

Testing the efficacy of typical urban pest mammal control in two BACI experiments

Christopher K. Woolley^{1,2*} , Deborah J. Wilson³ , John G. Innes⁴ , Neil Fitzgerald⁴  and Stephen Hartley² 

¹Zealandia Te Māra a Tāne, Karori, Wellington, New Zealand

²Centre for Biodiversity and Restoration Ecology, Te Herenga Waka Victoria University of Wellington, New Zealand

³Bioeconomy Science Institute, Dunedin, New Zealand

⁴Bioeconomy Science Institute, Hamilton, New Zealand

*Author for correspondence (Email: christopher.k.woolley@gmail.com)

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Abstract: Introduced mammalian predators have had dramatic impacts on the ecosystems of oceanic islands. While conservation strategies have been developed to suppress or eradicate them in a wide range of unpopulated habitats, their management in human-dominated landscapes is less advanced. Here, we assess the efficacy of urban predator control using two years (four sessions) of mammal monitoring data in before-after control-impact (BACI) experiments in Ōtepoti Dunedin and Kirikiriroa Hamilton. Results of the two BACI experiments provided no evidence for an effect of intensified predator control on rat, mouse, or possum abundance. Short experimental timeframes and low rat numbers in the before condition (especially for rats at non-treatment sites) may have made it difficult to identify effects. Further research is required to understand relationships between urban predator control and pest mammal abundance, and how control may be optimised to maximise cost-effectiveness.

Keywords: introduced mammalian predators, *Mus*, pest monitoring, pest control, *Rattus*, *Trichosurus*

Introduction

Predators are important components of ecosystems and can play critical roles controlling the distribution, abundance, and diversity of their prey (Sinclair & Krebs 2002; Richie & Johnson 2009). In doing so, some keystone predators exert top-down pressure with regulatory effects that cascade down trophic levels (Estes 1996; Terborgh et al. 2001). The loss or introduction of predators from or into an ecosystem can therefore have dramatic and far-reaching ecological impacts, as has been learned from numerous examples of invasion (Croll et al. 2005; Fukami et al. 2006; Fleming et al. 2014) and population reduction or loss (Myers et al. 2007; Taylor et al. 2016). To mitigate these impacts, predator populations in some systems are highly managed (Hecht & Nickerson 1999). On oceanic islands with few or no native terrestrial mammals, the impact of introduced mammalian predators has been notably severe (Fritts & Rodda 1998; Blackburn et al. 2004). Predatory mammals are implicated in 58% of modern bird, mammal, and reptile species extinctions globally, with rodents alone linked to 30% (Doherty et al. 2016).

The science and tools available for eradication and suppression of predatory mammals have increased considerably in the last 30 years, particularly with the availability of anticoagulant toxins and refinement of methods for aerial application of toxins (Hess & Jacobi 2011; Russell & Broome 2016). These advances have enabled pest mammal

eradication at increasingly large scales on islands and in fenced ecosanctuaries (Townes & Broome 2003; Innes et al. 2019) and have increased the efficacy of mammal suppression at unfenced ‘mainland islands’ (Saunders & Norton 2001). These interventions have in turn facilitated the recovery of vulnerable species (Townes 1991; Courchamp et al. 2003; Sharp et al. 2015; Jones et al. 2016; Innes et al. 2024).

A significant challenge to advancing the management of introduced predators is the habitation of larger islands by humans, especially in urban centres, and the need for wildlife management to consider human interests and activities (Allen et al. 2018; Russell & Stanley 2018). Typically, pest mammal management in peopled landscapes has been motivated by disease risk (Meerburg et al. 2009), damage to crops or other plants, and nuisance behaviours (Wilson et al. 2018). However, as awareness of the potential for biodiversity conservation in cities grows (Ives et al. 2016; Knapp et al. 2021), urban pest control is increasingly being undertaken to achieve ecological outcomes (Russell & Stanley 2018).

