

Effects of aerial 1080 operations on rodent and mustelid tracking rates on New Zealand's conservation land

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Abstract: We describe the effects of aerial 1080 operations on the tracking rates of ship rats, house mice, and mustelids in 13 New Zealand (NZ) regions across public conservation land between 2013 and 2022 using models fitted to 591 573 records of small mammal tracks collected over 24 years. Simulated managed and unmanaged tracking rates show predictable cyclic patterns of response over the six years after aerial 1080 operations, but also strong variation among regions and with environmental variation. Across regions, aerial 1080 operations immediately reduced ship rat tracking rates which remained lower than in unmanaged sites for 1–2 years before rebounding to levels higher than in unmanaged forests for the next 2–3 years. Ship rat rebounds were larger in warmer zones and in northern regions with more diverse low-elevation forests, including red beech and rimu, and smaller in southern and eastern South Island regions with more constrained food resource productivity. Mouse tracking rates were reduced less than those of ship rats and rebounded to levels higher than in unmanaged forests within 6–12 months after aerial 1080 operations in all regions before decreasing to unmanaged rates again. Aerial 1080 operations immediately reduced mustelid tracking rates, which recovered more slowly than rodent tracking rates, especially in cooler and drier South Island regions. Generalised linear mixed effects models showed ship rat irruptions following mast seedfall in 2019 were larger in areas that had received aerial 1080 within the previous four years, and that ship rat abundance increased by the same proportion at all temperatures. Spatial variation in the effects of aerial 1080 operations across NZ has important implications for outcomes for indigenous fauna and hence conservation management. Aerial 1080 operations need to be repeated regularly in sustained programmes to protect NZ's indigenous forest fauna populations and avoid adverse outcomes for them.

Keywords: aerial baiting, black rat, boosted regression tree models, forest conservation management, house mouse, mast seedfall, regional variation, ship rat, stoat, temporal dynamics

Introduction

Predation by introduced mammals is the primary cause of population declines in indigenous fauna in New Zealand's forests (e.g. Innes et al. 2010), and the scale of predator management to protect fauna has increased greatly in recent years (Elliott & Kemp 2016). Management of introduced mammals by aerial sowing of baits containing the acute toxin sodium fluoroacetate (hereafter aerial 1080 operations) was initiated in the 1950s, enables coverage of vast remote areas, and has been widely used for conservation purposes on public land (Brown et al. 2015; Department of Conservation [DOC] 2023). Individual aerial 1080 operations may now cover up to 100 000 ha and usually reduce numbers of brushtail possums (*Trichosurus vulpecula*) and ship rats (or black rat, *Rattus rattus*) directly (Nugent et al. 2011; Elliott & Kemp 2016) and also reduce stoat (*Mustela erminea*) numbers through secondary poisoning (Murphy et al. 1998). Mouse (*Mus musculus*) populations have been reduced less consistently (Fisher et al. 2009; Nugent et al. 2011).

Previous research has shown that indirect effects following on from predator management operations can produce changes in mammal assemblages with important implications for populations of indigenous fauna. A prominent example in New Zealand is that ship rats can recover after aerial 1080 operations to higher densities than in unmanaged forests. For example, Sweetapple and Nugent (2007) recorded increases in ship rat abundance indices to levels higher than before aerial 1080 operations for up to six years following control in podocarp-broadleaved forest at Pureora in the North Island. Increases in ship rat numbers to levels higher than in equivalent unmanaged forests (hereafter rebounds) following rat and possum suppression have also been reported in other North Island podocarp-broadleaved forest (Ruscoe et al. 2011), in mixed-beech and podocarp forests up to 900 m a.s.l. in the Tararua Range (Griffiths & Barron 2016), in the Marlborough Sounds (Bell et al. 2021), and in South Island west coast podocarp-broadleaved forests below 500 m a.s.l. (Kemp et al. 2018), but have not been reported at higher elevations or in pure beech forests. Removal of ship rats and stoats can also

release residual mouse populations from competition and predation, leading to increases in mouse populations (e.g. Kemp et al. 2018; Wilson et al. 2018).

In this paper we analyse DOC's large database of footprint tracking rates to investigate short- and medium-term (up to six years) effects of aerial 1080 operations on ship rat, house mouse, and mustelid tracking rates across 13 conservation land regions. We fitted models of tracking rates using a dataset spanning the period 1998 to 2022, but simulated tracking rate outcomes only between 2013 and 2022 when most data were collected. Most of the operations affecting those outcomes were undertaken in the late winters or springs of 2014, 2016, and 2019 (see Appendix S1 in Supplementary Material), and aimed to protect threatened fauna populations from rat and stoat irruptions following widespread beech (*Nothofagaceae*) forest mast flowering events (Elliott & Kemp 2016). However, some operations were undertaken in other years in response to regionally localised beech and rimu (*Dacrydium cupressinum*) mast events, to coincide with the vulnerable life stages of indigenous species, or on a rotational basis to protect forest canopies from possum browse (e.g. DOC 2023).

Our investigation was guided by the following conceptual model: (1) By removing possums, ship rats, stoats, and perhaps mice, we expected that every aerial 1080 operation would leave a relative surplus of their food (e.g. invertebrates, fruit, seed) in the system and release residual rodent populations from the competition and/or predation they previously experienced, (2) High survival and recruitment then follow, supplemented by immigration, leading to accelerated population growth (Herrando-Pérez et al. 2012) and temporary increases in rodent populations to levels higher than in equivalent unmanaged forests (population rebounds) until surplus food is exhausted and competitors (e.g. possums) and carnivores repopulate, (3) Finally, the vital rates of rodents are expected to decrease again with decreasing per capita availability of resources and full recovery of competitor and (where relevant) predator populations.

We first investigated how the timing and magnitude of responses varied in each mammal species regionally and with broad-scale environmental patterns, time, and management by fitting boosted regression tree (BRT) models to rodent and mustelid footprint tracking data. Our second analysis used a generalised linear mixed effects model to test the prediction that ship rat irruptions driven by beech mast seedfall will be magnified if inter-mast populations have become elevated following a previous aerial 1080 operation. Because ship rat populations can grow exponentially for 10 to 12 months following a mast seedfall (Elliott et al. 2018) we predicted that even modest differences in inter-mast populations could be magnified into significantly larger populations in the following irruption.

Methods

Response data: rodent and mustelid tracking data

Our data comprised 591 573 records of tracking by rats and/or mice collected by DOC or Greater Wellington Regional Council at 32 026 unique tracking tunnel stations over the period between December 1998 and June 2022 (Fig. 1; Appendices S2 & S3). Most tunnels were set and sampled approximately quarterly and we assigned records to one of four seasons: spring (October to December), summer (January to March), autumn (April to June), or winter (July to September).

Sampling used the same standard protocol (Gillies & Williams 2013) with ten tracking tunnel stations set at 50 m intervals along lines. For overnight sampling (82% of records) each tunnel was provisioned with fresh ink and a footprint card and baited at each end with peanut butter and cards collected the next day. The remaining tunnels were baited with rabbit meat for mustelids and cards collected after either 3, 7, 14, or 21 days. Data from all cards were recorded as either tracked or untracked for rats, mice, and mustelids. We assumed all rat tracks were from a single taxon (ship rat), although some tracks may have been of Norway rat (*Rattus norvegicus*) and a very few of kiore (*Rattus exulans*). Mustelid species were not differentiated because juvenile ferret (*Mustela furo*), stoat, and weasel (*Mustela nivalis*) footprints are not easily distinguished (Elliott & Kemp 2016).

Footprint tracking rate is an index of activity which does not account for changes in detectability and is limited by saturation at high animal densities. Cautious interpretation is also needed because reported correlations between tracking rates and measured density in short-term site-based studies have been mixed (e.g. Brown et al. 1996; Ruscoe et al. 2001) and stoat tracking rates have never been calibrated against measured densities.

Sampled environmental space

To define the area covered by the types of environments represented in the tracking dataset, we fitted a model using the machine learning BRT method (Elith et al. 2008). The response variable was the number of times that each of the 32 026 tracking stations had been sampled (with an assumed Poisson error distribution) and the predictors were eleven environmental variables (Appendix S4). Sampling frequencies were predicted from these models onto a truncated national 500-m grid which excluded Stewart Island | Rakiura and offshore islands where there were no tracking records. Points with predicted sampling frequencies of ≥ 2.7 ($\ln \geq 1.0$) were collectively used as our definition of sampled environmental space because they are assumed to represent similar environments to those sampled in the tracking dataset.

A geographic region predictor variable based on forest sequences

Within sampled environmental space we expected responses to aerial 1080 to vary regionally, because regions represent similar sets of environmental conditions and vegetation sequences, and hence background resource productivity. Responses to 1080 also vary because food resource pulses driving irruptions are not always synchronous between regions, and different canopy tree species produce different amounts of food when masting. For example, seeds of hard beech | tawhairaunui (*Fuscospora truncata*) and red beech | tawhairaunui (*Fuscospora fusca*) are larger than those of mountain beech | tawhairauriki (*Fuscospora cliffortioides*) and silver beech | tawhai (*Lophozonia menziesii*) (Ledgard & Cath 1983).

