in the relationship between footprint tracking and estimated density (i.e. the observed footprint tracking rate divided by the model averaged density estimate) disaggregated by block and vegetation type.

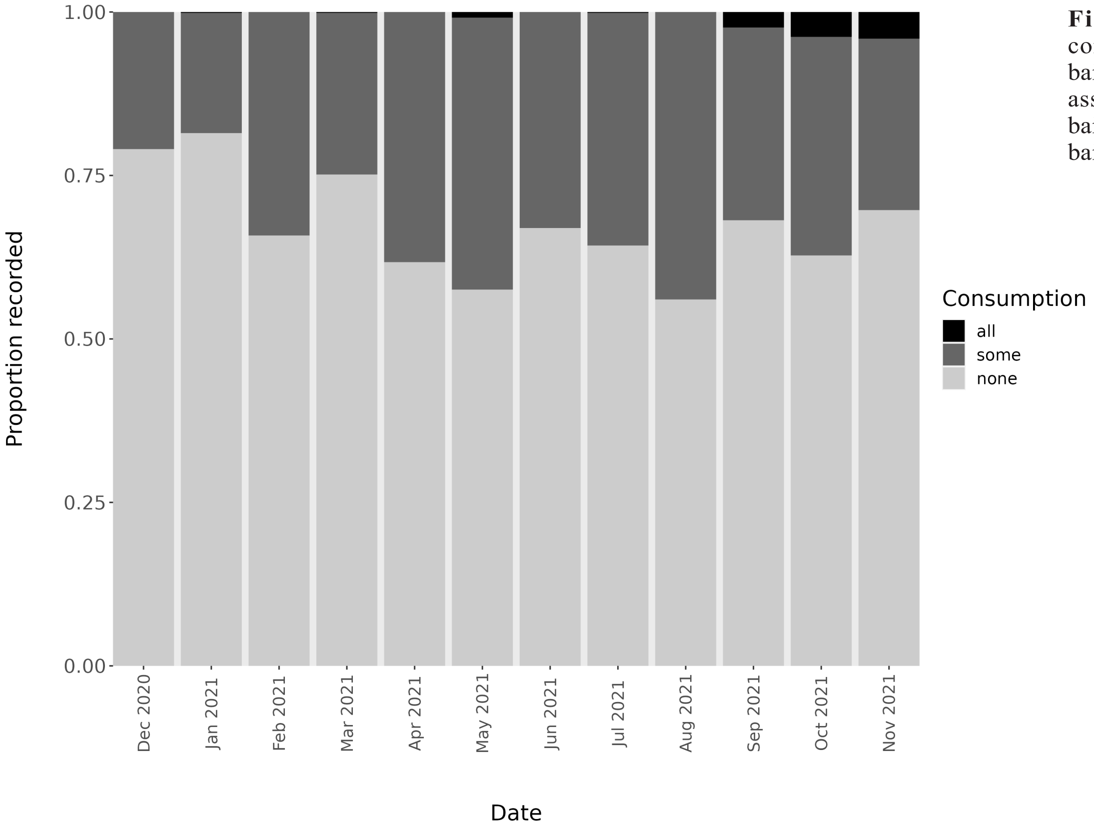

Figure 9. The apparent consumption of bait from bait stations. Based on a visual assessment of the residual bait at the end of the monthly baiting period.

Discussion

Mouse density responses to toxicant

Whilst mouse densities were suppressed for extended periods in the study block treated with cholecalciferol, they were not suppressed to the extent, nor for a duration, that suggests the tool can reliably mitigate mouse impacts on threatened taxa, noting that we still lack a nuanced comprehension of the patterns and drivers of mouse predation impacts needed to validate this assessment. Additionally, our results suggest that, in this form, cholecalciferol is not suitable for mouse eradication.

Spatially explicit capture-recapture derived mouse density patterns clearly show that cholecalciferol bait appeared to ameliorate mouse density through the late summer to autumnal mouse population peak (to c. 40% of expected density) but could not mitigate the rapid population growth observed in the first four months. The moderate suppression we recorded appeared to be sustained from March 2021 onwards and raises the question of whether the suppression effect might have extended into the subsequent year had the poison treatment been maintained. Our finding that vegetation type was an important factor is not unexpected given that house mice have been shown to be highly responsive to productivity cycles (Murphy 1992; Ruscoe et al. 2003; Ruscoe et al. 2004) and have a predilection for grassland habitat (Harper 2010).