In Aotearoa New Zealand, there is a growing desire to support native species and ecosystems in cities through the control of introduced mammalian predators (henceforth pest mammals). Biodiversity management in cities is administered at a local scale and many city councils have plans and strategies that describe control of pest mammals, including ship rats (*Rattus rattus*), Norway rats (*Rattus norvegicus*), mustelids (*Mustela nivalis*, *Mustela erminea*, and *Mustela furo*), and

brush-tail possums (*Trichosurus vulpecula*) (e.g. Dunedin City Council 2007; Auckland Council 2012; Wellington City Council 2015; Hamilton City Council 2020). Control programmes are highly variable, ranging from localised control in significant natural areas to operations that span networks of urban reserves and even residential areas (Wellington City Council 2015; Whitburn & Shanahan 2022). In addition to their own programmes, many councils in New Zealand support and partner with community restoration and backyard trapping groups to make the most of the large volunteer resource available in cities (e.g. predator-free community groups; Peters et al. 2015; Gerolemou et al. 2024). Recently, predator control initiatives have burgeoned as a result of the Predator Free New Zealand 2050 policy (New Zealand Government 2016) which aims to eradicate rats, mustelids, and possums from the entire country (including cities) by 2050. One notable urban example funded in part through Predator Free 2050 Ltd (the Crown-owned, charitable company established to help deliver this goal) is Predator Free Wellington, which aims to eradicate these pests from Wellington City and since July 2019 has substantially reduced pest populations on the suburban Miramar Peninsula (Whitburn & Shanahan 2022).

However, urban pest control is not yet a mature regime with proven best practice methods. Unlike rural forests and national parks, where the impacts of control operations have been studied both for their targeted pests and the native species they seek to protect (Brown et al. 2015), urban areas have received little such research. There are several respects in which urban predator control in New Zealand must differ from that undertaken in non-urban environments. The pest mammal community in cities has more Norway rats and cats (*Felis catus*), and fewer mustelids (King & Forsyth 2021) than elsewhere. Habituation to human activities and responses to lures may also differ due to the resources available in cities (e.g. abundant food waste, gardens, compost bins, etc.), bright lights, and noise. Predator control methods available for use in cities differ from those suitable in more remote locations due to the accessibility of devices to the public (especially children and pets), and the small parcels into which land ownership is broken. Furthermore, little is known about the behaviour and ecology of pest mammals in urban areas because they are less studied there (though see Morgan et al. 2009, 2011; Fitzgerald et al. 2017; Mackenzie et al. 2022; Miller et al. 2022). Biodiversity restoration outcomes too, may not reflect what has been learned in less modified ecosystems. In cities, remnant or restored native vegetation is typically fragmented, and hence native species may be limited by the availability of suitable vegetation rather than by pests (Elliott Noe et al. 2022).

To achieve positive outcomes for biodiversity restoration in cities, there is a need for research into current methods of urban predator control and into biodiversity outcomes with and without such control. Here, we report on two before-after control-impact experiments: one assessing the impact of a new predator control operation in Dunedin (Te Waipounamu | South Island, New Zealand) targeting ship rats, Norway rats, and possums, and the other assessing the intensification of existing ship rat and Norway rat control in Hamilton (Te Ika-a-Māui | North Island). These three pest species are those most commonly targeted in cities because they are the most tractable and often the most important predators of nesting forest birds (Innes et al. 1999, 2010; Armstrong et al. 2006a; Fea & Hartley 2018) and other fauna. In addition, ship and Norway rats (also known as black rats and brown rats, respectively) have a long history of control in cities to limit disease spread and damage to buildings (Wilson et al. 2018).

Methods

Mammal monitoring was carried out at eight study sites in Ōtepoti Dunedin and four in Kirikiriroa Hamilton (Fig. 1a & b) in Spring (late October–early December) 2017 and 2018 and Autumn (late May–June) 2018 and 2019. A further session of monitoring was completed in Hamilton only in Spring 2019. While we were primarily interested in the effects of predator control on the target species (ship rats, Norway rats, and possums), we were also interested in the effect of rat control on mice (*Mus musculus*) because mice compete with and are preyed upon by rats and interact with control devices targeting rats (Caut et al. 2007; Norbury et al. 2013; Bridgman et al. 2013, 2018).