To create a predictor variable able to fit regionally differentiated responses of small mammals to 1080 in our models, we identified a set of 12 contiguous geographic regions within which we expected food resource cycles to be broadly similar and synchronous. We defined a region as a contiguous area with a particular composition of mast-seeding forest canopy trees known to drive rodent irruptions. Each needed to be large enough to offer reasonable numbers of tracking records between 2013 and 2022 and to include monitored tunnels that were both managed with aerial 1080 and not managed at

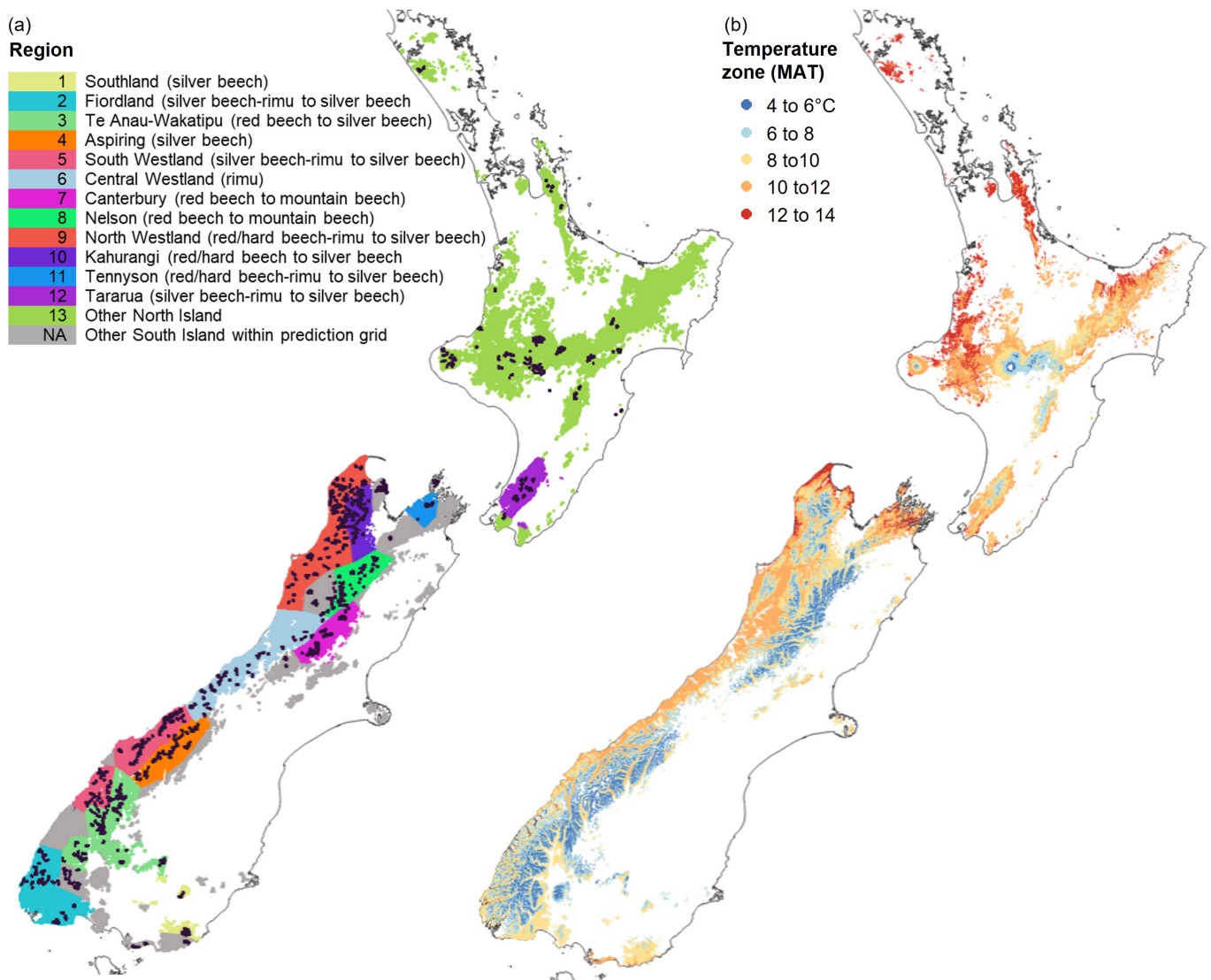


Figure 1. Maps of New Zealand's North and South Islands showing 262 235 500-m grid coordinates with similar environments to the tracking station locations (sampled environmental space). Map (a) shows the locations of tracking stations (black points) across 13 identified regions (colours) of which 12 are characterised by mast-seeding canopy tree sequences (named in parentheses). Grey shading (NA in the key) shows the extent of sampled environmental space in the South Island outside the 13 identified regions. Map (b) shows the distribution of mean annual temperature (MAT) across sampled environmental space.

different times. The predominant masting tree species at lower elevations in a region was identified as either rimu or one of four categories of beech (silver, hard, red, or mountain) with or without rimu; upslope species were one of the four beech categories (except in the Central Westland beech gap). Seven types of canopy tree composition or sequence were identified from expert knowledge and published sources (e.g. Leathwick 2001) and these characterise our 12 regions as follows:

(1) silver beech and rimu forest grading into pure silver beech upslope, as found in wet and infertile forests in three regions: Fiordland, South Westland, and the Tararua Range (Fig. 1),
 (2) red beech at lower altitudes with few or no rimu and a minor silver beech component, grading into silver beech towards treeline. This pattern largely occurs in the Te Anau and Wakatipu catchments (hereafter Te Anau-Wakatipu region),
 (3) silver beech only, as found in the Catlins and the Blue Mountains in Southland, and in the Makarora and Landsborough valleys in our Aspiring region,

(4) rimu only: forests in the Central Westland beech gap are characterised as rimu-dominated up to the altitudinal limit of that species (above which few tracking tunnels have been monitored),

(5) valley floors with red beech forest grading into predominantly mountain beech near treeline, as found in most Canterbury valleys (Canterbury region) and in Nelson region (stretching from the Lewis Pass and Springs Junction to Nelson Lakes),

(6) hard beech-rimu forest at low altitude, with some red and silver beech, which grades into silver beech near treeline (the Paparoa Range and the North Westland regions have this pattern, as well as our Tennyson region in the Marlborough Sounds),

(7) hard and red beech forest at lower elevations grading predominantly into pure silver beech (or less-commonly mountain beech) towards treeline, typical of eastern, central, and northern Kahurangi National Park (Kahurangi region).

We identified ‘other North Island’ as a 13th region. It covers a very wide range of North Island forest types and sequences, offers reasonable numbers of tracking records between 2013 and 2022, and includes monitored tunnels that were managed with aerial 1080 and not managed at different times across many different environments (Appendix S5). Tracking tunnels outside these regions were assigned to four other South Island quadrants (northwestern, northeastern, southeastern, and southwestern) (Table 1).

Effects of aerial 1080 operations on rodent and mustelid tracking rates

Boosted regression tree models

We used the regression trees method as described by Elith et al. (2008) to fit models of small mammal tracks to the full dataset of 591 573 tunnel-level records. Three separate BRT models were fitted (of tracks of ship rats, mice, and mustelids, respectively) using functions in the R library “gbm” (Ridgeway 2024) and following the procedures set out in Elith et al. (2008). We assumed Bernoulli error distribution in tracked or untracked responses, and predictor variables included regions, timing, and management history of each unique tracking record, and environmental variables extracted from GIS layers at the locations of each tracking station (Appendix S4) as follows:

(1) The region predictor was the geographic region or South Island quadrant in which the tracking station was located, coded as a factor. Regions were expected to show different temporal patterns of food resource productivity and to differ in background productivity due to their different abiotic and biotic environments.

(2) Timing predictors were the rodent year of sampling (starting on 1 October of the previous calendar year and finishing on 30 September of the calendar year) and season

of sampling, coded as spring (October to December), summer (January to March), autumn (April to June), or winter (July to September), both modelled as factors. A factor representing the setting period (overnight, 3, 7, 14, or 21 days) was included in each model.

(3) Two variables described management: number of days since the last aerial 1080 operation and the total number of aerial 1080 operations before the sampling date. Preliminary analyses suggested that effects of aerial 1080 were negligible after seven years. Thus, if there were no prior operations, values were set to 2554 days and zero, respectively, and if the last operation had been > 7 years ago, values were set to 2554 and the true number of previous operations, respectively. No attempt was made to include data on ground poisoning and trapping histories, which were available for only a small subset of tunnel locations.

Models of ship rat and mouse tracks included eight environmental variables expected to influence rodent tracking rates, and the model of mustelid tracks (which had fewer presence records) included four (Appendix S4). The long-term mean annual temperature (MAT; Fig. 1) has a strong positive effect on ship rat tracking rates (Walker et al. 2019a) and was included as an environmental predictor in each model. Models of mouse tracks included a factor recording whether rat tracks were present or absent, to account for top-down effects on mouse activity (Appendix S4).