Our estimates of mouse density fell well within the bounds recorded by many other SECR studies in NZ (Vattiato et al. 2023). It is possible our density estimates for mice may be slightly inflated due to immigration, which would violate the assumption of population closure. However, there was no evidence of higher trap catch on the boundary of the study areas which would have been expected if there was extensive immigration; as such, levels of immigration are likely to have been low. Density estimates may have been influenced by behavioural responses that resulted in trap-shyness or trap-happiness. Indeed, we undertook preliminary SECR analyses exploring the existence of simple and block dependent behavioural effects. Model selection incorporating the simplest behavioural effect (a universal behavioural component affecting detection probability) hinted that behavioural effects were not consistently present, but when present tended to show trap-happiness in winter and trap-shyness in summer, likely explained by resource availability (Appendix S3).

Footprint tracking interpretation

The relationship between footprint tracking rates and density of rodents recorded across previous studies has been inconsistent (Ruscoe et al. 2001; Nathan et al. 2013; Wilson et al. 2018). In our study footprint tracking rates appeared to be an unreliable proxy for mouse density because the relationship between footprint tracking rates and density oscillated through time, which could produce a c. 25-fold variation in mouse density for a given tracking rate. Consequently, we caution wildlife managers that footprint tracking rates may not always serve as a reliable proxy for density and require careful, context-specific interpretation.

Not only did we record high footprint tracking rates during peak mouse density in autumn, but we also recorded high footprint tracking rates during periods of low mouse density in late winter and spring in the non-poison block. Although footprint tracking indices may not be a reliable indicator of relative mouse abundance for management purposes, they likely retain value as an index of foraging intensity. Indeed, we surmise that the high footprint tracking rates we recorded during periods of low mouse density might be indicative of greater mouse foraging activity due to limited resources. Interestingly, this pattern was not pronounced in the woody vegetation area of the non-poison block, a finding which is potentially due to lower mouse densities, and therefore reduced competition for resources, although we lack data to validate this.

Norbury et al. (2023) have recommended that mice need to be controlled to a level which yields a footprint tracking rate < 5% in order to allow the recovery of NZ lizard populations. This has been described as a pest density impact function (DIF), which is derived from the relationship between pest density (mice) and its impact on non-pest species (lizards) (sensu Norbury et al. 2015). In the case of Norbury et al. (2023), their finding was based on modelling counts of different lizard species in artificial refuges against nearby mouse footprint tracking rates. Our finding suggests that as the relationship between mouse footprint tracking and mouse density is not constant it violates an implicit assumption underpinning the validity of the Norbury et al. (2023) pest density function: that the footprint tracking rate is a constant and reliable proxy of density through time, an assumption that Norbury et al. (2023) question in their discussion. This does not dispute the negative relationship between lizard abundance and mouse footprint tracking found by Norbury et al. (2023), or the value of metrics for triggering management, but it does raise concerns about the validity of using mouse footprint tracking as the basis for a universal conservation threshold that claims to describe density. In our study, footprint tracking appeared to be strongly influenced by local phenology.

Currently, there are few affordable estimation methods for monitoring mouse populations. Spatially explicit capture-recapture density estimates, while robust (in that they account for variable detection), are much more expensive and technically demanding than footprint tracking, and therefore will be unaffordable in most conservation management settings in NZ. Similarly, while there is now a large suite of estimation models available for modern wildlife monitoring, e.g. distance sampling and its variants (including random encounter models, random encounter and staying time models, N- mixture models, occupancy models, and a plethora of mark-recapture variants; Iijima 2020), these will also be out of reach for most practitioners due requirements for repeated surveys, specialist equipment, and a high level of analytical expertise. Another monitoring tool increasingly used for estimating density or indexing abundance in small mammals is camera trapping (Villette et al. 2016; Wearn & Glover-Kapfer 2019; Gracanin et al. 2022). Whilst methodologies and supporting technology continue to improve, camera trapping for density estimation, much like mark-recapture techniques, continues to be out of reach for many conservation management scenarios. We acknowledge that, in the absence of practical alternatives, tracking tunnel indices remain the only cost-effective mouse monitoring option for most conservation programmes in NZ, but we caution that users must be aware of the method's flaws and its potential unreliability as a metric of relative abundance.