At each site, a line of ten stations of monitoring devices were deployed at 50 m spacing. Each station consisted of a plastic footprint tracking tunnel (Black Trakka, Gotcha Traps, NZ) with pre-inked card (Gotcha Traps, NZ) used to detect rats (ship rats and Norway rats could not be distinguished from their footprints) and mice, and a plastic chew card pre-baited with peanut-butter-flavoured Possum Dough (traps.co.nz) used to monitor possums. Tracking tunnels were pegged into the ground and baited at both ends of the tunnel with rabbit paste (Erayz, Connovation, NZ). Chew cards were folded and nailed to a tree or other suitable object approximately 300 mm from the ground and 2–5 m from the tunnel. Both tracking tunnels and chew cards were deployed for 6 nights following the protocols of Miller et al. (2022). For each device, presence/absence of rats, mice, and possums was recorded according to standard practice (Manaaki Whenua n.d., Gillies & Williams 2013) over the 6 nights. Binary data were used in statistical models but tracking and chew indices (proportion of devices that recorded presence) are reported in results.

Predator control was intensified at some study sites in each city according to a before-after control-impact (BACI) experimental design. Sites for intensification were selected in collaboration with Dunedin and Hamilton City Councils, based in part on where predator control was planned, and hence assignment of treatments was non-random. In Dunedin, a new predator control operation, undertaken by contractors on behalf of Dunedin City Council, was implemented from July 2018 until the conclusion of the BACI study (July 2019). Rat (both ship and Norway) and/or possum control was undertaken at the treatment ('impact') sites: three sites received both possum and rat control, two rat control only, and a further two possum control only (Fig. 1a). Sites where control was not undertaken for either rats or possums were considered non-treatment for that species ($n = 5$ treatment sites and $n = 3$ non-treatment sites for both rats and possums; Fig. 1a). We summarised the rat and possum control effort before (two monitoring sessions) and after (two monitoring sessions) the intensification. In Hamilton, rat control was intensified at two study sites in July 2019 (Fig. 1a). The Hamilton BACI experiment therefore included four sessions of before-treatment monitoring and one session of after-treatment monitoring for two treatment and two non-treatment sites.

Based on information provided by city councils, we summarised pest control for annual periods (July–June), during which pests were monitored along the transect at each study site, as densities of each type of control device in use for rats or possums. Each summary applied to the area centred on a monitoring transect, using a buffer distance from the monitoring devices that approximated the radius of a 95% circular home range (130 m for ship rats and Norway rats, and 250 m for