We did not screen variables for multicollinearity, which is handled implicitly by decision trees so that fitting and prediction are robust to correlated variables (although variable importance scores are influenced). We carried out BRT model fitting and optimisation procedures and calculated cross-validation goodness-of-fit statistics on ten random 10% subsets of holdout records following Elith et al. (2008).

Table 1. Numbers of unique records of tracking by rodents and mustelids, of unique tracking tunnel stations, and of points within the prediction grids in each of 13 geographic regions and in four quadrants of the South Island outside the 13 geographic regions. The mast-seeding forest canopy species (or species elevation sequences) that characterise each region are shown in parentheses.

Region	Number of unique stations	Number of unique records	Number of prediction points
1 Southland (silver beech only)	680	33 426	2172
2 Fiordland (silver beech-rimu to silver beech)	1467	38 862	15 248
3 Te Anau-Wakatipu (red beech to silver beech)	3422	96 601	16 950
4 Aspiring (silver beech only)	1920	28 061	10 220
5 South Westland (silver beech-rimu to silver beech)	4423	55 651	18 643
6 Central Westland (rimu only)	1378	30 135	19 182
7 Canterbury (red beech to mountain beech)	2183	70 813	8205
8 Nelson (red beech to mountain beech)	2201	33 321	11 751
9 North Westland (red/hard beech-rimu to silver beech)	5090	56 792	30 972
10 Kahurangi (red/hard beech to silver beech)	2659	36 719	11 148
11 Tennyson (red/hard beech-rimu to silver beech)	240	8325	3560
12 Tararua (silver beech-rimu to silver beech)	592	18 633	8330
13 Other North Island	3259	56 583	66 129
Quadrant of remaining sampled environmental space in the South Island			
A Other northeastern South Island	157	1146	9509
B Other northwestern South Island	1791	19 403	12 062
C Other southeastern South Island	544	6944	13 665
D Other southwestern South Island	20	158	4489

Simulated effects of aerial 1080 on rodent and mustelid tracking rates

Simulated datasets were produced by predicting tracking rates from the fitted models at each point on the sampling grid in each season of each rodent year (i.e. quarterly). Although our BRT models were generated from all tracking data collected from 1996 to 2022, we summarise predicted tracking rates only for the 35 seasons between spring 2013 and autumn 2022 when records were most numerous and environmentally representative (Appendices S2 & S3) and tracking rates could have been affected by the aerial 1080 operations undertaken between late 2007 and early 2022 (Appendix S1). For ship rat and mouse predictions the tunnel setting period was overnight, and for mustelid predictions it was 21 days. When predicting mouse tracking rates, we set the ship rat tracks predictor by drawing 0 or 1 at random from the binomial distribution of the predicted unmanaged ship rat tracking rate at the same grid coordinate and date.

We first predicted unmanaged tracking rates by setting time since the last aerial 1080 operation variable to 2554 days (i.e. seven years) and the total number of aerial 1080 operations to zero. We then predicted tracking rates at different lengths of time after aerial 1080 by varying the ‘time since last aerial 1080 operation’ parameter between 23 days ($1/16^{\text{th}}$ of the first year) and six years and setting the total number of aerial 1080 operations to one.

To ensure that summarised predictions from the BRT models were well supported by data collected in the field, we summarise predictions for our 13 identified geographic regions only (i.e. excluding the four other South Island quadrants; Table 1). Within these regions we made quarterly (seasonal) predictions within a rodent year only if: (1) ten or more records were collected within the relevant interval of time since the last aerial 1080 operation and within the same rodent year and geographic region (Appendix S5), and within the same two-degree zone of MAT; and (2) raw data from unmanaged tunnels (i.e. > 7 years since the last aerial 1080 operation) were also available for the same combination of conditions. These constraints meant that the simulated dataset represented different rodent years in different combinations of geographic region, time since last aerial 1080 operation, and MAT zone.

We summarised the simulated data in each two-degree zone of MAT in each region by calculating medians, quartiles, and 95th percentiles of the predicted managed and unmanaged tracking and the net effects of 1080 (i.e. managed tracking rates minus unmanaged tracking rates) at different times since the last aerial 1080 operation.

Effects of previous aerial 1080 on the ship rat irruption in 2019

To test our prediction that a previous aerial 1080 operation would magnify a subsequent ship rat irruption (by elevating the starting population) we fitted generalised linear mixed models (glmm) using the “glmmTMB” library for R (Brooks et al. 2017) of ship rat tracks in the autumn and winter of 2019, immediately following a very large and widespread beech seedfall event. The response data were 599 records of tracking along 392 unique lines of ten tracking stations set in forests in sites across the North and South Island. Tunnels on each line had been set baited for stoats over 21 days within the summer (January to March) of seedfall and set overnight for ship rats in the autumn (between April and June) and/or winter (between July and September).

Ship rat tracking rates on each tracking line were modelled as a binomial (number of tunnels tracked, number untracked) with a complementary log-log link transformation (Elliott et al. 2018) in response to the presence or absence (0/1) of aerial 1080 within the previous four years (prior operations at most lines were undertaken one and a half to three years earlier so subdividing this period was not possible). Covariates were season of rodent sampling (autumn or winter, because we anticipated lower ship rat tracking rates at an earlier stage of the irruption), MAT (a proxy for forest productivity, which was expected to increase ship rat tracking rates), and the presence or absence (0/1) of summer mustelid tracks (an indicator of predation pressure which we expected to lower ship rat tracking rates). We used tracking line nested within geographic region as random intercepts to account for spatial non-independence of records. We fitted a set of models of all additive combinations of fixed-effect predictors and used Akaike’s information criterion corrected for small sample size (AICc) to select the best model.

Results

BRT models

Our sampling frequency model (Appendices S6 & S7) predicted log sampling frequencies of ≥ 1.0 at 262 235 500-m grid coordinates, which we adopted as our grid for predictions of rodent tracking rates.

Our three models of small mammal tracks (Appendices S8– S10) all discriminated much better than expected by chance (cross-validation areas under the curve of 0.91 to 0.94) and had acceptable cross validation correlation coefficients of 0.61 to 0.66 (Table 2). Rodent year, region, and time since last aerial 1080 operation were the most influential predictors in the models of ship rat and mouse tracks (Table 2; Appendices S8 & S9). The relative influence of individual environmental variables was muted because variation among regions also represents major environmental gradients; nevertheless, MAT was the most influential individual environmental predictor variable in the model of ship rat tracks. Setting period and mean annual rainfall were more important in the model of mustelid tracks than in models of rodent tracks (Table 2; Appendix S10). The total number of past aerial 1080 operations was the least important predictor in all models.

Effects of aerial 1080 operations

Ship rats

Our simulated dataset showed that ship rat tracking rates were immediately greatly reduced by aerial 1080 operations in all of the 13 geographic regions examined, and in all temperature zones within those regions (Figs. 2 & 3). Across the full prediction grid, the overall median predicted managed overnight tracking rate of ship rats at our earliest prediction time (23 days after 1080) was just 0.002 (95% confidence intervals [CI] 0.000, 0.042), on the tracking-rate scale of 0 to 1, compared to 0.119 (95% CI 0.011, 0.535) without management (Appendix S11 shows predicted unmanaged tracking rates in regions 1 to 12). Tracking rates then remained lower than in equivalent unmanaged environments for one to two years in all regions except Tennyson, where tracking rates in managed areas exceeded unmanaged rates within one year after management (Figs. 2 & 3; Appendix S11).

Ship rat tracking rates rebounded to levels higher than

Table 2. Model statistics for our boosted regression tree (BRT) models of rodent and mustelid tracks (columns). (a) Cross validation correlation coefficient (cvCC) and cross-validated area under the ROC curve (cvAUC); (b) The relative influence (RI) of predictor variables (RI is the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, averaged over all trees and scaled to sum to 100).