Temporal mouse dynamics

A strong autumnal mouse irruption was evident in both our density estimates and footprint tracking indices over the first six months (Fig. 5). Our modelling suggests there was an initial knock down effect by poison in December 2020 for mice in the grassland habitat. This might be indicative of mice being neophilic (sensu Crowcroft 1973; Barnett & Dickson1989), but this effect, if real, appeared to be very weak. Except for this minor dip, the application of poison appeared to have no effect on mouse density until March 2021. We speculate that this pattern relates to seed and invertebrate prey availability (Ruscoe et al. 2003; Wilson & Lee 2010) and hypothesise that during late winter and early spring mice might be more susceptible to toxic bait because of food resource limitation (Brown et al. 2024). This assertion is supported by the increases seen in the frequency of both 'some' and 'all' bait consumed per bait station during this period in the poison block (Fig. 9). Given that bait was rarely fully consumed from the bait stations we infer that our results were not impacted by limited bait availability. Under such circumstances, we speculate that low food resource availability was driving the uptake of cholecalciferol-laced bait, aligning with findings from similar studies (Brown et al. 2024). In the non-poison block where there was no alternate food source (i.e. no poison bait) mice may have responded by increasing their foraging area and therefore increasing the probability of an interaction with a tracking tunnel (Mitchell et al. 1990) which may explain why the relationship between footprint tracking rate and density was generally more elevated in the non-poison block compared to the poison block.

Management targets

Only occasionally did the footprint tracking rate fall in the poison area below the 5% tracking rate recommended for biodiversity protection (Romijn 2013; Hitchmough et al. 2016; Norbury et al. 2023). It is important to recognise that this threshold has only been demonstrated for a small number of lizard species in one location and ecotype (Norbury et al. 2023) and might vary according to species life-history traits and habitat characteristics. The apparent mouse density at a 5% tracking rate in our study equated to 0.4 –10.7 mice per hectare (based on our 95% prediction interval). We suspect the upper density we recorded at this threshold still may be insufficient to prevent harmful ecological impacts on vulnerable lizard species given that food limitation has been shown to drive greater foraging of rodents (e.g. Anderson 1986; Gutman et al. 2007).

We hypothesise that the predation risk to threatened fauna will differ at the same mouse density, depending on whether the mice have adequate food resources and are in a population growth or decline phase. Such conditions may force mice into greater foraging activity and, potentially, prey-switching onto less preferred prey, as has been observed in other predators (Rutz & Bijlsma 2006; Jaworski et al. 2013). Based on our observations we speculate that there may be two seasonal periods when predation by mice may be heightened on Quail Island: (1) when mouse density is declining at its fastest rate in autumn, coinciding with increasingly cooler and wetter climate conditions and the likely depletion of the seed and invertebrate resources which fuelled the initial irruption, and (2) in spring, when mouse footprint tracking reached a peak, which possibly indicates a secondary spike in resource limitation and/or climatic release of mouse foraging behaviour. Regardless, given the strong phenological pattern we observed, and which has been recorded elsewhere in rodent populations (Ruscoe et al. 2003; Ruscoe et al. 2004), we conclude that effective mouse management is better built around site-specific phenological risks and biodiversity vulnerabilities rather than arbitrary thresholds. Clearly, much more research will be required to understand these dynamics and ultimately improve user-friendly monitoring protocols.

Study design limitations

We acknowledge that our study design, by being unreplicated, is essentially a case study and therefore may not be generalisable. Additionally, this study was intended to include a poison to non-poison block reversal, but the required funding did not eventuate. We are cognisant of the power of BACI study designs (Smith 2002; Christie et al. 2019), but recognise that there is often resistance to robust study designs in applied conservation research due to perceptions of urgency (Coetzee and Gaston 2021) and limited resourcing.

Conclusion

High frequency, extensive poisoning using cholecalciferol in the form of Feracol paste appears to be ineffective in maintaining the suppression of seasonal mouse irruptions on Ōtamahu | Quail Island to the low levels recommended for conservation management (e.g. < 5% footprint tracking threshold). The maximal suppression we achieved in our study (c. 60%) only emerged in mid-summer, likely in response to a change in food availability. The utility of such moderate suppression of mice in the context of conservation management is not clear. Additionally, we found footprint tracking rates were not a reliable proxy of density. Our findings suggest that the success of future mouse toxicant interventions will rely not only on the effectiveness of the toxicant itself but also on determining the optimal timing for its application, which requires a deeper understanding of the phenological dynamics linking mouse density to the species they affect and a dynamic rather than static view of conservation risk.

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Supplementary Material

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

Appendix S1. Vegetation zones on Ōtamahua | Quail Island.

Appendix S2. Monitoring occasion detection probabilities**.**

Appendix S3. Behavioural effect of trap shyness and trap happiness during monitoring sessions**.**

Appendix S4. Statistical summary of the capture and recapture histories for each session disaggregated by block**.**