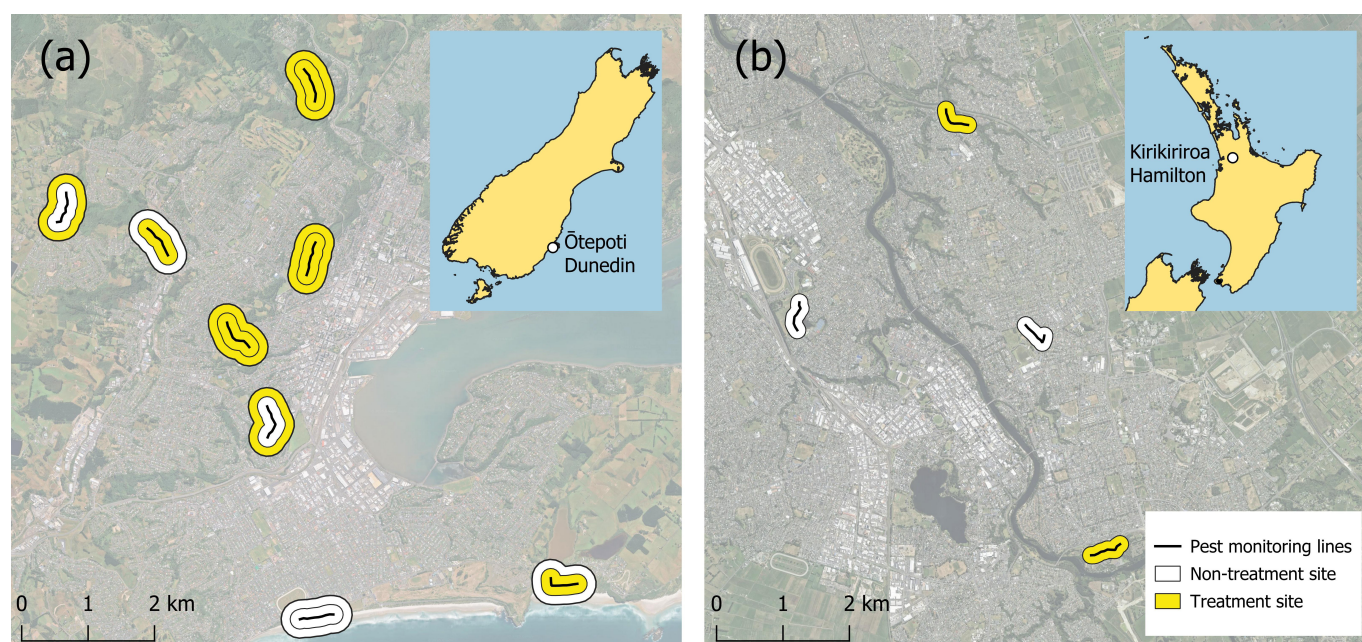


Figure 1: Locations of study sites in each of (a) Ōtepoti Dunedin ($n = 8$; location on Te Wai Pounamu South Island) and (b) Kirikiriroa Hamilton ($n = 4$; location in Te Ika a Māui North Island inset), New Zealand. Black lines show tracking card monitoring lines; polygons indicate 130 m buffers around lines for rats (both cities) and 250 m buffers for possums (Dunedin only). Polygon colour indicates intensification of management control for rats (inner polygon) and/or possums (outer polygon): yellow for treatment, white for non-treatment.

possums; Adams et al. 2014; Fitzgerald et al. 2017; Mackenzie et al. 2022). These site areas ranged from 15.1–20.0 ha (mean = 17.2 ha) for ship and Norway rats and 36.6–47.2 ha (mean = 41.9 ha) for possums.

Statistical analyses

We assessed effects of the intensification of control in Dunedin and Hamilton using separate mixed effects logistic regression models. Using presence/absence of rat or mouse prints (tracking tunnels) or possum chew (chew cards) as responses, we fitted separate models for each city, accounting for season (spring vs autumn), time (before vs after intensification of predator control), treatment (treatment vs non-treatment), and the interaction of time and treatment as fixed effects. Station nested within site was a random effect. A significant time \times treatment interaction in this BACI design indicates a treatment effect, i.e. a response to predator control. For Hamilton, models produced a warning that the Hessian was numerically singular, likely because there were no observations in the after category during autumn. To assess the robustness of the model estimates, we therefore fitted reduced models without the interaction and compared estimates with those of the full models.

All statistical analyses were performed in R version 4.2.1 (R Core Team 2022). Mixed-effects models were carried out using the lme4 package version 1.1-35 (Bates et al. 2015) and fit was assessed by plotting residuals and running Kolmogorov-Smirnov and Levene's tests using the DHARMA package version 0.4.7 (Hartig 2024). Results were visualised using the ggplot2 package version 3.5.0 (Wickham 2016).

Results

Urban predator control

In Dunedin, there was no consistent council-led predator control undertaken at the study sites in the year prior to Spring 2018; since the intensification, Dunedin City Council has continued and expanded the pest control effort across the city. The intensification in Dunedin used Protecta Sidekick bait stations (Bell Laboratories) baited with either bromadiolone or diphacinone for rodent control and single-kill Timms traps (Stallion Plastics Ltd, NZ) for possums (Table 1).

Prior to intensification of predator control in Hamilton, rodent control existed at three sites in the form of pindone in Pied Piper bait stations (Key Industries). In Spring 2019, this was temporarily intensified by the addition of A24 multi-kill traps (Goodnature Limited) (Table 1).

Rodent and possum control in Dunedin

In Dunedin, rat and mouse tracking indices showed no significant relationships with treatment, time or their interaction in the mixed effects logistic regression models. Season was a significant predictor of both rat and mouse tracking indices, with higher rates observed in autumn than spring (Table 2). Higher rates of possum chew were recorded at treatment sites than non-treatment, but this pattern was observed both before and after the intensification of control (Fig. 2a) and the interaction term was not statistically significant. Season was a significant predictor of possum chew index, with higher rates observed in spring than autumn (Fig. 2a, Table 2).