	Ship rats	Mice	Mustelids
(a) Model statistics			
cvCC	0.66 ± 0.00	0.69 ± 0.00	0.61 ± 0.00
cvAUC	0.91 ± 0.00	0.92 ± 0.00	0.94 ± 0.00
(b) Relative influence of predictor variables			
<i>Time</i>			
Rodent year	22.95	34.83	19.52
Season	2.87	5.81	2.97
Setting period	3.31	2.55	25.72
<i>Zone</i>			
Region	25.59	23.05	11.73
<i>Environment</i>			
July ground frost	5.21	3.70	-
Landscape element	3.47	2.53	-
Mean annual temperature	7.74	2.16	3.61
Mean annual rainfall	6.18	5.55	14.45
Rainfall: potential evapotranspiration ratio	2.65	2.14	-
Annual Penman moisture deficit	1.37	1.75	2.61
October vapour pressure deficit	2.61	1.92	-
<i>Nothofagus</i> stem density	4.27	2.73	4.99
<i>Biotic</i>			
Presence of rat tracks	-	0.44	-
Management	-	-	-
Time since last aerial management operation	10.62	9.47	13.05
Total number of past aerial management operations	1.17	1.36	1.34

in unmanaged sites following aerial 1080 operations in all 13 regions (Figs. 2 & 3; Appendix S11). Rebounds were generally largest in the warmer MAT zones of any region, but there were also some pronounced regional differences (Table 3, Fig. 2). The smallest rat rebounds followed operations in Canterbury, where valley floors are > 600 m a.s.l. and red beech is present but of limited extent, and the median difference in rat tracking rates in the warmest zone (8 to 10°C MAT) was just 0.004 higher than in equivalent unmanaged environments. Rebounds were also small (i.e. median tracking rates just 0.023 higher than in unmanaged forests) in Fiordland where rimu is present but red beech is absent in lower elevation zones. Rebounds were somewhat larger in the silver beech forests of our Southland and Aspiring regions (median increases were 0.048 and 0.047 higher, respectively, than unmanaged tracking rates in the 8 to 10°C MAT zone; Table 3), and larger again (a median increase of 0.077) in the Te Anau-Wakatipu region where red beech occurs in extensive contiguous stands at lower elevations (Fig. 2).

Ship rat rebounds were larger still in three West Coast regions, which include low-elevation forests zones with a significant component of rimu (Table 3, Fig. 2). In these three regions, median tracking rates after 1080 reached 0.102 to 0.184 higher than in unmanaged forests in the 8 to 10°C MAT temperature zone, 0.132 to 0.210 higher in warmer (10 to 12°C MAT) zones, and 0.280 higher in the very warmest forests of North Westland (i.e. 12 to 14°C MAT). The largest ship rat rebounds occurred in the Nelson, Kahurangi, Tennyson, and

Tararua regions and across the rest of the North Island (Table 3, Figs. 2 & 3). Here, median differences show tracking rates became elevated by 0.204 to 0.284 in 8 to 10°C MAT zones after aerial 1080 operations, and by 0.196 to 0.314 in the warmer (10 to 12°C MAT) lower-elevation zones which support more significant components of red beech, hard beech, and rimu.

Ship rat rebounds peaked (i.e. the positive difference between managed and unmanaged rates was greatest) between two and a half to three years after operations in most regions (Fig. 2). Rebounds were over by four years after operations in all South Island regions but extended to five to six years after operations in warmer zones of Tararua region and the rest of the North Island (Figs. 2 & 3). In Southland, Nelson, Kahurangi, and Tennyson regions, a second period of rat tracking higher than in unmanaged forests was predicted around five years after an aerial management operation (Fig. 2).

Mice

Our model predicted that the suppression of mouse tracking rates by aerial 1080 operations would be regionally variable (Figs. 3 & 4). For example, mouse suppression was more successful in Southland and Aspiring regions than in Te Anau-Wakatipu, Canterbury, and Nelson across the operations represented in the dataset. Across all regions and temperature zones, the median predicted overnight tracking rate across regions 23 days after an operation was 0.033 (95% CI 0.002, 0.336) compared to 0.068 (95% CI 0.011, 0.364) without management (Appendix S12 shows unmanaged mouse tracking

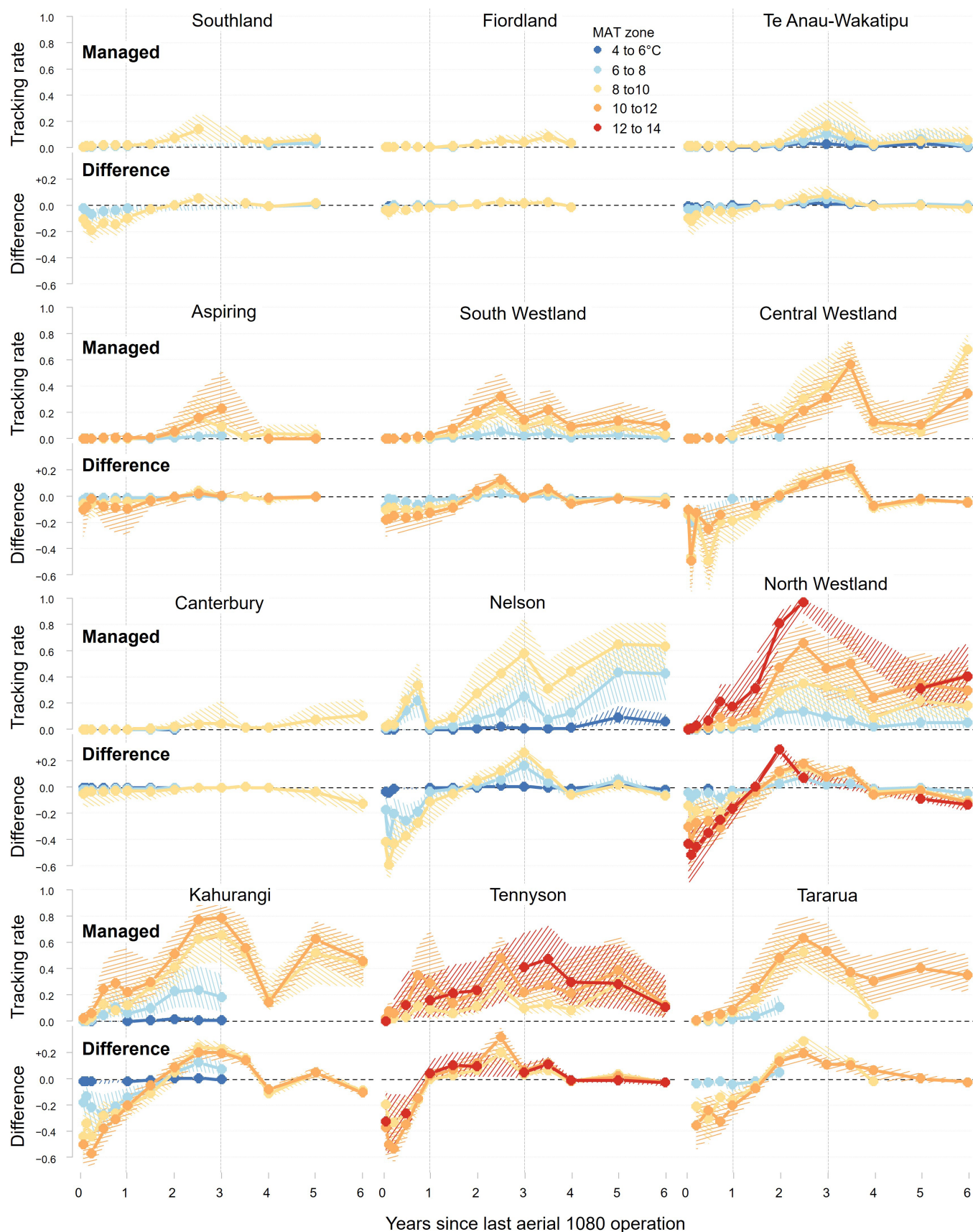


Figure 2. Medians (lines and symbols) and interquartile ranges (hatched polygons) of the predicted managed tracking rates of ship rats (Managed: upper subplot in each pair), and the differences between predicted managed and unmanaged tracking rates (Difference: managed minus unmanaged; lower subplot in each pair) in 5 zones of mean annual temperature (MAT; °C) in 12 geographic regions at different lengths of time after the last aerial 1080 operation. Appendix S5 in Supplementary Material shows the years in which tracking tunnel records were available for each data point.