Rodent control in Hamilton

Due to the concerns that some model parameters were not identifiable, models using data from Hamilton were run with and

Table 1: Summary of predator control targeting rats (ship and Norway) and possums at n study sites in Hamilton and Dunedin before and after intensification. Predator control was intensified in Dunedin in July 2018 and in Hamilton in July 2019. ‘NA’ indicates ‘not applicable’.

| Sampling period and location | Device type | No. sites where used | Mean density at sites where devices used (ha^{-1}) | Service frequency (year^{-1}) range (mean) |
|-------------------------------|-------------------|----------------------|---|---|
| Before intensification | | | | |
| <i>Dunedin</i> ($n = 8$) | | | | |
| Rat control | Bait stations | 0 | 0 | NA |
| Possum control | Single-kill traps | 0 | 0 | NA |
| <i>Hamilton</i> ($n = 4$) | | | | |
| Rat control | Bait stations | 3* | 0.41 ± 0.01 | 1–2 (1.6) |
| Rat control | Multi-kill traps | 0 | 0 | NA |
| After intensification | | | | |
| <i>Dunedin</i> ($n = 8$) | | | | |
| Rat control | Bait stations | 5 | 0.66 ± 0.26 | 5–9 (7.4) |
| Possum control | Single-kill traps | 5 | 0.34 ± 0.05 | 1–4 (2.0) |
| <i>Hamilton</i> ($n = 4$) | | | | |
| Rat control | Bait stations | 3 | 0.41 ± 0.01 | 1–2 (1.6) |
| Rat control | Multi-kill traps | 2 | 1.64 ± 0.57 | 1–2 (1.5) |

* The three sites with existing control consisted of one non-treatment and two treatment sites.

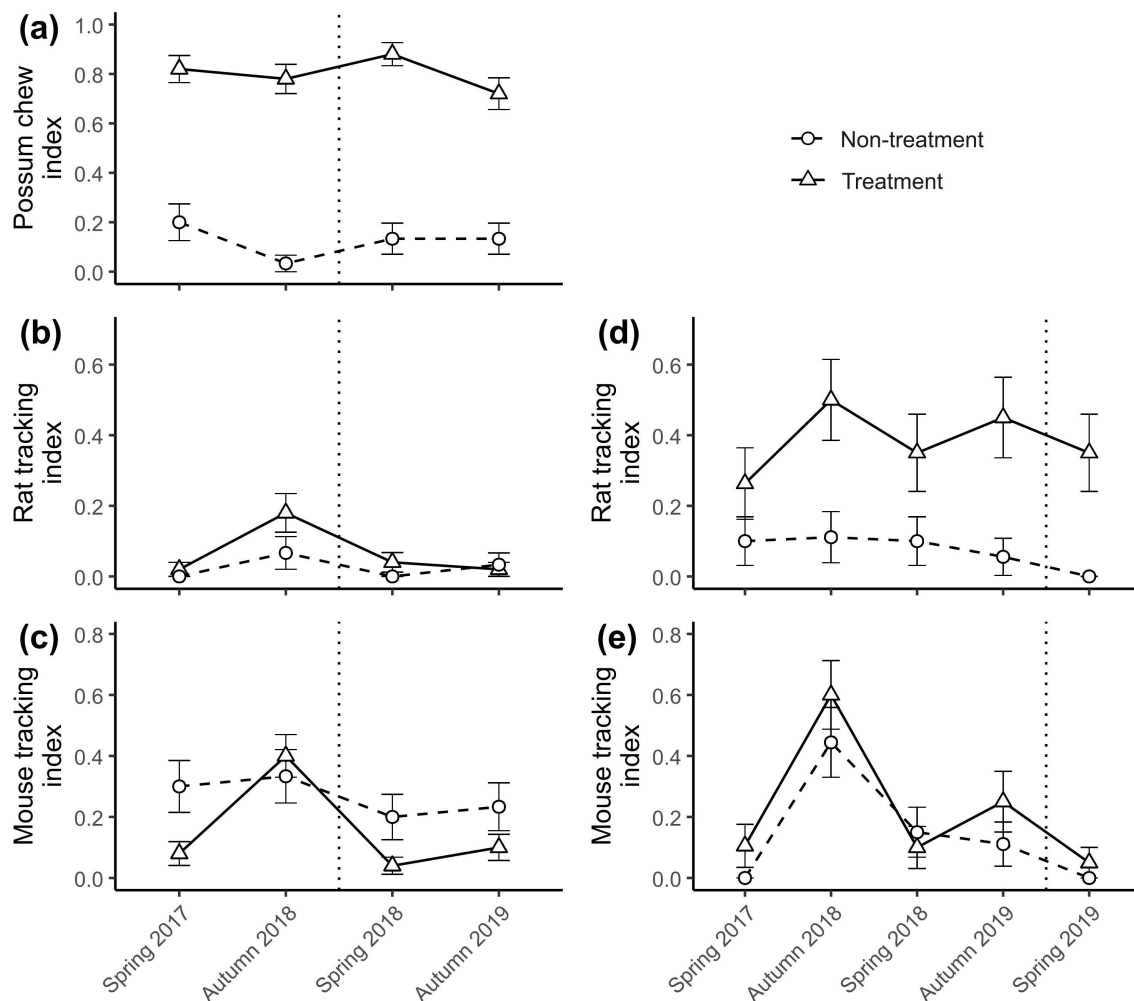


Figure 2: Pest mammal abundance indices in Dunedin, (a) possums, (b) rats, and (c) mice, and Hamilton (d) rats and (e) mice, prior to and during the intensification of predator control. Vertical dotted lines indicate commencement of intensification. Error bars are ± 1 SEM. Sample sizes: Dunedin, $n_{\text{treatment}} = 5$, $n_{\text{non-treatment}} = 3$; Hamilton, $n_{\text{treatment}} = 2$, $n_{\text{non-treatment}} = 2$.

Table 2: Results of mixed effects logistic regression modelling the outcome of intensification of predator control at study sites in Dunedin. Dependent variables in *italics*, significant effects ($P < 0.05$) are in bold typeface. Reference levels for factors are in parentheses.

| Factor | Estimate | z value | p-value |
|----------------------------------|------------------------------------|---------------|--------------|
| <i>Rat tracking index</i> | | | |
| Time period (before) | -0.74 ± 1.26 | -0.586 | 0.558 |
| Treatment (non-treatment) | 1.08 ± 1.27 | 0.850 | 0.395 |
| Season (autumn) | -1.70 ± 0.69 | -2.457 | 0.014 |
| Time \times treatment | -0.72 ± 1.46 | -0.495 | 0.621 |
| <i>Mouse tracking index</i> | | | |
| Time period (before) | -0.63 ± 0.46 | -1.365 | 0.172 |
| Treatment (non-treatment) | -0.43 ± 0.78 | -0.550 | 0.583 |
| Season (autumn) | -1.03 ± 0.33 | -3.153 | 0.002 |
| Time \times treatment | -0.97 ± 0.66 | -1.470 | 0.141 |
| <i>Possum chew index</i> | | | |
| Time period (before) | 0.29 ± 0.76 | 0.377 | 0.706 |
| Treatment (non-treatment) | 8.32 ± 2.85 | 2.916 | 0.004 |
| Season (autumn) | 1.32 ± 0.46 | 2.881 | 0.004 |
| Time \times treatment | -0.29 ± 0.91 | -0.313 | 0.754 |

Table 3: Results of mixed effects logistic regression modelling the outcome of intensification of predator control at study sites in Hamilton. Dependent variables in *italics*, significant effects ($P < 0.05$) are in bold typeface. Reference levels for factors are in parentheses.