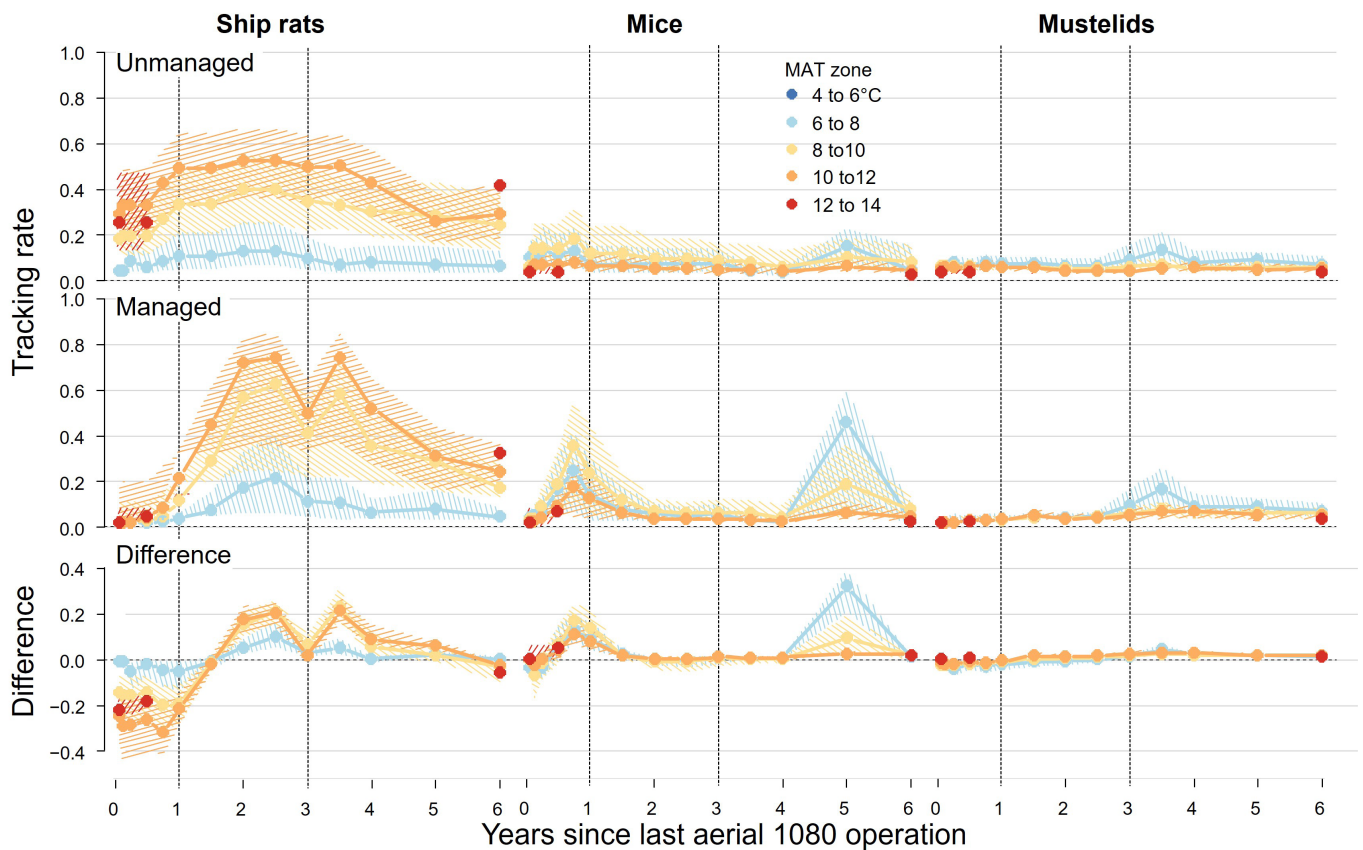


Figure 3. Medians (lines and symbols) and interquartile ranges (hatched polygons) of the predicted unmanaged and managed tracking rates of ship rats, mice, and mustelids, and the differences between predicted managed and unmanaged tracking rates (Difference), in five zones of mean annual temperature (MAT; °C) in the North Island outside the Tararua region at different lengths of time after the last aerial 1080 operation. Appendix S5 in Supplementary Material shows the years in which tracking tunnel records were available for each data point.

rates in regions 1 to 12). In most regions, mouse tracking rates became higher than in unmanaged sites within six months of operations and peaked within a year of the operation, and mouse rebounds ended within 18 months of an aerial 1080 operation (Figs. 3 & 4). However, mouse rebounds lasted relatively longer (two to three years) in Aspiring, South and Central Westland, Canterbury, and cooler parts of Kahurangi and Tennyson regions.

Initial mouse rebounds were larger in the cooler (but not necessarily coldest) zones of regions, but there was no clear latitudinal pattern (Table 3): for example, similarly large mouse rebounds were predicted in the 8 to 10°C MAT zones of Southland and in the wider North Island (excluding Tararua region). The largest mouse rebounds were predicted in cooler zones (8 to 10°C MAT) of Kahurangi and Tennyson regions, where overnight mouse tracking rates in forests briefly exceeded those in unmanaged forests by more than 0.4 (Table 3, Fig. 4). Our simulations show that a second mouse rebound occurred about five years after aerial management, most notably in Southland, Te Anau, Aspiring, Nelson, and Tennyson, where median overnight mouse tracking rates again were elevated by 0.10 to 0.20 over those in unmanaged areas (Fig. 4; Appendix S12).

Mustelids

Mustelid tracking rates were greatly reduced after 1080 and recovered more slowly than those of rodents. The median

predicted 21-day mustelid tracking rate across all regions and zones at our earliest prediction time (23 days after 1080) was 0.006 (95% CI 0.001, 0.040; Figs. 3 & 5) compared to 0.128 (95% CI 0.015, 0.440) without management. (Appendix S13 shows predicted unmanaged mustelid tracking rates in regions 1 to 12.) Our simulations show that most recoveries of mustelid tracks began within a year of an operation, but time to full recovery was considerably shorter in warmer regions (Figs. 3 & 5). Mustelid tracking rates took less than 18 months to fully recover to levels in unmanaged forests after operations in warmer (10 to 12°C) North Island zones outside Tararua region, 30 months in South and Central Westland and Tennyson regions, three years in North Westland, Kahurangi, Tararua, and other parts of the North Island < 10°C, and four years in Southland and Te Anau. Tracking rates had not yet fully recovered in Fiordland, Aspiring, Canterbury, or Nelson regions within six years of an operation (Table 3, Figs. 3 & 5; Appendix S13).

The largest mustelid rebounds were predicted in warmer forest zones in Southland and South and Central Westland, and at mid-elevations in Tararua region, where median differences in 21-day tracking rates between managed and unmanaged forests were 0.057 to 0.080. Smaller mustelid rebounds (median differences in 21-day tracking rates of 0.004 to 0.048) were also predicted in cooler forests in Southland and South Westland, and in the warmer zones of North Westland, Kahurangi, and Tennyson regions (Fig. 5).

Table 3. Largest median difference between managed vs. unmanaged rodent and mustelid tracking rates (expressed on the scale of 0 to 1) at any time following an aerial 1080 operation in each mean annual temperature (MAT; °C) zone in each of 13 regions. (a) Ship rats, (b) Mice, (c) Mustelids. Regions are ordered and grouped based on similarities in patterns of ship rat rebounds (i.e. positive median differences). The mast-seeding forest canopy species in the simplified canopy tree sequences that characterise each region are shown in parentheses.

No.	Region	MAT zone (°C)				
		4–6	6–8	8–10	10–12	12–14
(a) Ship rats						
1	Southland (silver beech only)	-	0.004	0.048	-	-
2	Fiordland (silver beech-rimu to silver beech)	-0.001	-0.002	0.023	-	-
3	Te Anau-Wakatipu (red beech to silver beech)	0.016	0.046	0.077	-	-
4	Aspiring (silver beech only)	-	0.010	0.047	0.027	-
7	Canterbury (red beech to mountain beech)	-	-0.002	0.004	-	-
5	South Westland (silver beech-rimu to silver beech)	-	0.024	0.102	0.132	-
6	Central Westland (rimu only)	-	-	0.184	0.210	-
9	North Westland (red/hard beech-rimu to silver beech)	-	0.074	0.157	0.180	0.280
8	Nelson (red beech to mountain beech)	0.020	0.163	0.256	-	-
10	Kahurangi (red/hard beech to silver beech)	0.010	0.129	0.242	0.201	-
11	Tennyson (red/hard beech-rimu to silver beech)	-	-	0.204	0.314	0.112
12	Tararua (silver beech-rimu to silver beech)	-	0.054	0.284	0.198	-
13	Other North Island	-	0.085	0.214	0.196	-
(b) Mice						
1	Southland (silver beech only)	-	0.314	0.252	-	-
2	Fiordland (silver beech-rimu to silver beech)	0.057	0.038	0.164	-	-
3	Te Anau-Wakatipu (red beech to silver beech)	0.264	0.291	0.202	-	-
4	Aspiring (silver beech only)	-	0.211	0.202	0.217	-
7	Canterbury (red beech to mountain beech)	0.121	0.078	0.090	-	-
5	South Westland (silver beech-rimu to silver beech)	-	0.261	0.234	0.101	-
6	Central Westland (rimu only)	-	0.041	0.056	0.024	-
9	North Westland (red/hard beech-rimu to silver beech)	-	0.113	0.073	0.065	0.138
8	Nelson (red beech to mountain beech)	0.231	0.278	0.199	-	-
10	Kahurangi (red/hard beech to silver beech)	0.127	0.450	0.133	0.103	-
11	Tennyson (red/hard beech-rimu to silver beech)	-	-	0.332	0.387	0.145
12	Tararua (silver beech-rimu to silver beech)	-	0.153	0.086	0.069	-
13	Other North Island	-	0.306	0.154	0.098	-
(c) Mustelids						
1	Southland (silver beech only)	-	0.022	0.065	-	-
2	Fiordland (silver beech-rimu to silver beech)	-0.027	-0.143	-0.001	-	-
3	Te Anau-Wakatipu (red beech to silver beech)	0.002	-0.003	0.002	-	-
4	Aspiring (silver beech only)	-	-0.058	-0.016	-0.002	-
7	Canterbury (red beech to mountain beech)	-0.014	-0.041	-0.020	-	-
5	South Westland (silver beech-rimu to silver beech)	-	0.048	0.044	0.092	-
6	Central Westland (rimu only)	-	-0.022	0.031	0.080	-
9	North Westland (red/hard beech-rimu to silver beech)	-	-0.022	-0.019	0.008	-0.001
8	Nelson (red beech to mountain beech)	-0.006	-0.026	-0.025	-	-
10	Kahurangi (red/hard beech to silver beech)	-0.010	-0.069	0.025	0.024	-
11	Tennyson (red/hard beech-rimu to silver beech)	-	-	-0.011	0.012	0.004
12	Tararua (silver beech-rimu to silver beech)	-	-0.133	0.057	0.026	-
13	Other North Island	-	0.028	0.009	0.016	-

Effects of previous aerial 1080 on the ship rat irruption in 2019

The two best glmms of ship rat tracks in the autumn and winter of 2019 included three fixed effects: MAT, season of measurement, and an aerial 1080 operation within the last four years ($K = 6$; Table 4). Including summer mustelid tracks (model 14, $K = 7$) made only a small difference to AICc, so we consider Model 13 more parsimonious, although both models have similar support (Burnham & Anderson 2002).

Positive parameter estimates in Model 13 (Appendix S14)

showed that ship rat tracking rates increased as irruptions developed from autumn (Fig. 6a) to winter (Fig. 6b) in 2019 and were significantly higher in warmer forests than in cooler forests, consistent with the patterns shown in our BRT model of tracking rates in all years and seasons. Ship rat tracking rates on lines that had previously received aerial 1080 were higher than on lines that had not, at all temperatures and in both seasons (Figs. 6a, b).

Increases in ship rat tracking were quantitatively larger in warmer forests: for example, the median winter tracking rate

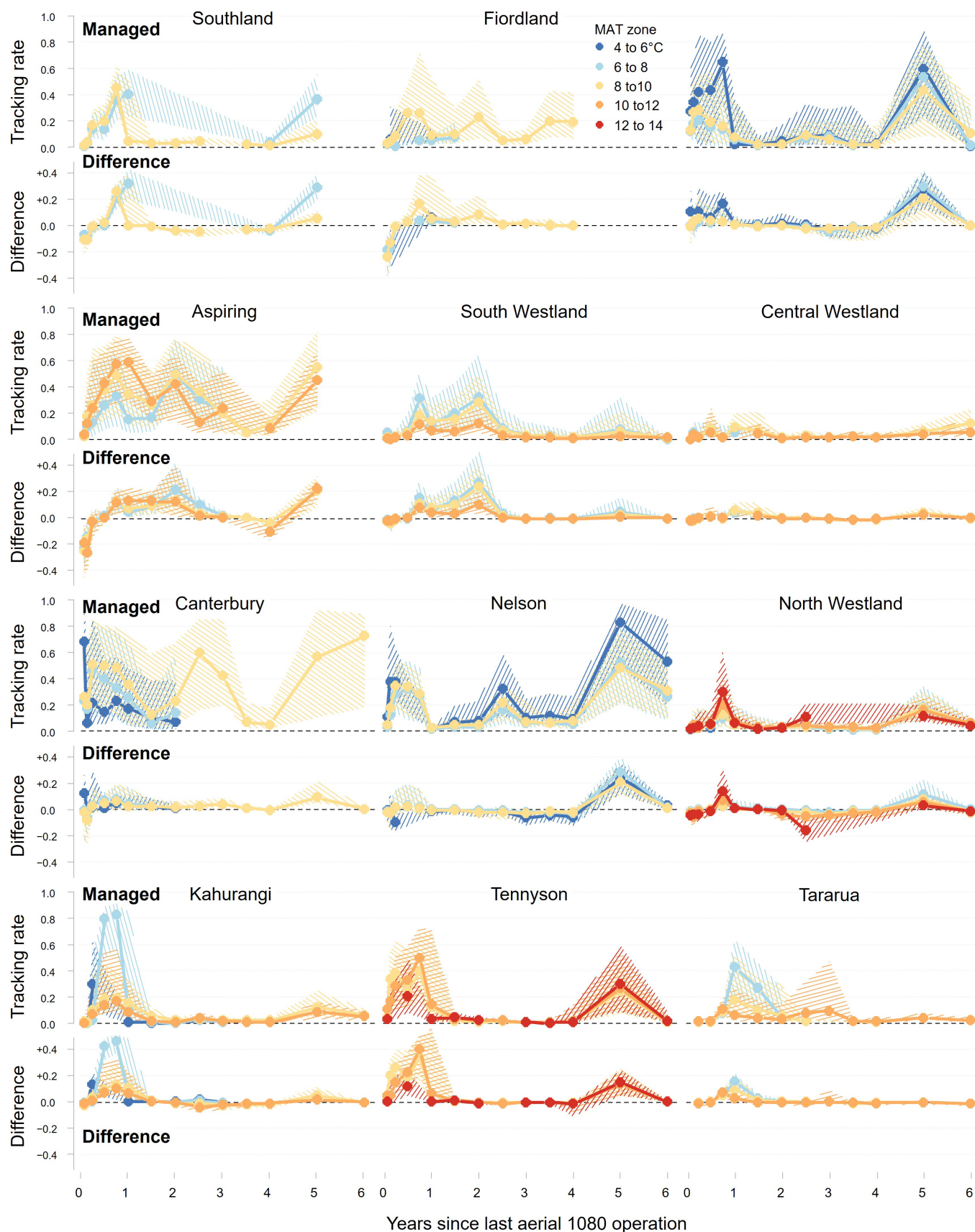


Figure 4. Medians (lines and symbols) and interquartile ranges (hatched polygons) of the predicted managed tracking rates of mice (Managed: upper subplot in each pair), and the differences between predicted managed and unmanaged tracking rates (Difference: lower subplot in each pair) in 5 zones of mean annual temperature (MAT; °C) in 12 geographic regions at different lengths of time after the last aerial 1080 operation. Appendix S5 in Supplementary Material shows the years in which tracking tunnel records were available for each data point.

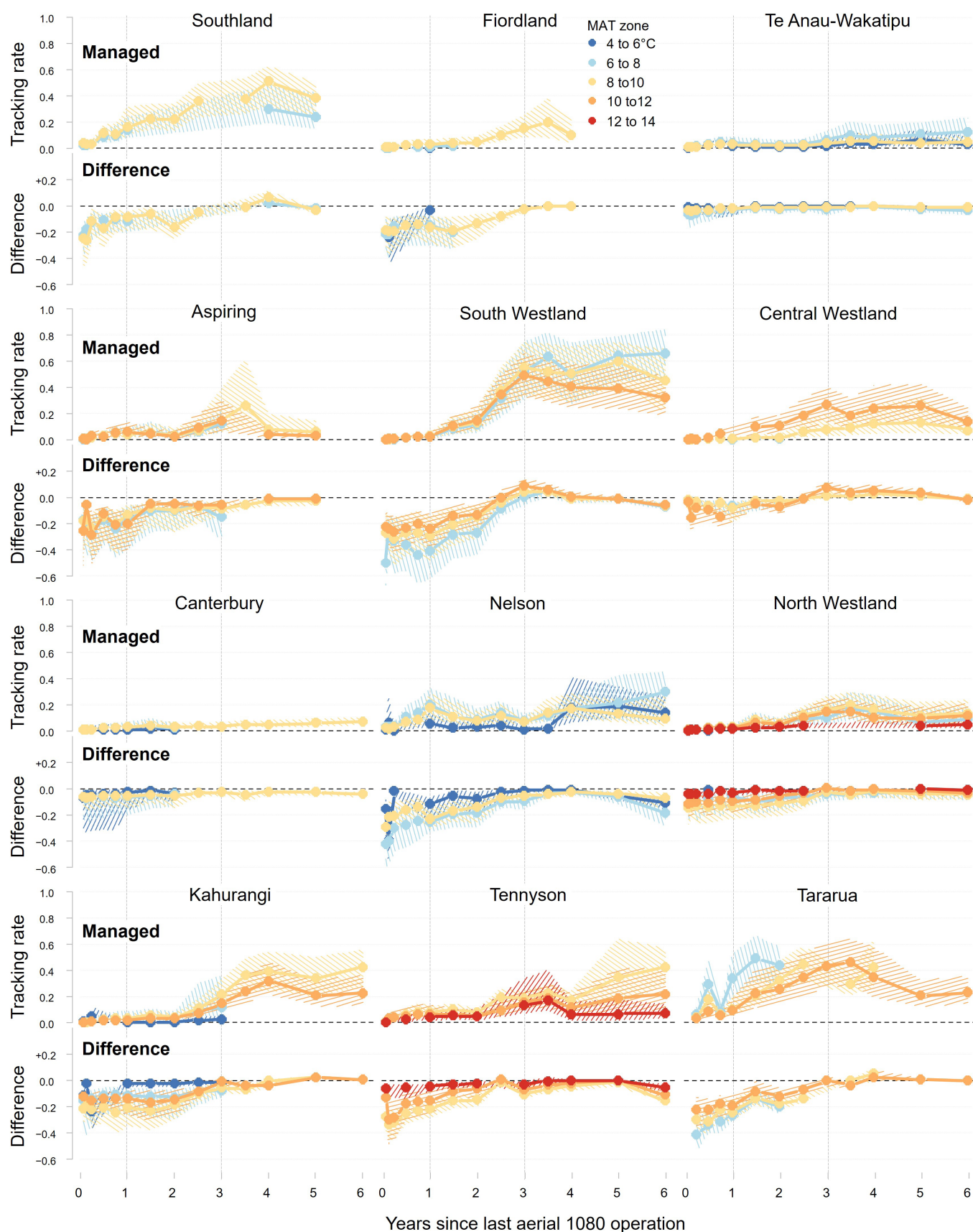


Figure 5. Medians (lines and symbols) and interquartile ranges (hatched polygons) of the predicted managed tracking rates of mustelids (Managed: upper subplot in each pair), and the differences between predicted managed and unmanaged tracking rates (Difference: lower subplot in each pair) in 5 zones of mean annual temperature (MAT; °C) in 12 geographic regions at different lengths of time after the last aerial 1080 operation. Appendix S5 in Supplementary Material shows the years in which tracking tunnel records were available for each data point.