| Factor | Estimate | z value | p-value |
|----------------------------------|------------------------------------|---------------|-------------------|
| <i>Rat tracking index</i> | | | |
| Time period (before) | -15.84 ± 2402 | -0.007 | 0.995 |
| Treatment (non-treatment) | 2.03 ± 0.63 | 3.211 | 0.001 |
| Season (autumn) | -0.55 ± 0.42 | -1.305 | 0.192 |
| Time \times treatment | 15.92 ± 2402 | 0.007 | 0.995 |
| <i>Mouse tracking index</i> | | | |
| Time period (before) | -17.28 ± 5070 | -0.003 | 0.997 |
| Treatment (non-treatment) | 0.64 ± 0.52 | 1.230 | 0.219 |
| Season (autumn) | -1.84 ± 0.49 | -3.794 | < 0.001 |
| Time \times treatment | 16.37 ± 5070 | 0.003 | 0.997 |

without the time-treatment interaction. Comparing the models we found that the interaction term made little difference to the estimates of the main effect and did not affect their direction or statistical significance (model outputs of the reduced models are in Appendix S1 in Supplementary Material).

In Hamilton, rat tracking rates were higher at treatment than non-treatment sites prior to intensification of rat control (Table 3), and this pattern persisted after the intensification of control (Fig. 2b); hence the interaction term was not statistically significant ($p = 0.995$). Mouse tracking rates showed no significant relationships with treatment, time or their interaction in the mixed effects logistic regression model (Table 3). Season was a significant predictor of mouse tracking rates, with higher rates observed in autumn than spring.

Discussion

Impact of predator control on pest mammal abundance

Predator control is increasingly being applied in urban systems by councils, community groups, and landowners, with the goal of enhancing or restoring biodiversity (Russell & Stanley 2018;

Leathwick & Byrom 2023). While predator control undertaken in indigenous ecosystems has been demonstrated to reduce predator numbers with positive effects on species recovery (e.g. Innes et al. 2024), evidence is largely lacking in cities.

Our BACI experiments in Dunedin and Hamilton detected no effect of rodent and possum control upon their target species despite the intensified control in both cities being typical of common urban predator control operations. It is possible that the scale and intensity of control or duration of the treatments and follow-up monitoring used in the BACI experiments were not sufficient to show an effect. Where bait stations and traps have been shown to significantly reduce rat and possum densities, e.g. in remote forest environments, control intensities have been high and spatially extensive. For example, ship rat control (brodifacoum bait stations) at Paengaroa Mainland Island deployed at densities of 0.96 ha^{-1} and service frequency of 12 year^{-1} reduced ship rat tracking rates to 0–9% (increasing to 100% within 18 months of baiting cessation; Armstrong et al. 2006b). In our study, bait station densities at intensified sites were only 0.66 ha^{-1} in Dunedin and 0.41 ha^{-1} in Hamilton (although Goodnature A24 traps were used at densities of 1.08 ha^{-1}). Although there is little

existing research on the effects of predator control on residual pest abundance in urban environments, two notable projects in Wellington have successfully reduced pest densities through widespread, intensive control programmes. A possum control operation on the 822 ha Miramar Peninsula between February 2003 and February 2004 appeared to have eliminated the population (evidenced by a cessation of bait take, no possum sign in two wax tag monitoring operations and no credible public reports; Greater Wellington Regional Council, unpubl. report). The initial knock-down phase of control used monthly checks of 647 bait stations at just under densities of 1 ha^{-1} across the peninsula (Greater Wellington Regional Council, unpubl. report). Also on the Miramar Peninsula, a rat eradication attempt that commenced in 2019 as part of Predator Free Wellington reduced average rat tracking rates at three rodent monitoring transects to zero in the four monitoring sessions (over two years) following the beginning of the operation, from rates of between 0.05 and 0.3 over the four monitoring sessions prior (Whitburn & Shanahan 2022). This operation used a grid of bait stations (4 ha^{-1}) and single-kill traps (1 ha^{-1}).

The intensity and scale of rat and possum control in our urban sites was substantially lower than these urban regimes that achieved high reductions in pest mammal numbers. Sites where control is undertaken by councils in most cities are comparatively small and limited to the areas that they are responsible for managing (i.e. parks and reserves), making them prone to high rates of reinvasion by pest species from the edge. Nonetheless, current possum management in Wellington appears to be maintaining very low densities of possums (Miller et al. 2022).