Table 4. The top six models of ship rat tracking rates in the 2019 year of mast seeding in beech forests. MAT = mean annual temperature, Season = autumn (April to June) or winter (July to September), Management = aerial 1080 within the last four years, and Mustelid tracks = mustelid tracks in the previous summer. K = number of parameters included in model, AICc = Aikake’s information criterion corrected for small sample size, Δ AICc = difference in AICc value from that of the best model, AICc weight = relative support for models.

No.	Model	K	AICc	Δ AICc	AICc weight
14	MAT + Season + Management + Mustelid tracks	7	1343.53	0.00	0.51
13	MAT + Season + Management	6	1343.64	0.11	0.49
10	MAT + Season + Mustelid tracks	6	1362.55	19.01	0.00
4	MAT + Season	5	1363.81	20.28	0.00
8	MAT + Management	5	1413.87	70.34	0.00
12	Season + Management + Mustelid tracks	6	1414.94	71.41	0.00

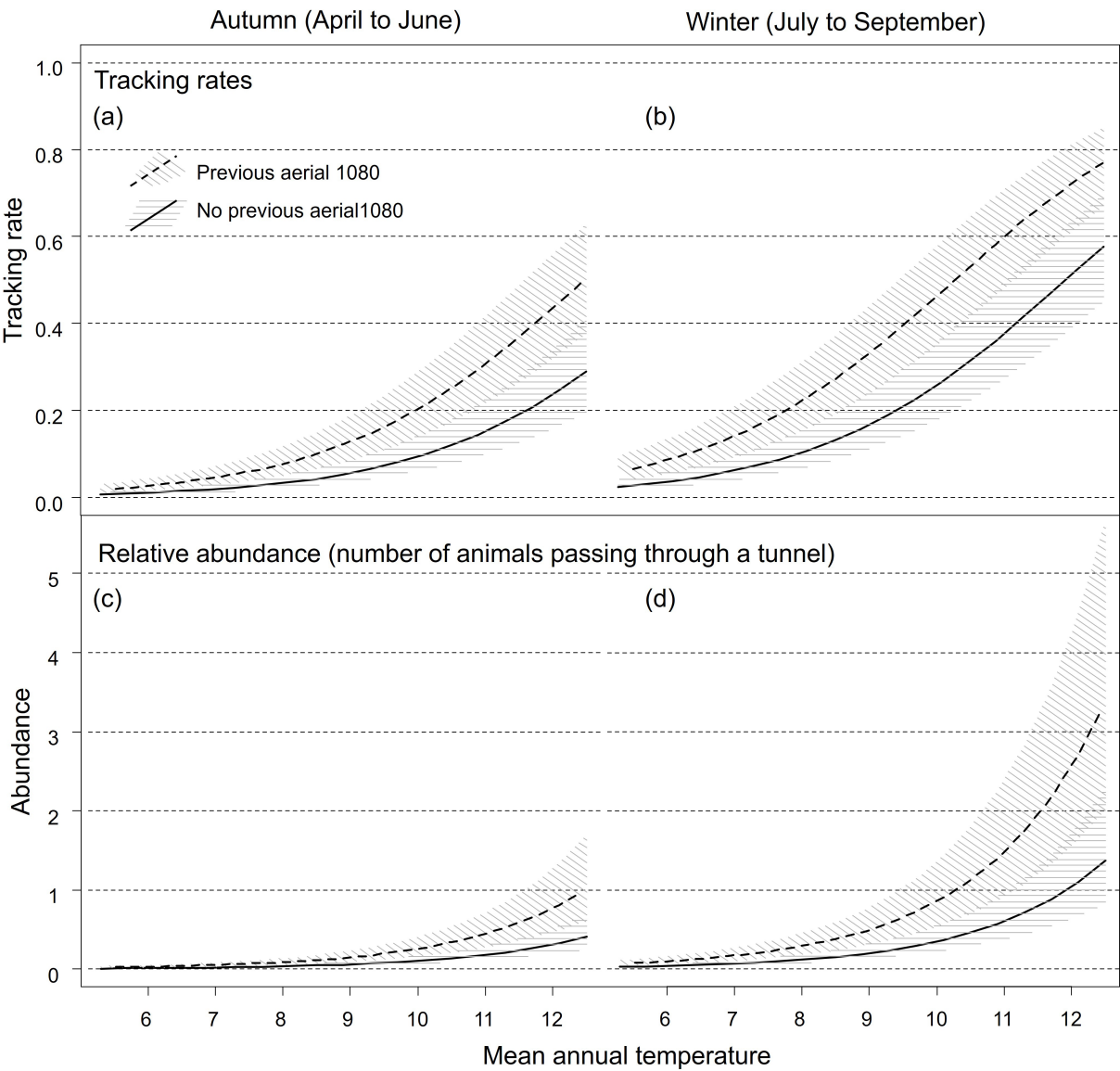


Figure 6. Medians (lines) and standard errors (hatched polygons) of the fitted tracking rates (upper plots) and numbers of ship rats passing through tunnels (lower plots) in beech forest in the autumn and winter following beech seedfall in 2019, from Model 13 (Table 4). Numbers passing through tunnels is estimated as $\log(1 + \text{tracking rate})$ after Elliott et al. (2018). The different line styles show fitted values with and without an aerial 1080 operation within the last four years. The left panel shows fitted values for autumn and the right panel shows those for winter. Parameter estimates from the model are shown in Appendix S14 in Supplementary Material.

increased from 0.449 to 0.711 after an aerial 1080 operation in a warm forest (10.5 °C MAT), and from 0.027 to 0.080 in a cool forest (6.0 °C MAT). However, the proportional change made by aerial 1080 to the number of animals passing through tunnels ($-\log(1-\text{tracking rate})$; Elliott et al. 2018) did not change with temperature. The number of animals passing through a tunnel was about 2.5 times greater in managed forests than in unmanaged forests at all temperatures and in both seasons (Figure 6c, d).

Discussion

We found predictable responses and strong overall regional and environmental patterns in the responses of small mammal tracking rates to the aerial 1080 operations undertaken on conservation land. Following 1080 operations, which were mostly undertaken between August and November (late winter to spring), ship rat and mustelid tracking rates reliably and immediately dropped to low levels, but mouse tracking rates were reduced less consistently across regions. Tracking rates of mice recovered first, followed by ship rats, and lastly mustelids. Mouse and then ship rat tracking rates rebounded to exceed levels in unmanaged forests in most regions before decreasing again. Effects on small mammal tracking rates remained evident up to six years after an aerial 1080 operation. Autumn and winter ship rat irruptions in response to the early 2019 beech mast seedfall were larger where a 1080 operation had been undertaken in the previous four years.

Tracking rates must be interpreted with caution as, at best, a coarse estimate of relative abundance. Nevertheless, the broad-scale, recurring patterns of tracking rate responses to aerial 1080 operations shown in this study provide new ecological insights and have implications for conservation management, which we discuss below.

Ship rat responses

Although aerial 1080 operations immediately and substantially reduced ship rat tracking rates in all regions, ship rat activity then recovered to higher levels than in equivalent unmanaged forests, as also reported by other studies (Sweetapple & Nugent 2007; Ruscoe et al. 2011; Griffiths & Barron 2016; Kemp et al. 2018; Bell et al. 2021). However, our data showed wide variation in rebounds among regions and the temperature zones within them.

Rebounds in ship rat tracking rates were small in the least productive regions in the south or east of the South Island. Those regions either lack red beech forest (Southland, Fiordland, and Aspiring) at lower elevations, or support red beech or rimu under relatively cool, infertile, or dry conditions (e.g. Fiordland and Canterbury). Rebounds were largest in warmer northern and western South Island regions where there is red beech, hard beech, and/or rimu forest at lower elevations (e.g. Nelson and Kahurangi regions) and across the North Island where both ship rats and possums are normally abundant (Forsyth et al. 2018; Walker et al. 2019a). The alignment of this pattern with expected patterns of resource productivity (albeit unmeasured in our study) is consistent with our expectation that the quantity of residual food available is the primary determinant of ship rat rebounds after mammal populations are reduced. Large rebounds after aerial 1080 operations also appeared to depend on a comparatively benign (warm, moist) climate regardless of the canopy tree composition of a region. Release from predation by stoats after 1080 operations may

contribute to behavioural and/or numerical changes in ship rat populations. However, the largest rebounds in ship rat tracking rates occurred across North Island sites where mustelid tracking rates usually recovered most rapidly from 1080. It therefore it seems unlikely that mesopredator release is a primary driver of ship rat rebounds.