In our experiments, we cannot rule out the potential for confounding resulting from non-random assignment of control intensities across sites due to areas with high mammal numbers being targeted for higher levels of control, possibly as councils responded to complaints from the public. Despite low initial rat detections in the treatment sites in spring (Fig. 2b & d), successful reproduction and/or reinvasion from outside these sites may have made it difficult to detect an effect of the intensified rat control in a localised area. Such departures from ideal experimental design are often characteristics of landscape-level quasi-experiments that rely on third-party management (Butsic et al. 2017) and underscore the importance of further rigorous study and the need for more widespread quantification of predator control intensities and pest mammal densities from a range of situations. Similarly, we were unable to consider the effects of past control on the current pest abundance. Finally, our study, like many others, relied on indices of detection to estimate abundances rather than estimates of animal population density (e.g. Patterson et al. 2021; Mackenzie 2022) as the latter are considerably more costly to collect.

Determining the impacts of current urban predator control tools and regimes on mammalian pest abundance is an important first step for improving methods used to restore urban biodiversity. A crucial second step requires desired biodiversity outcomes to be linked in a formal way with residual pest abundances (i.e. a density-impact function; Norbury et al. 2015, 2022; Fea and Hartley 2018) to assess benefits to species and ecosystems when pests are reduced. Benefits may not accrue if native prey species are limited by lack of habitat, or by untargeted pests such as domestic cats, in which case management should focus on resolving these other limiting factors (Linklater & Steer 2018; Elliott Noe et al. 2022). In fact, objectives of urban restoration are frequently unstated or vague. Even Predator Free New Zealand 2050 is a predator

control and eradication target, not a biodiversity restoration target. Most studies supporting the relationship between these two target outcomes took place in native forests or other large-scale natural environments with relatively undisturbed vegetation (Armstrong et al. 2006a; Baber et al. 2008, 2009; Dowding et al. 2020).

Some well-known restorations of forest bird populations in New Zealand cities have resulted from diverse, widespread pest control. In Wellington, widespread pest control operating in concert with a pest-free ecosanctuary (Zealandia – Te Māra a Tāne) has resulted in city-wide increases of tūi (*Prosthemadera novaeseelandiae*), kākā (*Nestor meridionalis*), and kererū (*Hemiphaga novaeseelandiae*) (Miskelly et al. 2005; Miskelly 2018; MacArthur et al. 2022). Numbers of tūi in Hamilton and korimako (New Zealand bellbird, *Anthornis melanura*) in Christchurch increased after urban planting combined with pest control in peri-urban forest reserves outside the city where the birds were nesting (Crossland 1999; Spurr et al. 2014; Fitzgerald et al. 2021). Many bird species move freely between urban and peri-urban environments, demanding careful assessments of how and where predator control and other habitat improvements can best assist them (Innes et al. 2022).

The timing of control relative to the ecology of the predator and prey may also be important. For species such as ship rats and Norway rats, whose populations can recover quickly, control might be best targeted at a time that will improve population viability of the species being protected (e.g. by providing pulses of protection during its breeding season; Innes et al. 1999; Dowding et al. 2020). Expertise of operators, such as selection of the best microsites in which to place control devices, may also make a difference to their effectiveness.

These complexities make the empirical linking of biodiversity outcomes with predator control effort in urban landscapes an important area for future research. As new technologies and understanding emerge, best practice urban pest control continues to evolve. Nonetheless, quantification of predator control effort, along with rigorous measurement of residual pest abundance and biodiversity outcomes in a range of urban contexts, are essential to accelerate improvements in the efficacy and cost-effectiveness of urban biodiversity management.

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Additional information and declarations

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Ethics: Pest control was undertaken by city councils working to current best practice and legal standards. The use of tracking tunnels and chew cards has been assessed by Te Herenga Waka Victoria University of Wellington's Animal Ethics Committee as not requiring formal approval because animals are not captured and behavioural manipulation is minimal.

Conflicts of interests: The authors have no relevant financial or non-financial interests to disclose.

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Supplementary Material

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

Appendix S1. Mixed effects logistic regression models for Hamilton with no interaction terms.

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