The tracking data supported our expectation that the larger inter-mast ship rat populations which follow aerial 1080 operations would generate larger subsequent ship rat irruptions: ship rat tracking rates through the autumn and winter of 2019 were significantly higher where there had been an aerial 1080 operation within the previous four years. Our model suggested that prior operations boosted irruptions by a similar proportion regardless of temperature, leading to substantially larger ship rat irruptions especially in warmer forests. Despite the much larger absolute increases in ship rats in warmer forests, adverse effects of more ship rats on indigenous prey species might be greater in the cooler forests which generally support fewer ship rats between and after mast seedfall events (Innes & Russell 2021). Cooler forests are thermal refuges for rat-sensitive indigenous bird species (Walker et al. 2019b), and many warmer forests have already been cleaned out of sensitive species, presumably because inter-mast rat populations are seldom held below damage thresholds. There could be severe adverse effects on the persistence of populations of sensitive indigenous fauna in cooler forests if aerial 1080 operations boost inter-mast and irruptive ship rat numbers above damage thresholds.

Mouse and mustelid responses

We found that aerial 1080 operations undertaken in the late winters and springs of mast years had variable effects on mice, backing up others' observations (e.g. Fisher et al. 2009; Nugent et al. 2011). Mouse rebounds quickly followed aerial operations but lasted longer in cooler, less productive regions and zones and were briefer in the warmer environments where ship rats rebounded more strongly. This pattern suggests that the effects of strongly recovering ship rats quickly negated any early bottom-up effect on mice of food surplus and/or release from top-down predation.

Mustelid tracking rates consistently fell to low levels after aerial 1080 operations suggesting that secondary poisoning (Murphy et al. 1998) was highly effective. Tracking rates of mustelids remained lower than in unmanaged forests for four years in cooler southern and eastern South Island regions, and for three years in Taranaki and warmer South Island regions. It is possible that stoat trapping programmes slowed stoat recovery in some of these regions, but we do not have the spatial data to test this. Mustelid tracking rates recovered most rapidly—within 18 months—across most of the North Island where unmanaged tracking rates were generally very low. Rapid recovery perhaps reflected comparatively high mustelid reinvasion rates in the generally fragmented forest habitats that remain there.

It is possible that recovering mustelid numbers contributed (through behavioural or numerical effects) to curtailing rat rebounds across our regions. However, in warmer northern forests, intraspecific competition for food and interspecific competition from recovering possum populations (Sweetapple & Nugent 2007) are both plausible alternative explanations for the eventual decreases in ship rat tracking rates. Furthermore, in cooler forests, our results show that the comparatively modest ship rat rebounds were largely over before mustelids had completed their slower recoveries.

Implications for conservation management and indigenous fauna

The ship rat and mustelid responses we describe provide plausible explanations for patterns of benefit and harm to bird populations observed in the field within the geographic range of the data. For example, in North Island podocarp-hardwood forest near Tongariro, two years of post-1080 population gains for stoat-vulnerable North Island brown kiwi | kiwi-nui (*Apteryx mantelli*) and improved nesting success in rat-vulnerable fantails | pīwakawaka (*Rhipidura fuliginosa*) were followed by declines in the following three years that largely negated these benefits (Robertson et al. 2019). Our simulations for warm North Island zones suggest that aerial 1080 operations provide for, at most, two seasons of improved breeding for kiwi and for fantails, because both mustelid and ship rat tracking rates returned to unmanaged levels within 18 months of operations and became higher than in unmanaged sites thereafter.

Regional and environmental context is likely to influence the frequency of aerial 1080 operations needed to provide long-term benefit to an indigenous species. For example, Bell et al. (2021) concluded that aerial 1080 operations would have long-term benefits for South Island robins | kakarui (*Petroica australis*) in the Marlborough Sounds (in our Tennyson region) only if repeated at three-yearly or shorter intervals. This conclusion matches our predictions that ship rat tracking would fully recover within 12 months of a 1080 operation. However, the situation in Tennyson was unusual because only two operations were undertaken and were just one year apart, and in most other monitored regions, ship rat recoveries were less dramatic and took longer. It is therefore possible that robins could benefit under longer intervals between operations in some other regions (if mast seedfalls do not occur and cause ship rat irruptions within that period).

Malham and Elliott (2023) found that nesting success in stoat-vulnerable kākā (*Nestor meridionalis*) in South Westland mixed beech forests declined two years and more after aerial management operations, and declines were probably mostly caused by a recovery in stoat abundance. Our models predicted high (i.e. > 0.2) and fully recovered mustelid tracking rates in South Westland from between 24 and 30 months after operations, which matches their result and assumption. Malham and Elliott (2023) concluded that kākā populations in South Westland would grow if 1080 operations were undertaken every second year to prevent stoat recoveries. Our results concur, but also reveal that mustelid recoveries were slower (taking three to four years) in most other South Island regions, and kākā populations might therefore increase elsewhere under a regime with longer (i.e. > 2 year) management intervals.

Although regional patterns of rodent and mustelid response can provide broad guidance to conservation managers, local context and the biology of individual species will determine the outcomes of any regime. For example, our results show that in the Kahurangi region, mustelid tracking rates usually recovered slowly, and recovery was still incomplete within three years of aerial 1080. Yet in southern Kahurangi National Park, aerial 1080 improved nest and duckling survival of blue duck | whio (*Hymenolaimus malacorhynchus*), a large-bodied, stoat-sensitive species, mainly within the first six months of an operation, and there was no significant effect of aerial 1080 on adult survival (Steffens et al. 2022). Models showed that whio survival increased with distance to farmland, and the authors concluded that stoats were able to reinvade rapidly after aerial 1080 operations in this location. Furthermore, adult whio were highly vulnerable to stoats in the non-breeding season, making

the population potentially vulnerable to the presence of stoats in very low numbers.

A major goal of aerial 1080 operations on conservation land is to protect forest birds and bats from predation by ship rats and mustelids (Elliott & Kemp 2016). Our results support field studies of fauna outcomes which demonstrate that this goal can be achieved, but only if operations are undertaken at frequencies appropriate to protect the target species. Where ship rats rebound to higher numbers, operations that are not repeated (or are repeated after too long an interval) may worsen conservation outcomes for some species of birds and bats. The (mainly) austral late winter and spring aerial 1080 operations covered by our data led to increases in mice, which are generally less important predators of indigenous birds and bats than ship rats and stoats but can have adverse effects on lizard populations (Monks et al. 2024) and invertebrate composition (Bertoia et al. 2024). It remains a challenge to develop effective predator control tools, tactics, and strategies that can control a wide range of pests and protect more of the full range of indigenous fauna.

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Author contributions: Susan Walker: conceptualisation, methodology, analysis, writing – original draft. Josh Kemp: conceptualisation, data curation, writing – review and editing. Graeme Elliott: analysis, writing – review and editing.

Data availability: The data and analysis used in this study will be made available in the permanent Landcare Research Repository <https://datastore.landcareresearch.co.nz/>.

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Supplementary Material

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

Appendix S1. Dates of aerial 1080 management operations in different regions and the frequency distribution of operations across calendar months.

Appendix S2. Numbers of unique records in the dataset from tracking tunnels in different elevation zones in each rodent year.

Appendix S3. Number of unique records in the dataset from tracking tunnels in different zones of mean annual temperature in each rodent year.

Appendix S4. Predictor variables included in boosted regression tree models, showing the range of values along with units of measurement.

Appendix S5. Representation of tracking data in regions over time and intervals of days since the last aerial 1080 operation.

Appendix S6. Partial dependence plots for the eight most influential variables in our BRT model of sampling frequency.

Appendix S7. Partial dependence plots for the eight most influential variables in our BRT model of ship rat tracks.

Appendix S8. Partial dependence plots for the eight most influential variables in our BRT model of mouse tracks.

Appendix S9. Partial dependence plots for the eight most influential variables in our BRT model of mustelid tracks.

Appendix S10. Relative influence of variables in our model of sampling frequency.

Appendix S11. Predicted unmanaged tracking rates of ship rats at different lengths of time after the last 1080 operation.

Appendix S12. Predicted unmanaged tracking rates of mice at different lengths of time after the last 1080 operation.

Appendix S13. Predicted unmanaged tracking rates of mustelids at different lengths of time after the last aerial 1080 operation.

Appendix S14. Parameter estimates for the best model of ship rat tracking rates through the winter and spring of the 2019 mast seeding year.

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